FRDC FINAL REPORT

POPULATION DYNAMICS AND REPRODUCTIVE ECOLOGY OF THE SOUTHERN CALAMARY (*SEPIOTEUTHIS AUSTRALIS*) IN TASMANIA

Natalie Moltschaniwskyj, Gretta Pecl, Jeremy Lyle,
Malcolm Haddon, & Michael Steer

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Tasmanian Aquaculture and Fisheries Institute, University of Tasmania, Private Bag 49, Hobart, Tasmania 7001. E-mail: Natalie.Moltschaniwskyj@utas.edu.au.

Ph. (03) 6227 7277 Fax (03) 6227 8035

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Non-Technical Summary

2000/121 Population dynamics and reproductive ecology of the southern calamary (*Sepioteuthis australis*) in Tasmania

PRINCIPAL INVESTIGATOR: Dr Natalie Moltschaniwskyj
ADDRESS:
School of Aquaculture
Tasmanian Aquaculture and Fisheries Institute
University of Tasmania
Locked Bag 1370
Launceston
Tasmania 7250
Telephone 03 63243802, Fax: 03 63243804

OBJECTIVES

1. Describe temporal and spatial variability in rates of growth, size and age distributions and reproductive status of populations of southern calamary.
2. Describe the spatial and temporal patterns of spawning activities and quantify the reproductive output of southern calamary populations.
3. Determine the age, size, spawning condition and sex composition of the southern calamary caught by commercial fishers using different fishing gear.
4. Develop performance indicators to be used with southern calamary populations and other short-lived marine species.

OUTCOMES ACHIEVED TO DATE

- Provided a description of reproductive ecology that allowed managers to make decisions on fishing closures during the spawning period.
- Assessed the spatial and temporal variability in life history characteristics of calamary that was required for input into management decisions.
- Determined that abundance of squid & life history characteristics were unrelated and simple environmental correlates not evident
- Identified region specific patterns in population biology, fishing methods, and harvest rates that indicate the possibility of region specific management.
- Identified the potential suitability for egg production by squid to be a useful fishery independent indicator of biomass
- Identified that for the fishery to remain sustainable a more precautionary approach is required, including consideration of options that will effectively reduce harvest rates.

This report presents the results of two years (July 2000 – July 2002) of fieldwork funded by FRDC that described the reproductive and population status of southern calamary in the eastern and southern regions of Tasmanian. To increase the scope and context of the research this report also presents data collected as part of TAFI funded research, and research carried out by doctoral students (Dr Gretta Pecl and Mr Michael Steer).

Currently the dominant fishing method for collecting southern calamary in the state is hand jigs, accounting for 67-79% of state-wide catch since 1998/99. Following a sharp increase in catches in the late 1990s commercial landings of southern calamary have fluctuated between 75 and 100 tonnes in recent years. Fishing effort focuses on the spawning aggregations that occur in shallow sheltered bays over the austral spring and early summer. The calamary fishery was centred initially in Great Oyster Bay and as the fishery developed catches in most of the main regions in Tasmania increased. Regional differences in the contributions of the various fishing methods reflect a range of factors including gear preferences of fishers, squid behaviour and availability, and levels of targeted fishing for calamary. The calamary fishery is highly seasonal, with greatest catches taken from late winter to early summer, with catches and catch rates peaking between September and November. The recreational harvest was in the order of 37,000 calamary, equivalent to about 22 tonnes or almost 30% of the 2001/02 commercial catch

Small-scale temporal and spatial variability in egg production by southern calamary was described over four years in an area known to attract spawning aggregations. Egg deposition on inshore seagrass beds occurred predominantly during the austral spring and early summer. A large loss of egg masses from the seagrass was associated with storms, suggesting physical dislodgment. The introduction of short-term closures in Great Oyster Bay during the peak catching period each year since 1999 has been a significant factor in contributing to the stability in catches in that region whilst encouraging expansion into other areas such as Mercury Passage. Information about the spatial and temporal patterns of egg production was used to make recommendations about the use of fishing closures to protect spawning adults from over-fishing. There was evidence that egg densities on the beds were correlated to squid biomass at the time, providing an immediate assessment of the size of spawning populations.

To assess the effect and potential management value of short-term fishing closures (two-week closures) egg surveys and squid sampling was done at the end of periods when the spawning grounds were open and closed to fishing. During one fishing closure, densities of eggs increased six-fold, suggesting that either the closure provided protection to the spawning aggregation or promoted an increase in spawning activities. However, increased egg production during fishing closures was not always evident possibly reflecting relatively low levels of spawning activity and low reproductive condition of females during the closure. That is to say the actual timing of the closures in relation to the dynamics of reproductive activity will ultimately determine the benefits of the closure in terms of egg production. Daily CPUE information suggested that closing Great Oyster Bay to fishing did not result in increased numbers of squid aggregating in the spawning areas, implying continual movement onto and away from the areas. However, the reduced contribution of Great Oyster Bay catch to the State-wide total production over the study period suggests that short closures were of value in protecting the spawning aggregation. However, the total annual catch remained relatively stable as the closures forced effort into adjacent areas, particularly Mercury Passage.

During each of the spring/summer spawning periods of 1999 and 2000 the reproductive status, abundance, and reproductive output of the stock declined. However, the average age of squid in the spawning aggregation was c. 6 months over the three months of peak spawning activity. Therefore, it was concluded that new squid were entering the spawning aggregation throughout the spawning period which is consistent with inferences made from the daily CPUE data. Given that squid in the aggregation were hatched at different times during the year, it seems that a series of micro-cohorts with different biological characteristics were entering the spawning aggregations throughout the duration of the spawning season. The strategy of micro-cohorts with a diversity of life history characteristics coming together in a single spawning aggregation maybe a way in which short-lived species can ensure successful recruitment. Given the biological and life history characteristics of the spawning aggregation are changing during the season due to the arrival of new micro-cohorts, then consideration needs to be given to protecting these micro-cohorts to ensure maintenance of genetic diversity.

Squid encase their eggs in a protective mucus shell, and while the eggs are attached to the benthos they are vulnerable to mortality processes. During 2000, egg mortality was initially low (4%) but increased significantly to 20% in late November and remained above 10% until late December. This dramatic increase in mortality was not strongly associated with increasing water temperatures, but coincided with a period of heavy rainfall suggesting that potentially salinity affects mortality rates.

Inter-annual changes were evident in both the life-history characteristics of individuals and the population structure in the five years of data analysed. During the five years for which data are available (1996, 1996/97, 1999/00, 2000/01, and 2001/02) there was a reduction in reproductive investment in both males and females, the average size of individuals and weight-at-length increased, males became more prevalent in the population, and growth rates became more variable. However, there does not appear to be a simple relationship between water temperature and growth and condition of squid. Furthermore, it appeared that the life history characteristics of squid populations were not related to biomass levels (based on CPUE data). Therefore, it will be difficult to use water temperature or stock size as a simple predictor of growth, size and reproductive condition.

In a comparison of the population biology and life-history characteristics of southern calamary between the east coast and southern regions of Tasmania, it was evident that there were important differences. There was a difference in the proportion of individuals in the reproductive stages between the regions due to the south having proportionally more immature and spent individuals compared with the east coast. Spawning intensity differed significantly between the two regions, with three times the density of egg masses in the east. Overall individuals in the south-east were older and smaller than those in the east, although in any one season the fastest growing individuals were in the south-east spring population. Differences between the two regions in the biology, and particularly reproductive ecology, suggested that different management strategies may need to be adopted in the different regions.

Preliminary surplus production models of the Tasmanian calamary fishery suggest that harvest rates are very high within the main area of the fishery, implying that the fishery has impacted significantly on stocks and current catch levels are not sustainable. This observation is set against the fact that there is growing interest in the fishery and substantial capacity within the Tasmanian scalefish industry to increase effort. Although there is a high degree of uncertainty with the present assessment, key

indicators suggest that maintaining the status quo for the Tasmanian southern calamary fishery is a high-risk strategy. For the fishery to remain sustainable a more precautionary approach is required, including consideration of options that will effectively reduce harvest rates.

KEYWORDS: southern calamary, population structure, growth, reproductive status, egg production, embryo mortality, sex ratios, spatial variability, temporal variability, growth, population structure, environment-recruitment, reproduction, condition

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Chapter 5 includes data that was collected as part of Dr Gretta Pecl's PhD prior to the start of this project, and was funded by Tasmanian Department of Primary Industries and James Cook University. Dr George Jackson also provided support for some of the 1996 work and aged some of the individuals.

Chapters 1, 2, 4, 5, and 6 include data that was collected in 1999 and this fieldwork was funded by TAFI.

The tagging fieldwork in Chapter 5 was carried out during a 10 day cruise of the RV Challenger. This cruise was funded by TAFI and we thank the crew of the RV Challenger, Mat Francis and Jac Gibson, for their logistic support during the cruise.

Background

The aim of this project is to describe the life history characteristics and spawning ecology of southern calamary (*Sepioteuthis australis*) in Tasmania. High variability in growth ratas and reproductive characteristics of squid prevents us from producing general population models using data from a single place or time (Triantafillos 1998, Pecl 2001). Therefore, this project extends the existing spatial and temporal scale of biological information about southern calamary in Tasmania and aims to generate population dynamic models for use in managing this unique species.

The ecological significance of the short life span of most squid species is that only a single generation spawns at any one time. Therefore, if this generation fails to spawn, recruitment failure with subsequent population collapse is likely. In contrast, most fish populations have a buffer against inter-annual recruitment fluctuations provided by the presence of a number of year-classes in the spawning biomass. 'Failures' in squid fisheries to date, eg *Illex illecebrosus* (NW Atlantic) and *Todorodes pacificus* (NW Pacific), appear to have been brought about by life-cycle responses to environmental changes, probably aggravated by heavy fishing pressure.

Given the vulnerability to recruitment failure in any year it is thought that spatial and temporal variability in the life history characteristics of many squid species provides a mechanism to ensure survival of the population. In other words, variability in growth and reproduction maybe used to enhance survival, and provide an alternative way of buffering recruitment variability.

Interest in this species from the commercial sector is increasing because of the relatively high market value ($5-15/kg), the low set-up costs (fishing is conducted from dinghies in sheltered waters), and the open access to the fishery for all persons with a marine Scalefish licence. Fishers use a range of methods; principally jigs and nets (seine and haul), to target reproductively mature fish as they aggregate to spawn in shallow inshore areas. The South Australian marine Scalefish fishery caught approximately 425 t of southern calamary worth more than $2 M in the financial year of 1998/99. The commercial fishery in Tasmania first developed in the early 1980's with landings of 10-30 t per annum up until 1997/98 but increased markedly in 1998/99 to 93 t, valued at over $0.5 M. Catches in Victoria and New South Wales are currently relatively low, however, there is potential for increased effort. Southern calamary are also important recreationally. For instance, in South Australia it has been established that southern Calamary is the third most targeted species amongst recreational boat fishers (McGlennon & Kinloch 1997) and there is anecdotal evidence that in Tasmania the species is being increasing targeted by recreational fishers off the east and north coasts.

As southern calamary is associated with reefs and seagrass beds in shallow, sheltered inshore waters of southern Australia, they are increasingly accessible to most fishers. For those reasons, there has been a substantial increase in the amount of fishing effort directed at this species by both commercial and recreational sectors. This species is a significant natural resource across southern Australia. Squid are an ecologically important component of coastal systems, both as primary consumers of crustaceans and fishes, but most significantly as a food source for numerous teleost fishes, sharks and seabird (Coleman 1984, Gales *et al.* 1993). Therefore, their exploitation raises concerns, not only about the sustainability of the fishery, but also about the effect on populations of other marine animals.

However, despite the increasing annual catches and more fishers entering the fishery, questions are being raised about what level of fishing effort is sustainable. There are concerns that unless correctly managed these stocks of southern calamary will be easily over-exploited. Already there is evidence that localised depletion of stocks in certain areas of both South Australia (Triantafillos 1997) and Tasmania has occurred. Set against this, it is recognised that potential also exists for expansion into areas that are currently lightly exploited.

Need

Squid differ from fish in more than just short life spans. They also have a relatively long juvenile phase, non-asymptotic growth, short spawning periods, spatial and temporal variability in population dynamics and considerable inter-individual variability. Therefore, existing fish management strategies are unlikely to adequately address the spatial and temporal variability evident is squid populations. This project directly addresses the key areas of squid fisheries research, which is the need to clarify the variability in the life history characteristics in space and time. It will only be through the quantification of this information and the application of modelling techniques that we will be able to determine the appropriate management strategy for squid eg closures vs. limited access vs. total allowable catch.

A need for research on southern calamary has arisen because the fishery targets sexually mature individuals on the spawning grounds while they are mating and laying eggs. This is a short-lived species (<1 year) and populations are entirely dependent on successful production of young by each generation. Therefore we need to determine the impacts of fishing upon adult populations and egg production, which may compromise future recruitment.

Fishers and managers in Tasmania have raised questions about the current status of southern calamary stocks, with suggestions that increasing exploitation my place the stocks at high risk of collapse. A number of factors such as the short life span, low fecundity, non-overlapping generations and high inter-annual recruitment variability of this species exacerbate the risk. Especially since managing a species with these biological characteristics cannot be based on previous catch history. We need to develop numerical models that can use biological indicators to manage stocks that are vulnerable to recruitment given that the primary targets are spawning individuals.

The current state of biological and ecological knowledge about Southern calamary does not allow management decisions to be made to allow this fishery to develop at sustainable levels. Consequently, there is urgent need to quantify the productivity of southern calamary populations and determine which components of the population are fished by different gears.

Objectives

1. Describe temporal and spatial variability in rates of growth, size and age distributions and reproductive status of populations of southern calamary.

2. Describe the spatial and temporal patterns of spawning activities and quantify the reproductive output of southern calamary populations.

3. Determine the age, size, spawning condition and sex composition of the southern calamary caught by commercial fishers using different fishing gear.

4. Develop performance indicators to be used with southern calamary populations and other short-lived marine species.

General Introduction

The 'live-fast die-young' life history of many squid species makes managing squid fisheries a balancing act. Southern calamary (*Sepioteuthis australis* Quoy/Gaimard, 1832) typically lives for approximately 6-8 months and females are capable of producing multiple batches of eggs during their short adult lifetime (Pecl, 2001). Mature southern calamary are present throughout the year, but in areas around southern Australia spawning aggregations appear during warmer months each year to deposit eggs in areas of shallow seagrass. This species deposits eggs in white finger-like strands, approximately 60-70 mm long. Clusters of egg strands (egg masses) are attached in aggregations to macro-algae and seagrass in sheltered, shallow inshore areas. Egg masses may be made up of several egg strands to more than six hundred egg strands, with each strand containing between three to nine eggs.

As a result of the aggregative spawning behaviour highest commercial catches of southern calamary are landed during the late winter to early summer period. Most of the fishing effort and expansion has focused on Great Oyster Bay, on Tasmania’s east coast. This large embayment attracts aggregations of spawning southern calamary into sheltered, shallow areas that are easily accessed by the fishers. Catches of southern calamary from Tasmanian waters ranged between 5.8 and 32.8 tonnes for the period 1990/91 to 1997/98. However, catches increased markedly in 1998/99 to 90.6 tonnes, reaching historically high levels. Effort using jigs has increased six-fold in the past year and currently all holders of a commercial scale-fish license have access to the southern calamary fishery.

The population consequences of over-exploitation are likely to be more dramatic if reproductive individuals are removed from the population before producing the next generation. In the case of southern calamary there is concern that over-fishing of the aggregations could jeopardise production of the next generation. This is of concern as the “storage effect” that protects populations of long-lived species from recruitment failure (Warner & Chesson 1985) is absent in short-lived species. Long-lived species with overlapping generations are able to survive, or tolerate, years in which reproductive events fail (Warner & Chesson 1985). However, for annual or sub-annual species that do not have a demographic buffer for poor reproductive years, population persistence depends upon successful reproduction in each generation (O’Dor & Coelho 1993). Such populations can persist by broadly distributing reproductive effort in time (within a season) and space (O’Dor 1998). Reproductive characteristics are important life-history variables determining successful production of offspring. Success of reproductive events depends on when adults are reproductively mature, the location of spawning, and when conditions are favourable for embryo and hatchling survival

Removal of reproductive individuals from the spawning grounds before and during spawning has the potential to shorten the reproductive period of the female, reduce lifetime fecundity and jeopardise the size of the next generation. In the case of southern calamary the individuals spawning in the summer produce the winter population, and the winter population produces the following summer population. This means that over-fishing of adult spawning populations, combined with a recruitment failure will affect population structure and dynamics very quickly (Boyle, 1990, Brodziak, 1998, Rodhouse *et al.* 1998).

Chapter 1: Small-scale spatial and temporal patterns of egg production by the temperate loliginid squid *Sepioteuthis australis*

(Authors: NA Moltschaniwskyj & GT Pecl)

Note that the full details of this work have been published in the following paper:
Moltschaniwskyj, N.A & Pecl, G.T. (2003). Small-scale spatial and temporal patterns of egg production by the temperate loliginid squid *Sepioteuthis australis*. Marine Biology 142: 509-516. © Springer-Verlag – reproduced with permission.

Introduction

Based on evidence from macroscopic and microscopic analyses of reproductive organs many squid species appear to spawn repeatedly over extended periods during the adult lifetime (eg, *Photololigo* sp., Moltschaniwskyj 1995; *Loligo vulgaris* and *Loligo forbesi*, Rocha & Guerra 1996; *Loligo vulgaris reynaudii*, Melo & Sauer 1999). Population level information also suggests that many species of squid spawn over extended periods of the year (*Loligo chinensis*, Jackson 1993; *Loligo duvauceli*, Mohamed 1993). However, describing spatial and temporal patterns of egg production of squid from information gathered by destructive sampling of individuals from a population is difficult. This is largely because of the mobility of squid and the absence of information about the length of time between ovulation and depositing of eggs. Even temporally intensive sampling of the adult population over the spawning ground would not determine exactly where and when eggs were laid. Patterns of egg production by marine organisms are usually estimated indirectly from plankton trawls, adult density or batch fecundity. Only in benthic spawners is it possible to directly describe patterns in egg production and understand the processes responsible for this variability (eg *Clupea harengus*, Stratoudikis *et al.* 1998).

Loliginid squid lay well-protected benthic eggs with multiple eggs per strand in coastal areas, attached either to sand (eg *Loligo vulgaris reynaudii* Sauer *et al.* 1993), coral (*Sepioteuthis lessoniana* Segawa *et al.* 1993), or algae (*Loligo gahi* Arkhipkin *et al.* 2000). For those loliginid squid for which mating and spawning information is available, populations display some predictability in the general location of spawning grounds (eg *Loligo opalescens,* Vojkovich 1998, *Loligo vulgaris reynaudii,* Sauer *et al.* 1993), with mature males and females aggregating to court, mate and lay eggs (Smale *et al.* 1995, Hanlon & Messenger 1996). However, the density of eggs laid varies both spatially and temporally (Sauer *et al.* 1993). For benthic spawners, factors such as substrate (eg *Clupea harengus* Kääriä *et al.* 1997, *S. lessoniana* Ueta 2000) and physical characteristics of the water masses (Roberts & Sauer 1994) may determine the location and intensity of spawning in any one year.

The aim was to describe the spawning dynamics of egg production by southern calamary and factors that may influence the presence and loss of eggs on the beds. This was done by estimating the small-scale temporal and spatial variability in egg density in areas known to attract spawning aggregations. Using sub-tidal techniques, surveys of the seagrass beds determined the timing and location of egg deposition. Changes in the density of eggs on the spawning grounds as a function of seagrass bed characteristics and weather patterns were explored. This information allowed us to estimate the reproductive output of the southern calamary population and to ascertain if the spatial variability in egg laying patterns could be explained by the physical characteristics of the seagrass.

Materials and Methods

This work focused upon shallow inshore (<10 m) areas of seagrass (*Amphibolis antarctica)* that are known to have aggregations of spawning squid present during spring and summer. Surveys of egg masses were carried out at three random sites at each of two locations, Coles Bay and Hazards Bay, in Great Oyster Bay on the east coast of Tasmania, Australia (Fig. 1.1). The two locations were approximately 6 km apart and the sites within each location were along a 1.4 km section of coastline. Each site was characterised by a discrete bed of *A. antarctica* delimited by sand and/or macroalgae. The area of *A. antarctica* at each site was determined, on a calm day when the water clarity was high, using differential GPS and a high-resolution depth sounder. The areas of *A. antarctica* differed among the sites, ranging from 0.17 ha to 2.02 ha. The smaller sites were in Coles Bay and as a result the total area of seagrass surveyed at the two locations differed (Table 1.1). At Hazards Bay more than three seagrass sites were available, therefore three random sites were chosen each summer. At Coles Bay only three sites were available and, therefore, these were used in both years.

Figure 1.1: Map of Tasmania and Great Oyster Bay showing the two locations surveyed.

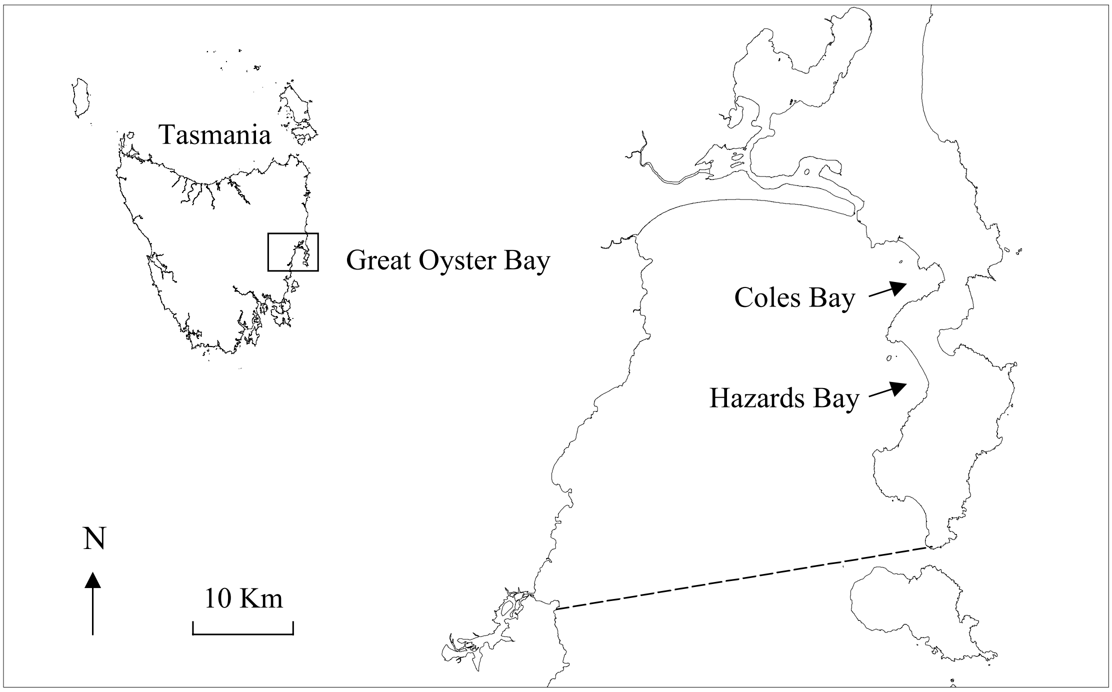


Table 1.1: Summary of the area (hectares) of the sites surveyed during 1999 and 2000. In Hazards Bay seagrass beds surveyed totalled 3.68 ha in 1999 and 4.21 ha in 2000. In Coles Bay seagrass beds surveyed totalled 1.36 ha in both 1999 and 2000.

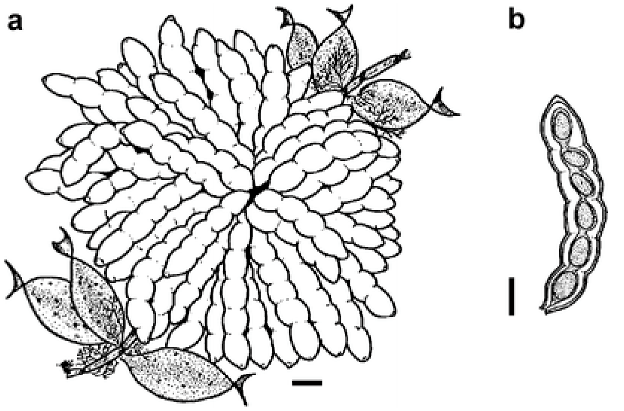
	Hazards	Coles Bay
Site 1	0.17	0.63
Site 2	2.02	0.22
Site 3	1.49	0.51
Site 4	2.02	

Southern calamary deposits the eggs in white finger-like strands attached to seaweed in sheltered, shallow inshore areas along the southern Australian coast. Each strand is approximately 60-70mm long with 3-7 eggs inside (Fig 1.2). The egg strands are often attached to one another to form an individual egg mass made up of 10's to 100's of egg strands. The density of the egg masses at each site was assessed on SCUBA using 20 m^2 belt-transects (10 m by 2 m), the most suitable size based on precision and logistics. At most sites 20 belt-transects were used and the seagrass searched for egg masses present, however, at the two smallest sites (Sites 1 and 3 in Coles Bay) 14 belt-transects were used. On each occasion that egg densities were estimated the belt transects were haphazardly laid in the seagrass beds.

Surveys of the egg masses on the seagrass beds in Great Oyster Bay were carried out from November 1999 to December 2000. During the spring/early summer months (October to December) surveys were carried out fortnightly on three sites at each of the two locations. These surveys were timed around two-week fishing closures to both commercial and recreational fishing, implemented as a management measure to provide some protection to the spawning squid and their subsequent egg production in the Great Oyster Bay area (Chapter 2). Therefore, when estimating the spatial and temporal pattern of egg production only surveys carried out during periods of fishing (the 'normal' situation for most of the year) were used. The fortnightly surveys were used to estimate loss of egg masses (see below). During late summer, autumn and most of winter surveys were done every second month due to the absence of spawning activity. Development time of the embryos was expected to be slower in the winter months and therefore egg masses laid during the non-survey months would have been detected in the next survey.

Most egg masses were made up of more than 50 strands and it was not logistically possible to count the strands in each mass while underwater. The number of strands is a better indicator of spawning intensity than the number of egg masses. Therefore, we used egg mass length as a predictor of the number of strands in a mass. The length of an egg mass was determined to be from the attachment point on the *Amphibolis* to the tip of the terminal strand when laid along the edge of an underwater slate marked with centimetre increments. Egg masses were measured to the nearest centimetre. Three observers over two days (Nov 4 and 27) measured and collected a total of 61 egg masses across a range of stages and sizes. Back in the laboratory the number of strands in each mass was counted each egg mass. A Model II regression was used to generate a predictive equation for calculating the number of strands from the length of the egg mass. The correlation coefficient of 0.75 (df 59, P<0.001) was lower than preferred for predictive purposes, however, given the limitations of counting the strands underwater it was felt that this provided an indicative estimate of spawning intensity. The density of egg strands was compared among times and between locations using an orthogonal ANOVA. The assumptions of the ANOVA were checked using residual plots and no transformation was found to be necessary. A Tukeys HSD post-hoc test was used to explore terms in the ANOVA that were significant.

Figure 1.2: An egg mass made up of a number of egg strands (A). Each egg strand contains between three and nine eggs (B).



Each egg mass measured in the field was allocated a development stage ranging from I (newly laid) to IV (hatching) based on the external appearance of the strands (Table 1.2). It was not possible to measure the length of Stage IV masses because the masses were reduced in length by the hatching out of the juvenile squid and also at this stage the egg masses were starting to disintegrate. To determine if the broad 'in-situ' four-stage classification of the egg masses was valid, twenty newly laid egg masses (ten from each location) were monitored from laying to hatching in November and December 1999. Each week from laying to hatching three randomly selected egg strands were removed from each egg mass. The embryos from each strand were dissected out and the developmental stage determined using Segawa's (1987) thirty stage developmental series for *Sepioteuthis lessoniana.* Eggs laid during November 1999 took at least 30 days to get to the final stages of development. Therefore, it was likely that over the period when most egg masses were present, hatching would have occurred at approximately 5 weeks. As a result, on our classification scale Stage I and II egg masses were less than 14-20 days old. Stage III egg masses were characterised by pigment around the eye, a feature that is evident in embryos that Segawa (1987) describes at developmental Stage 22-24. Also recorded along each transect was the presence of single strands, attached to the top of the plant. The significance of these single strands was unclear, and these were not included in the estimates of egg mass density on the seagrass beds.

Table 1.2: Description of the staging of egg masses used in the field

Stage	Description
I	Newly laid strands, pearly white, no fouling by algae, individual eggs not obvious
II	Strands no longer shiny, some fouling evident, the eggs are starting to become obvious
III	Eggs within the strand are clearly obvious, extensive fouling is present on the egg mass. The embryos have eye and body pigmentation and can be seen.
IV	Most of the embryos in the egg mass have hatched or are hatching and the egg mass is starting to fall apart

To provide a description of the type of habitat used by the squid for egg attachment, seagrass density, percent cover, and plant length were assessed at each site once each year (November 1999 and December 2000). A grided 0.25 m^2 quadrat provided 36 interstices used as points to estimate the percent cover of plants using the point-count method (Kingsford & Battershill 1998). The quadrat was placed randomly on the seagrass and the number of interstices over sand was counted to calculate percent cover of vegetation. In the same quadrat the numbers of individual Amphibolis plants were counted and the length of a random plant was measured to the nearest centimetre. At most sites 20 quadrats were examined, but at the two smallest sites 14 quadrats were used.

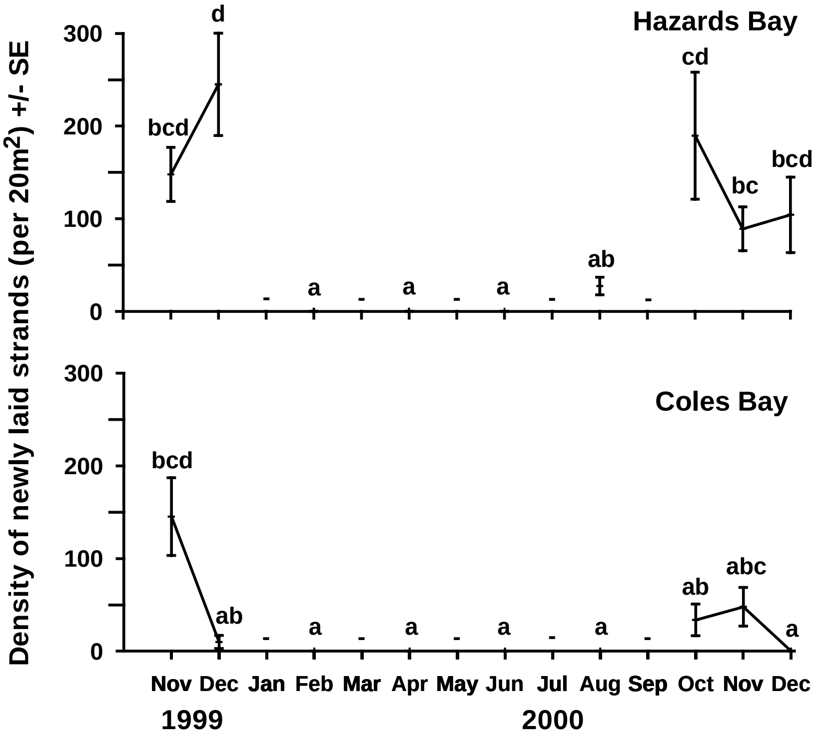
Observations of egg masses washed up on beaches near the spawning sites suggested the possibility of egg masses being dislodged from the seagrass beds by storms. Using average egg mass density (number of egg masses per 20 m^2) at each site through time, based on data from the summer fortnightly surveys, it was possible to estimate the loss of egg masses. The difference between the average density of egg masses classified as Stage I to III at Time 1 and the average density of the Stage II, III, and IV egg masses at Time 2 was calculated. Note that Stage IV egg masses were not included in the Time 1 calculations because these egg masses would have disintegrated before Time 2. If the difference in the average density of egg masses between Time 2 and Time 1 (± 95% confidence limits of the difference) was less than zero, then this was considered a loss of egg masses. Atmospheric pressure and wind direction and strength data were obtained from a local weather station (Australian Commonwealth Bureau of Meteorology's climate archive). The spawning sites in this survey were exposed to winds from the SW through to NW, therefore only these data were examined to determine when the sites might have experienced storm conditions.

Results

The temporal pattern in the production of newly laid egg strands was not the same at both locations ($F_{location*month}$ = 2.94, df 8, 954, P=0.003). It was evident that spawning activity of southern calamary on shallow seagrass beds in Great Oyster Bay was concentrated over spring and early summer in both years (Fig. 1.3). However, spawning activity appeared to occur earlier in 2000 at Hazards than at Coles Bay, with egg masses present as early as August, the austral winter. A comparison between the two years, month by month at each location, shows that the density of newly laid eggs was not significantly different in both years (Fig. 1.3).

The large standard error bars around the means in Fig. 1.3 are indicative of the extreme spatial patchiness of egg production among sites within each location. This spatial variability of egg production within each location was notable because the sites within a location were on average less than one kilometre apart. The laying activities of squid did not show the same temporal pattern at the two locations in 1999. In November and December 1999, the production of eggs in Hazards Bay was similar. In contrast, there was a four-fold drop in egg production between November and December in Coles Bay (Fig. 1.3). From October to December in 2000 the production of eggs at each location was at a similar level throughout the three months (Fig. 1.3).

Figure 1.3: The average density of newly laid egg strands at each of the two locations during the thirteen months of monitoring. - = no data. Hazard Bay n=60, Coles Bay n=48. Letters above the means are results of the post-hoc test; means sharing the same letter are not significantly different. (from Moltschaniwskyj & Pecl 2002)

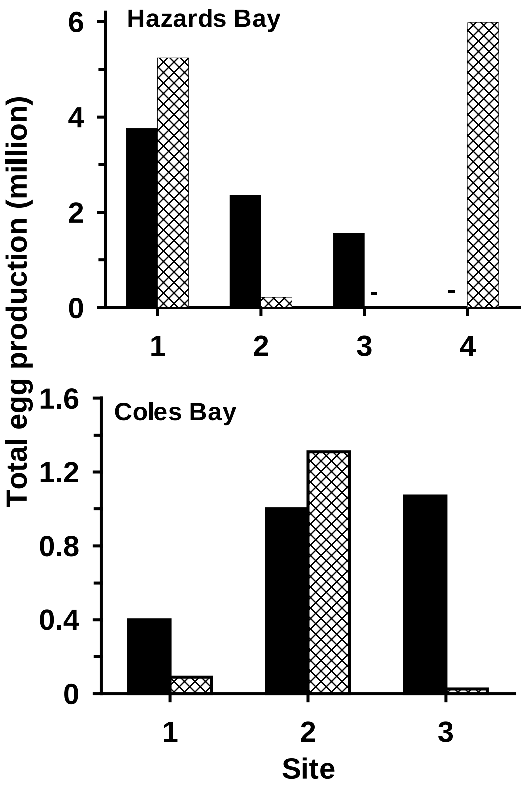


With respect to total egg production Hazards Bay was the most productive in absolute terms in both 1999 and 2000, with slightly higher productivity in 2000 (Table 1.3). In contrast, spawning production in Coles Bay showed almost a four-fold drop between 1999 and 2000 (Table 1.3). Productivity was not consistent among the seagrass beds at each location, and a breakdown of the egg production at the site level again highlights the spatial variability in spawning activity, with sites separated by 0.5 kilometres differing by over 150% in some cases (Fig. 1.4).

Table 1.3: Total egg production (x 10^6), and seagrass characteristics in 1999 and 2000 at each location. Values in brackets are SE.

Location		1999	2000
Hazards Bay	Total egg production	7.68	11.40
	Egg production per hectare	2.09	2.72
	Average percent cover seagrass	87.64 (1.57)	91.52 (0.33)
	Average plant height (cm)	24.75 (0.83)	43.38 (1.54)
	Average seagrass density (per $0.25m^2$)	18.78 (0.91)	12.25 (0.59)
Coles Bay	Total egg production	2.47	1.43
	Egg production per hectare	1.82	1.05
	Average percent cover seagrass	90.11 (1.29)	96.63 (0.42)
	Average plant height (cm)	24.98 (0.81)	42.00 (1.37)
	Average seagrass density (per $0.25m^2$)	20.52 (1.05)	11.60 (0.55)

Figure 1.4: The number of Stage I eggs produced in the sites monitored in each of the two locations in 1999 (solid bars) and 2000 (cross-hatched bars). Note different scale for each location. - = no data. (from Moltschaniwskyj & Pecl 2002)



Dramatic and significant differences in the density and length of *A. antarctica* plants and the percent cover of vegetation were evident between 1999 and 2000 (Table 1.4). Percent cover of vegetation increased from 88% in 1999 to 94% in 2000 however, this was not a function of *A. antarctica* becoming denser during 2000. At many sites during late 2000 a mat of brown epiphytic brown algae developed, covering the *A. antarctica*. Between the two census dates there was a 39% decline in the density of *A. antarctica* plants across the two locations (Fig. 1.5). Additionally, there was a 72% increase in the average height of the plants (Fig. 1.5). No differences in any of the three variables measured were detected between the two locations, but it was evident that considerable variation was present among the sites at each location (Table 1.4). At the scale of sites there was no evidence, across the years, of correlations of egg production with *Amphibolis* density (r=-0.15, n=12, P=0.63), percent cover (r=-0.11, n=12, P=0.73), or plant height (r=0.06, n=12, P=0.86).

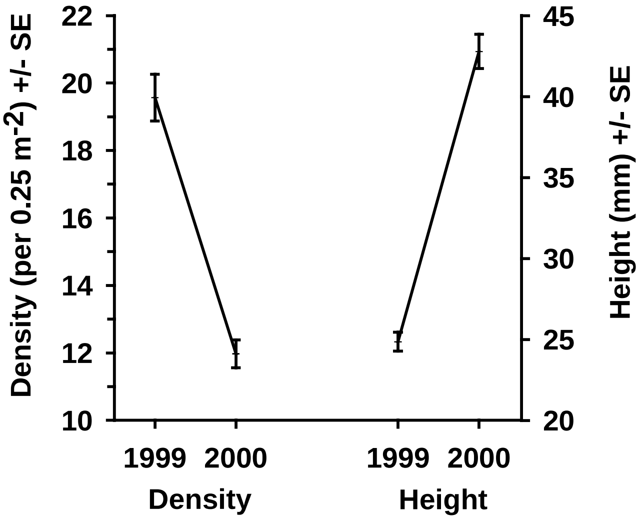
Table 1.4: Mixed model ANOVA results for percent cover, density of *Amphibolis antarctica* plants and the height of the plants. Type I error rate used is 0.017, using the Bonferroni adjustment for tests on the three variables.

	Percent Cover		
Source of Variation	F	df	P
Year	5.80	1,8	0.42
Location	2.87	1,8	0.13
Year*Location	0.41	1,8	0.54
Site(Year*Location)	3.84	8,196	<0.001

	Density		
	F	df	P
Year	26.18	1,8	0.001
Location	0.09	1,8	0.78
Year*Location	0.47	1,8	0.51
Site(Year*Location)	3.48	8,196	0.001

	Height		
	F	df	P
Year	91.85	1,8	<0.001
Location	0.002	1,8	0.96
Year*Location	0.61	1,8	0.46
Site(Year*Location)	2.45	8,196	0.02
Site(Year*Location)			

Figure 1.5: The average density of *Amphibolis* plants and the average height of the plants across the two locations in summers of 1999 and 2000. (from Moltschaniwskyj & Pecl 2002)



The only significant loss of egg masses was detected on two occasions at sites in Hazards Bay (Fig. 1.6). The most dramatic reduction in the density of egg masses occurred at Site 1 between November 4 and 20 1999 when 54% of the egg masses were lost. At this time Site 2 had very low densities of egg masses (on average approximately 2 masses per 20 m^2) possibly explaining why losses were not detected at this site. A second loss occurred during 1999 in Hazards Bay between December 6 and 20 when Site 1 and Site 2 experienced smaller losses of on average four and two egg masses per 20 m^2 respectively (Fig. 1.6). During the 2000 season neither of the Hazards Bay sites suffered significant losses of egg masses (Fig. 1.6). The Coles Bay sites did not show any loss of egg masses in either 1999 or 2000.

During November and December 1999 a series of low-pressure systems passed over Tasmania, causing strong winds into both Coles Bay and Hazards Bay. In contrast the 2000 season was characterised by consistently high atmospheric pressure and as a result relatively light winds affected the sites (Fig. 1.7). The first storm event in 1999 occurred between November 4 and 20, 1999 (Fig. 1.7). However, the second occurred between November 20 and December 6 1999, when no loss of egg masses was detected. Furthermore, when losses of egg masses were seen between December 6 and 20 1999, no high winds were recorded.

Figure 1.6: Differences in the average density of egg masses deposited at two sites in Hazards Bay between two consecutive survey dates approximately two weeks apart. If the confidence limits do not encompass zero then the average difference in the density of egg masses is significantly different from zero. (from Moltschaniwskyj & Pecl 2002)

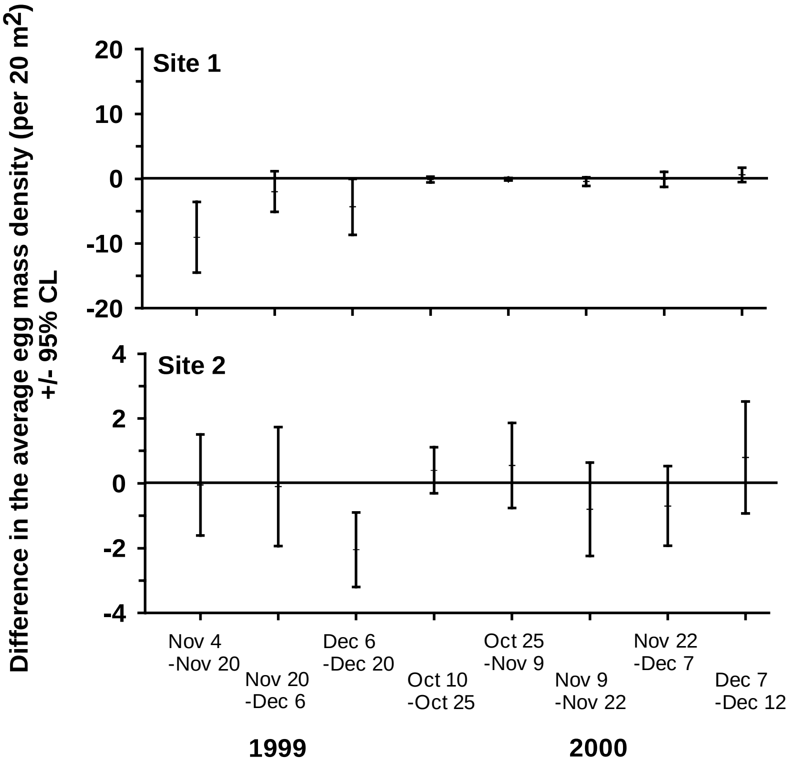
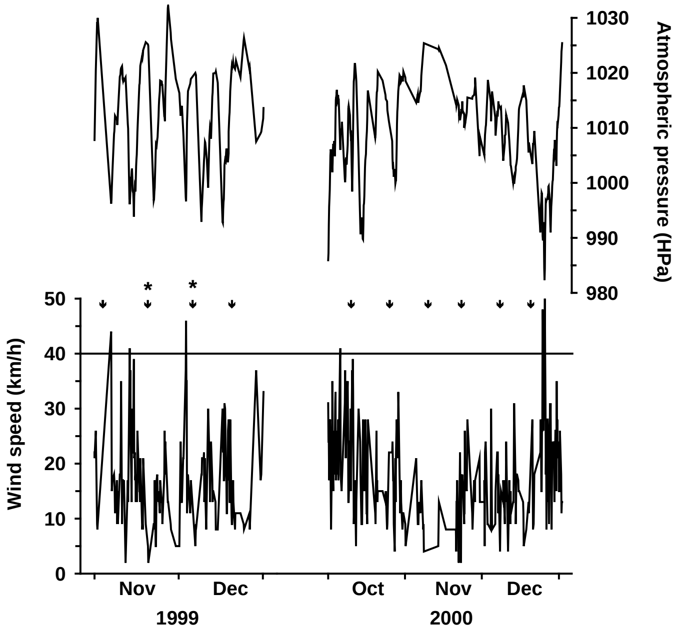


Figure 1.7: The wind speed (km/hr) and atmospheric pressure (HPa) during the spring/early summer of 1999 and 2000. The arrows indicate the days on which surveys of the eggs masses were conducted. The asterisks indicated times at which egg mass loss had been detected. (from Moltschaniwskyj & Pecl 2002)



Discussion

In Great Oyster Bay the extensive use of the shallow, inshore seagrass beds for spawning activities by *S. australis* during the 14 months of this study was limited to the austral spring and early summer time. This temporal pattern was consistent over the two summers. Spawning occurred as early as September, but peaked in October and November and by January no new egg masses were seen. Based on more extensive surveys throughout the year and in the south-east of Tasmania, this aggregation represents one of the largest seen on the east and south-east (Chapter 6). It is possible that spawning takes place during the rest of the year either in different habitats (eg reefal areas or deeper water). Female squid are present in the Great Oyster Bay area during winter months, but lower proportions are mature compared with summer (Pecl 2001). Furthermore, landings of squid are lower in winter than during the spring/summer period (Tasmanian Department of Primary Industries, Water and the Environment, unpub. data). Anecdotal information from fishers suggests that eggs have been seen and trawled from deeper waters (c. 20 m); however the recent absence of trawling and dredge fishing operations makes it difficult to determine if spawning still occurs in deeper habitats. .

The spatial variability in the density of newly laid eggs was very high at all scales examined. This was particularly surprising given the close proximity of seagrass beds within a location. Although the sites differed with respect to the seagrass bed characteristics assessed, there was no evidence of a correlation between egg production and seagrass characteristics. Patchy or clumped distribution of eggs on the spawning grounds has been observed for *Loligo vulgaris reynaudii* (Sauer *et al.* 1993). In contrast, surveys on the spawning grounds of *Loligo opalescens* found a random distribution of eggs throughout the study area (Okutani & McGowan 1969). Specificity in the type and use of substrates for egg laying is seen in teleosts (eg the Japanese surf smelt *Hypomesus japonicus* Hirose & Kawaguchi 1998). However, to date there is limited evidence that cephalopods display specificity in laying substrate. In both Tasmania (this study) and South Australia (Triantafillos 1997) southern calamary extensively use *A. antarctica* as a laying substrate, but we have also seen eggs attached to macrophyte algae and embedded in the sand. *Sepioteuthis lessoniana* lays eggs on a range of artificial substrates displaying a lack of specificity (Ueta 2000). Many of the other loliginid squid (*L. opalescens*, *L. plei* and *L. vulgaris reynaudii)* do appear to prefer sand as a substrate to attach eggs (Shimek *et al.* 1984, Vecchione 1988, Sauer *et al.* 1993), but the specificity with respect to physical and biological characteristics is unknown. The assessment of the seagrass was done once a year; therefore it is possible changes in the seagrass during late summer and winter reduced the preference of *Amphibolis* as a spawning substrate. Specificity of laying substrate and selection of spawning sites are assumed to benefit the survival of eggs and maximise hatching rates.

The spatial variability in the use of spawning areas may also be related to behavioural interactions among mature adults and the daily patterns of movement of these individuals. Little is known about the behavioural dynamics of the spawning adults, and the extent to which courtship and mating in the immediate spawning area is important in determining where laying takes place. The presence of eggs or spawning adults encourages more spawning to take place in the immediate vicinity for

Loligo pealeii (Maxwell & Hanlon 2000). There is a strong possibility that the visual stimulus of eggs is also important for *S. australis*, resulting in suitable attachment substrate being apparently ignored.

Much of the temporal and spatial variability in egg production may be a function of changes in the population structure and fecundity of the *Sepioteuthis* aggregations. There is no information about the abundance of squid at the spatial scales of this study. Direct counts were not possible because the behaviour of the squid and water clarity meant that adults were rarely seen underwater. Catch and effort data are also not available at that scale. However, biological data of squid populations in that area suggest that over short periods of time different cohorts of adults are moving onto the spawning grounds to deposit eggs (Chapter 4, Jackson & Pecl 2003). However, there was no evidence that size or reproductive investment changed between the months to explain temporal differences in egg production. Given that more than 75% of the females on the spawning area had empty stomachs (Jackson & Pecl in review), it is unlikely that presence of prey was a major determinant in the spatial use of the *Amphibolis* seagrass beds.

Loss of egg masses from the spawning areas monitored was detected on two occasions, but only on the first occasion was the loss correlated with storms. However, large swells associated with storms can continue to occur for longer than the winds that generated them, therefore it is possible that storm associated wave action may have been responsible for dislodging the egg masses. It is possible that the loss of egg masses could be attributed to hatching out of the juveniles, although our surveys found no hatching egg masses in November. However, during December hatching was occurring when low level of egg mass loss was evident. Given that counts of egg masses were estimates it was possible that a significant difference in egg mass numbers between times may be due to chance. However, it would also be possible, by chance, to find an increase in egg mass density, a situation that did not occur, suggesting that the losses detected were real. In past studies the loss of egg masses on squid spawning beds has been attributed to predation (Sauer & Smale 1993, Hixon 1983) and anchor damage (Sauer 1995). Although anchor damage may occur during commercial fishing activities for the squid, the small size of the seagrass areas means that fishers tend to drop their anchors over the sand so the boat is hanging over the seagrass beds. Therefore, anchor damage was not considered to be a source of egg mass loss, furthermore the loss of egg masses would have been more prevalent given that fishing occurs over much of the spawning season. Predation of *S. australis* egg masses by fish and smaller invertebrates may violate the integrity of egg masses and cause dislodgement from the seagrass.

Currently in Tasmania closures over the spawning period have been implemented in this area (Chapter 2). Several points can be made with respect to the decisions surrounding fishing closures in this case. The first is that within Great Oyster Bay spatial variability in spawning activities and intensity means that areas closed to fishing need to encompass relatively large areas i.e. bays, rather than single seagrass beds. The second point is that the temporal variability in the magnitude of egg production and losses of egg masses means that spawning adults need to be protected for extended periods throughout the spawning period.

Chapter 2: An assessment of the use of short-term closures to protect spawning southern calamary aggregations from fishing pressure in Tasmania, Australia

(Authors: NA Moltschaniwskyj, GT Pecl & J Lyle)

Note that parts of this work have been published in the following paper:
Moltschaniwskyj, N.A., G.T. Pecl & J. Lyle (2003). An assessment of the use of short-term closures to protect spawning southern calamary aggregation from fishing pressure in Tasmania, Australia. Bulletin of Marine Science 71: 501-514

Introduction

Unfortunately many squid fisheries target spawning aggregations (eg *Loligo vulgaris reynaudii,* and *Loligo opalescens* Hanlon, 1998). The impact of fishing spawning aggregations can range from removal and disturbance of spawning and mating individuals to the physical damage of eggs by anchors (Sauer, 1995). There is a need to consider some protection of squid populations from high fishing pressure given evidence that fishing will remove healthy spawning animals from the population (Leos, 1998). There is also evidence that squid jigs will selectively remove animals from the spawning beds (Sauer, 1995), potentially modifying the processes of sexual selection and mating systems of the spawning populations (Hanlon 1998). Given these potential effects, particularly on reproductively mature animals, there is an increasing needed to impose controls on fishing activities that allows sustainable use of these resources.

A variety of management approaches towards squid fisheries has been achieved by spatial and/or temporal exclusions (Augustyn and Roel, 1998, Leos, 1998), or regulating effort (Haimovici *et al.*, 1998). The different approaches range from total allowable catches and limited entry in the long-finned squid (*Loligo pealeii*) fishery (Brodziak, 1998), proportional escapement via effort control for the short finned squid (*Illex argentinus*) in Falkland Islands waters (Beddington *et al.* 1990), to effort control via licences, and temporal and spatial closures in the Falkland Island loliginid squid (*Loligo gahi*) fishery (Hatfield and des Clers, 1998). In many cases management policy is designed explicitly to protect and reduce fishing effort targeting reproductively mature individuals and allow spawning to take place (eg *Loligo vulgaris reynaudii* Augustyn and Roel, 1998). As a result of dramatic increases in catch and effort in the southern calamary fishery and the perceived vulnerability of spawning aggregations to over-fishing, effort control via closures to fishing were put in place in Great Oyster Bay. However, it will be necessary to assess the value of the management strategies in providing the protection that is claimed.

Based on previous observations and information obtained from fishers it was known that within this area *Amphibolis antarctica* patches periodically support large aggregations of spawning squid. Therefore, this work was restricted to and focused upon areas of *A. antarctica* seagrass that occur in isolated patches. The total closure time was 4 weeks, split into 2 two-week blocks separated by two weeks, over the spring and early summer of 1999 (Table 2.1). This study explored the effect and value of short temporal closures in protecting spawning aggregations of the loliginid squid southern calamary in Great Oyster Bay. We achieved this by directly assessing spawning intensity, as well as describing changes in the population and fishery in the time periods around the closures. Over a ten-week period that included before, during and after the closures, we estimated egg production on seagrass beds, CPUE in and out of the closed region, and the size structure, somatic condition and reproductive status of the spawning squid.

Materials and Methods

Monitoring of the spawning activity of squid was carried out at two locations within Great Oyster Bay: Hazards Bay and Coles Bay in 1999 and 2000 (Fig. 2.1). Within each location three sites that we knew were regularly used by southern calamary for spawning were monitored throughout the study in each year (Chapter 1). In 1999 each site was surveyed on four occasions; at the end of each two-week closed period, at the end of the two-week open period between the closures, and two weeks after the area was permanently re-opened (Table 2.1). In 2000 there were three closure periods and we looked at open periods between each closure and at the end of each closure (Table 2.1).

Figure 2.1: Map of Tasmania and Great Oyster Bay showing the location of the study area.

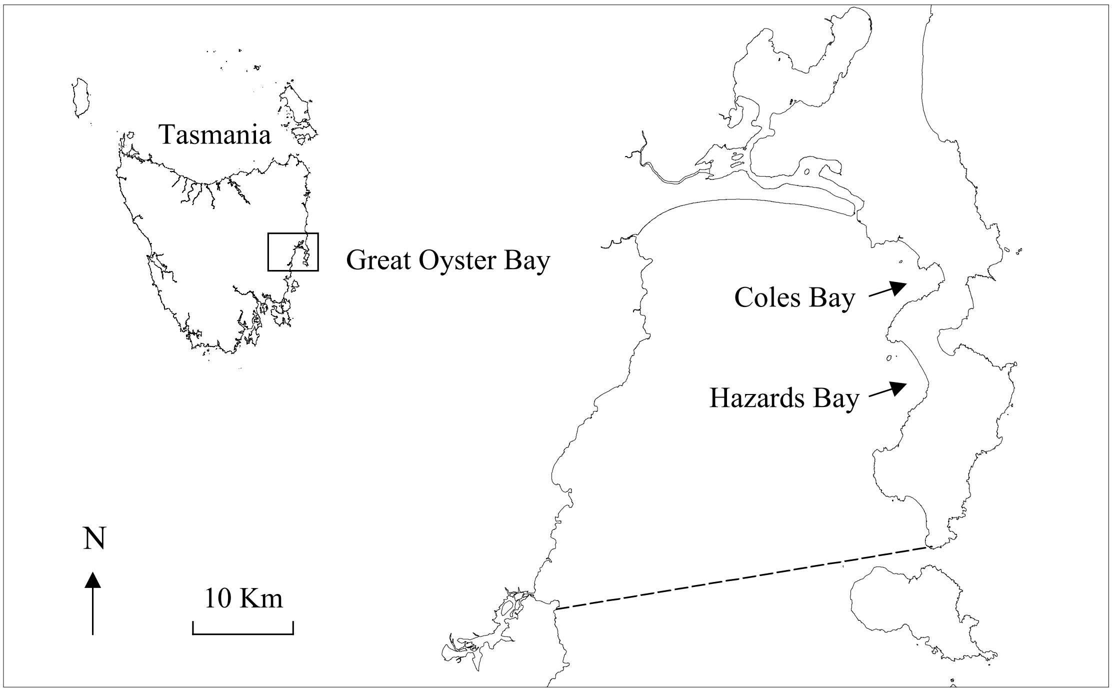


Table 2.1: Timetable of activities, the ticks indicates time periods for which data is available. Note that egg mass counts were conducted at the end of each block of time. The early November 1999 egg mass counts included Stage III masses, while the rest of the surveys only included Stage I and II masses (see text for more detail).

Date 1999	**11/10-24/10** Open 1	**25/10-7/11** Closure 1	**8/11-21/11** Open 2	**22/11-5/12** Closure 2	**6/12-19/12** Open 3
Egg mass counts	✓	✓	✓	✓	✓
Catch records	✓	✓	✓	✓	✓
Research Samples	10 d before Closure 1	✓	✓	✓	✗

Date 2000	**25/9-8/10** Closure3	**9/10-22/10** Open 4	**23/10-5/11** Closure 4	**6/11-19/11** Open 5	**20/11-3/12** Closure 5	**4/12-17/12** Open 6
Egg mass counts	✓	✓	✓	✓	✓	✓
Catch records	✓	✓	✓	✓	✓	✓
Research Samples	✓	✓	✓	✗	✓	✗

Egg density was determined using strip transects (see Chapter 1 for details). At four of the sites twenty transects were used and at of the two smaller sites only fourteen transects were used. Stage I and II egg masses (Table 1.2) were likely to be less than two weeks old (Chapter 2). As we were only interested in the output of females during the two-weeks prior to each survey only the data for Stage I and II egg masses were analysed. No survey was undertaken before Closure 1, therefore the density of Stage III egg masses was counted in early November as these egg masses represented eggs laid at the end of October.

Catch records for Great Oyster Bay and the rest of Tasmania, as reported by the fishers, were compiled for the two-week periods during the study (Table 2.1). Catch records for the same or similar periods were also obtained for 1997 and 1998. In Tasmania southern calamary are caught using a variety of fishing methods, which include a range of netting techniques, hand-jigs, dip-nets and hand-spears. There has been a general shift to hand jigging as the dominant method for catching squid, partly in response to management changes that restricted the use of nets via licensing since 1996/97. To allow the use of all effort and CPUE data during the study period, effort was calculated on the number of fishing days in which the species was caught, regardless of the fishing method(s). However, to reduce the inclusion of records for which southern calamary represented an incidental by-catch rather than target species, landings of less than 10 kg for Danish-seine nets, beach-seine nets, gill-nets, dip-nets and hand-spears were excluded. Since hand jigging and purse-seine nets are used specifically to target southern calamary all catches using these gears have been included in the analyses. CPUE was calculated as the geometric average of the catch per fishing day across each two-week period.

Collections of squid on the spawning beds, using hand-jigs, were made to obtain biological information over the October to December period (Table 2.1). From each individual, the dorsal mantle length (mm), total body weight (g), sex and the weight of the reproductive organs (g) were recorded. Using this data the sex ratio, gonosomatic index (GSI)[1] and mantle length-body weight relationships were examined for changes during the periods open and closed to fishing. Trends in the GSI through time were analysed using a combination of ANOVA and regression. Length-weight relationships among the times were compared using an ANCOVA.

Results

Spawning Activities

The average density of egg strands within transects in Great Oyster Bay ranged between 0-62.8 strands.m^{-2}. In 1999 changes in strand density through time were different between the two locations (time*location interaction F=2.98, df 4,557, P=0.019), largely due to a 6-fold increase in the production of egg strands in Hazards Bay during October Closed period that did not occur in Coles Bay (Fig. 2.2). In contrast a significant increase in the density of new strands was not seen in Coles Bay until the November Open period (Fig. 2.2). Following these increases the density of newly laid eggs in each two-week period thereafter was relatively constant at both locations. There was evidence that more spawning activity occurred in Hazards Bay during the closures (four times higher during the October Closed period and two times higher during the November/December Closed period, but new egg strand density was similar at both locations during open periods (Fig. 2.2). In 2000 the variation in egg strand number was only a function of time (F=3.85, df 5,636, P=0.002), where the lowest density of egg strands occurred during the October opening and the highest during the December closure (Fig. 2.2). The density of egg strands was highest in Hazards Bay (F=21.88, df 1,636, P<0.001), with more than twice as many egg strands (mean ±SE; Hazards 14.6±1.4, Coles 6.58±0.9).

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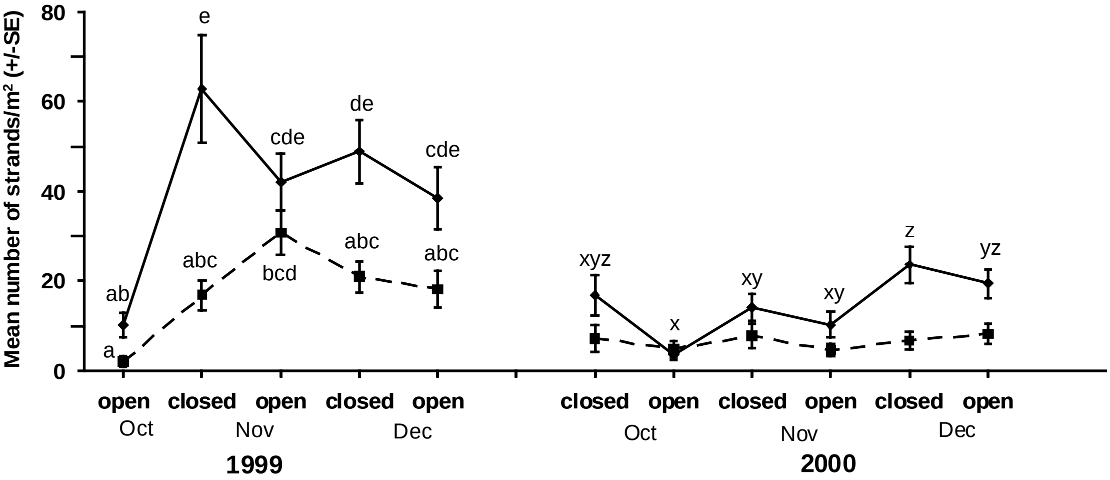
[1] GSI = ((weight of reproductive structures) / total body weight) * 100
Reproductive structures for females include ovary and oviduct; for males testis, spermatophoric complex, penis and needhams sac.

Figure 2.2: The mean number of egg strands.m^{-2} (± standard error), in Hazards Bay (solid line) and Coles Bay (dashed line). Means with different letters are significantly different from one another based on post-hoc Tukeys HSD test among the ten means. In 2000 the letters refer to means at each time across locations.



Size and Reproductive Status

In 1999 female GSI decreased significantly from a mean of 6.4% prior to the first closure to 4.5% in late November (F=9.29, df 3,65 P <0.001; Fig. 2.3); furthermore this decrease was linear through time (F=19.93, df 1,2, P=0.047). There was a 15% decrease in the male GSI between Open 2 and Closure 2 (Fig. 2.3), which was significant (F=2.91, df 3,159 P=0.036). However, no linear decline through time in the male GSI was evident (F=0.05, df 1,2, P=0.0975).

In 2000 the females GSI also changed through time (F=3.64, df 3,37, P=0.21), the highest GSI seen during the first open period and the lowest during the December closure (Fig. 2.3). There was no significant change in GSI during the open and closed periods for males (F=2.12, df 5,636, P=0.062).

In 1999 among the four time periods the average females body weight ranged from 727.8-839.8 g (Fig. 2.4), which was not significantly different (F=0.89, df 2,66, P=0.415). In contrast in 2000 there was a significant decline in body size (F=5.48, df 6,119, P<0.001), although this does not appear to be related to period open and closed to fishing (Fig. 2.4). The male average body weight declined significantly in both 1999 (F=9.75, df 3,159, P<0.001) and 2000 (F=22.43, df 6,363, P<0.001). The decline was as much as 33-41% from mid-October to the end of November (Fig. 2.4). The length-weight relationships did not differ among the time periods for either males (F=1.45, df 3,155, P=0.23) or females (F=0.44, df 2,63 P=0.64), suggesting that somatic condition of the individuals in the spawning aggregation did not decline during the spawning season.

Figure 2.3: The mean gonosomatic index for females and males for the open and closure periods in 1999 and 2000 for the two locations combined. The sample size is indicated above each mean.

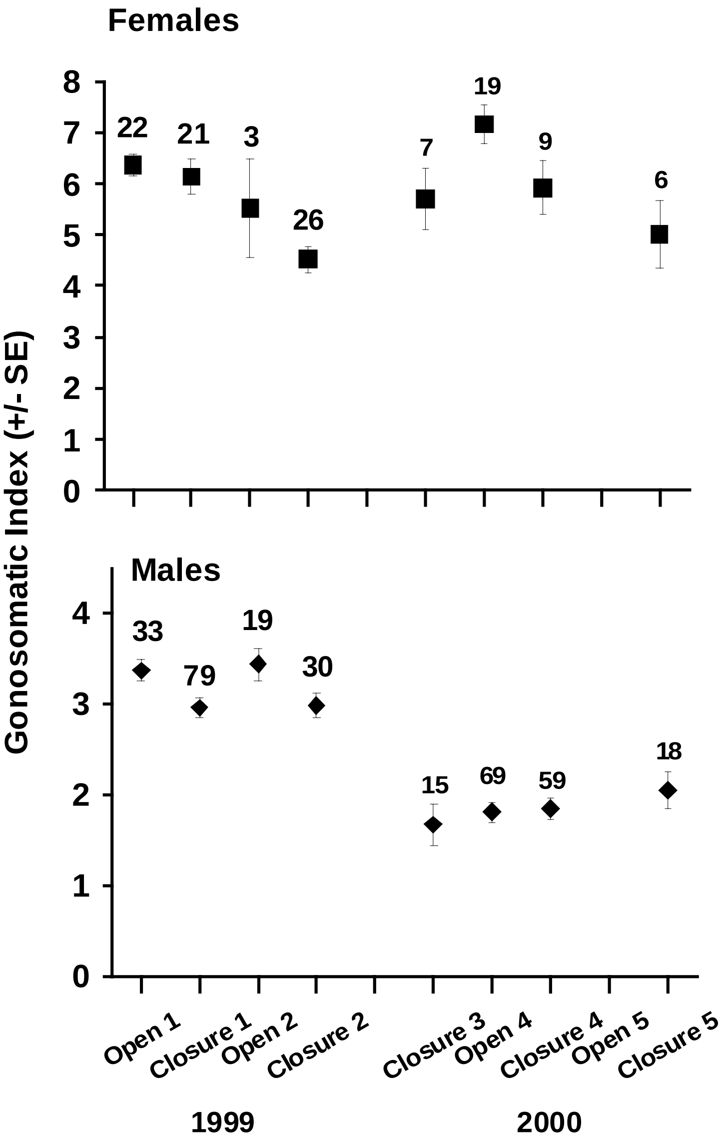
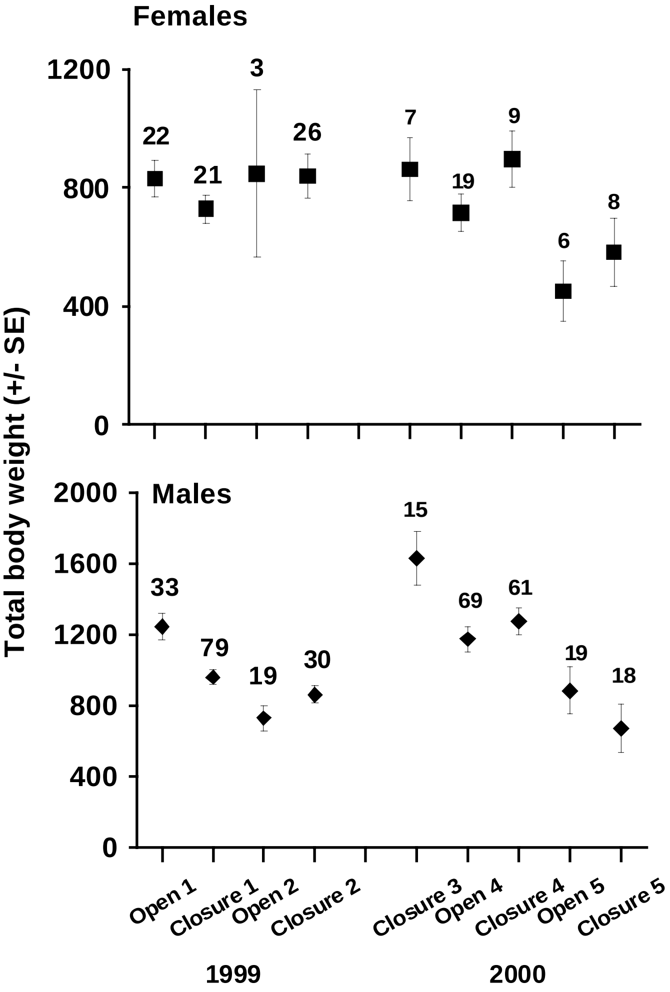


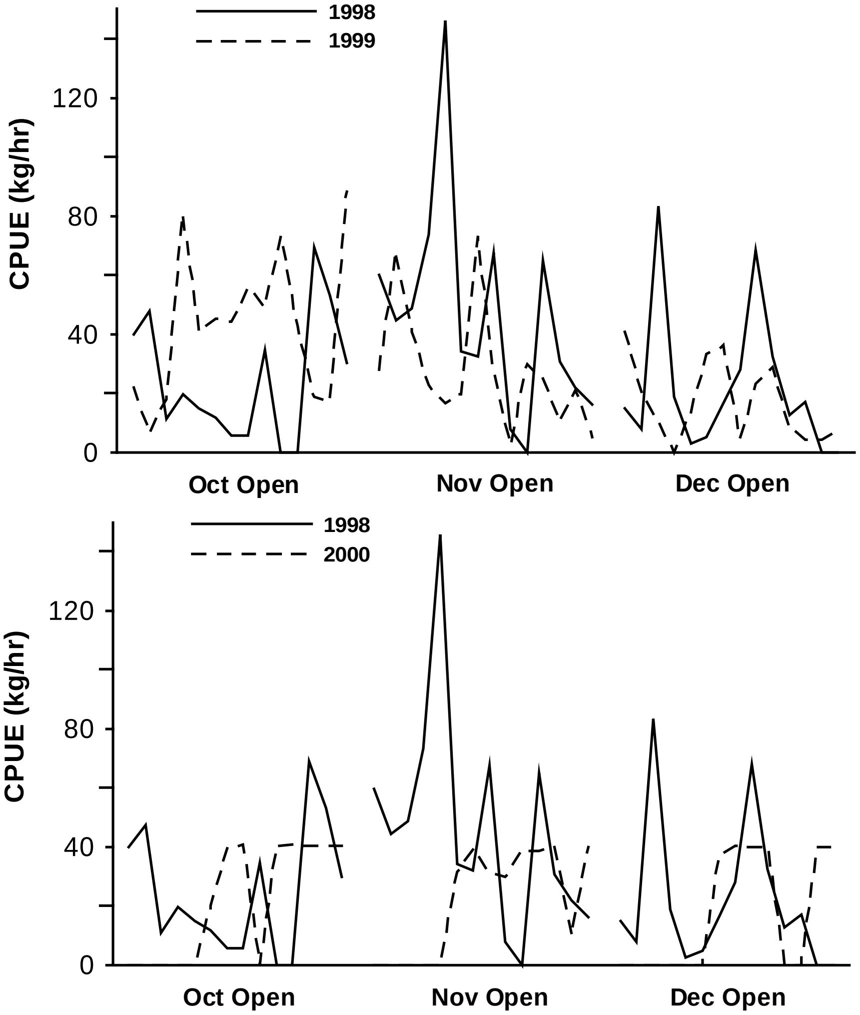
Figure 2.4: The total body weight for females and males for the four occasions during the study across the two locations. The sample size is indicated above each mean. Females caught during Open 2 were not included in the analysis because only three were caught.



Catch per Unit Effort

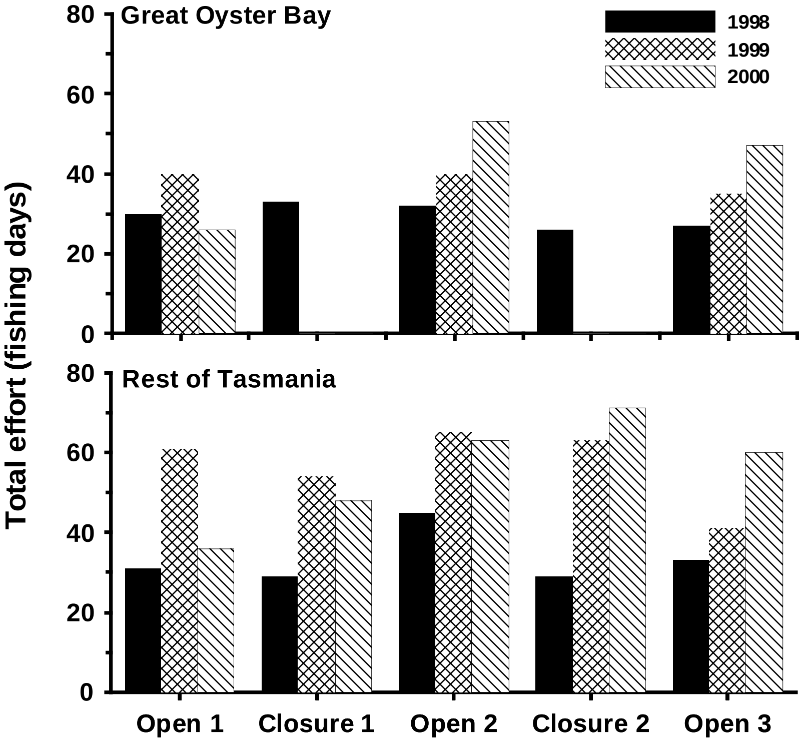
An industry expectation of the closures was that by preventing fishing the concentrations of squid on the spawning beds would increase such that once fishing was resumed there would be a dramatic fish-down of the spawning population. However, it was evident from the daily CPUE data in Great Oyster Bay that there were considerable fluctuations, with no evidence of a marked decline in catch rates following the opening of the fishery. Furthermore, the magnitude of the fluctuations in CPUE during 1999 and 2000 were comparable to those seen in 1998 (Fig. 2.5), suggesting that densities of squid did not increase during the closure. Rather this may reflect squid moving in and out of the area daily, and/or changes in the catchability of the squid. Most notable in 2000 was the consistent absent of catch early in the open fishing period (Fig. 2.5), most probably a function of weather preventing fishing.

Figure 2.5: CPUE data for the 14 days that the fishing was open in October, November and December in 1999 and 2000, and corresponding days for 1998. Note that zero values are indicative of no fishing effort.



It had been anticipated that during the closures fishing effort would be transferred to other areas along the Tasmanian coastline. One of the effects of both a growing interest in the southern calamary and the closure of Great Oyster Bay over the spring and early summer was an increase in fishing activity outside of Great Oyster Bay. In, 1997 and 1998, 43% (of 284 fishing days) and 39% (of 955 fishing days) respectively of the total southern calamary fishing effort occurred in Great Oyster Bay. During the period of the study fishing effort in Great Oyster Bay and the rest of Tasmania increased dramatically, with only 25% and 45% of these occurring in Great Oyster Bay in 1999 and 2000 respectively. In 1998 and 1999 during the periods comparable to the open and closed times in Great Oysters Bay in 1999, the allocation of effort between Great Oyster Bay and the rest of Tasmania was very similar. However, during the 1999 study period fishing effort in areas outside of Great Oyster Bay was 50% higher than in Great Oyster Bay, and was sustained even after fishing resumed in Great Oyster Bay (Fig. 2.6). This suggests that not only is the fishery attracting greater interest and effort, but that the closures encouraged fishers to look for fishing areas outside of Great Oyster Bay. Notwithstanding this, Great Oyster Bay still continued to attract considerable effort.

Figure 2.6: Fishing effort for Great Oyster Bay and rest of Tasmania from mid-October to mid-December during 1998-2000.



During the six weeks of fishing around the closures (before, between and after) the total catch landed in Great Oyster Bay was 40% of the total Tasmanian catch (Fig. 2.7). In contrast, during the 10 weeks of interest in 1998 the catch from Great Oyster Bay represented 58% respectively of the total southern calamary catch in Tasmania. The effect of the closures was to decrease the total Tasmanian catch contribution of Great Oyster Bay for the summer, indicating that short closures were effective at reducing fishing pressure. The Great Oyster Bay CPUE, averaged for each two-week block, was relatively constant during the 1999 open periods; only during the Open 3 period was there a slight decline, while in 2000 the lowest levels were seen earlier in the season (Fig. 2.8). During 1999 and 2000 the CPUE in Great Oyster Bay did not reach the levels seen during similar time periods in 1998, suggesting that closing the area to fishing was not increasing the densities of animals in the area (Fig. 2.8). However, despite increasing effort in areas outside of Great Oyster Bay, the 50% higher CPUE in Great Oyster Bay during 1999 suggests that this site may have characteristics that are conducive to aggregating southern calamary. The CPUE for the rest of Tasmania remained constant throughout the 10 weeks of the study, and was approximately 50% of the CPUE for Great Oyster Bay. This suggests that Great Oyster Bay continued to be an important focus for fishing activity.

Figure 2.7: Total catch for Great Oyster Bay and rest of Tasmania from mid-October to mid-December during, 1998-2000.

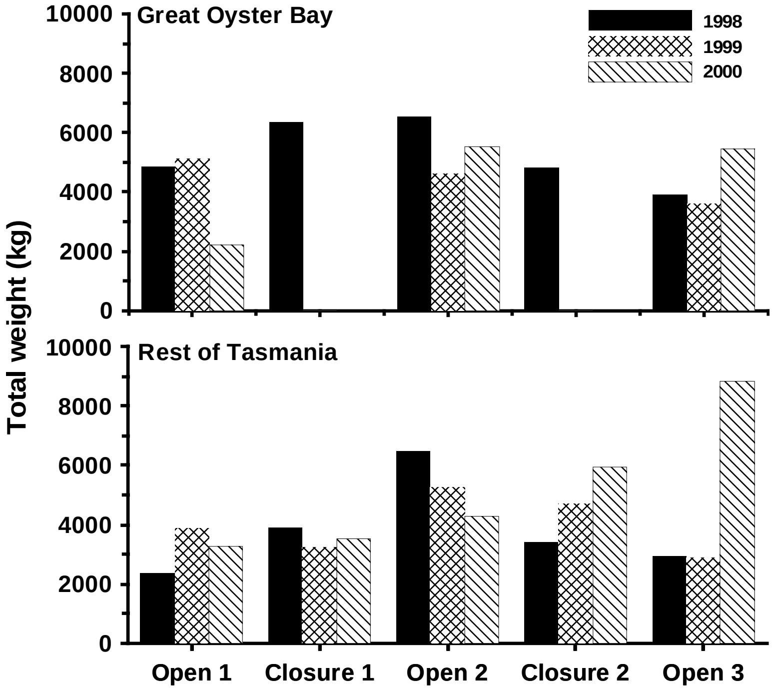
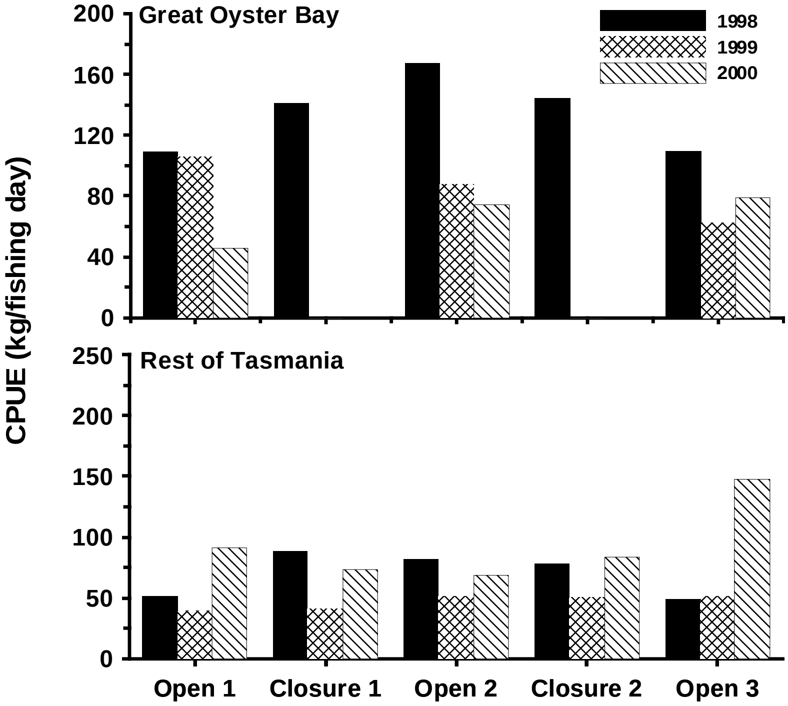


Figure 2.8: CPUE for Great Oyster Bay and rest of Tasmania from mid-October to mid-December during, 1998-2000.



Discussion

It is not an unusual phenomenon for loliginid squid to form aggregations in specific areas for egg laying. Targeting of spawning aggregations of fish and squid by fishers represents a cost-efficient way of harvesting, but may cause concern for resource sustainability. In Tasmania as a short-term emergency measure to offer some protection to the southern calamary spawning aggregations that are targeted by fishers a series of two short (two week) closures was implemented in Great Oyster Bay. This strategy was similar to that which has been implemented in South Africa, where a four-week closed season for commercial and recreational fishers is in place (Augustyn and Roel, 1998).

Immediately prior to the first closure in both years the female gonosomatic index was the highest seen in the study and the CPUE data suggested that animals were present in high numbers. Despite this very low densities of eggs were present in the areas surveyed. Assuming that minimal mortality of eggs had occurred, the very low egg abundances during the first open period indicated that little spawning activity had occurred. A possible explanation for this is that the bulk of the mature squid present on the *Amphibolis* seagrass beds were being caught prior to spawning. Alternatively, spawning may have occurred elsewhere within the area. Given squid were caught in high numbers on the seagrass beds that later had high numbers of eggs present, and the females had ovulated eggs, this presents strong evidence to suggest that animals were present to spawn.

In 1999 a dramatic and significant increase in the density of newly laid eggs occurred during the first closure. This may have happened because the suspension of fishing in Great Oyster Bay allowed the animals to spawn without disturbance, or because the first closure was coincident with a peak in spawning activity in that year. However, in 2000 the levels of spawning were considerably lower and the difference between open and close periods was not as dramatic. This study does not allow us to demonstrate a cause and effect relationship between the closure and spawning activity. The difficulty in assessing the value of the closures is two-fold. The first is that there is no baseline information about the spawning activities of southern calamary in Tasmania; therefore it is not known what typically happens in Great Oyster Bay either during or in the absence of fishing activities. The second problem is that given the unique features of Great Oyster Bay there were no control sites available to provide baseline information about spawning activities during 1999 and 2000. Therefore, it was not possible to compare the locations under the management protocol with those without and make conclusions about the effect of the closures on reproductive behaviour. In spite of this, it must be stressed that the closure was successful in providing protection to the spawning individuals. Future work needs to assess to what degree the fishing activity actually modifies reproductive behaviour, or if it is simply that fishing removes spawning animals.

The timing of the closures in Great Oyster Bay was intended to correspond to the period when peak spawning activities of the southern calamary was occurring. A closure in October may have provided some protection for the reproductively mature females that were present on the beds at this time. Results of modelling the South African chokka squid fishery, which has a closure, suggest in this fishery the closure may have limited value until fishing effort exceeds one million fishing hours (Roel *et* *al*., 1998). This is largely because the overall reduction in annual effort due to closures is slight as fishing effort is intensified during the open periods. In Tasmania there was evidence that fishing effort in both Great Oyster Bay and the rest of Tasmania was higher during the open periods in 1999 and 2000 than during similar periods in 1998 and 1997. This may have occurred because a limited amount of time was available to the fishers to fish and/or because high catches in 1998 and advertising of the closure has increased awareness of the fishery encouraging new fishers to enter the fishery. The use of closures in this fishery was for the purpose of limiting effort during periods of spawning activity.

A major problem associated with the timing of imposing short-term closures on a fishery that targets spawning squid is that we have little information on the temporal and spatial predicability of spawning activities. Environmental cues such as temperature, current and turbidity influence spawning aggregations in other loliginids (eg *Loligo gahi*, Hatfield and des Clers, 1998, *Loligo vulgaris reynaudii*, Roberts and Sauer, 1994). These factors are likely to be important for southern calamary especially since these squid spawn in shallow (3-5m) areas. However, no quantitative information about the temporal patterns of spawning activities of squid in Great Oyster Bay was available at the time of the decision. Research is underway to obtain this information in the hope that the timing of any future short-term closures of this fishery can be made on a biological basis that offers maximum protection to the spawning aggregations.

Egg strand densities on the seagrass beds suggested that continuous low levels of spawning occurred throughout November and December following the peak in early November. It is possible that, despite the removal of mature males and females by fishing, there is continual movement of reproductively mature females into the area thereby allowing spawning activities to continue. Although by December the gonosomatic status of the females was lower than in mid-October, the size of females was no different between those two times. However, the males were significantly smaller towards the end of the study. The effect of intensive fishing pressure on the reproductive behaviour of the squid is unknown. Spawning aggregations of chokka squid in South Africa do not appear to be disturbed by fishing despite high densities of jigs and boat noise (Sauer 1995). However, cephalopods have a complex behaviour associated with reproduction (Hanlon & Messenger 1996). The response of individuals to jigs when courting, mating, and spawning needs to be assessed to determine the impact of jig fishing on spawning dynamics. Therefore our understanding of the effectiveness of closures to protect spawning aggregations of southern calamary will benefit from quantitative studies of the behaviour of squid on the spawning areas like that done by Sauer *et al.* (1992 & 1997).

The CPUE data for 1999 and 2000 suggests that the numbers of squid on the spawning beds were relatively constant over the 10-week period. The slight decrease in CPUE towards the end of the year mirrors the pattern seen more dramatically in 1998. This may reflect a general fish down of individuals that moved into the area to spawn, or that the numbers of squid moving into the shallow areas during spring to reproduce gradually declines over early summer. However, daily CPUE data suggests that squid are not aggregating and increasing their numbers on the spawning beds, but instead are moving in and out of the bays over a period of days.

There are difficulties associated with estimates of biomass of squid and the CPUE data needs to be used with caution. Typically fishers do not record search times for squid as part of CPUE and zero catches are not recorded. There is also evidence that jigs are selective with respect to the individuals that will take the jig (Lipinski, 1994). Our observations of squid when collecting the research samples using hand jigging suggest that there was daily variability in the catchability of squid. As a result of both fisher and squid behaviour the CPUE may be under- or over-estimating biomass with no predictability. Difficulties in using CPUE data for biomass estimates and to determine the effect of closures have been noted before (Leos, 1998). There is considerable value in exploring the use of egg density on the seagrass beds as an indirect method to estimate the biomass of southern calamary on the spawning areas.

In the absence of biomass estimates for southern calamary the use of closures appears to be the best approach to limiting effort on spawning aggregations under a precautionary management approach. Improved descriptions of the use of the inshore spawning grounds and clarification of the movement patterns of southern calamary on a number of temporal scales will allow appropriate management to be put in place. This will allow the balance in squid fishery management between allowing time for the adults to spawn, and removal of these short-lived animals for commercial value rather than as a function of natural mortality.

Based on these considerations the use of short-term fishing closures has been implemented in Tasmania. However, several points can be made with respect to the decisions surrounding fishing closures:

1. Spatial variability in spawning activities and intensity means that areas closed to fishing need to encompass relatively large areas i.e. bays, rather than individual seagrass (spawning) beds.
2. Temporal variability in the magnitude of egg production and losses of egg masses means that spawning adults need to be protected for extended periods throughout the spawning period.
3. Short term closures that encompass only very discrete times, as is the current situation for southern calamary in Tasmania, or fisheries that are managed by monitoring throughout season and then calling a halt to fishing when catch triggers have been reached, or escapement levels breached, only provide full protection for some micro-cohorts but not others

Chapter 3: Temporal variability in embryonic development and mortality in the southern calamary *Sepioteuthis australis*: a field assessment

(Authors: MA Steer, NA Moltschaniwskyj & FC Gowland)

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Introduction

Quantitative estimates of mortality rates for squid species are virtually non-existent. However they have been vaguely defined as being higher than mammals, similar to marine plankton, and lower than fish (O'Dor 1998). This description arises purely as a function of the logistical and technical complexities associated with reliably sampling the animals through the egg, paralarval and juvenile phases in the wild. However, the need to quantify early mortality rates and identify processes responsible is important, especially from a fisheries management perspective, as it can potentially be used to predict recruitment strength.

For most fish species egg and larval mortality rates are generally high, but extremely variable (Ferron & Legget 1994). This variability is largely attributed to the larva's vulnerability to physical and biological interactions, e.g., predation pressure, starvation and the physical environment (Sissenwine 1984). Such variability contributes significantly to variation in recruitment to the adult population (Narimatsu & Munehara 1999). Loliginid squid, however, differ fundamentally from fish, as they do not exhibit a true larval phase (Young & Harman 1988). Instead they undergo direct embryonic development within well-protected, sedentary egg capsules to hatch as behaviourally and structurally adept paralarvae (Boletzky 1987, Boyle *et al.* 2001). As a consequence some of the risks associated with a planktonic metamorphosis phase are reduced resulting in higher survivorship than many marine fishes (Caddy 1983).

Unfortunately direct embryonic development in squid is typically a lengthy process, representing up to 30% of their short lifespan, depending on the species (Boletzky 1987). During this time the developing embryos are potentially at risk to fluctuating environmental conditions (Augustyn *et al.* 1994). Temperature defines embryonic developmental limits (Segawa 1988) and influence rates of development (Boletzky 1994) and is therefore considered the principal environmental factor governing cephalopod embryonic development. Although some loliginid squids spawn sporadically during the winter months or in deep, cold water (e.g. *Loligo forbesi* Lordon & Casey 1999, *Loligo. gahi* Arkhipkin *et al.* 2000) most species aggregate with some predictability in shallow waters during warmer months to spawn (Hanlon 1998). Spawning during this time and in these regions is assumed to maximize hatching success and survival by effectively accelerating developing embryos through the early vulnerable phase. However, the developing embryos are still potentially vulnerable to rapid temperature and salinity fluctuations resulting from prevailing weather conditions, whilst also being at risk of dislodgment due to storm activity (Augustyn *et al.* 1994, Chapter 1) and excessive biofouling.

In the laboratory, large fluctuations in temperature and salinity are responsible for major structural deformities and high embryonic mortality (Boletzky & Hanlon 1983, Palmegiano & D'Apote 1983, Hanlon 1990, Ueta et al. 1999). In the wild, survivorship may be affected by epiphytic growth on the egg strands' surface, especially for those laid in shallow, nutrient-rich waters and during the later stages of development (Chapter 1). The effect of epiphytic growth on the developing embryos is unclear, but it may contribute to 'unsatisfactory hatching' (Choe 1966). To date, the relative importance of biotic and abiotic factors on egg development and survival in nature has not been directly assessed due to the difficulties associated with *in situ* investigations. The southern calamary, *Sepioteuthis australis*, however, reliably aggregates in shallow protected waters on the east coast of Tasmania to mate and spawn, allowing researchers regular access to extensive spawning beds. Spawning in *S. australis* is typical of the loliginids; once mated, females attach a series of digitate egg strands to seagrass/macroalgae holdfasts to collectively form discrete egg masses. Individual egg masses may comprise <10 to >500 strands, with each strand containing between 2 and 8 longitudinally aligned egg capsules (Chapter 2).

This field-based study aimed to quantify variability in rates of development and mortality for calamary embryos throughout a spring/summer-spawning season. Due to the collective egg packaging strategy exhibited by this species, this study also described variation in development within individual egg strands to determine if certain eggs were at a higher risk to mortality. Furthermore, the effect of biofouling on the capsule surface and its effect on mortality rates were quantified.

Materials and Methods

Four southern calamary spawning sites located on the east coast of Tasmania, Australia (42°07'34"S, 148°17'51"E) were visited fortnightly from early November 2000 until early January 2001. All sites were within 5 km of each other, within 100 m of the shoreline, less than 4 m depth and subjected to a maximum tidal range of 1.2 m. On each trip divers searched areas of *Amphibolis antarctica* seagrass beds for egg masses containing embryos close to hatching. From each egg mass three biofouled (F) egg strands (75-100% of the surface supporting filamentous algae) and three unfouled (UF) egg strands (0% of the surface supporting filamentous algae) were collected, bagged and stored in fresh seawater prior to dissection.

Embryos were dissected from each strand within 8 hours of collection and examined under a stereo dissection microscope. Developmental stage was assigned to each embryo according to the criteria described by Steer (In review) that differs slightly (in terms of the chronological appearance of the eye vesicle, ventral chromatophores, anal papillae and ink sac) from the developmental scheme proposed by Segawa (1987) for *Sepioteuthis lessoniana*. The position of each embryo within an egg strand was recorded; position 1 identified the embryo located at the fixed/proximal end of the strand and progressing consecutively to the free/distal end of the strand. Eggs that were identified as unfertilised or undergoing abnormal development were scored as “dead”. To avoid over-estimating the within strand developmental differences, all embryos that had hatched to leave an obviously vacant egg capsule were assumed to have hatched prematurely (stage 29). This assumption was based on the observation that premature hatching readily occurs during collection (pers obs).

Seawater temperature was measured within seagrass beds using 32K StowAway® TidbiT® temperature dataloggers located at three collection sites. Dataloggers were secured to the substrate (<4m deep) one month prior to the first sampling occasion and logged temperature hourly. Daily rainfall data (as a proxy of salinity) were obtained from a local weather station maintained by the Australian Bureau of Meteorology.

To examine conditions experienced by developing embryos sampled on each trip we back-calculated the approximate date the eggs were laid. Oviposition dates were calculated using Laptikhovsky’s (1999) predictive equation for decapods. This equation takes mean egg size (L mm) and incubation temperature (T °C) in consideration to generate the duration of embryogenesis (D days). The equation was applied as follows:

$D = (1220.94 \cdot T^{-1.68194})\, L^{k}$,
where $k = 2.5139 \cdot T^{-0.3574}$

Two problems were evident in this equation. Firstly, as the predictive estimates are calculated for eggs developing under constant temperature regimes, they do not account for unknown effects of natural temperature fluctuations observed in the field. Secondly the equation does not incorporate development stage at the time of collection, but rather calculates the time to hatching. In an attempt to counteract these problems T was derived from the average field temperature recorded 3-weeks prior to collection and mean egg development stage at time of collection was factored in to provide approximate oviposition dates (Table 3.1.). Egg length (L) was determined by measuring a total of 375 ovulated eggs collected from the ovaries of 13 mature females (mean 6.18 ± 0.06 SE).

Table 3.1: Back-calculated oviposition date for field-collected *Sepioteuthis australis* eggs using Laptikhovsky's (1999) model. Mean incubation temperature three weeks prior to collection and developmental stages at time of collection are factored into the equation.

Date collected	Mean temperature in previous three weeks (°C)	Predicted development time until hatching (days)	Mean development stage	Predicted development time at collection (days)	Approximate date laid
08-Nov-00	14.5 ±0.04	78.8	27.3 ±0.10	72.3	28-Aug-00
22-Nov-00	15.2 ±0.05	70.7	26.5 ±0.08	55.9	27-Sept-00
06-Dec-00	17.3 ±0.04	52.9	26.2 ±0.09	40.7	20-Oct-00
21-Dec-00	18.7 ±0.05	44.2	27.8 ±0.12	38.8	10-Nov-00
08-Jan-01	18.0 ±0.07	48.2	27.9 ±0.08	43.9	24-Nov-00

To determine variability in embryonic development within egg strands the average development stage and the deviation of each embryo from the strand average was calculated for all egg positions. If embryonic development was synchronous within an egg strand, each embryos' deviation from the strand mean would be zero. These differences in developmental deviation within strands were then examined as a function of sampling time, biofouling, and position within the strand using a 3-factor Model 1 ANOVA. Only egg strands containing 4 and 5 eggs were included in the analyses to avoid severely unbalancing the dataset. All dead embryos were included in the analysis as missing values as developmental stage could not be ascertained. Assumptions of ANOVA were checked by visual inspection of variance and normality plots. No data transformations were required.

To determine if developmental asymmetry was a function of the number of eggs within a strand, the difference in developmental stage between the fixed and free ends was calculated for all strands containing between 4 and 7 eggs (n=226). Strands containing the extremes (3 and 8 eggs) were not included in the analysis due to insufficient replication. A one-way ANOVA with unequal replication was used to compare mean values. The Hochberg GT2 post hoc test for an unbalanced dataset (Sokal & Rohlf 2000) was used to highlight significant differences amongst means.

Temporal effects on the frequency of mortality as a function of biofouling and the eggs' respective position within the egg strand were estimated via a series of non-parametric log-likelihood ratio (G) tests. Incorporation of Williams's correction (G_{adj}) ensured a more conservative estimate of G and therefore reduced the risk of type I errors (Sokal & Rohlf 2000).

Results

Rates of development of *Sepioteuthis australis* embryos within a strand differed among egg positions, but the pattern and magnitude of the difference along the strand depended upon time ($F_{16,601}$=3.48, P=<0.001). On most occasions the embryos located at the fixed (proximal) end of the strand developed more slowly than those located at the free (distal) end (Fig. 3.1). However, in late November position 2 embryos were slowest to develop, on average lagging 0.7 developmental stages from the distal embryos (Fig. 3.1). The within-strand difference in development was greatest for those eggs collected in early December with proximal embryos on average lagging 1.1 developmental stages behind distal embryos. This difference coincided with the largest incremental change in water temperature, where embryos were subjected to a 7.3°C increase over a 41-day developmental period (Fig. 3.2a). Development rates of embryos within the strand were most synchronous in early November where proximal and distal embryos exhibited a mean difference of 0.4 in developmental stage (Fig. 3.1.). Temperatures experienced by developing embryos collected in early November were relatively constant with embryos experiencing a 3.8°C range throughout development (Fig. 3.2a). There was a weak positive correlation between within-strand development variation and rate of temperature change (Pearson's correlation, r = 0.87, n=5, P=0.05).

Fouling on the egg strands had a large effect on rates of development within the strand, with greater within-strand variation in unfouled than in fouled egg strands ($F_{4,601}$=13.76, P=<0.001). While proximal embryos in unfouled egg strands on average lagged 1.0 development stage behind distal embryos, those in fouled embryos lagged by only 0.4 (Fig. 3.3).

Figure 3.1: Mean differences in the development of *Sepioteuthis australis* eggs during a spring/summer spawning season. Mean developmental deviation per embryo is calculated as a function of strand mean. Only egg strands containing 4 or 5 egg capsules were included in the analysis (n=226). Dashed line represents synchronous development within an egg strand, error bars represent standard error. (from Steer *et al.* 2001)

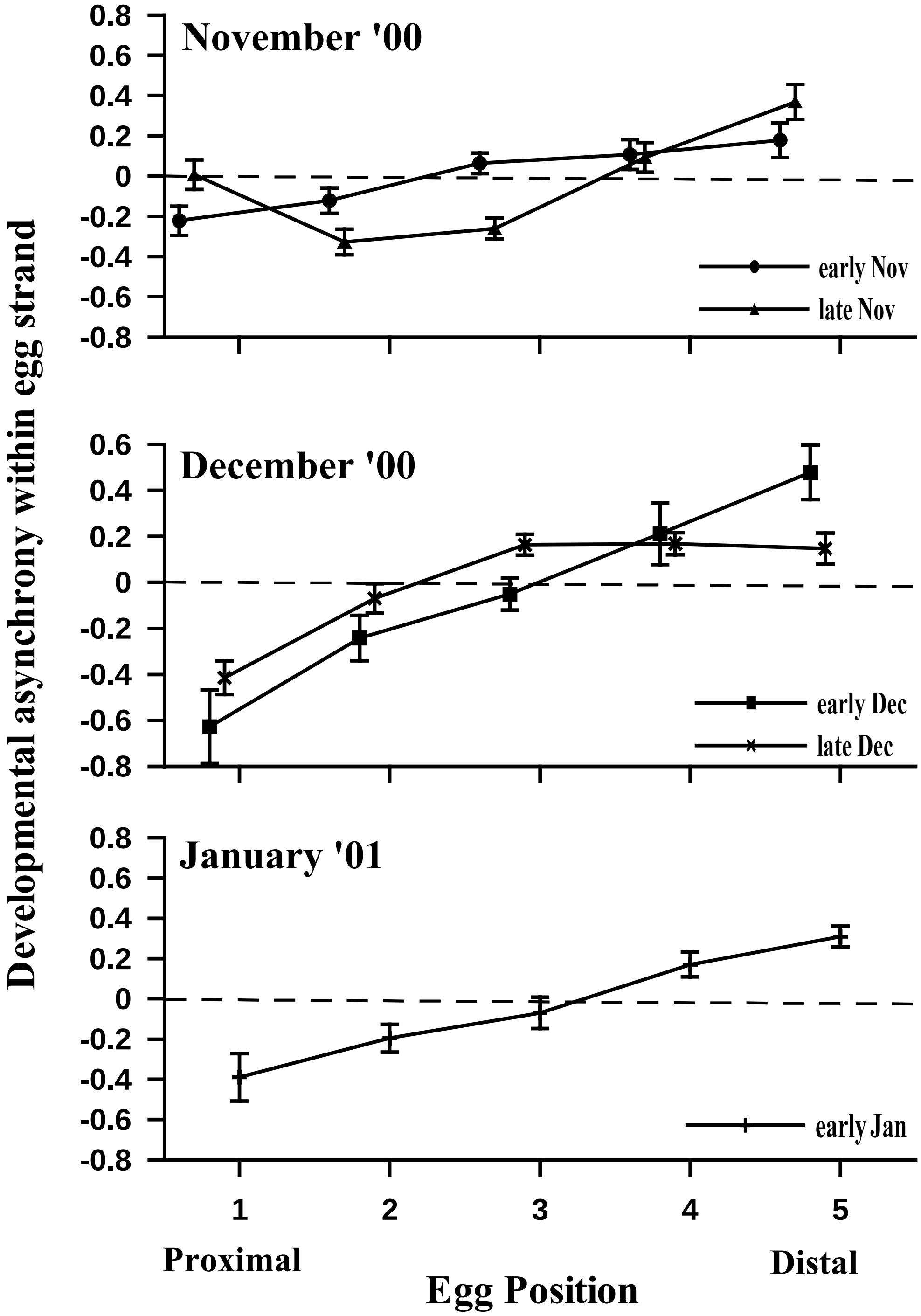


Figure 3.2: (a.) Benthic water temperature (°C) measured hourly; dashed horizontal lines represent duration of embryonic development of collected egg samples calculated using Laptikhovsky's (1999) predictive equation for decapods. Arrow indicates the greatest temperature spike observed during the study period. (b.) Daily rainfall (mm). (from Steer *et al.* 2001)

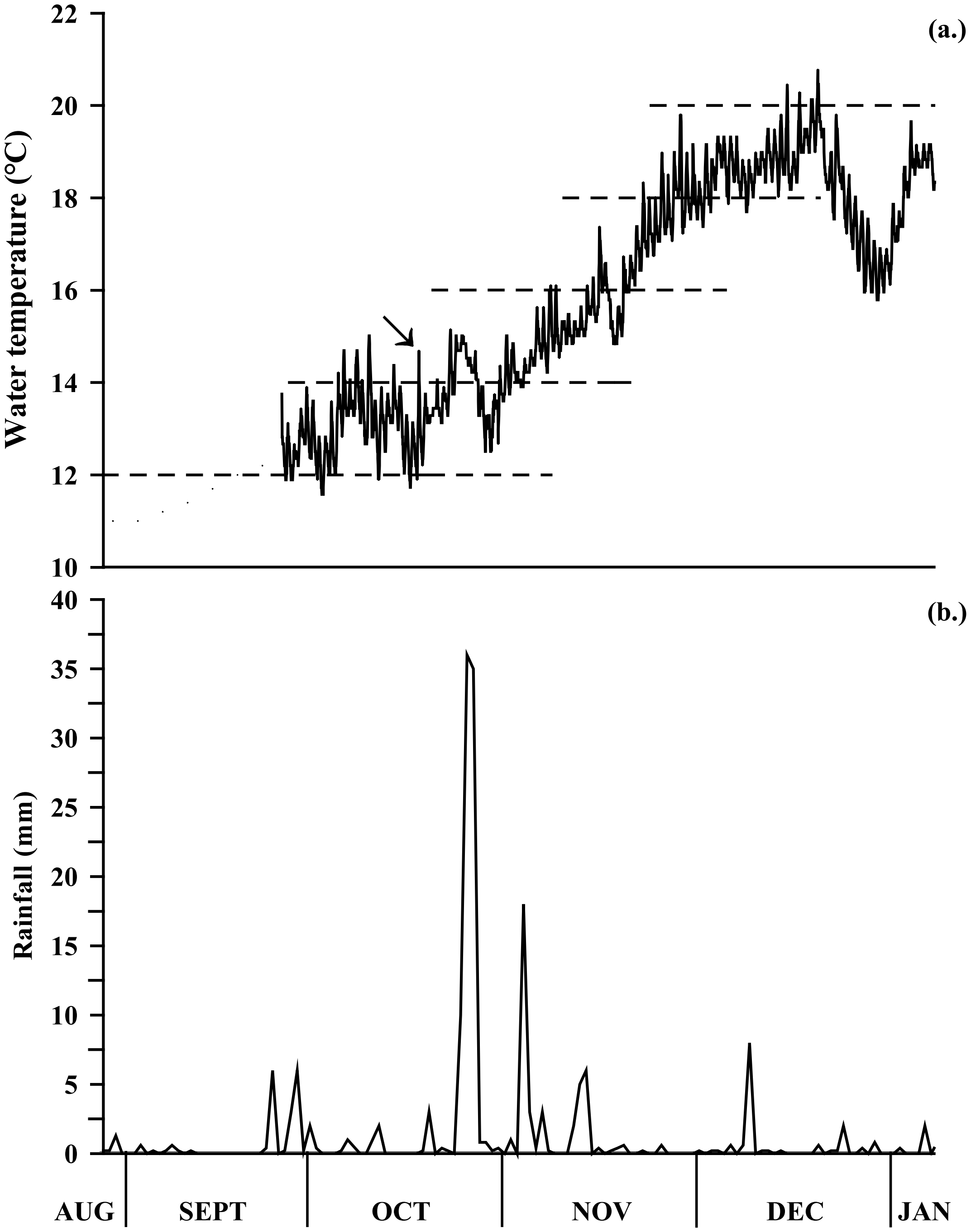
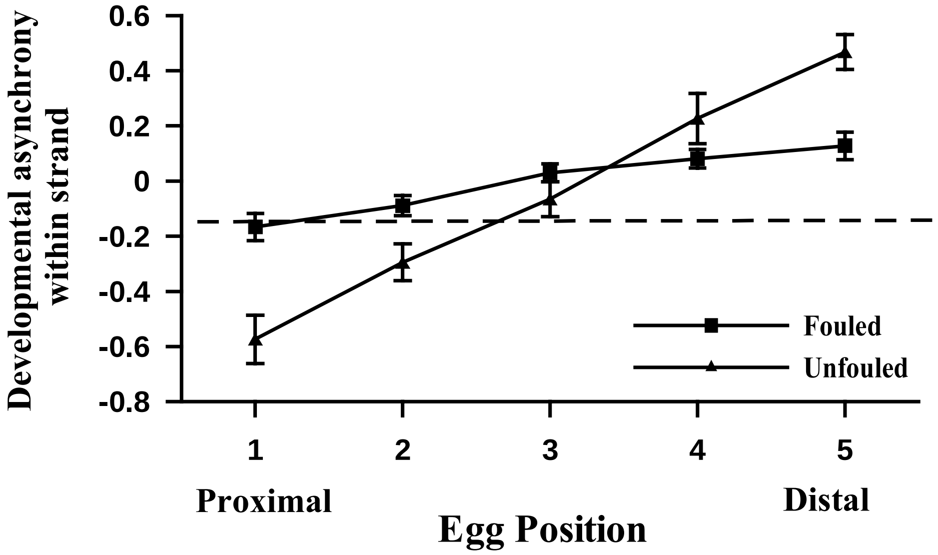


Figure 3.3: Mean differences in the development of *Sepioteuthis australis* eggs between fouled (n= 350) and unfouled strands (n= 301). Mean developmental deviation per embryo is calculated as a function of strand mean. Fouled = 75-100% surface coverage, Unfouled = 0% surface coverage. Dashed line represents synchronous development within an egg strand, error bars represent standard error. (from Steer *et al.* 2001)



The number of eggs in the strand affected the difference in the rate of development between the proximal and distal end (F3, 222=3.31, P=0.021). The shortest egg strands showed minimal difference, with proximal embryos lagging 0.57±0.17 developmental stages behind distal embryos. Longer egg strands, however were observed to display greater asynchrony in development with 1.2±0.2 developmental stages separating proximal and distal embryos.

Incidence of embryonic mortality changed over the summer, ranging from ~4% dead in early November to 19.5% in late November (Fig. 3.4). Total mortality remained above 10.0% in early December and January periodically dropping to 6.4% in late December, however greatly varied as a function of biofouling (G_{adj}= 89.27 P=<0.001). From late November onwards the incidence of mortality in unfouled egg strands was as much as 90% higher than that in fouled strands. Except in early November mortality rates were very similar in both fouled and unfouled egg strands.

Using Laptikhovsky's (1999) predictive equation it was possible to back-calculate the approximate oviposited dates from sampled embryos. Embryos collected in the initial sample were back-calculated to be laid on the 28th August marking the 'beginning' of the study period (Table 3.1.). By calculating oviposited date it is possible to identify potential environmental perturbations throughout embryonic development (i.e. from when eggs were laid to when they were sampled) (Fig. 3.2a). Diel temperature fluctuations were small throughout the study (mean 1.18ºC ±0.55 SD). The largest temperature change occurred on 17th October where there was an increase of 2.8°C over a 7-hour period (Fig. 3.2a.). All embryos collected in November would have experienced this subtle temperature spike during their developmental process, however, there was no correlation with increased mortality rates and changes in water temperature throughout the study (Pearson's correlation, r=0.19, n=5, P=0.49) (Fig. 3.2a.). Embryos collected in November and early December experienced a period of heavy rainfall where a total of 83.2 mm fell over 7 days (from 24th to 30th October, with major downpours occurring on the 25th and 26th measuring 36 and 35 mm respectively (Fig. 3.2b.). Rainfall during this period considerably exceeds the October average of 50 mm (Australian Bureau of Meteorology).

Embryos developing at the proximal end of an egg strand suffered mortality rates more than seven times higher than those at the distal end, a pattern that was consistent in both fouled and unfouled strands (G_{adj}=147.74, P=<0.001) (Fig. 3.5). No dead embryos were found in positions 7 or 8 regardless of biofouling (Fig. 3.5).

Figure 3.4: The percent frequency of dead embryos at each sampling time across all strand positions for fouled and unfouled egg strands. Numbers in parentheses indicate total number of embryos examined. (from Steer *et al.* 2001)

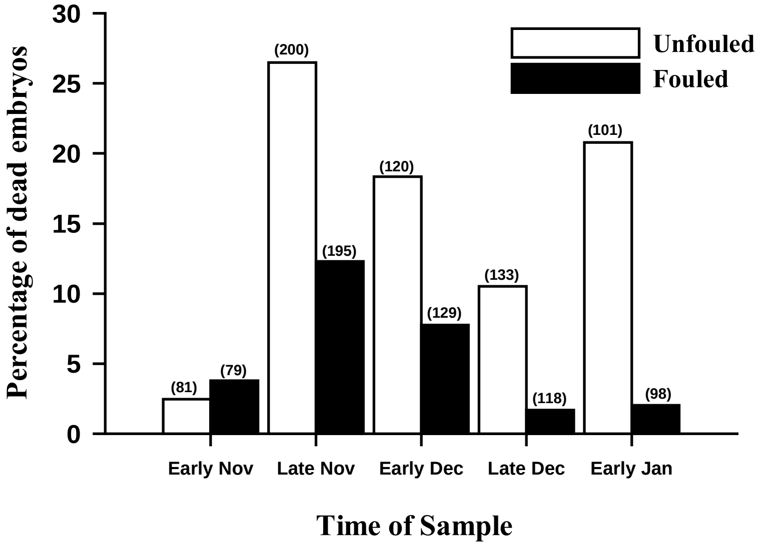
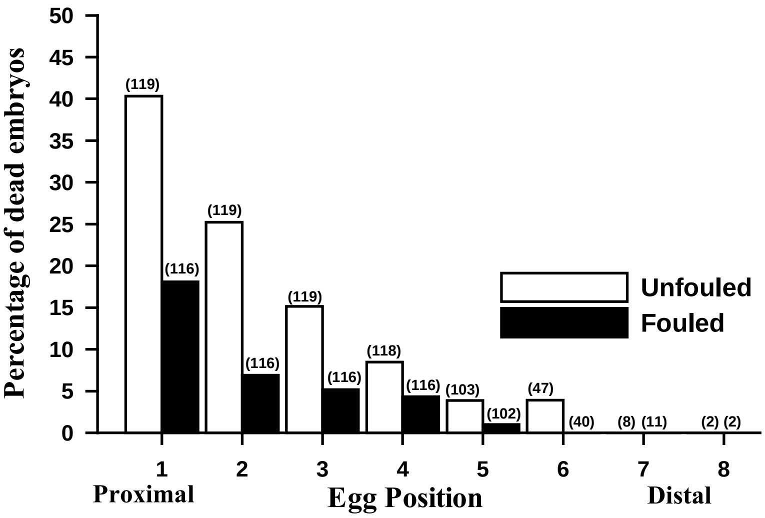


Figure 3.5: The percent frequency of dead embryos at each position along the egg strand for fouled and unfouled egg strands. Numbers in parentheses indicate total number of embryos examined. (from Steer *et al.* 2001)



Discussion

Southern calamary embryos develop asynchronously within individual egg strands with proximal embryos consistently developing slower and suffering higher mortality than their distal siblings. Variable development within an aggregated egg mass has been reported in a variety of marine species e.g. gastropods *Lymnaea stagnalis, Melanochlamys diomedeai* and *Haminaea vesicula*, polychaete *Nereis vexillosa* (Marois & Croll 1991, Cohen & Strathmann 1996), and fish *Clupea harengus* (Stratoudakis *et al.* 1998). In each instance embryos in the distal or outer perimeter of the egg mass develop faster and hatch first. This difference in developmental rate is attributed to the interior embryos not getting sufficiently oxygenated and/or accumulating excess excretory products and responding by either retarding or arresting development (Strathmann & Strathmann 1995). Given the high density of eggs in the squid egg masses, particularly at the attachment point, it would be valuable to determine the micro-environmental characteristics experienced by the embryos.

Temporal variations in developmental rate and mortality estimates were explored as a function of incubation temperature. The positive correlation between the magnitude of within strand developmental variation and incubation temperature range suggests that asynchronous development was greater when embryos were subjected to a wider temperature range. Importantly, this can translate to differential hatch times, suggesting that an entire egg mass will hatch over a longer period when incubation temperatures change, compared to egg masses experiencing relatively stable temperatures. Similar results have been observed in shallow-water, benthic spawning fish (e.g. Pacific Herring *Clupea pallasii* and Capelin *Mallotus villosus*), where the hatching interval was negatively correlated with the average incubation temperature (Taylor 1971, Frank & Leggett 1981). Given that temperature intrinsically defines developmental rates it is likely that when embryos are subjected to progressively warmer temperatures, typical of a seasonal increase, embryonic development speeds up, exaggerating the within strand variation. It is unclear if survival of remaining embryos is compromised once hatching begins.

Although seasonal increases in temperature are positively correlated with developmental rate their influence on embryonic mortality remains unclear. Temporal differences in embryonic mortality have been observed in the long-finned squid *Loligo gahi* where the incidence of mortality during the winter months is more than four times greater than during spring and summer (Arkhipkin *et al.* 2000). It remains to be investigated whether this seasonal difference was purely a result of differing temperatures, or other environmental conditions, or a combination of both. Extreme temperature fluctuations are suggested to be detrimental in laboratory reared eggs, especially during the earlier developmental stages, and controlled temperature shifts are advised not to exceed 1°C per day (Hanlon 1990). As temperature fluctuations during this study were generally between 1 and 2°C per day it is unlikely that thermal conditions contributed to elevated mortality. A previous study of late stage *Sepioteuthis lessoniana* embryos showed that short-term exposure (<1 hr) to temperatures 3-7°C above natural conditions does not adversely affect development (Kinoshita 1982). As the maximum rate of temperature elevation recorded in this study equated to 2.8°C over a 7-hour period, it is unlikely to have promoted developmental arrest. A study by Pedersen & Tande (1992) suggests that invertebrates living in environments characterised by natural increases in temperature during the developmental period are physiologically adapted to cope with slight fluctuations. By this rationale *Sepioteuthis australis* embryos may be relatively robust with regard to coping with temperature fluctuations.

Heavy rainfall and subsequent fresh-water run-off, in October may have contributed to elevated mortalities observed in late November and early December. As all eggs examined in this study were collected in shallow, near shore waters (< 4m) their development may have been perturbed by rapid changes in salinity. Cephalopods are generally thought to be stenohaline and supporting field evidence suggest that low salinities have a significant inhibitory effect on hatching success in the cuttlefish *Sepia officinalis* (Palmegiano & D' Apote 1983). Embryos that were collected in early November, and would have experienced this change in salinity, however, displayed a relatively low incidence of embryonic mortality, suggesting that if salinity was to have an effect on development, the timing of such events may prove to be an important factor.

Biofouling did not seem to have any obvious detrimental effect upon embryonic development. Embryos developing within fouled strands displayed relative synchrony in development and a low incidence of mortality compared to those developing within unfouled strands. This result was unexpected, as epiphytic growth upon amphibian eggs typically creates hypoxic conditions during the night (Pinder & Friet, 1994). It has been suggested that colonisation of the fouling organisms on *S. australis* egg strands is delayed by a chemical defence present on the strands' surface. Therefore any resultant growth is not rapid enough to interfere with development as embryos hatch in sufficient time before fouling has any affect (Benkendorff 1999). Conversely, the photosynthetic abilities of fouling organisms coupled with the surrounding *Amphibolis* vegetation may enhance oxygen levels during the day and water movement during the night may cancel out any negative effect of epiphyte respiration (Cohen & Strathmann 1996). Excessive biofouling may additionally benefit developing embryos by protecting them from potentially damaging solar radiation that has been known to cause problems in development in other taxa (Biermann *et al.* 1992) and perhaps explain why mortality was higher in strands that were free of fouling.

The present study demonstrates temporal variability in development rates of *Sepioteuthis australis* embryos. The dynamic nature of shallow water spawning sites makes it difficult to single out the major contributing factor(s) responsible for embryonic mortality. As a result, future work should focus upon defining tolerance levels in developing embryos exposed to a variety of fluctuating environmental conditions and determine their relative effect on different phases of development. In addition, the size and density of an egg mass needs be factored into any analysis to determine if this is contributing to rates of mortality (see Strathmann & Strathmann 1995).

Commercial catches of *Sepioteuthis australis* off Tasmania have increased in recent years and a series of fishery closures aimed at protecting the spawning stock and maximizing recruitment strength were implemented (Chapter 2). Understanding the effect of the environment on embryonic development and hatching success can reduce some of the variability encompassed within existing stock-recruitment relationships, which are currently based on spawner biomass/ parental stock sizes. Reducing variability within predictive stock-recruitment relationships will allow fisheries managers to make more informed and accurate decisions about the fishery.

Chapter 4: Spawning aggregations of squid (*Sepioteuthis australis*) populations: fisheries management of a continuum of ‘micro-cohorts’

(Authors: NA Moltschaniwskyj & GT Pecl)

Introduction

In free-spawning sedentary invertebrates (eg: bivalves, Honkoop *et al.* 1999) and broadcast spawning teleost fish, synchrony in the timing of gamete release is crucial to reproductive success. Aggregative spawning behaviour in these species may occur on a range of temporal scales, with aggregation and spawning activity associated with time of day, lunar phase, or maximum declination of the moon (Robertson 1991). Aggregative spawning behaviour of cephalopods appears to be widespread across taxonomic groups and ecological types (eg *Sepia apama*, Hall & Hanlon 2002; *Loligo vulgaris reynaudii,* Sauer, Smale & Lipinski 1992; *Dosidicus gigas,* Tafur *et al.* 2001).

The direction of management for many squid fisheries appears to be based on the concept that within a fishing season there is a single cohort with similar characteristics being fished, and that the absence of over-lapping cohorts makes these populations vulnerable to recruitment failure. Therefore, when managing the stock there is an assumption that the stock structure changes through time in a predictable way, i.e. the population as a whole is composed of individuals that are getting bigger, older, and closer to senescence. As a result the concept of “proportional escapement” has been used to manage fishing effort in many squid fisheries around the world (eg *Illex argentinus* Beddington *et al.* 1990; *Dosidicus gigas* Hernandez-Herrera *et al.* 1998). Under this strategy the level of fishing effort is set at a point at which there is a proportion of animals in the population that will escape capture and be able to produce offspring that will comprise the next generation (Basson & Beddington 1993). However, if a series of “micro-cohorts” (O’Dor 1998), with different genetic make-up and life-history characteristics, move into the spawning aggregation throughout the fishing season each of the micro-cohorts needs protection (O’Dor 1998). In some loliginid squid species spawning aggregations do not consist of well-defined or stable population units. Instead there may be influxes or waves of new individuals with others effectively leaving the spawning population at a scale of months (eg *Loligo opalescens* Leos 1998) to weeks (eg *Sepioteuthis australis* Jackson & Pecl 2003). Variability in the structure of spawning aggregations and the biological characteristics of the individuals during the spawning season need to be described for more effective management of fishing effort.

The implementation of a series of short (two weeks) fishing closures over the last four years (1999-02) encompassed the major spawning aggregations during October-December. The timing of the closures was flexible and been principally based upon reducing effort when catches and egg deposition were highest in previous years (Chapter 1). However, this approach has largely ignored temporal variation in size and age structure of the populations and the somatic and reproductive condition of animals in the spawning aggregation. Recent work has demonstrated changes in the spawning population on a scale of weeks, as new individuals move in and become part of the aggregation (Jackson & Pecl 2003), and also years (Chapter 5).

The aim was to develop a set of recommendations for management of the southern calamary fishery based on the biological traits of the spawning population and temporal variability of these traits during the spawning period. We examined monthly and yearly changes in size, age, somatic and reproductive condition, and relative abundance of individuals. Furthermore, we explored the relationship between these population and individual characteristics and the level of egg production measured on the inshore spawning grounds of Great Oyster Bay.

Methods and Materials

Spawning aggregations of *Sepioteuthis australis* are present for up to four months (October-January) each year on the east coast of Tasmania, Australia. Therefore, collections of southern calamary were undertaken on the inshore spawning grounds in Great Oyster Bay, east coast of Tasmania from October-December when egg deposition is greatest (Chapter 1). This area is characterised by the presence of discrete beds of seagrass (*Amphibolis antarctica)*, delimited by sand and/or macroalgae, occurring predominantly along a 10 km section of coastline (location details provided in Chapter 1). Animals were either purchased from commercial fishers, or caught by the research team. Most of the animals were caught using jigs (97%), but commercial fishers using purse-seine nets collected some of the samples. Fishing effort was particularly focussed on six areas of shallow (<10 m) seagrass (0.17 ha to 2.02 ha) within Great Oyster Bay that are known to have aggregations of spawning squid present for intensive periods over the spring and summer (Jackson & Pecl 2003, Chapter 1). On one occasion we were able to obtain size dorsal mantle length (DML) and gender information about individuals caught by the same fisher using jigs and purse seine nets in the same area and on the same day. There was no evidence of gear selectivity in either average DML of individuals (F<1, df 1,68, P=0.984), or in sex ratios (χ^2=0.087, df 1, P=0.768) between the two fishing methods. Therefore, jig and purse seine caught samples were pooled.

Research sampling was undertaken monthly over two to four days. At least six areas of *A. antarctica* seagrass were visited in each month with a minimum of 30 minutes fishing time spent at each site, if no squid were caught after this time the next site was visited. Under ideal conditions 60 to 120 squid were caught in each month, however, due to variable weather conditions and catchability of squid this target was not always reached (Table 4.1). If possible additional squid were purchased from fishers working in the same area and month. Due to the low numbers caught in 2001 the data from this year was not analysed.

Table 4.1: Counts of the number of males and females by month for which DML, total body weight, and age were obtained.

Year	Month	Females			Males			Fishing (hrs)
		DML	Weight	Age	DML	Weight	Age	
1999	Oct	22	22	12	33	33	18	9
	Nov	143	32	15	346	114	58	26
	Dec	51	26	15	65	30	22	7
2000	Oct	35	19	8	111	69	18	13
	Nov	17	17	8	80	80	37	9
	Dec	12	12	6	33	33	16	11

Animals were stored frozen until dissections were completed in the laboratory. From each animal the DML, total weight, sex, reproductive stage (based on Pecl 2001), and gonad weight (testis or ovary) were obtained. From a sub-set of individuals the age was estimated from daily rings in the statolith. The preparation of the statoliths and counting protocols are described in Pecl (2000) and Chapter 6. Additional to the research sampling, some market sampling of commercial catches was undertaken with the DML, sex and maturity stage determined for all individuals in catches from fishers operating in the same area over the period of the study.

To assess the movement of squid among the seagrass beds within Great Oyster Bay all squid caught during a six-day period in November 2001 were tagged. Squid were jigged, measured (DML), sexed and a numbered t-bar tag was inserted mid-mantle on the dorsal side through the muscle and pen. The reproductive status of females was assessed based on the degree of oviduct fullness (0, 25, 50, 75, and 100% full). To assist with healing of the tag injury site each animal was injected with 2-4 ml of 6 mg/ml tetracycline into the muscle at the base of the arms. A total of 216 individuals were tagged, with most animals caught over two 24-hour periods. The data from the tagged squid were analysed separately from the 1999 and 2000 individuals.

As a fishery independent assessment of abundance was not available, catch-effort data from the commercial fishery was used to provide a relative measure of abundance of squid on the spawning grounds. As 86% of the southern calamary in Great Oyster Bay are landed using squid jigs on handlines, and the fishers recorded the number of hours spent jigging, it was decided that the best measure of catch-per-unit-effort (CPUE) was the geometric average of kg.jig hour^{-1} across the number of fishing days in each month. Given that there was often more than one fisher onboard the number of jig hours in each day was multiplied by the number of fishers. The average weight of individual squid varied among the months, so CPUE values (kg.jig hr^{-1}) were adjusted using the average weight of squid in each month to determine relative abundance as individuals.jig hour^{-1}.

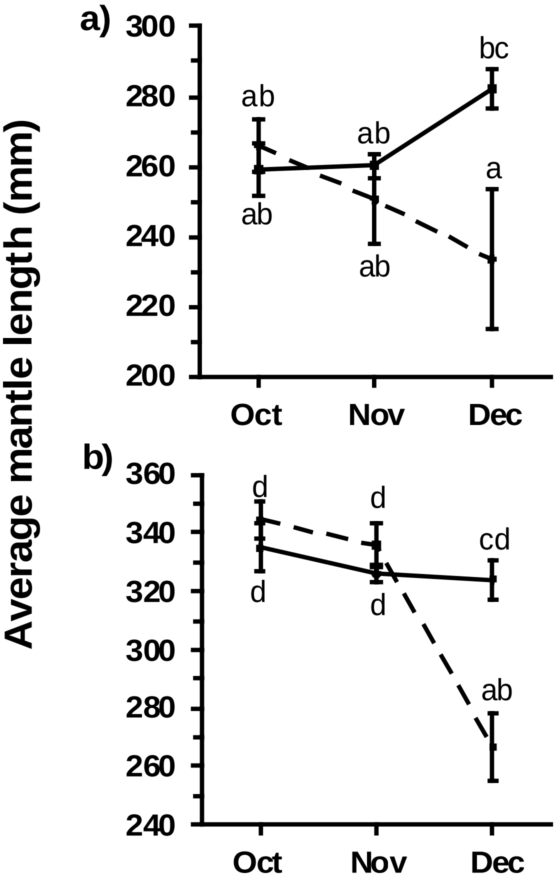
Southern calamary lay benthic eggs attached to the seagrass, with each finger-like strand containing 3-7 eggs, and 10 to >300 egg strands attached at the same point to form an egg mass. The density and size of the egg masses across the six *A. antarctica* seagrass beds was assessed each month by SCUBA divers using 108 20m^2 belt-transects (Chapter 2). The length and stage of each egg mass was assessed, and number of egg strands in the egg mass was estimated from the length (for details see Chapter 1). Estimates of egg production were made at the same time that animals were collected by the research team.

Results

Size and Somatic Condition

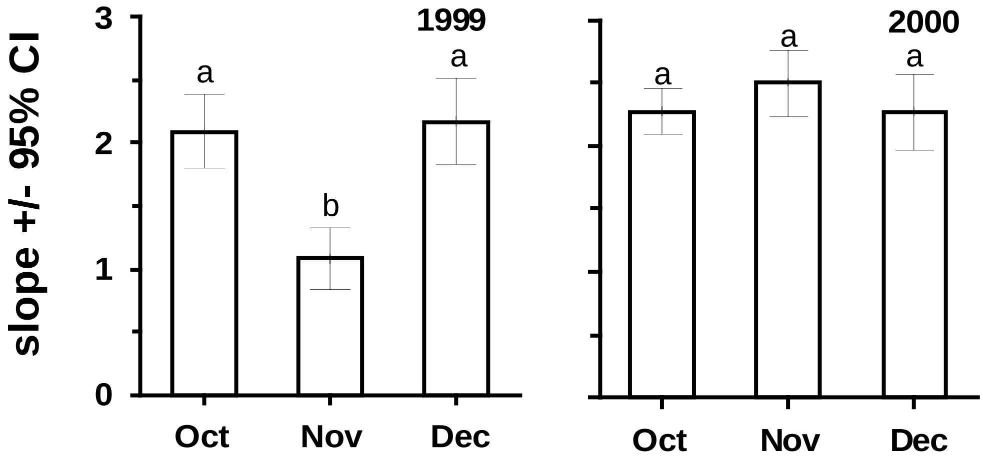
Variation in the DML of squid was explored as a function of the year and month of capture, and the sex of the individuals. There were differences in the average DML among the squid that was a function of an interaction among the three factors of interest ($F_{year*month*sex}$=31.43, df 11, 936, P<0.001). Female squid were similar in size among the three months, a pattern that was consistent between both years (Fig. 4.1a). In a comparison between the years, it was evident that in October and November the average DML of the females was not different between 1999 and 2000. In contrast, females in December 2000 were 17% smaller than females in December 1999 (Fig. 4.1a). Male southern calamary were approximately 6% larger than the females in October and November (Fig. 4.1b). However, there was no significant difference between the two sexes in December, and this pattern was consistent in both years (Fig. 4.1b). In 1999 the average size of male squid was relatively constant throughout October to December (Fig. 4.1b). However, in December 2000 males were 20% smaller than males in all other months (Fig. 4.1b).

Figure 4.1: The average DML for a) females and b) males for each month across 1999 (solid line) and 2000 (dashed line). Across the two figures the means with different letters are significantly different from one another.



To explore the length-weight relationships of the population the sexes were combined, as in some months the number of weighed animals was low. There were significant differences in the length-weight relationships of the squid population on the spawning grounds among the months (F_{month}=43.60, df 5, 424, P<0.001). In November 1999 the relationship between total body weight and DML in squid was half as steep as that relationship for any other month (Fig. 4.2). In other words squid caught in this month were increasing their body mass relative to length at half the rate compared with individuals in other months, suggesting that these individuals were in poorer somatic condition.

Figure 4.2: Slope values for the DML-total weight relationships for each month in 1999 and 2000. The 95% CL are adjusted using a Bonferroni correction for multiple comparisons among the six means. Means with different letters do not have overlapping confidence limits and are considered to be statistically different.



Size-at-Age

Individuals in the aggregation ranged in age from approximately four to nine months old (Table 4.2). For the individuals aged in each month the average age was approximately 6 months. The presence of young (< 6 mo) individuals in all months indicates that new squid were moving into the spawning aggregation during the three months (Table 4.2). In most months 37-41% of the individuals were < 6 mo old, suggesting that younger squid could be part of the spawning aggregation in the following month. Conversely, 11-20% of the individuals in any one month were > 7 mo old, indicating older squid were either staying around the spawning grounds or moving in from other locations.

Table 4.2: Age (days) parameters for individuals aged in each month.

Year	Month	Mean	Minimum	Maximum
1999	October	188.6	139	233
	November	191.2	131	275
	December	187.1	133	246
2000	October	171.5	130	229
	November	189.3	145	244
	December	188.7	145	226

There was no evidence of a strong relationship between size (DML or total body weight) and age in any single month ($R^2 = 0.08$-0.30), therefore size-at-age curves were not generated. The average weight of individuals (adjusted for age) was significantly different among the three months across years ($F_{month}=13.35$, df 2, 195, $P<0.001$). This was the result of December caught squid being 28 and 34% lighter for their age than the individuals from October and November respectively (Fig. 4.3). This suggests that at some stage during their life individuals present on the spawning grounds in December had slower growth than individuals present in October and November. The slower lifetime growth of December caught individuals may well be a function of the time that these individuals hatched (Fig. 4.4). Most of the October and November caught squid were born in autumn (March-May). In contrast, the December caught animals were predominantly hatched during late autumn/early winter (Fig. 4.4). In October and November there were individuals from cohorts hatched during summer through to winter. While in December the range of hatch dates was less, spring to winter (Fig. 4.4).

Figure 4.3: Average weight-at-age of individuals in each month across the two years.

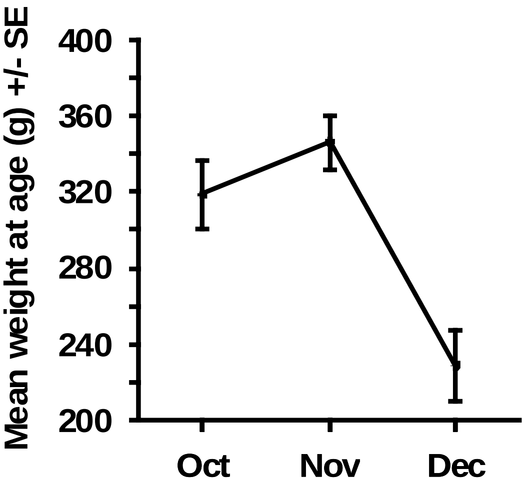
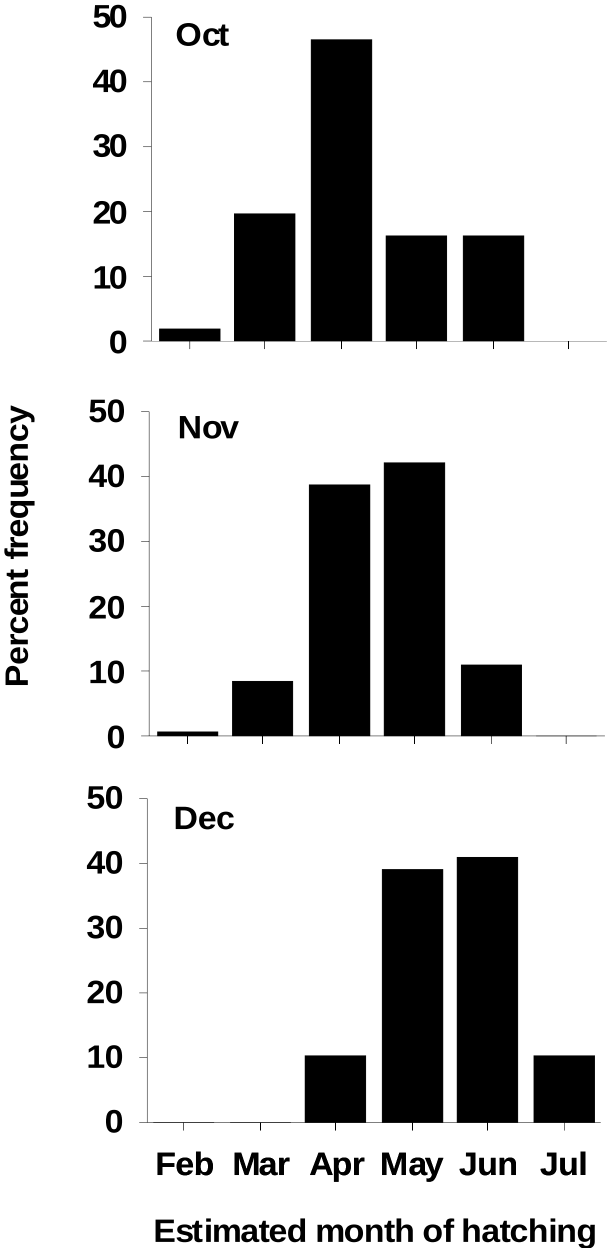


Figure 4.4: Percent frequency of aged individuals that hatched from February to July from each month of capture on the spawning grounds.



Abundance

The highest biomass in the spawning aggregation, based on CPUE (kg.jig hr^{-1}), occurred in October 1999 (Table 4.3). Although averaged over the entire spring/early summer period the highest biomass of squid were present in 2001 (Table 4.3). In 2000 all three months showed low levels of squid biomass. In each year the biomass consistently declined from October through to December, with low catches in September and January, either side of the spawning period (Table 4.3). When CPUE is converted from kg to individuals the effect of heavier animals in 2000 makes the decline in abundance less obvious, however, there is still a decline in the number of animals in the spawning aggregations during the spawning period (Table 4.3).

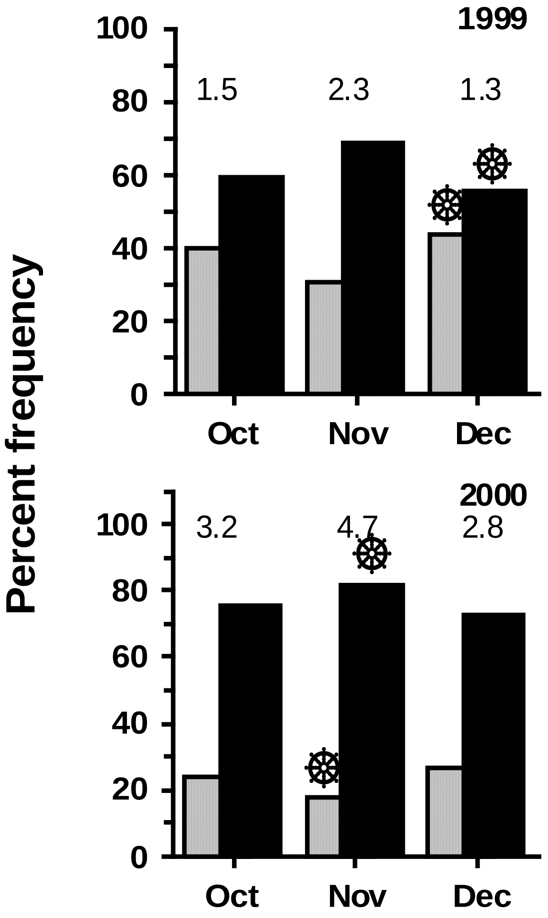
Table 4.3: Catch, effort, and CPUE for the jig fishery in Great Oyster Bay. Note that in 1999 and 2001 the fishery was closed for 4 weeks, while in 2000 the fishery was closed for 6 weeks.

Year	Month	CPUE ($kg.jighr^{-1}$)	Catch (kg)	Jig hours ($ind.jighr^{-1}$)	Fishing Days	CPUE
1999	Sep	6.6	5546	696	65	-
	Oct	11.2	8948	858	73	10.4
	Nov	7.8	5003	629	49	8.8
	Dec	5.8	4011	615	47	6.8
2000	Jan	2.4	113	44	6	3.7
2000	Sept	4.6	5857	959	66	3.4
	Oct	6.1	4594	694	49	5.7
	Nov	4.6	3446	631	40	4.2
	Dec	1.9	366	122	12	3.2
2001	Jan	0	0	0	0	0
2001	Sep	7.0	4036	465	28	7.6
	Oct	8.0	7962	738	52	-
	Nov	8.3	5913	650	28	7.86
	Dec	6.2	2099	319	17	9.92

Reproductive Ecology and Biology

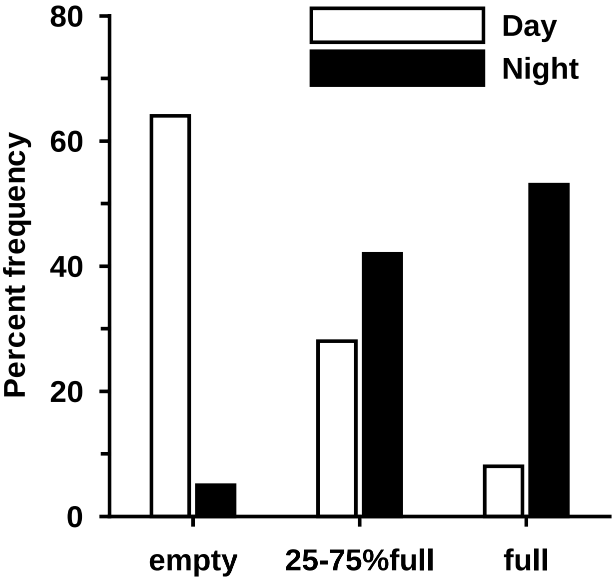
The sex ratios of the populations on the spawning grounds consistently favoured males, with between 1.3 to 4.7 males caught for every female (Fig. 4.5). There was a significant difference in the sex ratio between months in the two years (χ^2=23.5, df 5, P<0.001). The change in ratio occurred in December 1999 when there was an increase in the relative numbers of females. The reverse happened in November 2000 (Fig. 4.5) when the highest ratio of males to females (4.7:1) occurred. A similarly high ratio of males to females (3.2:1) was also seen during the tagging study in November 2001, and the ratio of males to females did not change between night and day (χ^2=0.99, df 1, P=0.320).

Figure 4.5: Percent frequency of males and females by month for 1999 and 2000. The arrows indicate the direction of significant differences between observed and expected frequencies based on the χ^2 test



All animals caught on the spawning grounds from October to December were fully mature and classified as Stage 5. The females had large ovaries and ovulated eggs in the oviduct (i.e. eggs ready to be laid), and the males had spermatophores present in the penis. There was evidence that the proportion of females with eggs in the oviduct changed as a function of time of day (χ^2=16.39, df 2, P<0.001). In a comparison of oviduct fullness between daylight and dark periods it was evident that during the day females had predominantly empty oviducts, while during the night most females had full oviducts (Fig. 4.6). This suggests that females were accumulating eggs in the oviduct during the night and depositing these eggs during the day.

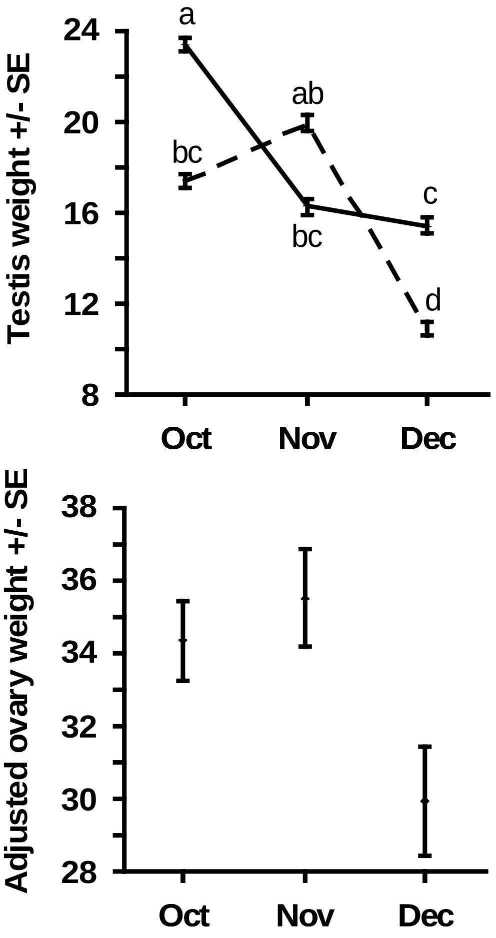
Figure 4.6: Percent frequency of tagged females that showed three levels of oviduct fullness during night and day (November 2001).



Males showed a very weak relationship between body mass and gonad mass which was considered biologically non-significant despite being statistically significant (b=0.007, se 0.001, $r^2=0.25$, n=322, P<0.001). Average testis weight (adjusted for body weight using ANCOVA) did change monthly, but the pattern of change was not consistent between 1999 and 2000 ($F_{year*month}=20.53$, df 2, 317, P<0.001). A decline in testis weight was evident in both years, but in 1999 a 20% decrease in weight occurred between October and November, while in 2000 a 50% decrease in weight was seen between November and December (Fig. 4.7a). When comparing testis weight between the two years, males had lighter testes in October and December of 2000 when compared to 1999 (26% and 29% lighter respectively), but 23% heavier in November 2000 than 1999.

There was a positive relationship between body mass and gonad mass for females throughout the spawning period, and this relationship was similar in all months (F=1.58, df 5, 101 P=0.174). In both years the weight of the ovary adjusted for total body mass, declined during the spawning season ($F_{month}=4.19$, df 2,106, P=0.018), with a 13% decrease in weight from October to December (Fig. 4.7b). There was no difference in adjusted ovary weight between 1999 and 2000 ($F_{year}=1.96$, df 1, 106, P=0.164).

Figure 4.7: Average gonad weight for a) males for each year and b) females combined across both years. Ovary weights are adjusted for total body weight. Means with the different letters are significantly different from one another. Solid line 1999, dashed line 2000.



Egg Production

The egg masses laid by females ranged in size from several egg strands to more than six hundred strands in a single mass. The size of the masses was different among months (χ^2=23.15, df 8, P=0.003). In most months the greatest percentage of egg masses contained 100-199 egg strands, except for October 1999 when larger egg masses (200-299 egg strands) were present (Fig. 4.8). Egg masses with >300 strands were not common (c. 4% of the egg masses), but in October 2000 more egg masses than were expected were in this largest size class (Fig. 4.8). While in November 1999 fewer egg masses than expected were in this size class (Fig. 4.8).

Differences in the density of egg strands deposited among months varied as a function of year ($F_{year*month}$=13.66, df 2, 1182, P<0.001). In 1999 the density of new egg strands laid was low in October, there was then a dramatic three-fold increase in the density of strands in November, followed by a slight non-significant decrease in December (Fig. 4.9). In contrast, during 2000 the density of new egg strands produced remained low throughout October to December (Fig. 4.9). No egg masses were found in January 2000 or 2001. There was no correlation (r=0.62, n=8, P=0.103) between average egg strand density and CPUE (individuals.jig hr^{-1}). However, if October 1999, in which there was high landing and low egg strand density, was excluded a positive correlation was found (r=0.87, n=7, P=0.011).

Figure 4.8: Size frequency distribution of eggs masses in each month 1999 (grey bars) and 2000 (black bars). The arrows indicated size classes that had more (↑) or less (↓) masses than expected on the assumption that the size frequency of egg masses would be similar in each month.

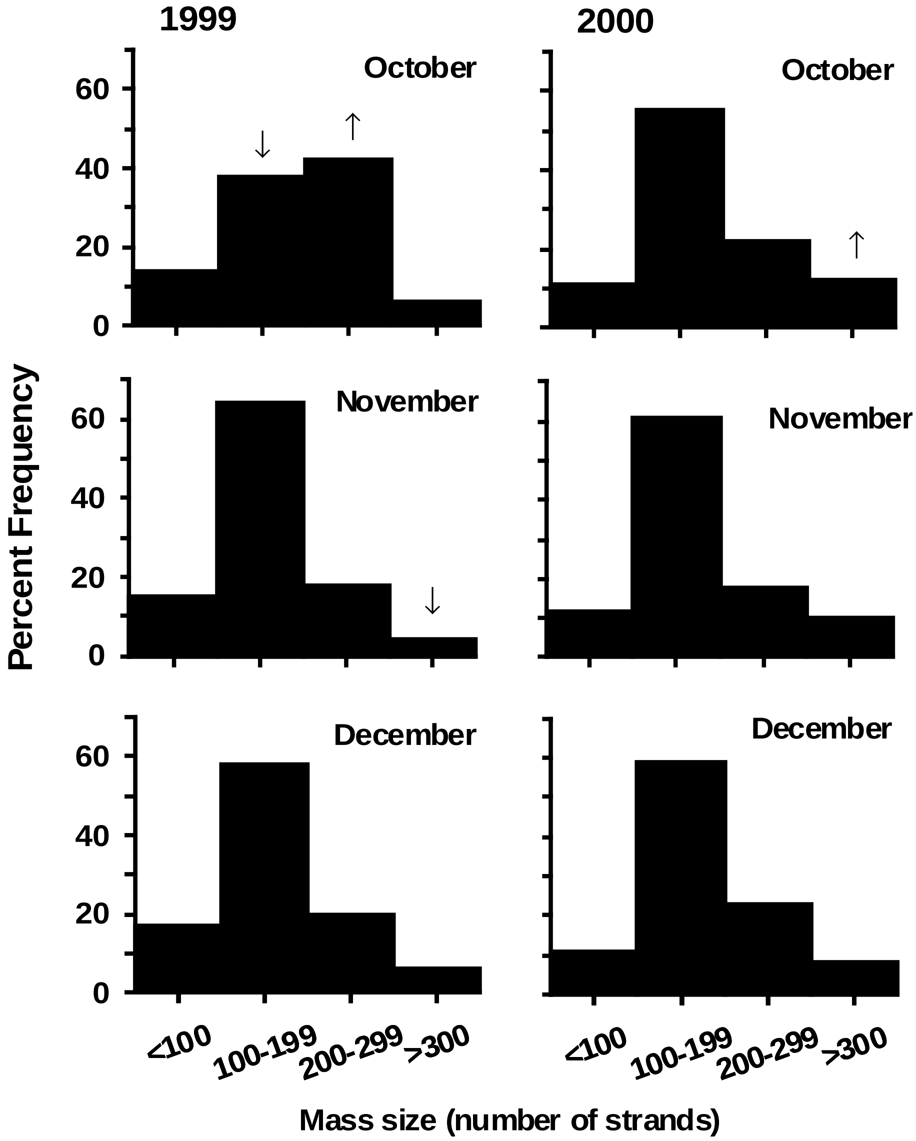
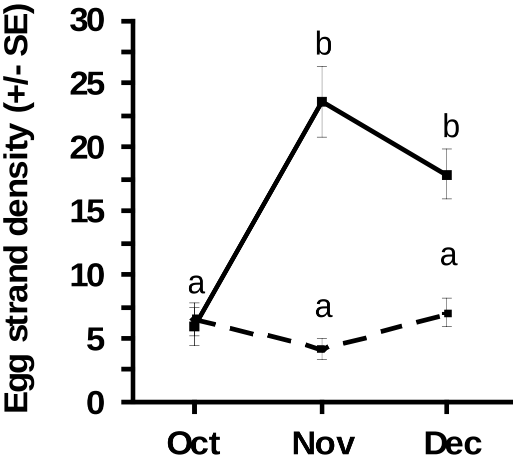


Figure 4.9: Average egg strand density (per m^2) in each month of 1999 (solid line) and 2000 (dashed line). Means with the different letters are significantly different from one another.



Movement

Of the 216 individuals tagged, 14 squid were recaptured, seven within 24 hrs of originally being tagged, and seven individuals between 10 and 19 days later (Table 4.4). All individuals were caught within 10 km of the original capture site, with more than 90% caught within a kilometre of the capture site. The rapid recapture (within 24 hrs) of squid was reassuring from a handling perspective, supporting the idea that the techniques used had minimal effect on the immediate behaviour of the individuals. This data provided preliminary evidence that spawning squid are spending considerable time in the spawning area, and reinforces the idea that fishing closures encompassing the broader Great Oyster Bay region are most probably providing substantial protection to the spawning populations during the closure dates.

Table 4.4: Summary of tag recapture data.

Date tagged	Sex	ML	Number of days before recapture & distance from tag site
5/11/2001	M	36	1 d, same site
5/11/2001	M	42	1 d, same site
5/11/2001	M	48.5	1 d, same site
5/11/2001	M	31	1 d, same site
5/11/2001	M	42	1 d, same site
6/11/2001	F	31	1 d, same site
3/11/2001	M	34.8	2 d, 1.7 km
5/11/2001	M	34	10 d, same site
5/11/2001	M	45	10 d, same site
5/11/2001	M	41	10 d, same site
5/11/2001	M	30	10 d, 0.4 km
3/11/2001	M	28	14 d, same site
3/11/2001	M	34	19 d, 8.5 km

Discussion

An examination of the structure of the spawning aggregations of southern calamary during the spawning season revealed that reproductive status, abundance, and reproductive output of the stock declined from October to December. This is due to either removal of stock by fishing, or completion of spawning activities, resulting in animals moving off the grounds or not returning to the spawning aggregation. This initially suggested that the spawning aggregations were composed of a single cohort that was showing signs of overall senescence. However size and size-at-age data suggested that younger individuals are continually entering the spawning aggregation throughout the October-December period. The presence of older squid, and preliminary tagging information, suggests that individuals stay in the aggregations for several months. Furthermore differences in the biological characteristics (growth rates, and somatic and reproductive condition) among months indicate variable growth rates and reproductive characteristics that are likely to be a function of genetic and environmental factors. Therefore, management of the fishery needs to consider protection of what appears to be a continuum of micro-cohorts that participate in contributing to the next generation.

Aggregative spawning behaviour suggests that synchronisation of spawning activity is advantageous to the population. Fertilisation of eggs produced by cephalopods occurs as the female releases the eggs, to be either attached to a substrate (eg *Sepioteuthis lessoniana* Ueta *et al.* 1995) or released as a discrete mass into the water column (eg *Stenoteuthis* Nigmatullin & Laptikhovsky 1994). The behavioural interactions among individuals within a population are complex in squid, with extensive time spent obtaining a mate and courting prior to sperm transfer and egg deposition (eg: *Sepioteuthis australis*, Jantzen & Havenhand 2003). Synchronised spawning in species with benthic eggs and no parental protection has no benefits associated with predator swamping or the use of current systems to promote higher egg survival. However, the mixing of micro-cohorts in spawning aggregations of southern calamary, suggests that aggregative spawning may ensure that individuals with a wide range of life history traits, i.e. growth rates and size- and age-at-maturity, are part of a common spawning population. Maintaining a diversity of life history traits will be critical to ensuring the persistence of genetic variability and the observed flexibility of life history traits (Boyle, Pierce & Hastie 1995, Moltschaniwskyj 1995, Pecl 2001).

Estimates of abundance using CPUE with species that display aggregative behaviour and where those aggregations are targeted is problematic because depletion of the aggregation may not be occurring as new individuals move into the area (Carvelho & Nigmatullin 1998). Therefore, depletion of stocks maybe occurring at a larger spatial scale than the CPUE is estimating. Given the problematic nature of using catch data from the fishers to monitor spawning biomass (i.e. delay in obtaining the data and that it is based on fisher recollection and honesty), an independent assessment is necessary. Reasonable correlations between CPUE estimates of spawning biomass and egg production (this study, Triantafillos 2001), suggests that surveys of egg strand density on the beds could be a useful, relatively cheap and immediate proxy of biomass.

Uneven sex ratios, particularly in favour of the males, have been observed in spawning aggregations (eg *L. vulgaris reynauldii* Augustyn 1990; *Loligo forbesi* Holme 1974). There is evidence that selectivity of individuals by jigging may cause bias in the reported sex ratios (Lipinski 1994), however there is no evidence of this for southern calamary (Chapter 5). The significance of a male dominated population is unclear, although the competition among males for mates will be a dominant aspect to the behaviour on the grounds (Hanlon 1998). Given that males must fight to obtain a mate and repel other males, the removal of males by fishing must be a constant disruption to the mating process, possibly opening more opportunities for smaller "sneaker" males to mate. More importantly the male will guard females during egg deposition, and the removal of the male may result in the females spending less time depositing eggs and more time being courted by a series of new males. Therefore, under heavy fishing pressure less egg deposition may occur despite high spawning biomass.

Understanding the relationship between paternities and mating systems will be important to recognising how changes in population structure may influence the genetic structure of the next generation. It has been suggested that the mating systems of species such as *L. pealeii* and *L. vulgaris reynaudii*, may generate genetic diversity (Hanlon 1998). However, given a continuum of micro-cohorts are participating in the spawning aggregation the mating systems may not be sufficient to protect genetic diversity if differential fishing effort during the spawning season occurs. This would arise if poor weather periodically prevents fishing, or in the use of short fishing closures.

Deciding on the length or nature of the fishing closures has been problematic in managing the southern calamary fishery. Given daily variability in CPUE, spatial variability of egg deposition (Chapter 1), multiple spawning (Pecl 2001), and the age range of spawning individuals it appears that extended protection of the spawning aggregations will be essential. Extended spawning seasons, multiple spawning, variable growth rates and constant movement of animals in and out of the spawning population result in a more complicated population structure for the population as a whole, and are important mechanisms in maintaining the genetic diversity of populations. Mechanisms that help maintain genetic diversity balances the risks of mortality factors combining at any one time to cause periodic local extinction (Boyle & Boletzky 1996). As such, management strategies should aim to minimise impacts on the overall diversity of populations throughout the full extent of spawning seasons, and not just protect spawning populations for comparatively minor discrete periods.

Squid fisheries that are managed by monitoring throughout each season and then calling a halt to fishing when total allowable catches (TACs) have been reached, or escapement levels breached, only provide full protection for some micro-cohorts but not others. This may result in differential protection of life history characteristics and shield only a component of the population from exploitation and not necessarily the full genetic diversity and range of life history strategies. In contrast, short term closures that encompass very discrete times, as is currently the case for southern calamary and the Monterey bay squid (Leos 1998), may provide protection for the continuum of miro-cohorts. The strategy of micro-cohorts with a diversity of life history characteristics coming together in a single spawning aggregation is a way in which short-lived species can ensure successful recruitment. This strategy may complement the strategies of spreading reproductive effort in space and time (O'Dor 1998).

Chapter 5: Inter-annual variation in the spawning aggregations

(Authors: GT Pecl, NA Moltschaniwskyj, SR Tracey & AR Jordan)

Introduction

As a consequence of their fast growth and short life cycle, the size of cephalopod populations fluctuates over several orders of magnitude between years (Boyle 1990). This potentially limits more directed exploitation (Bellido *et al.* 2001) and creates difficulties for stock assessment and subsequent fisheries management. However, recent studies suggest that like fish (Cury *et al.* 1995), strong environment-recruitment relationships may exist for a number of squid stocks (eg: *Loligo forbesi*, Robin & Denis 1999; *Loligo gahi*, Agnew *et al.* 2000, Agnew *et al.* 2002; *Illex argentinus*, Waluda *et al.* 2001). The temperature dependence of squid growth has been suggested as an explanatory factor for environment-recruitment relationships (Robin & Denis 1999, Agnew *et al.* 2002). However, growth and reproductive processes are tightly linked (Mangold *et al.* 1993), and as such any impact of temperature or other factors on growth will also impact on the timing and level of energy allocated to reproductive effort. There is considerable variation in the reproductive strategies of individuals within some cephalopod populations, particularly age and size at maturation (Boyle *et al.* 1995, Moltschaniwskyj, 1995, Arkhipkin *et al.* 2000). Once mature many cephalopods show a high degree of individual variation in the degree of anatomical investment in reproductive structures, particularly females (Jackson 1993, Pecl 2001). The allocation of energy to reproduction will also directly affect population size as this determines the fertility and survival schedule (Brommer 2000).

Although causal links for relationships between stock abundance and environmental parameters have been suggested, there are still no rigorous working hypotheses explaining observed fluctuations in squid abundance. The progression of our understanding in this area is severely hindered by the lack of comprehensive multi-year studies examining changes in population structure and plasticity in a suite of individual life-history characteristics of wild populations. This is a critical knowledge gap as the ultimate effects of environment on stock abundance are transduced through individual organisms into population level phenomena, with the population response arising as the summation of individual responses (Dunham and Overall 1994). There is also a continuous interplay between population-level and individual-level processes (Brommer 2000), although for cephalopods the role that density-dependence may play in regulating population size and structure is unexplored. Without understanding the mechanisms through which population responses to environmental conditions are mediated, we cannot predict when or if established relationships might break down completely (Agnew *et al.* 2002). Identifying the growth, condition, and reproductive characteristics of recruits who have grown under different environmental scenarios may lead to an improved understanding of the mechanistic connections between environmental conditions and the temporal variation in life history characteristics that might ultimately affect recruitment. Establishing the characteristics of successful recruits may ultimately lead to improved forecasts of annual population size.

Southern calamary (*Sepioteuthis australis*) are a fast growing, short-lived (<1 year), and multiple spawning inshore species. All life-history characteristics of southern calamary examined to date have been shown to be extremely variable. Egg size and embryo mortality (Chapter 3), annual egg production (Chapter 1), hatchling size (Steer *et al.* in review), level of reproductive investment (Pecl 2001), and growth (Pecl 2000) are all highly plastic. Although low levels of spawning take place throughout the year, there is a distinct observable peak in the austral spring and summer (Oct-Jan) when southern calamary aggregate over shallow (<10m) inshore spawning grounds. The individual and population characteristics of southern calamary during the spawning season are variable at daily (Chapter 2), weekly (Jackson & Pecl 2003), and monthly (Chapter 1) time scales.

Much of the spawning activity on the east coast of Tasmania is concentrated in Great Oyster Bay; on the east coast of Tasmania (Chapters 1 & 6). This is an area of convergence between the northern warm, nutrient poor East Australian Current (EAC) water mass and the southern cool, nutrient rich water mass of sub-antarctic origin. The oceanography and productivity of these waters shows inter-annual variability due to the shifting location of the convergence. The relative position of the convergence annually is determined by zonal westerly wind strength and large-scale oceanographic circulation associated with El Niño/Southern Oscillation (ENSO) events (Harris *et al.* 1987). When the convergence is south of Great Oyster Bay and the warm water dominates, the shelf waters are strongly stratified and there is little recycling or influx of nutrients (Harris *et al.* 1991). The dominant large zooplankter, krill (*Nyctiphanes australis*) and pelagic fish disappear from the shelf (Young *et al.* 1993). There is a correlation between the El Niño-Southern Oscillation index, sea-surface temperature, variations in the direction and strength of the winds, and recruitment variability of southern rock lobster *Jasus edwardsii* (Harris *et al.* 1988), gemfish (Thresher, 1994), and jackass morwong *Nemadactylus macropterus* (Jordan 2001). The oceanographic variability evident within Great Oyster Bay makes this region an ideal area to study environmentally induced population and individual variability in loliginid squid.

The aim of this five-year study was to determine the association between life history characteristics of southern calamary (eg growth rate, body size, and patterns of repro-somatic energy allocation) and oceanographic conditions experienced by the individuals. The extended temporal scope of the study allowed a description of the variation in individual and population characteristics under a range of environmental conditions. An added dimension of this study was the approach of utilizing population and individual based information, with the aim of linking population level information with individual processes of energy allocation to somatic and reproductive growth. Understanding the inter-annual dynamics of this abundant, short-lived (<1 year) and highly flexible species may help generate mechanism-based environment-recruitment hypotheses worth exploring further in similar but less studied coastal squid.

Materials and Methods

Sepioteuthis australis individuals were collected using hand jigs, and to a lesser extent purse-seine, from the fishery and targeted research sampling from Great Oyster Bay on the east coast of Tasmania, Australia. Squid were collected during the austral summer over five spawning seasons; early 1996 (January), 1996/97, 1999/2000, 2000/2001 and 2001/2002 (all November, December and January).

A total of 1211 squid were examined throughout the study, with weight information recorded for 837 squid and a sub-sample of 484 individuals aged via increments in the statolith. Most individuals from January 1996 and 1996/97 were refrigerated or placed on ice within a few hours of capture and measured within 12 hours. All other squid were stored frozen until processed. Squid were assigned a maturity stage according to the relative size and colour of reproductive organs, following the six-stage maturity scale of Lipinski (1979), as per Pecl (2001). Under this scheme stages IV and V are mature and are hence part of the spawning stock. Dorsal mantle length (ML) was measured to the nearest millimetre, and gonad (ovary or testis) and total body weight to the nearest 0.01g.

To examine the relationship between somatic condition and level of reproductive investment by females, residuals were generated for the ovary-ML and body weight-ML relationships from model II regressions using log data. A residual is the difference between an individual's actual measured weight and the weight predicted by the regression equation. Residuals were standardised by dividing each residual by the standard deviation of the predicted values. Residuals of the weight-length relationship provide a size independent measure of the somatic condition of an individual at the whole animal level (Moltschaniwskyj & Semmens 2000). An individual that is lighter for its length than predicted from the regression equation (negative residual), is suggested to be in poorer somatic condition than an individual who is heavier for its length than predicted from the regression equation (with a positive residual). Residuals from the ovary-ML relationship provide an indicator of the level of reproductive investment.

Sepioteuthis australis statolith increments have been validated as daily in known age squid up to 102 days of age (Pecl 2000). Statoliths from January 1996, 1996/97 and part of 1999/00 were stored, treated and processed as detailed in Pecl (2000). Subsequent work in 2000 revealed that statolith microstructure was clearer towards the dorsal margins when statoliths were ground along the dorsoventral axis (as per Dawe and Beck 1993). Examination of 20 adult statoliths and 5 known age juvenile statoliths (from Pecl 2000) prepared using both methods revealed no statistical difference between the methods (paired *t*-test, *t*=-0.774, df=24, P=0.446). Statoliths from the remainder of the study were thus prepared using the method of Dawe and Beck (1993). All statoliths were read twice, most by two different readers, with one reader common to all statoliths. Statoliths from January 1996 and 1996/97 combined were read in a random order, as were statoliths from the last years of the study (i.e.: not all statoliths from one year were read and then all from the next year). Statoliths were discarded as unreadable if the natal ring was unclear, if two consecutive counts differed by more than 10%, or less than 90% of the rings were visible. From each sample 4-7% of statoliths were discarded as unreadable due to statolith microstructure.

Estimates of abundance

Fishery independent estimates of biomass are unavailable for southern calamary, however, as population parameters are affected by biomass, CPUE has been used as a proxy of relative abundance. Southern calamary are harvested commercially using squid jigs, hand-spear, dip net, and purse-seine, with squid jigs the primary method accounting for 61% of the total Tasmanian catch and 86% of the Great Oyster Bay catch in 2000/01. Therefore for CPUE analysis in this study only catch reported by the jig fishery in Great Oyster Bay was used, and was calculated as the geometric mean of kg/jig hour (Lyle and Hodgson, 2002). CPUE estimates were derived for each spawning season for the months of November, December and January combined. As the average weight of individuals varied substantially between years, CPUE values were also adjusted using the average weight of squid in each spawning season to determine the relative abundance as individuals/jig hour.

Oceanographic data

Estimates of sea surface temperature (SST) data were derived for an area encompassing the central east coast of Tasmania to provide an indicator of temperature variations for that region. Reynolds SST data was provided by the NOAA-CIRES Climate Diagnostics Centre, Boulder, Colorado, USA, from their Web site at http://www.cdc.noaa.gov/. The optimum interpolated (OI) SST analysis was produced weekly on a one-degree grid. The analysis uses in situ and satellite SSTs plus SSTs simulated by sea ice cover. Before the analysis is computed, the satellite data is adjusted for biases using the method of Reynolds (1988). A description of the OI analysis can be found in Reynolds and Smith (1994). The bias correction improves the large-scale accuracy of the OI SST. As the depth of the thermocline is generally below that of the maximum depth of Great Oyster Bay (Jordan *et al.* 1995), estimates of SST are likely to reflect the thermal conditions of the bay. Weekly SST data was used to generate a sine function[2] to formally characterise the temperature regime in each year in terms of mean location, amplitude, phase, and cycle. The best fit was decided by minimising the sums of squares residuals.

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[2] Temperature = mean location + amplitude. Sin ((t-phase)/cycle))

Results

Individual size and population sex ratios

In each year of sampling, individuals of both sexes were obtained over a wide size and age range (Table 5.1). Average size of males and females were significantly different, but the nature of the difference was dependent upon year ($F_{sex*year}$=5.85, df 9, 811, $P<0.001$). Males were between 31-88% larger on average in each year compared with females, except in January 1996 and 1999/01 when there was no difference (Fig. 5.1). The difference in size between the sexes was particularly dramatic in the later years of the study with males on average 59% and 88% larger than females in 2000/01 and 2001/02 respectively. Combined ANOVA regression revealed a significant positive linear relationship between average male size and year (F=402.31, df 1, 3, $P<0.001$); the rate of increase in weight through time was 167.36g (± 17.88) per year. Whilst female size varied over duration of the study, this was not as dramatic as the changes in average size of the males, with males in the later two years twice the size of males in the earlier years. The difference in average size was a function of proportionally fewer small (<400g) and medium (400-1000g) sized males in the population and a higher percentage of very large males (>1400g, Fig. 5.2).

In each year, 72-100% of the squid sampled were mature and in spawning condition. However, in January 1996, 23 juveniles and immature females were caught, and eight immature females were also caught in 1996/97. Between 1999/00 and 2001/02, only three immature squid were caught, and these were two stage two males and one juvenile caught in 1999/00. There was a significant difference in the sex ratios between the years ($\chi2$=27, df 4, $P<0.001$). In January 1996 there was a similar number of males and females sampled (51.5% females), however, in all other samples the sex ratios consistently favoured males (Table 5.1). The percentage of females decreased from 41.3% in late 1996 to 20.4% in 2000/01, with an increase in 2001/02 to 35.3%.

Table 5.1: Collection details of *Sepioteuthis australis* for this study.

Year	Month and no. of sampling days	Total no. caught	Number of mature adults	Total no. aged	Weight range (g)	ML range (mm)	Age range (days)	Sex ratio (M:F)
1996	Jan (6 days)	82	59	75	19-1270	66-382	92-203	0.94:1
1996/97	Nov (5 days) Dec (12 days) Jan (2 days)	271	264	201	43-2830	87-501	100-264	1.42:1
1999/00	Nov (7 days) Dec (2 days) Jan (1 day)	564	561	151	190-2009	151-434	128-275	2.01:1
2000/01	Nov (2 days) Dec (2 days)	142	142	67	141-2968	127-515	145-245	3.90:1
2001/02	Nov (3 days) Dec (2 days) Jan (1 day)	152	152	0	144-2623	105-485	N/A	1.83:1

Figure 5.1: Average body size of male and female *Sepioteuthis australis* in each of the years.

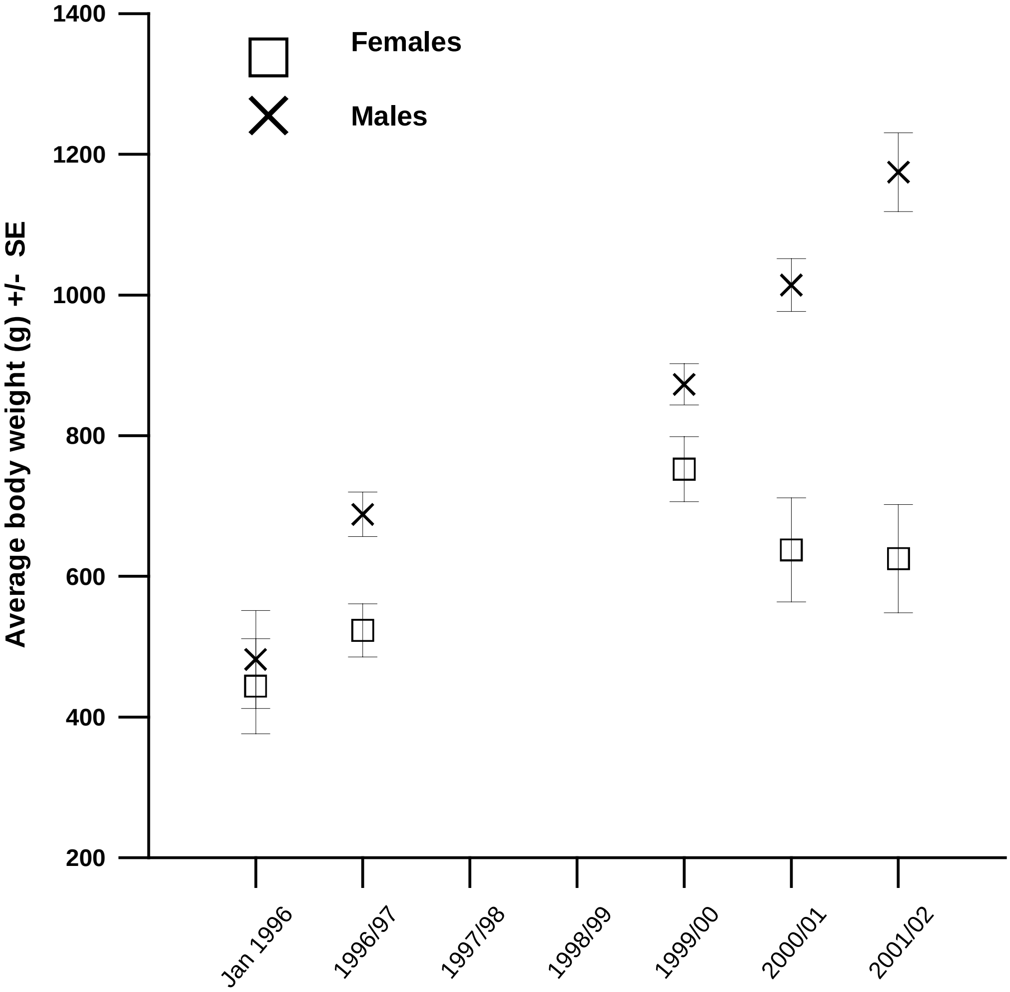
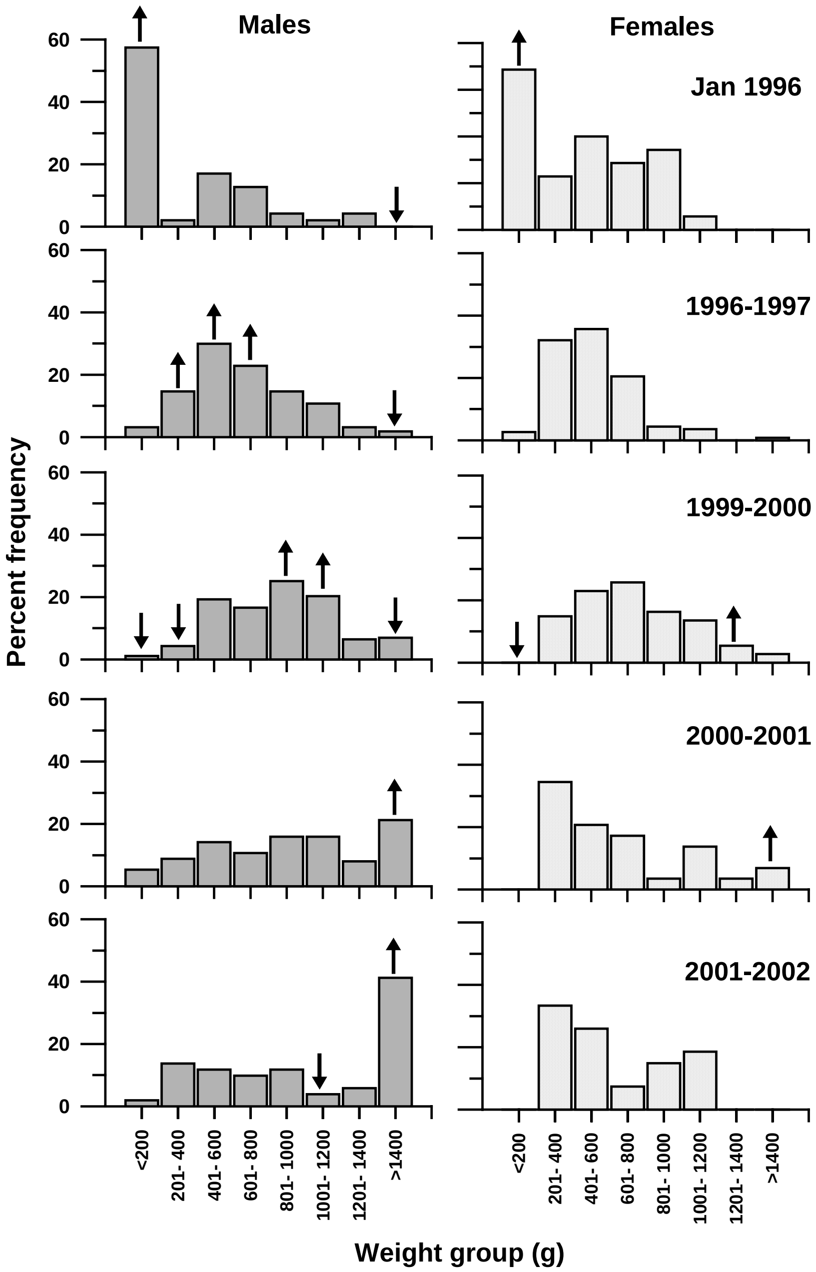


Figure 5.2: Size frequency distribution of male and female *Sepioteuthis australis*. The arrows indicate where more (↑) or less (↓) individuals were observed than expected, under the assumption that the size frequency distribution was independent of year.



A comparison of the average size of jig vs. seine caught individuals from 1996/97 (from all of Nov – Jan combined) and 1999/00 (seine and jig sample from the one commercial fisher, same location and day) show no evidence of differential selectivity between the gear types (F<1, df 1, 271, P=0.526; F<1, df 1, 68, P=0.984 respectively). The sex ratios in the jig vs. seine samples were also not significantly different in either 1996/97 (χ^2= 0.52, df 1, P=0.473) or 1999/00 (χ^2=0.87, df 1, P=0.768), with the percentage of females ranging between 37-44% for each combination of gear type and year.

Age

Relationships between size (ML or total weight) and age were weaker (although still significant) for squid caught in 1999/00 and 2000/01 compared with squid from the earlier samples, due to the paucity of younger and smaller squid (<200g) present in the population (Fig. 5.2). Differences in the range of ages and sizes across the years, and the unbalanced sample sizes made comparisons between the years difficult (Table 5.2). However, examination of the weight at age graph (Fig. 5.3) shows that squid from January 1996 and 1996/97 did not appear to have grown either comparatively very fast or very slow. In contrast, squid from 1999/00 display a high degree of variability in size-at-age and are found above and below the main group. This indicates that in this year, in addition to squid with 'average' growth rates, there was a component of the population that had grown very fast, and a component that had grown very slowly. Likewise, a component of the 2000/01 individuals also grew very fast, but slower growing squid were absent.

Using only age data over a range common to all samples (140-220 days), size-at-age was determined to be dependent upon sex (F=12, df 1, 386, P<0.001) and year (F=6.5, df 3, 386, P<0.001). Males were on average 21% heavier at a given age compared with females, indicating that they had grown faster for some duration of their life. On average, squid caught in 1996/97 had grown considerably slower than individuals caught in 1999/00 and 2000/01 (Fig. 5.4). Although the sex*year term in the model was not significant (F=2.46, df 3, 386, P=0.06), examination of the estimated marginal means show that the difference in size-at-age between males and females was relatively small in squid from January 1996 and 1996/97, compared to the later years where males appeared to be growing much faster than females. The non-significance of the ANCOVA may be due to the unbalanced model, and the low numbers of females aged in 2000/01.

Based on age, the back calculated hatch date was estimated for each individual and indicated significantly different hatching periods for each of the years. Squid caught in January 1996 were hatched mostly in July, August, and September, whilst those caught in 1996/97 were estimated to have hatched in May, June, and July. In contrast, squid caught in 1999/00 and 2000/01 appeared to have similar hatch peaks, mostly hatching in April, May, and June (Fig. 5.5).

Figure 5.3: Size-at-age of male and female *Sepioteuthis australis* from each year.

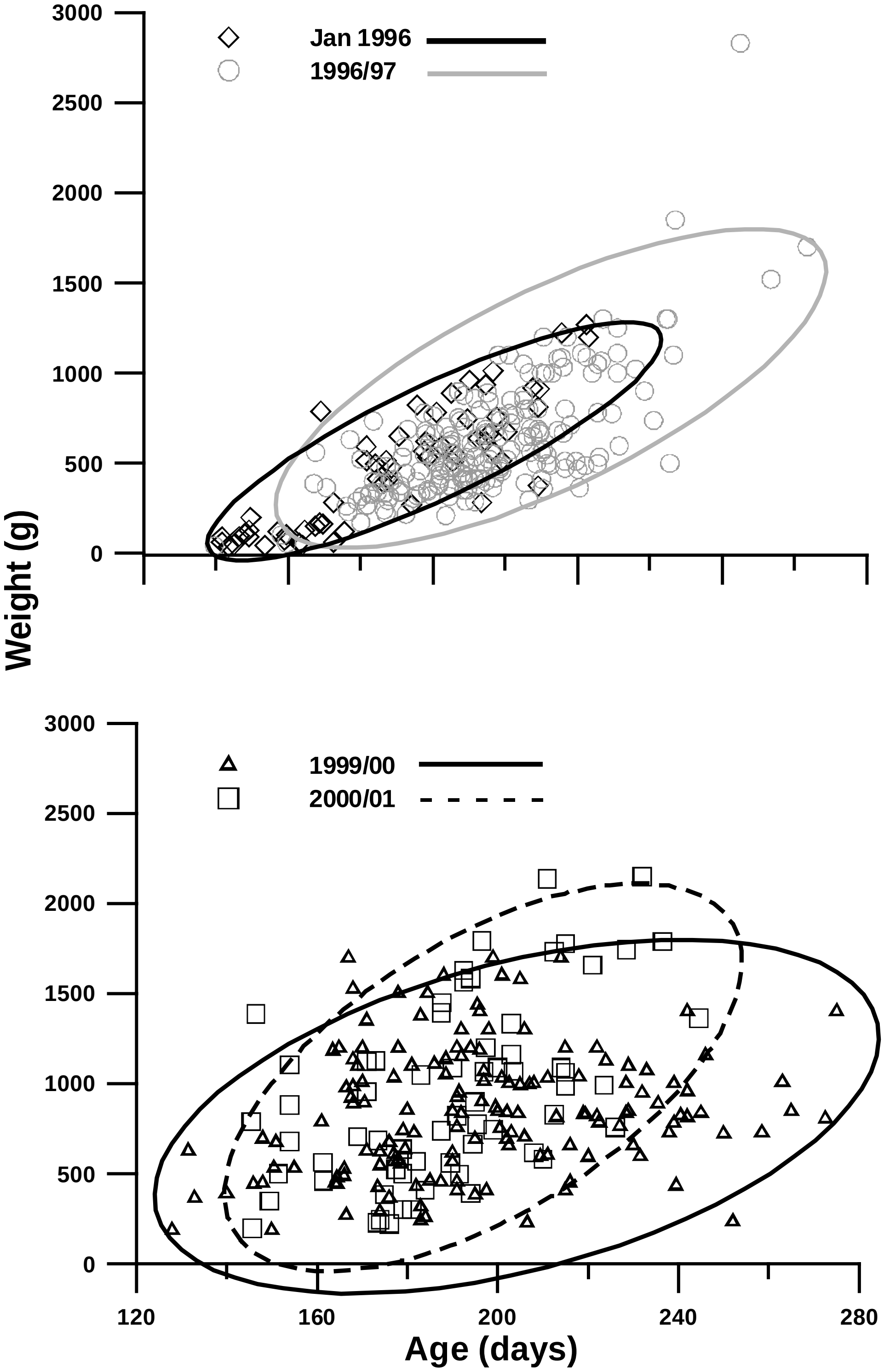


Figure 5.4: Average body weight of *Sepioteuthis australis* in each year, adjusted for age. Means with different letters are significantly different from one another.

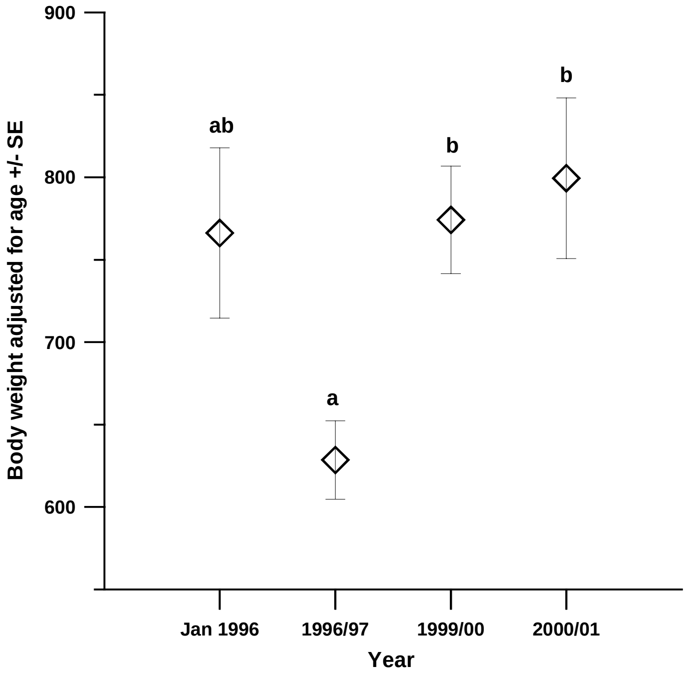
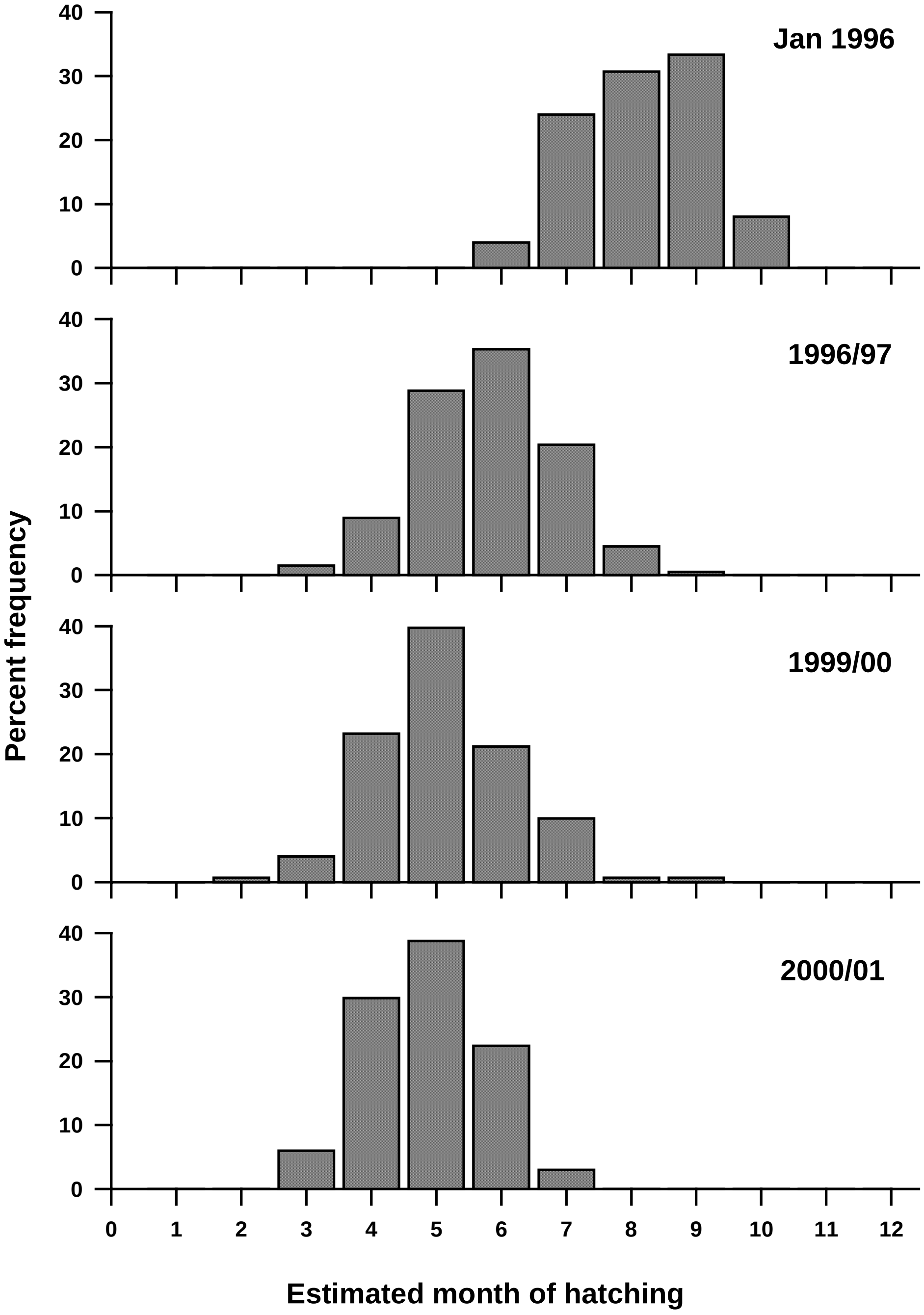


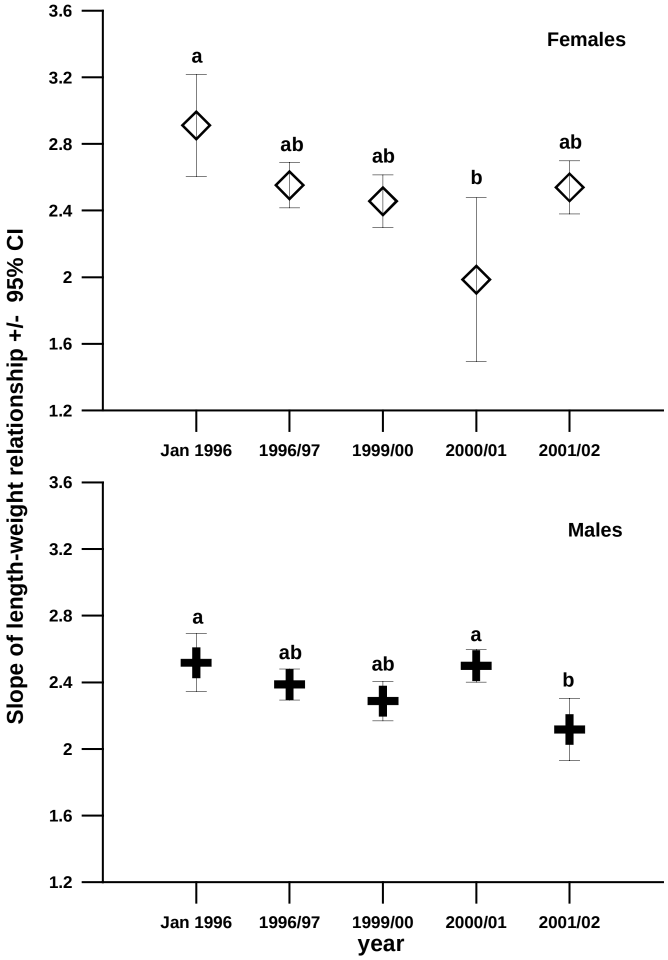
Figure 5.5: Frequency of estimated month of hatching for aged individuals from each year.



Reproduction and condition

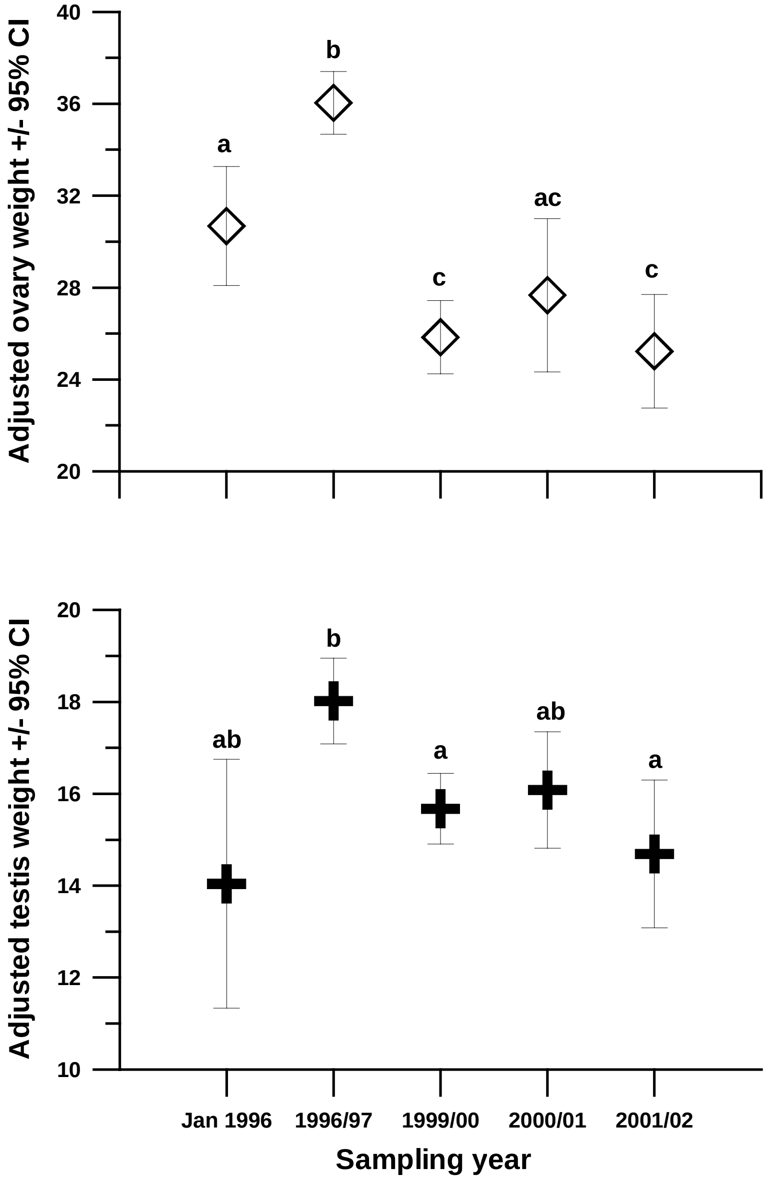
For both males and females, there were differences in the length-weight relationship of squid on the spawning grounds in each of the years (Males F=7.18, df 9, 524, P<0.001; Females F=7.28, df 9, 251, P<0.001). Comparison of the slopes of the length-weight relationship showed that this was because female squid caught in January 1996 were in better somatic condition than those caught in 2000/01 (Fig. 5.6). Male squid caught in January 1996 and 2000/01 increased their mass at a faster rate than males caught in 2001/02 (Fig. 5.6).

Figure 5.6: Slope of the length-weight relationship for males and females from each year. Means with different letters are significantly different from one another.



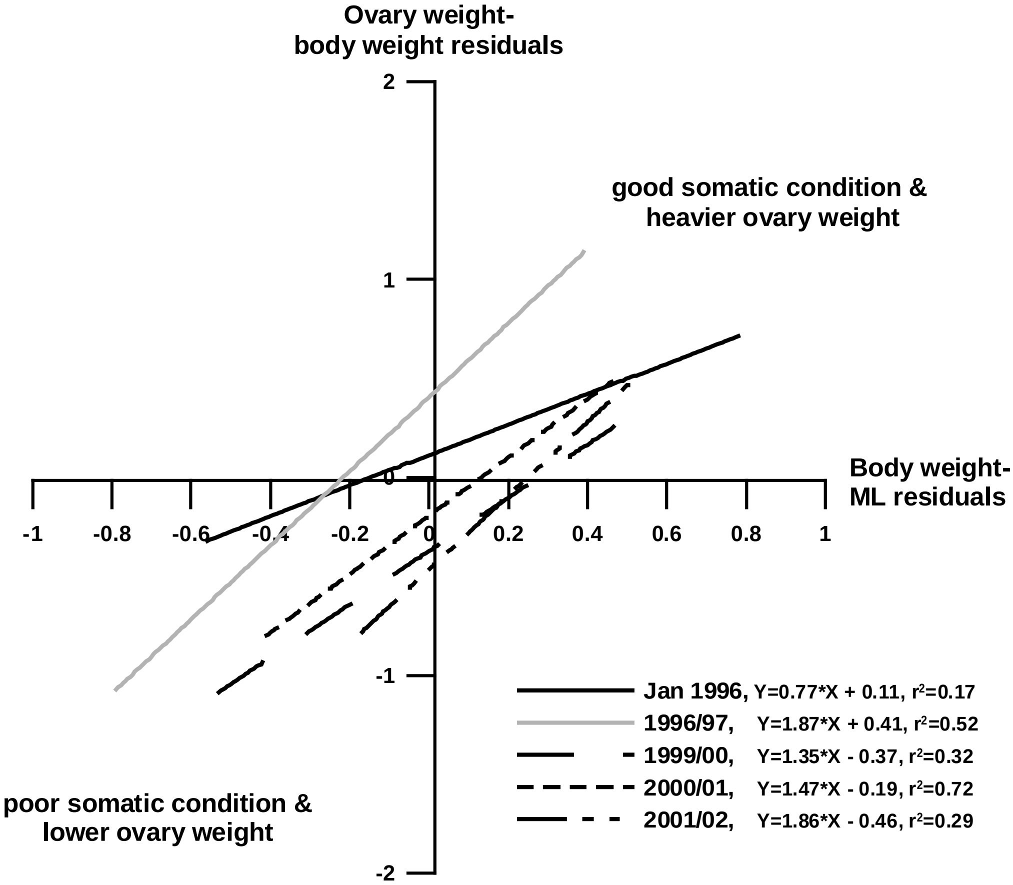
In each year males showed a very weak relationship between somatic and testis mass (r^2 = 0.26 - 0.36). An analysis of covariance showed that testis weight, adjusted for body weight, varied significantly as a function of year (F=2.331, df 9,489, P=0.014). Males caught in 1996/97 had an adjusted testis mass greater than males from 1999/00 and 2001/02. In contrast to the males, females caught in each year had a very strong relationship between somatic and gonad mass (r^2 = 0.83 - 0.97). Ovary mass, adjusted for body weight, varied as a function of year (F=2.52, df 9, 235, P=0.042). Females caught in 1996/97 had an adjusted ovary mass greater than females from all other years, and females caught in January 1996 had greater ovary weights than those caught in 1999/00 and 2001/02 (Fig. 5.7).

Figure 5.7: Average gonad weight, adjusted for total body weight, for females (ovary weight) and males (testis weight) in each year. Means with different letters are significantly different from one another.



Across all years, female squid in better somatic condition also tended to have a higher level of reproductive investment, as shown by the correlation between body weight-ML residuals and ovary-ML residuals (r=0.407, n=242, P<0.0001). The ovary-ML residuals were compared among years, using the body weight-ML residuals as a covariate. Reproductive investment by females was dependent upon year and body weight-ML residuals (F=2.42, df 9, 232, P=0.04). Generally, females from January 1996 and 1996/97 had higher levels of reproductive investment for their size at any given level of somatic condition compared with females from other years (Fig. 5.8).

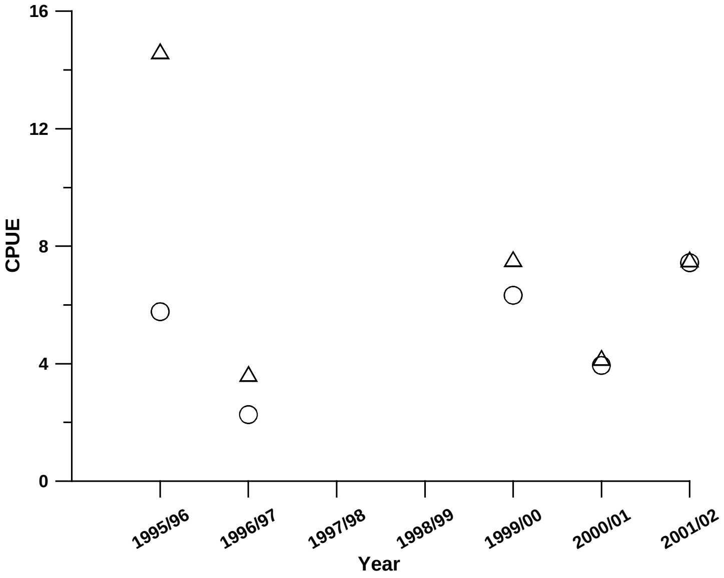
Figure 5.8: Residual values for each female from the body weight-ML and ovary weight-body weight relationships. Individuals with higher body weight-ML residuals are heavier than predicted from the regression equation, and individuals with higher ovary weight-body weight residuals have greater ovary weights than predicted from the regression equation.



Abundance

The highest biomass in Great Oyster Bay, based on CPUE (kg/hr), occurred during 2001/02 followed closely by that of 1999/00 (Fig. 5.9). Abundance of squid during these two years also appeared very similar using CPUE adjusted by the average size of individuals caught during each respective spawning season. 1996/97 and 2000/01 had the lowest abundance of squid during the study period, using both abundance indices (kg/hr or individuals/hr). During more recent years of the study abundance estimates based on kg/hr and individuals/hr were very similar. However, in the first two years where squid were on average much smaller, the two abundance indices differed, particularly for 1995/96. During 1999 and 2001, the fishery was closed to commercial and recreational fishing for four weeks (two, two-week closures) and in 2000 it was closed for six weeks (three, two-week closures). There was, however, no evidence that densities of squid increase during fishing closures (Chapter 2).

Figure 5.9: Catch per unit effort values for the jig catch reported for Great Oyster Bay in each year. Circles are CPUE estimates based on kg/jig hour and triangles are individuals/jig hour.



Oceanographic conditions along the east coast of Tasmania 1995-2001

SST's in the Great Oyster Bay region showed a distinct seasonal cycle, with temperatures highest between January and March, and lowest in September (Fig. 5.10). SST maximums varied by up to two months between years reaching a peak in mid January 1999 and mid March in 2000. There was also evidence of considerable variations in the maximum and minimum SST's between years with 1999, 2000, and 2001 being consistently warmer than 1995 and 1996. Only very small fluctuations in the Southern Oscillation Index were evident during the study period. A moderate La Niña event occurred in 1998/99, which weakened back to neutral conditions before reforming for a shorter period in 1999/2000, this last event finished in Autumn 2000.

Figure 5.10: Estimates of weekly SST's for Great Oyster Bay in each year.

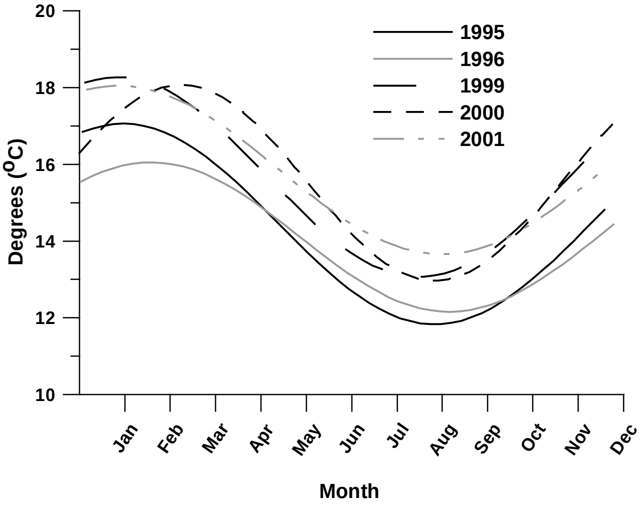


Table 5.2: Annual SST for Great Oyster Bay, Tasmania for each of the sampling years, and estimated average temperature at hatching for the individuals comprising each years spawning population. A summary of the biological parameters are also shown.

Annual temperature	**1995**	**1996**	**1999**	**2000**	**2001**
Mean Location (^{o}C)	14.45	14.11	15.67	15.52	15.86
Amplitude	2.61	1.95	2.60	2.55	2.19
Phase	349.42	354.29	334.85	329.22	358.06
Cycle	67.82	64.79	65.52	55.10	70.43
SSQ temperature curve	14.16	6.35	13.12	12.83	10.40
Hatching temperature					
Average (^{o}C)	12.17	14.40	15.51	16.15	15.91
Biological parameters	**Jan 95**	**96/97**	**99/00**	**00/01**	**01/02**
Age – weight overall correlation	0.852	0.708	0.191	0.425	N/A
Average age (days)- males	149	179	198	188	N/A
Average age (days)- females	147	168	191	194	N/A
Average size (g) - males	482	688	873	1014	1175
Average size (g)- females	444	523	752	637	625
Condition- males	good	average	average	good	poor
Condition- females	good	average	average	poor	average
Reproductive investment-males	average	good	average	average	average
Reproductive investment- females	average	good	poor	poor	poor
% Females	51.5	41.3	33.2	20.4	35.3
Sexual dimorphism	none	minor	none	high	extreme

Discussion

All aspects of *Sepioteuthis australis* life history and population dynamics are highly plastic in nature, a combination of phenotypic response to biotic (predators & prey) and abiotic factors, and possibly genetic differences. Across this five-year study, changes in squid size, condition, and possibly growth rate were sex-specific, indicating that males and females respond differently to similar factors. Importantly, populations of apparently similar abundance (eg: 1996/97 and 2000/01, 1999/00 and 2001/02) had very different population structures and were composed of individuals with strikingly different life-history characteristics. The population dynamics of cephalopods generally appear to be driven primarily by phenotypic plasticity in response to environmental variability (Boyle & Boletzky 1996). However, the relative roles of phenotypic plasticity vs. genetic diversity, and the extent to which density dependent processes may operate in shaping the observed life histories remain unknown.

The SST patterns identified in this study for eastern Tasmanian coastal waters reflect both seasonal trends and inter-annual variations in regional oceanography. As the duration of sunlight increases with the onset of spring there is a general warming of surface waters from a minimum in September. This solar warming continues during the following months with temperatures often increasing by c. 3-4 ^{o}C by early January. At that time there is often an intrusion of oligotrophic subtropical East Australian Current (EAC) water that floods the shelf, creating an environment low in nutrients and phytoplankton (Harris *et al.* 1991). The considerable inter-annual variability in the influence of EAC water on the east coast of Tasmania was evident during this study where there was a difference of up to 2.5 ^{o}C in SST's between years, a trend that was evident throughout most of the year. Overall, 1995 and 1996 were cooler than 1999, 2000 and 2001 with SST's during the summer of 1996 generally around 16 ^{o}C. This was indicative of periods of strong westerly winds driving colder nutrient rich waters of subantarctic origin up the east coast of Tasmania in summer disrupting the pycnocline (Harris *et al.* 1988). In contrast, in the latter years of the study the warmer nutrient poor EAC water dominated the region. There is also evidence that SST's peaked up to a month later in 2000 than in 1999 or 2001 reflecting the persistence of cooler water of subantarctic water on the shelf during January 2000.

In addition to variation in SST's, the changing influence of different water masses results in strong variations in productivity and biological structure of eastern Tasmanian shelf waters. In El Niño years prolonged westerly winds through spring and summer results in high productivity due to the vertical mixing and constant replenishment of nitrates from the cooler subantarctic waters (Harris *et al.* 1988). During La Niña years a decrease in wind mixing and the intrusion of warm water results in decreased primary and secondary production and a change in the structure of the zooplankton community (Harris *et al.* 1991, Young *et al.* 1993). While there are no direct estimates of productivity during the period of this study, the patterns of SST give a broad indication of the levels of productivity. Overall, the cool years of 1995 and 1996 can be defined as more productive than the warmer years of 1999, 2000, and 2001. Although the environmental regime during this study differed substantially between years, it did not encompass the extremes that may occur on the east coast of Tasmania (eg: during years with strong La Niña or El Niño signals).

This study identified two groups of years of similar abundance (eg: 1996/96 and 2000/01, and 1999/00 and 2001/02), but with very different population structure and characteristics. If we were generating environment-recruitment relationships these two populations would be considered equivalent. However, the factors responsible for generating a population consisting of smaller, slower growing squid with little sexual dimorphism and high levels of reproductive investment, are going to be very different to those factors resulting in a population of larger, faster growing squid with extreme sexual dimorphism in body size and low levels of reproductive investment. In the search for environment-recruitment relationships for squid the 'spawning stock' is considered as a single uniform unit. However, seeking a relationship between abundance and environmental parameters at such a gross level will not shed light on the mechanisms that lead to any given level of abundance. Therefore, use of environmental-recruitment relationships as predictive management tools may be limited.

Indices of stock abundance have relationships of varying strength with a number of environmental characteristics; sea surface temperatures preceding recruitment (*Loligo forbesi*, Robin & Dennis 1999; *Loligo gahi*, Agnew *et al.* 2002), proportion of hatching areas occupied by frontal waters in the previous year (*Illex argentinus*, Waluda *et al.* 2001), and water mass movement and river runoff (*Illex argentinus*, Chang 2001 in Agnew *et al.* 2002). For short-lived species with highly plastic life-history characteristics and where the standing crop is entirely replaced each year (Boyle & Boletzky 1996), environmental predictors of recruitment may be useful in highly variable environments (Agnew *et al.* 2002). Environmental predictors of recruitment are, however, going to be more useful and much more rigorous if we work towards incorporating life history processes and their plasticity into the models. This will involve accumulating longer time series of life history data, in addition to recruitment data.

Southern calamary exhibited sex-specific life history plasticity. The males varied more in size and growth, whilst females varied more in somatic condition and level of reproductive investment. Male squid have a relatively smaller anatomical investment in reproduction and therefore may have a larger energetic scope to respond rapidly to environmental changes (Jackson & Domeier 2003). The level of reproductive investment of female *Sepioteuthis australis* appeared related to temperature, with females from cooler (and possible more productive) years having a higher level of reproductive investment. Given the relationship between SST and productivity on the east coast of Tasmania, we are unable to identify the relative importance of temperature vs. food, although as female southern calamary derive their energy for reproduction primarily from food and not body stores (Ho *et al.* submitted), food availability is likely to have the larger influence.

Egg production by individuals that produce multiple batches of eggs can vary in response to food, growth, temperature, population size, and age structure (Lowerre-Barbieri *et al.* 1998). Given that squid with indeterminate and non-asymptotic growth allocate energy to growth and reproduction across all ages and sizes, we could not assess how the populations differed in longevity and total reproductive output. How the life history traits of the spawning stock affects subsequent recruitment would depend on the strength and nature of the stock-recruitment relationship. Agnew *et al.* (2000) found evidence of a negative density-dependent effect in the stock-recruitment relationship for *Loligo gahi*, with high spawning stock sizes leading to below-average recruitment. Perhaps this is evident in our study with the high spawning stock of 1999 resulting in an apparent low abundance of 2000.

Between years, differences in body size were extreme, both among the male component of the population and between genders. Size can influence food gathering, size selective predation or starvation, and reproductive success (Cargnelli & Gross 1996). Small individuals may survive and reproduce better when food is limited because they need less food to sustain themselves, however, larger individuals may survive better when there is no food at all (Nylin & Gotthard 1998). The mortality schedules of southern calamary populations with large fast growing males and small females with low reproductive output will differ from populations of smaller males and females of similar size. The influence of size dependent behaviours such as male-male competition, mate selection and cannibalism may also differ among years. Gender specific responses of growth rate to environmental factors such as photoperiod, temperature, diet and mortality risk occurs in insects (Nylin & Gotthard 1998). The sexual dimorphism in size of southern calamary maybe unrelated to temperature as the sexes were of equal size in 1999/00, and yet the populations of 2000/01 and 2001/02, under a similar temperature regime, displayed very large differences in size between the sexes.

During the two warmer years size-at-age relationships were weaker than those observed during the two cooler years. This has trend has also been seen in both laboratory reared and wild caught *Loligo pealeii* (Hatfield *et al.* 2001, Hatfield & Cadrin 2002). Additionally, potential variability in growth rate increases with temperature in many fish (Houde 1989). We found evidence of fast and slow growing squid in one warmer year (1999/00), however only ‘average’ and faster growing individuals were present in the other warmer year (2000/01). Several explanations are possible for this observation. The total annual catch and CPUE values for 1998 were the highest on record (Lyle & Hodgson 2001), and perhaps the huge population of 1998 generated a high diversity in the life history traits of subsequent populations. Alternatively, total catch, CPUE, and egg production (Chapter 1) in 1999/00 were also very high, and 1999/00 may have therefore been a very good year for survival. Individuals from 2000/01 may have been exposed to higher levels of size (or growth rate) dependent predation. For larval fish, as food abundance increases the mean and variance in growth rates increase. However, as predator abundance increases, the variance in growth rates, for any given mean, decreases via culling of slow growing larvae (Pepin 1989). It is important to note that factors other than temperature are playing a major role affecting the observed growth rates in adult southern calamary.

Embryonic duration, hatchling size (Bouchaud 1991) and juvenile growth rates (Forsythe 1993), are all influenced by temperature in cephalopods. With recruits of many squid species hatching over at least 4 months of the year (eg: *Sepioteuthis australis*, this study, *Loligo gahi* Hatfield 1991), a ‘spawning stock’ will be composed of individuals who have experienced very different environmental conditions during the critical early periods of their life-cycle. Partitioning the variance in cephalopod recruitment into its component sources, and establishing the basis behind environment-recruitment relationships is therefore going to be a challenging task. The mechanistic connections between environmental variation and population level rates and characteristics are complex and indirect, operating at the level of individual organisms (Dunham and Overall, 1994). Progress towards understanding recruitment processes will be accelerated by a systematic and in depth consideration of individual variability and the attributes of survivors (Rice *et al.* 1993). This study was by design exploratory in nature however, these findings provide a strong basis for the direction of future studies.

Chapter 6: Large scale temporal and spatial patterns of adult populations and spawning activities

(Authors: NA Moltschaniwskyj & MA Steer)

Introduction

Management of squid stocks using theories developed for temperate teleost species is inappropriate due to the dramatic differences in life history characteristics between the two groups. Squid typically have short life-spans and rapid growth, with aseasonal spawning that is followed shortly by death. Furthermore, there is evidence that many populations have individuals showing extreme variation in growth and age and size at reproductive maturity (Boyle *et al.* 1995, Moltschaniwskyj 1995, Pecl 2001). Some squid species appear to show strong correlations between environmental parameters and recruitment strength, allowing the development of responsive management (Agnew *et al.* 2002). However, southern calamary does not display clear simple associations between life-history characteristics and environmental factors such as water temperature, therefore predictions of future stock characteristics on this basis may not be feasible (Chapter 7).

There is a very comprehensive dataset for southern calamary populations on the east coast of Tasmania, particularly in the Great Oyster Bay area. Given the focus of fishing effort in this region and high densities of egg masses on shallow seagrass beds, management policies have focussed on protecting and controlling this part of the fishery. The use of fishing closures in this area only was explicitly implemented to allow some spawning to occur, thereby ensuring with greater confidence that offspring for future populations were being produced. However, increased fishing effort and landings has continued around Tasmania due to the increased value of southern calamary and diversified nature of the scale fish industry in Tasmania (Chapter 7). There has been a spatial extension of fishing closures to the south of Great Oyster Bay in 2002; however, there are concerns about stocks in the south-east of the State, prompting concern about if and how these should be managed. The current management policies will only protect Tasmanian squid stocks if the populations in the east and south-east are connected, either by active movement of adults or passive dispersion of the juveniles.

There is evidence that *Sepioteuthis australis* populations in east Tasmania are genetically similar to those in South Australia and New South Wales, but different to Western Australian and New Zealand populations (Triantafillos & Adams 2001). However, there are differences in life history characteristics of the South Australian and east Tasmanian populations, particularly in growth rates and longevity (Pecl 2001, Triantafillos 2002). Therefore, it is likely that there are population differences between the major regions of Tasmania that maybe due to environmental and habitat differences, or different genetic stocks.

Currently little is known about the fished populations of southern calamary outside of Great Oyster Bay. We know that there are some differences in growth rates, sex ratios, body size, and egg production among years within Great Oyster Bay (Chapters 1 & 5). However, the nature of large scale spatial differences is unclear. Implementation of a State wide management plan will require information on the following for southern and eastern populations over the same time period; size and age characteristics, reproductive and somatic condition, levels of egg production, and rates of embryo survival.

Back-calculated hatch dates based on statolith ages suggest that those individuals that are involved in the spring/early summer spawning aggregation in Great Oyster Bay were hatched during autumn/early winter. Furthermore, although mature females are found all year, there is no evidence of spawning aggregations occurring at any time other than spring/early summer. This raises the question about if and where spawning is occurring during autumn/winter. Combining the collections of adult squid to assess reproductive status, and the sub-tidal surveys of sites for egg masses where squid were caught, allowed a broad scale assessment of temporal and spatial variation in spawning activities of southern calamary.

The aim of this chapter was to describe and identify differences in the population biology and life-history characteristics of southern calamary on the east coast and southern regions of Tasmania. This was done with respect to determining a state-wide approach to managing southern calamary, especially with respect to protecting spawning aggregations of squid, and also to determine if spawning aggregations were occurring outside of the currently known spring/summer spawning period. The focus in this study was on the part of the population caught commercially, therefore there was no targeted collection of sub-adults or juveniles, and all conclusions made are restricted to the adult component of populations collected in shallow habitats (<10m) on the east and south-east of Tasmania.

Material and Methods

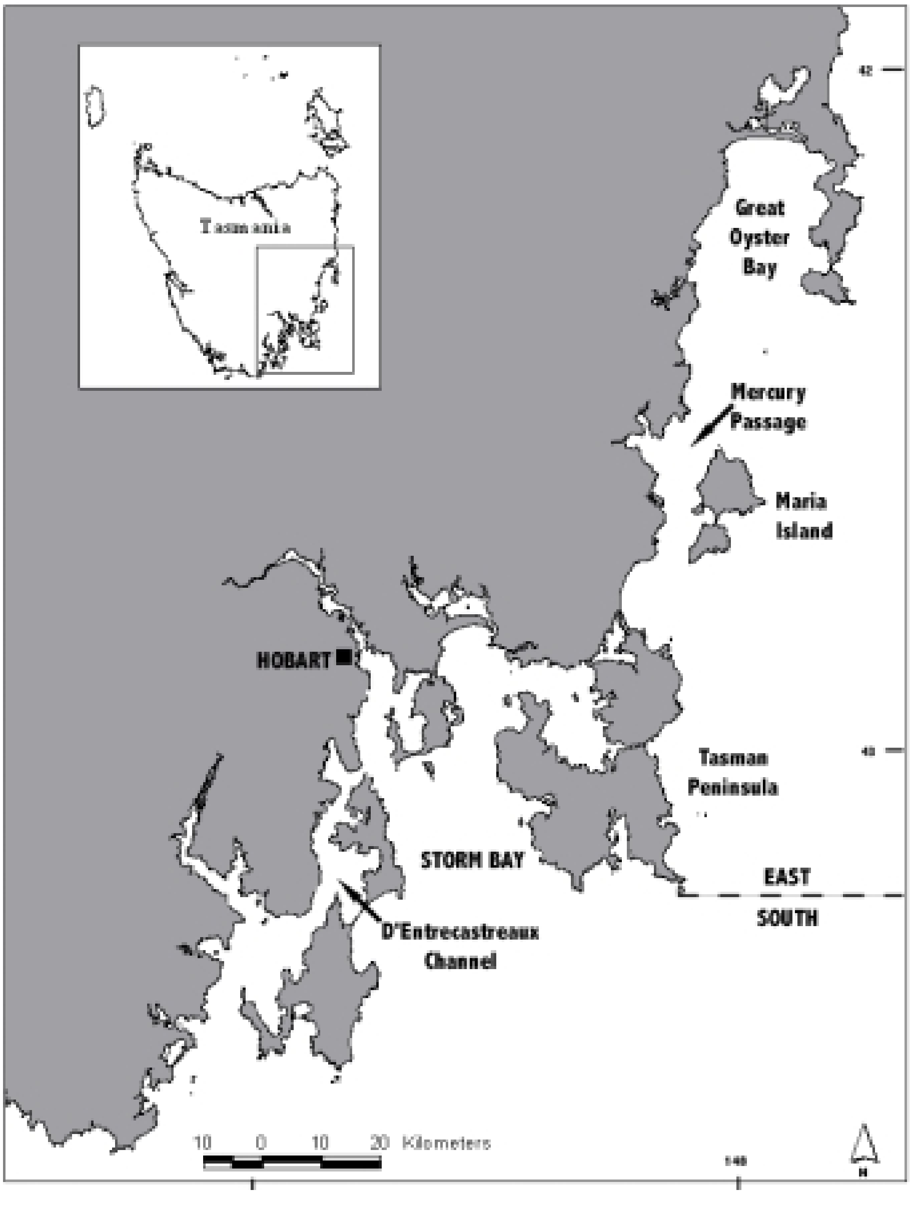
Collection of squid

Sampling of squid was carried out from October 1999 to April 2001, from two regions; the east (from Great Oyster Bay to Eaglehawk Neck on the Tasman Peninsular) and the south-east (Fortescue Bay on the Tasman Peninsular to D'Entrecastreaux Channel) of Tasmania (Fig. 6.1). Over this period between 16-22 sites were fished in each of the two regions. Sites in each region were targeted based on anecdotal information from commercial and recreational fishers as to where squid were being caught in reasonable numbers in the past and/or squid eggs had been sighted.

During 2001-2002 collections of adult squid were made from each region bimonthly from January-September, then monthly from October-December. To date, differences in the population structure of southern calamary have been explored at the scale of weeks, months and years (Jackson & Pecl 2002, Chapter 5). However, our interest is on seasonal large-scale differences that maybe occurring in the populations being fished around the state, and therefore seasonal comparisons were made among the regions. Collections of squid were made using the research group and commercial fishers. The research samplers would undertake at least 15 min of fishing by two fishers at each site. If no squid were caught during that time, then the next site was visited. If squid were caught at a site then fishing continued until either 60 squid were caught or until no squid were caught for 15 mins. In some months the research team was unable to catch enough squid; therefore if possible catch was bought from commercial fishers. The fishers would provide us with information about where the animals were caught and what fishing method was used.

A total of 2,396 animals were examined, with DML measured and gender recorded during the course of the study. Of these, 1,394 individuals had a more comprehensive set of biological data measurements taken (total weight and gonad weight). Stage of reproductive maturity was estimated macroscopically based on the size and colour of the reproductive organs, the modified Lipinski scale was used (Pecl 2000). The gonosomatic index (GSI) was calculated as a percentage of gonad weight (ovary and oviduct for females and testis for males) to total body weight. Due to difficulties in collecting adults during autumn and winter in the south-east of the state, insufficient individuals were aged for analysis. The age of 602 individuals was estimated from daily rings in the statolith. Details of the preparation of the statoliths and counting protocols are described in Pecl (2000) and Chapter 6.

Figure 6.1: Map of the eastern and southern region of Tasmania, indicating the major areas that from where squid were collected and subtidal surveys for egg masses were undertaken.



Egg surveys

Subtidal surveys were undertaken in both the east and south-east of the state. As for the collections of adults, sites in each region were chosen based on information from fishers about where animals had been caught in the past. Sites in Great Oyster Bay on the east coast were those used in earlier intensive egg surveys (Chapter 2). The habitat of the sites ranged from seagrass (*Amphibolis antarctica* and *Heterozostera* sp) covered soft bottom, to macroalgal dominated (*Ecklonia radiata*, *Sargassum* spp and *Macrocystis pyrifera*) covered reef.

Surveys for egg masses were carried out with the same periodicity as the adult collections, with 7-15 sites visited in each region in each season. Most sites were surveyed between one to three times in each season. To cover a greater area of the site, timed swims or manta-tows were undertaken at each site. Where the sites consisted of broken reef and patchy seagrass with large areas of sand a diver was towed behind the boat on a manta-board for 20 mins (c 500 m). The diver then recorded the number of egg masses seen and provided an estimate of development using the four stage development categories described in Chapter 1. In sites with dense macroalgae and/or seagrass that required searching, 1-2 divers completed 20 minute (c 300-340 m^2) swims searching for egg masses. In the spring/summer months when egg masses were more consistently seen, 20 min timed swims were completed at most sites.

For surveys conducted via timed swims, length of any egg mass encountered was measured (see Chapter 1 for details). To convert the number of egg masses seen on a timed swim to density, the area searched was determined by timing how long it took to search $20m^2$ under different densities of egg masses. This then allowed us to estimate how much substrate was searched during the 20 min swim.

To assess the mortality rates of eggs between the regions, six egg strands were randomly collected from egg masses that had embryos which were developed beyond Stage 20 (Steer *et al.*, 2003). Embryos were dissected from each strand within 8 hours of collection and embryos were scored as “dead” if they were unfertilised, had ceased development, or were undergoing abnormal development.

Catch-per-unit-effort

Commercial catch records accessed from the DPIWE database were broken down into the two regions, based on the location of the recorded fishing block. One block (6G4) spans both the east and southern region, therefore, all records of catches in block 6G4 were removed from the analysis, representing c. <1% of the total landings. However, 6G4 is broken down into estuary blocks, which are more commonly used by fishers in their records and do not span the two broader geographic areas. To reduce the inclusion of records for which southern calamary represented an incidental by-catch rather than a target species, landings <10 kg for Danish-seine nets, beach-seine nets, gill-nets, dip-nets and hand-spears were excluded. Since hand jigging and purse-seine nets are used specifically to target southern calamary all catches using these gears were included in the analyses.

Results

Size Frequency Distribution

Populations from both the east and south-east of the state had different size frequency distribution among the four seasons (χ^2_{east}=258.51, df 12, P<0.001; χ^2_{south}=78.45, df 12, P<0.001). This was a function of larger individuals (>300 mm) being present in spring at both locations compared with the other seasons (Fig. 6.2). In contrast, both summer and autumn populations had fewer larger (>300mm) individuals, and on the east coast there were relatively greater numbers of smaller (<200 mm) individuals (Fig. 6.2). Due to low numbers in the frequency distribution the only contrast that was possible between regions was for spring, which was significant (χ^2_{spring}=35.49, df 4, P<0.001). This was due to a greater proportion of individuals in the 200-299 mm size class on the east coast.

In a comparison of the size frequency distribution between the sexes in each region, there was significant differences (χ^2_{east}=310.68, df 4, P<0.001; χ^2_{south}=50.47, df 4, P<0.001). At both locations females in the larger size classes (>300 mm) were relatively less abundant compared with males (Fig. 6.3). On the east coast the samples had proportional more females than males in the sizes class <300 mm, a feature that was not seen in the south-east (Fig. 6.3). A comparison of male size frequency distributions across the regions showed proportionally more males <200 mm in the south-east compared with the east (χ^2_{male}=41.52, df 4, P<0.001).

Sex ratios

There was no difference in the proportion of males to females between regions in any one season; the sex ratio across all seasons and locations was 2.2 males to 1 female. However, there was a difference in the proportion of males to females among the season within each location (χ^2_{east}=24.56, df 3, P<0.001; χ^2_{south}=28.17, df 3, P<0.001). In both the east and south-east there was a consistent pattern of proportionally fewer females in spring, except in autumn in the south-east (Fig. 6.4).

Somatic condition

There was no evidence that the somatic condition of males or females differed between the regions in any season ($F_{regions}$=1.10, df 1,1383, P=0.294). There was however a difference among the seasons, but this was only seen in males ($F_{seasons}$=3.43, df 3, 1383, P=0.017). It was evident that males in the summer were in poorer somatic condition than in autumn and winter (Fig. 6.5). It appeared that within each season male and female somatic condition was similar (Fig. 6.5).

Figure 6.2: Size frequency distributions for each season at each region. The black arrows indicate differences between seasons within regions, while the red arrows are comparisons between east and south-east in spring. The direction of the arrow indicates where more (↑) or less (↓) individuals were observed than expected under the assumption that the size frequency was independent of season (black arrows) or region (open arrows). To adjust for the number of tests done using the same dataset P=0.008 was used as the critical probability.

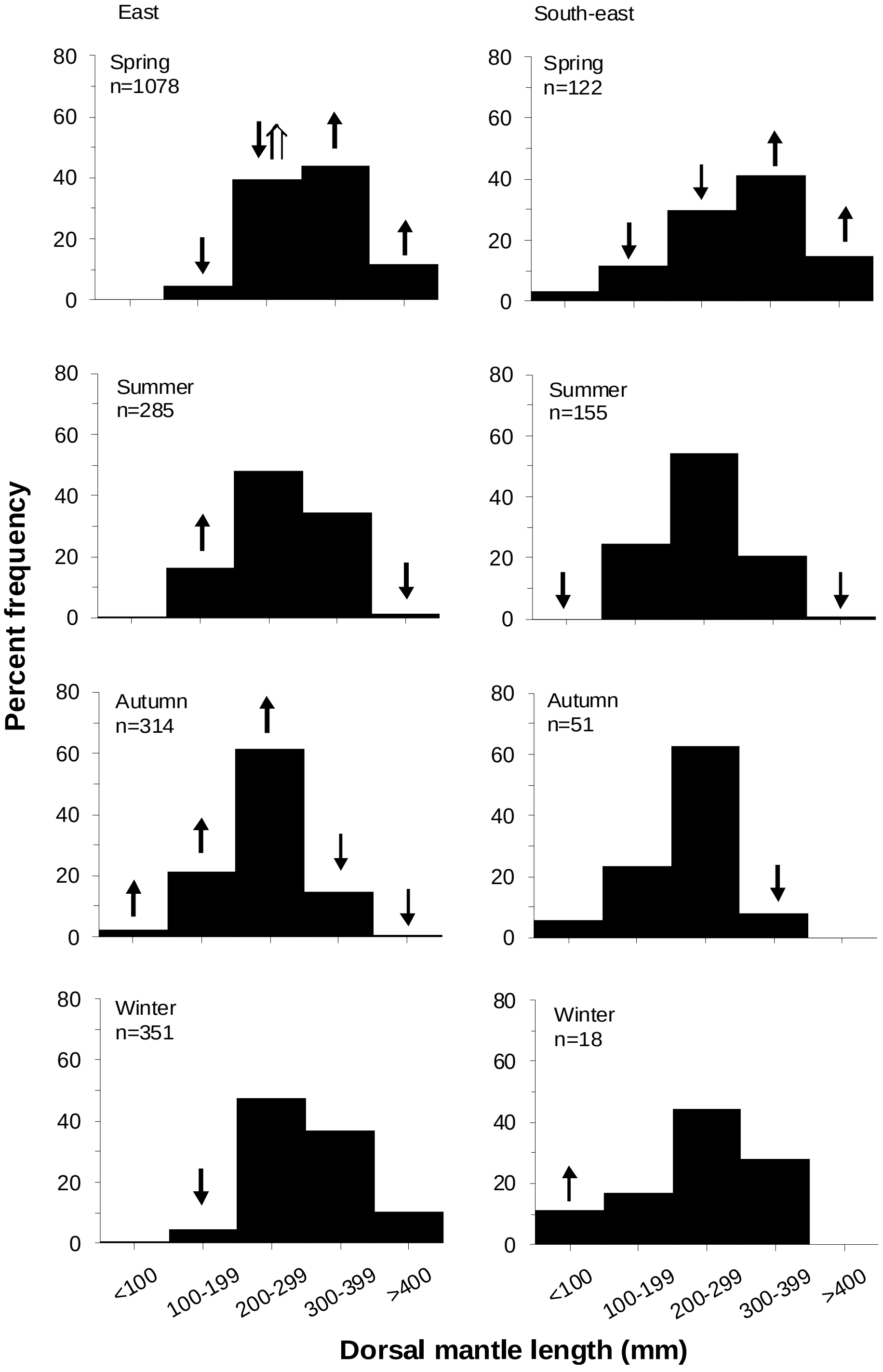


Figure 6.3: Size frequency distributions for each sex at each region. The black arrows indicate differences between sexes within regions, while the red arrows are comparisons between the regions within each sex. The direction of the arrow indicates where more (↑) or less (↓) individuals were observed than expected under the assumption that the size frequency was independent of gender (black arrows) or region (open arrows). To adjust for the number of tests done using the same dataset P=0.008 was used as the critical probability.

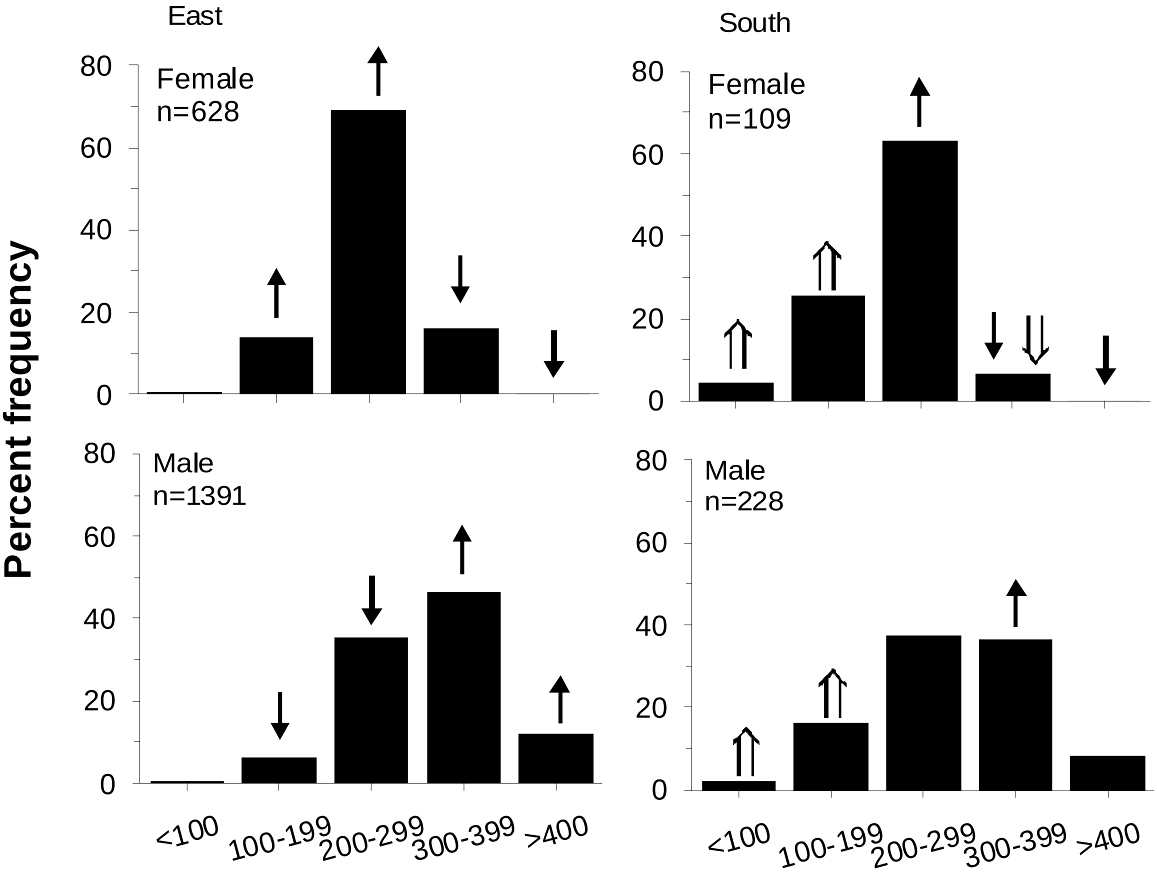


Figure 6.4: Percent frequency of females in each season and region. The values above each bar are the ratio of males to females. The direction of the arrow indicates where more (↑) or less (↓) females were found than expected under the assumption that the sex ratios were independent of season.

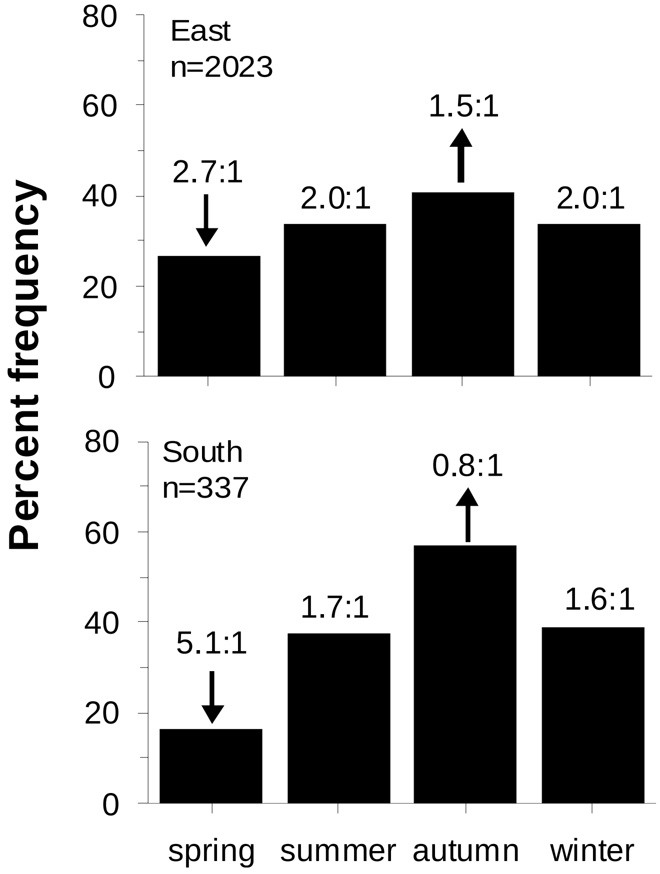
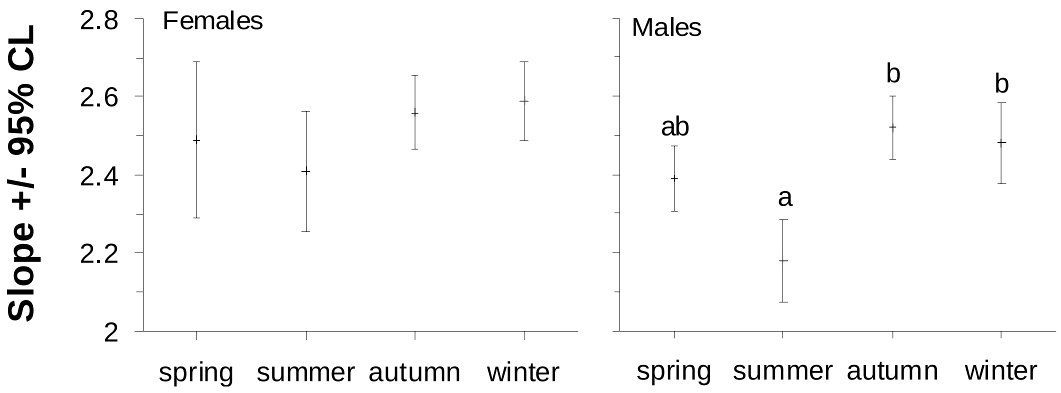


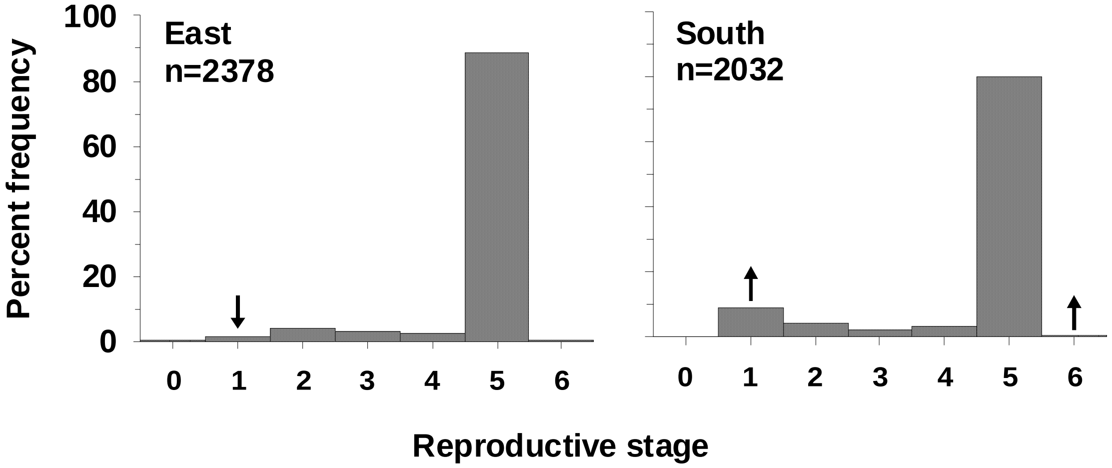
Figure 6.5: Slope of the length weight relationships for males and females across both regions and all seasons. Means with different letters for the males indicate seasons that are significantly different from one another.



Reproductive condition

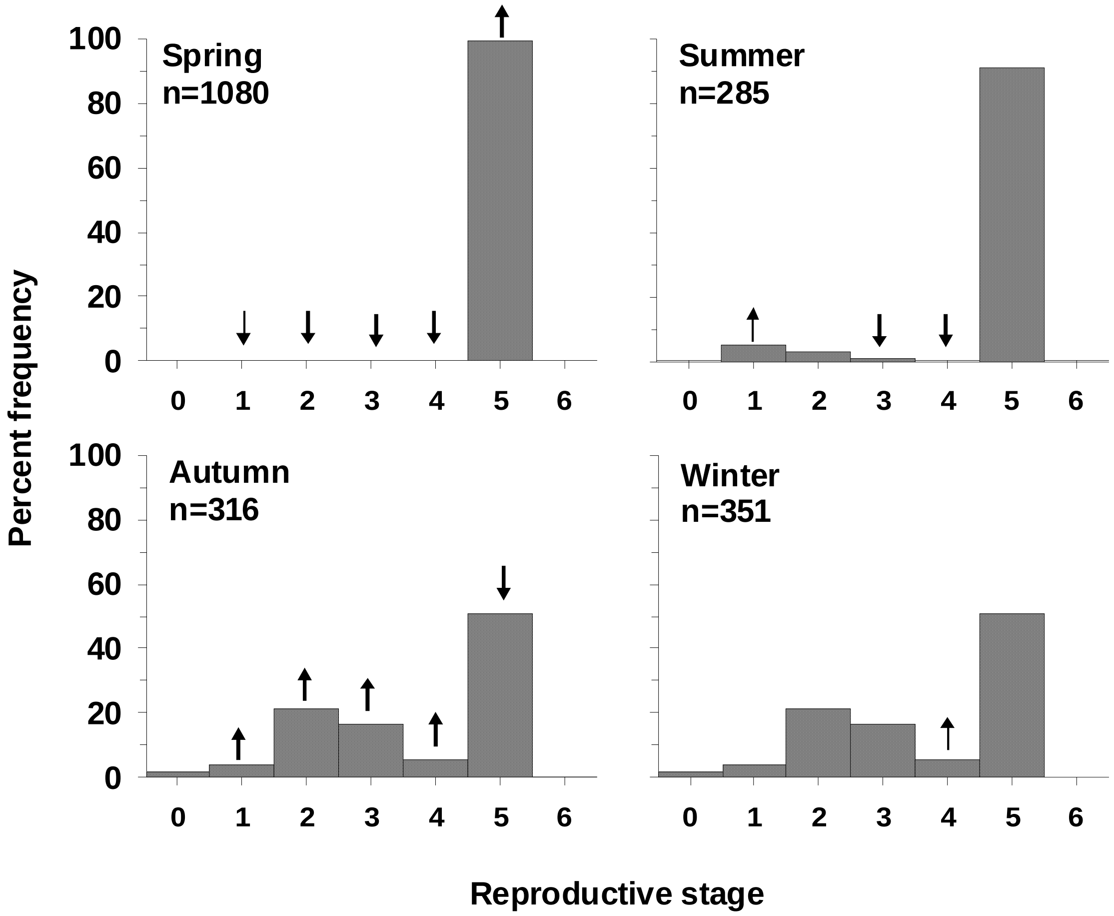
In both regions, across all seasons and both sexes, more than 80% of the individuals caught were reproductively mature (Stage 5), indicating that females had eggs in the oviduct ready to lay and males had spermatophores ready to be passed to the female (Fig. 6.6). There was a significant difference in the proportional of individuals at each stage between the regions (χ^2=78.54, df 6, P<0.001). This was due to the south-east having proportional more immature (Stage 1) and spent (Stage 6) individuals compared with the east coast (Fig. 6.6). At no time were spent females sampled despite the presence of spent males in the summer in both regions.

Figure 6.6: Percent frequency of males and females in maturity stages (0=immature – 6=spent), for the east and south-east regions of Tasmania for seasons combined. The direction of the arrow indicates where more (↑) or less (↓) individuals were found than expected under the assumption that stage of maturity was independent of region.



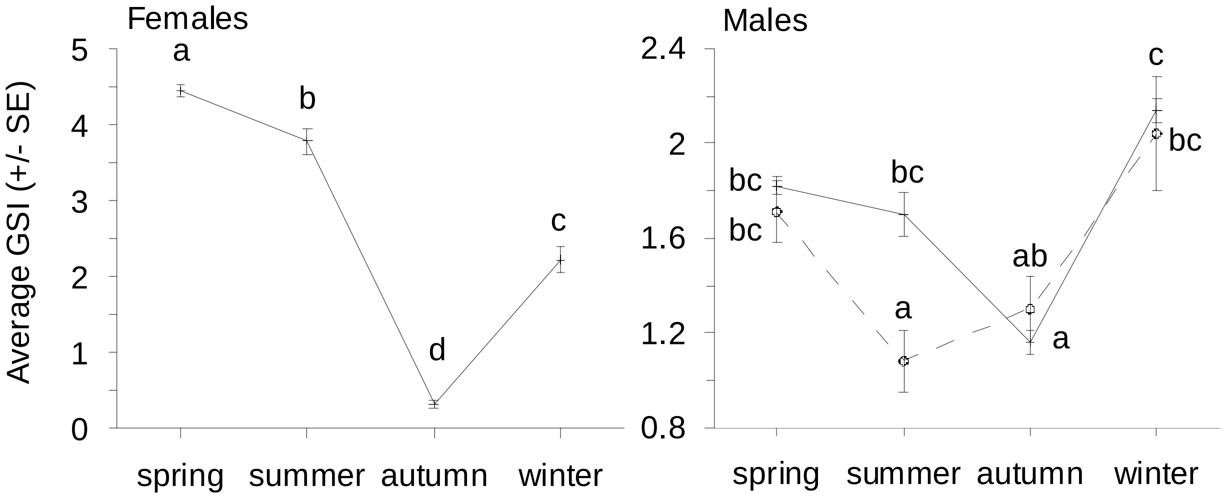
Comparisons of stage frequency distributions across seasons were only possible for the east coast. This was not due to low numbers of individuals from the south-east, but because there were low numbers in some seasons and stages, largely due to such high numbers of Stage 5 individuals. In the case of the east coast the juveniles (Stage 0) and spent (Stage 6) individuals were dropped from the analysis due to low numbers of individuals in these categories. There was a significant difference among the seasons in the frequency of individuals at each reproductive stage (χ^2=708.71, df12, P<0.001). It was evident that during the spring there were proportionally more mature individuals (Stage 5), with fewer individuals at all other maturity stages (Fig. 6.7). During the summer, although the proportion of mature individuals remained high, there were relatively more individuals that were immature (Stage 1). In contrast, during autumn, relatively fewer individuals were mature (Stage 5) and more were immature or in the earlier stages of reproductive maturity (Stages 1-4) (Fig. 6.7). The winter population had proportionally more individuals at Stage 4.

Figure 6.7: The percent frequency of individuals caught on the east coast at each reproductive stage for each season. The direction of the arrow indicates where more (↑) or less (↓) individuals were observed than expected under the assumption that the maturity stage was independent of season.



There were significant differences in the average gonosomatic index (GSI) in the population among the seasons. In the case of females the differences among the seasons (F_{season}=108.68, df 3,412, P<0.001) were consistent between the regions ($F_{region*season}$=1.71, df 3,412, P=0.164). The highest GSI was during the spring, with a decline during summer and autumn, and an increase in winter (Fig. 6.8). In contrast the nature of the difference in GSI among the seasons for males was different between the two regions ($F_{season*region}$=4.63, df3, 932, P=0.003). On the east coast, male GSI was similar among the season, with the only difference being between the autumn low and the winter high (Fig. 6.8). In comparison in the south-east of the state the lowest GSI was seen in summer and autumn, with the highest in winter and spring (Fig. 6.8).

Figure 6.8: Changes in gonosomatic index among the seasons for females across both regions and males for east (solid line) and south-east (dashed line)

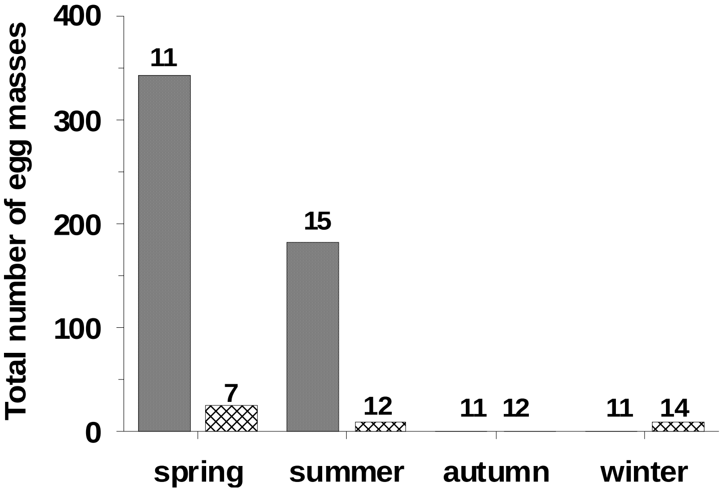


Egg Masses

Most of the egg masses were associated with shallow water (<6m) seagrass beds, with some attached to the holdfasts of deeper macroalgal species, and others either dislodged or partly buried in sandy sediments. The seagrass *Amphibolis antarctica* is the dominant shallow seagrass on the east coast of Tasmania, extending from Great Oyster Bay to the Mercury Passage (Edgar 2000), and the dominant substrate for egg deposition on the east coast. In the south-east of the state, where *A. antarctica* is largely absent, calamary eggs were attached to *Calurpa* and *Heterozosterous*. In deeper water (>6m) eggs were deposited on *Macrocystis, Sargassum,* and *Laminaria* macro-algae.

Egg masses were seen predominantly in the spring and summer at both sites. No egg masses were seen during the autumn months, and those counted in winter were only at one site in the south-east (Fig. 6.9). Spawning intensity, assessed using egg mass density, differed significantly between the two regions (F=4.59, df 1,102, P=0.035), but not among the six months (September-February) that egg masses were seen (F=0.77, df 5,102, P=0.577). The density of egg masses was more than three times greater on the east coast (mean=0.33 $20m^{-2}$, se=0.05, n=84) than in the south-east (mean=0.12 $20m^{-2}$, se=0.09, n=30). The failure to detect a difference among the months was due to the extreme variability in the density of egg masses among sites. Coefficients of variation were large, with variances of the egg mass density in the regions for each month ranging from 20-348% of the mean.

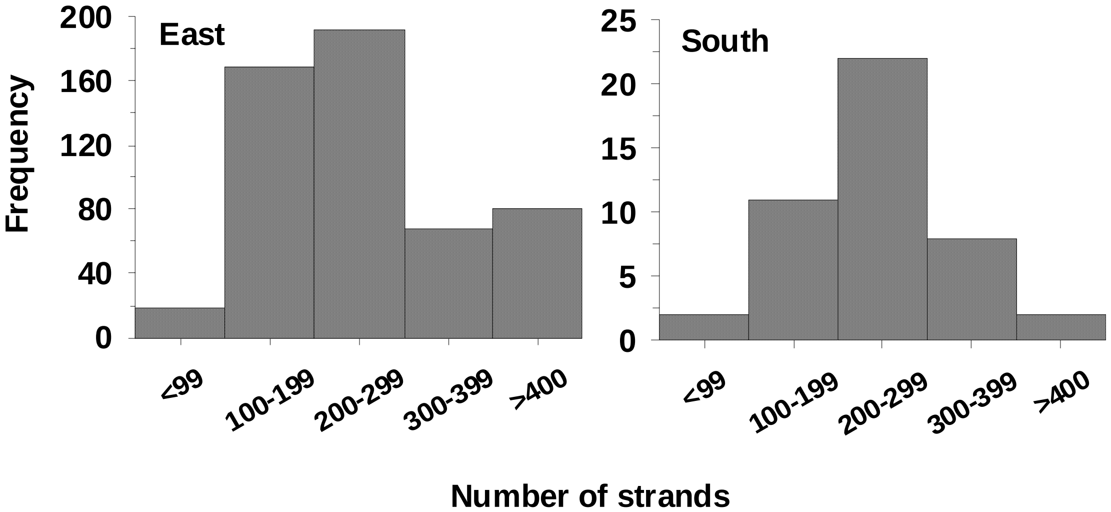
Figure 6.9: The total number of egg masses counted in the south-east and east coast for each season. The values above each bar are the number of sites surveyed. Stippled bars = east, and cross-hatched = south-east.



The size of the egg masses ranged from 3-1241 strands on the east coast and 10-619 strands in the south-east. However there was no significant difference in the size frequency distribution of the egg masses between the two regions (χ^2=6.69, df 4, P=0.153). Most of the egg masses at both regions had 200-299 strands (Fig. 6.10).

Approximately 10.2% of the embryos examined from both regions and across the spring/summer period (September-February) were dead. There was no difference in the proportion of dead embryos between the two regions (χ^2=0.01, df 1, P=0.982).

Figure 6.10: The size frequency distribution of egg masses measured in each region. Note the different scales on the y-axis.



Size at age

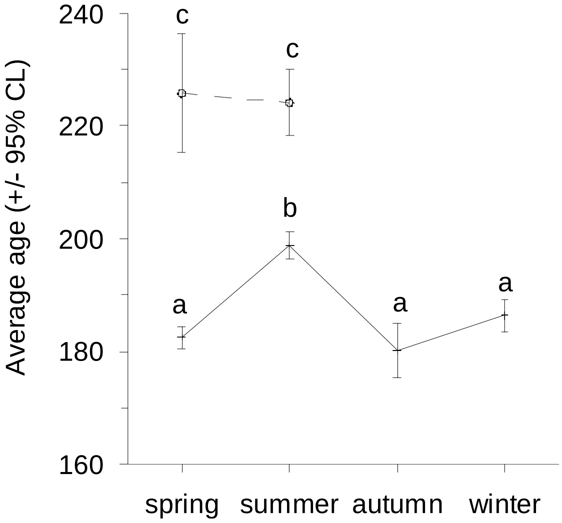
Size-at-age relationships were linear for many of the region-season combinations, and although weak, were all significant (Table 6.1). Although there was some evidence of a significant difference in the growth rates among the region-season combinations (F=7.65, df 5,590, P<0.001), the post-hoc test failed to detect where the difference occurred. Slowest growth was found for east coast populations in spring, while the fastest was the southern spring population (Table 6.1).

Table 6.1: Linear size-at-age relationships for each combination of region and season. The slope refers to the slope of the linear regression calculated using least squares.

Region		Slope	SE slope	r^2	F	df	P
East	Spring	0.017	0.004	0.11	23.03	1,192	<0.001
	Summer	0.050	0.008	0.22	35.77	1,130	<0.001
	Autumn	0.044	0.011	0.16	15.55	1,84	<0.001
	Winter	0.033	0.005	0.31	45.81	1,100	<0.001
South-east	Spring	0.057	0.008	0.49	52.43	1,52	<0.001
	Summer	0.047	0.01	0.42	23.01	1,32	<0.001

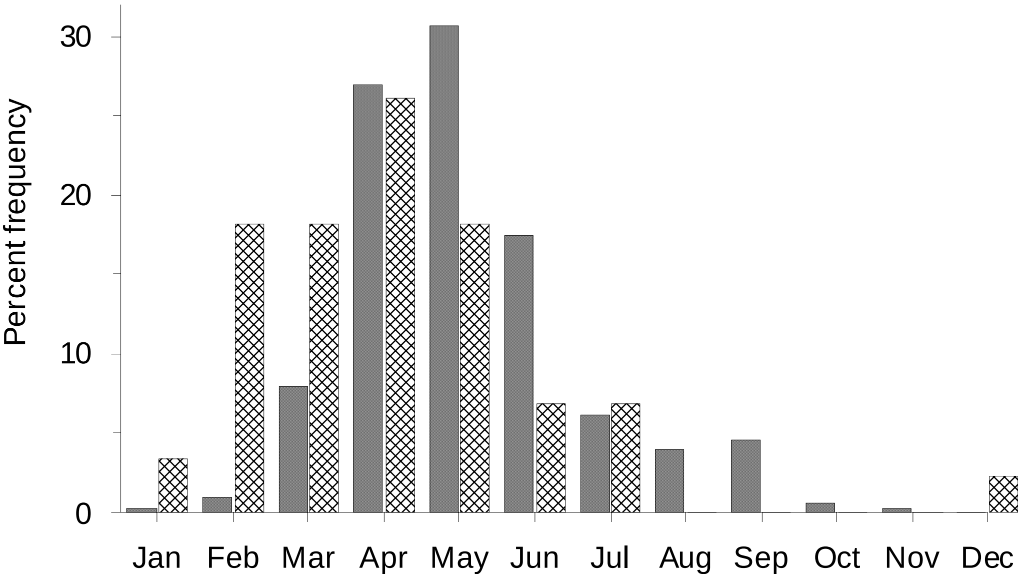
Given the dominance of reproductively mature animals found in both regions, a comparison of the average age of Stage 5 individuals was completed and found that the average age among the regions depended on season (F=4.33, df 5, 498, P <0.001). In both spring and summer the average age of southern individuals was c. 225 days (Fig. 6.11). In contrast the east coast individuals were c. 15-20% younger than the southern individuals. There was a difference in the average age of the mature individuals among the seasons on the east coast, with summer individuals as much as 7% older than individuals in the other seasons (Fig. 6.11).

Figure 6.11: The average age of all Stage 5 (mature) individuals in each combination of region and season. East = solid line and south-east = dashed line. Age in days on y-axis



The birth month of individuals caught in spring and summer were compared between the two regions. In the east there were proportionally fewer individuals born in March, while in the south-east proportionally more individuals were born in the summer months (December-February), but fewer in June (Fig. 6.12, χ^2=83.90, df 11, P<0.001).

Figure 6.12: The percent frequency of spring and summer aged individuals born in each month, from the east (stippled bars) and south-east (cross-hatched bars).



Gear Comparisons

To determine if there were differences in the size of animals targeted by different commercial fishing gears, comparisons in average DML were made between gears where animals were caught in the same month (Table 6.2).

There was no evidence of a difference in the average size between those animals caught with jig and spear, and between jig and purse-seine, or in the size frequency distribution of animals caught between jig and spear (Table 6.2). However, in the month when a comparison was made between jig and dip net, there was evidence that dip-netting caught on average larger squid (Table 6.2).

Table 6.2: Comparison of average DML and DML size frequency between gear types. All comparisons between gear types were made using samples caught on the east coast by commercial fishers. The t-test compared the average size of the animals, while the $\chi 2$ test compared the size frequency distribution.

Comparison	Month	*t*-statistic, df, P<t	χ^2-statistic, df, P<χ^2
Jig vs. Purse-seine	Nov ’99	1.99, 43, 0.053	insufficient data
Jig vs. Spear	Jun ’01	1.81, 119, 0.073	3.86, 3, 0.336
Jig vs. Spear	Aug ’01	0.33, 54, 0.747	insufficient data
Jig vs. Dip net	Apr ’00	7.59, 70, <0.001	38.15, 3, <0.001

In two comparisons of sex ratios between the gear types, it was found that there was no difference between jigging and spearing (χ^2=2.24, df 1, P=0.134; χ^2=1.46, df 1, P=0.227). On another occasion of purse seining and jigging by the same fisher on the same day at the same location, all squid caught were females. In contrast there was a difference in the sex ratios between jigging and dip netting (χ^2=16.85, df 1, P<0.001). During this month jigging caught no females, whilst the sex ratio of females to males caught by the dip-nets was 1:1.1.

Overall landings and effort were highest on the east coast, largely as a function of the spring landings (Fig. 6.13). The southern region had greatest catches and fishing effort during spring (Fig. 6.13). In a comparison of the two regions, only in autumn (in all years) and summer 2000/01 were greater landings recorded in the south-east autumn. On the east coast there was a distinct seasonal trend in catch and effort, with most occurring in the spring. Landings were as much as six times lower in the other seasons, and effort was five times lower (Fig. 6.13). In contrast, the seasonal changes in the south-east were less dramatic, although catches and effort was also greatest in the spring (Fig. 6.13). CPUE as a measure of abundance suggested that the biomass of squid was greater on the east coast in all seasons compared with the south-east, except for autumn 2000 and 2001, when the values were similar between the two regions. The southern biomass appeared to be relatively similar in all seasons, although as with the east coast, abundance appeared highest in spring

On the east coast most of the squid are landed by squid jigs, and in some cases this is 100% of the catch (Fig. 6.14). Minor components are taken by different methods in different seasons. The most notable is the increased proportion of catch taken by dip-nets during the autumn, a pattern consistent in all years, but most dramatic in 2000, when dip-net landings exceeded landings by jigs (Fig. 6.14). In the south-east in most seasons jigging was the dominant landing method, except for both the winters when dip nets, purse-seine, and spears were used extensively (Fig. 6.14). In contrast to the east, both spears and dip-nets were used extensively in the south-east in all seasons.

Figure 6.13: Total catch, effort and CPUE for each season from spring 1999 to winter 2002 on the east coast (solid bars) and south-east (stippled bars).

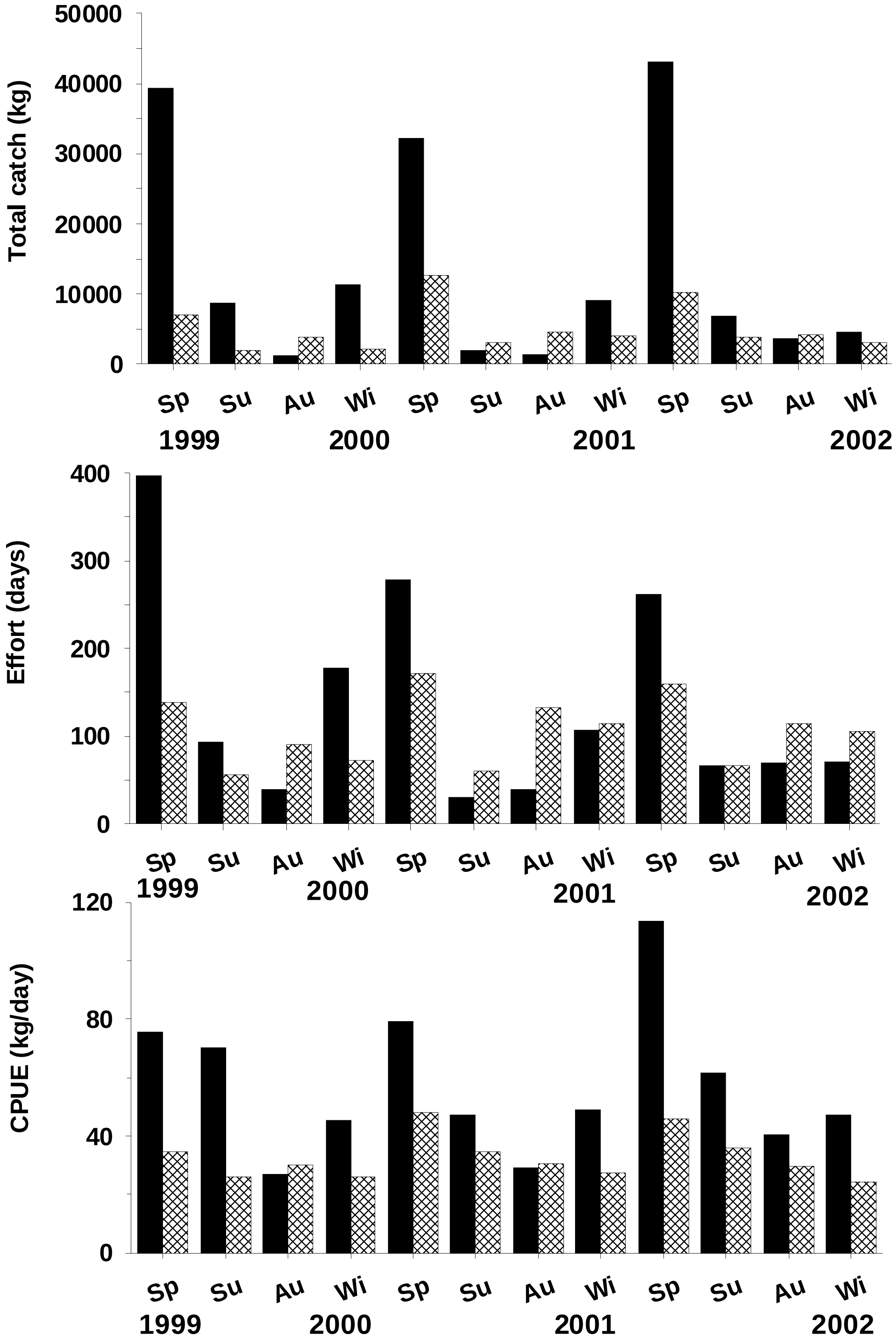
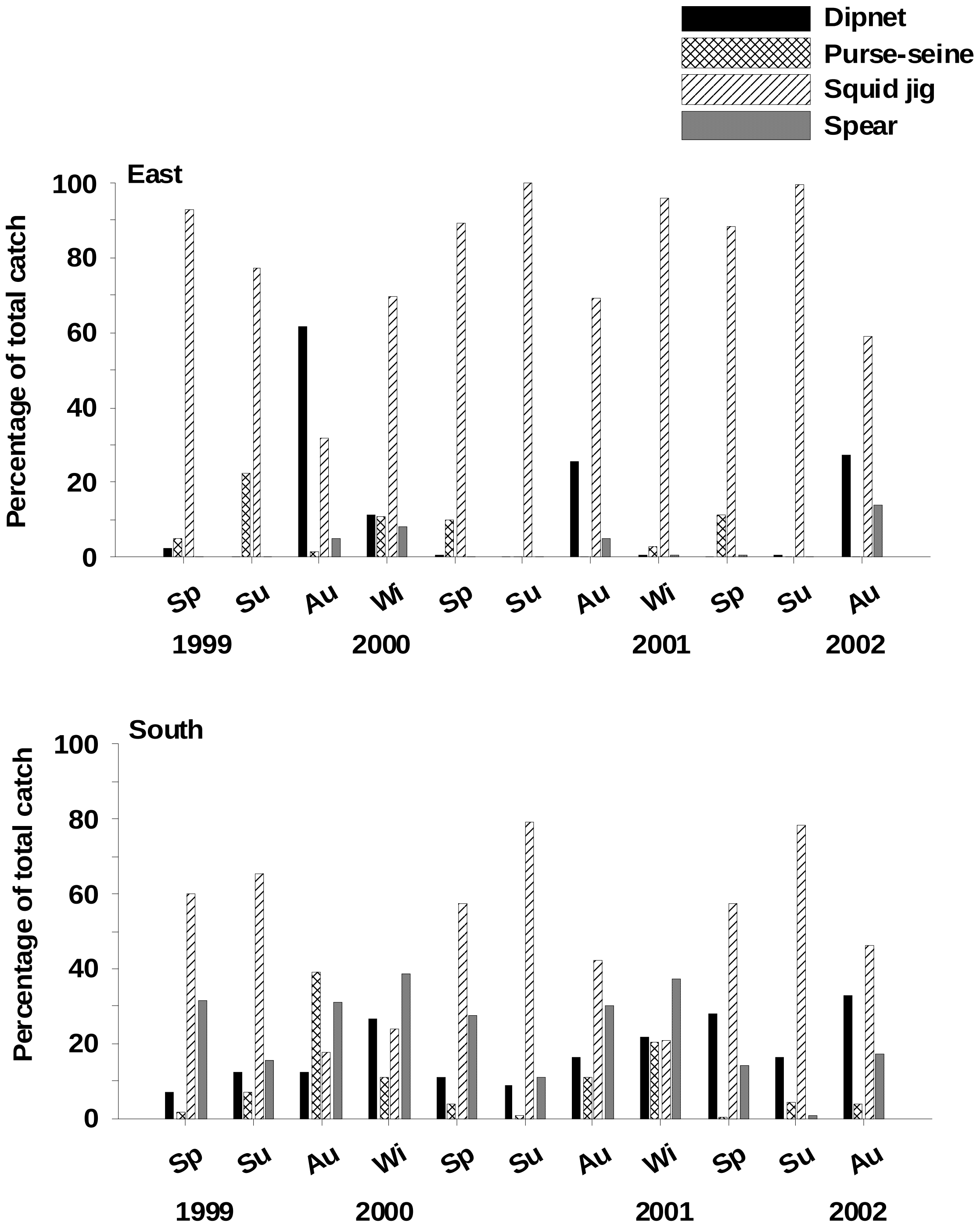


Figure 6.14: The breakdown of the landings for 1999-2001 by method for the east coast and south-east, in each season.



Discussion

The inshore populations of southern calamary show a consistent spatial and temporal trend of high gono-somatic index, high levels of reproductive output and large body size during the spring and early summer. During the autumn and winter there was little evidence of high levels of reproductive activity, based on low GSI and few egg masses observed inshore, although most animals caught in autumn and winter are reproductively mature. Yet these individuals in the spring/summer spawning were largely hatched during autumn. The populations in the south-east of the state appeared to be slower growing, with generally smaller and older individuals being caught. Interestingly this was a characteristic of summer caught individuals on the east coast (Chapter 5). Given those individuals that hatch out in January and February were likely to have been from eggs deposited some six weeks earlier, animals from the south-east were approaching an annual lifecycle. However, there is limited evidence to support the hypothesis of a single cohort, or even two cohorts as seen in other species (eg *Loligo gahi* Patterson 1988). Southern calamary in the eastern and southern populations largely targeted by the fishery are the product of extended spawning, during late summer and autumn.

Uneven sex ratios, particularly in favour of the males, have been observed in *L. vulgaris reynauldii* (Augustyn 1990). There is evidence that selectivity of jigging may cause bias in the reported sex ratios (Lipinski 1994), however, there is no evidence of this for southern calamary (this chapter). Therefore, we concluded that males are more abundant in the population than females, although the ratios vary seasonally and spatially. There are two possible reasons for the dominance of males in the populations. Females may have lower survivorship, possibly related to their smaller size. Alternatively, females may spend much of their time elsewhere, perhaps in deeper water, and the time spent in spawning areas is relatively short compared with males. It is unlikely that fewer females are born as sex ratios in captivity tend to be equal (Walsh et al 2002). *Loligo forbesi* populations during the spawning season in English Channel are comprised of up to 70% females (Holme 1974). However, this species displays spatial and temporal variations in sex ratios, with either the sexes in equal proportion, or females slightly more common than males (Boyle & Ngoile 1993). The dominance of males in loliginid spawning aggregations is not seen in teleosts, instead males move into the spawning area before the females, and the later arrival of the females reduces this dominance (eg Samoilys 1997, Rhodes & Sadovy 2002).

The significance of a male dominated population is unclear, although the competition among males for mates will be a dominant aspect to the behaviour on the grounds (Hanlon 1998). The importance of males in the spawning aggregation is difficult to assess given that females can store sperm for an undetermined period of time and the high GSI of males during winter suggests they may have mated with females before arriving on the spawning beds. The presence of eggs is an important cue for female ovipositing (Arnold 1962) and the increase in agnostic behaviour of males (King *et al.* 1999). Therefore, it is possible that the population structure and biomass of animals on the spawning beds is influenced by the amount of eggs present. Understanding the relationship between paternities and mating systems will be important to recognising how changes in population structure may influence the genetic structure of the next generation. It has been suggested that the mating systems of species such as *L. pealeii* and *L. vulgaris reynaudii*, may generate genetic diversity.

In the spring when densities were higher and bigger individuals were present, there were proportionally greater numbers of larger egg masses present than in other months. There is an ephemeral use of the spawning areas between months and years and it is not clear what cues the females use to attach egg strands in certain areas (Chapter 1). It is likely that visual cues are important and hence females may add eggs to an existing egg mass. Therefore, when there are higher densities of females, the addition of egg stands to existing egg masses maybe more prevalent than when individuals are at lower densities. It is also possible that large females with relatively larger ovaries may produce bigger batches of eggs and hence deposit more egg strands in an egg mass. However, larger egg masses suffer higher rates of embryo mortality Steer (unpub data), suggesting that this strategy may not be beneficial, but driven by the behaviour of the spawning animals.

It is possible the greater CPUE in the east may be a function of the well known and very predictable nature of the spawning aggregations in this region. The intensity of egg mass deposition seen in the east was not evident in the south-east. Along the southern coast occasionally high densities of egg masses were seen in localised areas, although these were not as temporally stable as the spawning seen in the east. However, during the spring the southern individuals were reproductively mature and had a high GSI, suggesting that egg deposition should be occurring. However, it is possible that unlike the eastern populations animals in the south-east do not form large spawning aggregations, and instead there is isolated low density deposition of egg masses spread over a broader spatial area. The biological significance of this is unclear, particularly with respect to understanding the mechanisms that drive the development of spawning aggregations, eg presence of egg masses encouraging further egg deposition. From a fishery management perspective concerns about targeting the spawning aggregations in the south-east may not be such an issue.

Estimates of abundance using CPUE with species that display aggregative behaviour and where those aggregations are targeted is problematic because depletion of the aggregation may not be occurring as new individuals move into the area (Carvelho & Nigmatullin 1998). Therefore, depletion of stocks may occur at a larger spatial scale than the CPUE is estimating. This poses problems for management; on one hand new individuals are moving into the aggregation and this is a short-lived species which is likely to suffer natural mortality after spawning. Given the flexibility of the mating system targeted fishing should then have limited effects on gene mixing and production of young (Hanlon 1998). On the other hand, depletion rates cannot be accurately estimated and constant interruption of the egg deposition process by fishing will ultimately compromise recruitment of the next generation. Also if east are aggregating and south-east not, our CPUE estimates may mean different things on a regional basis.

The comparison of the squid caught by jig versus other methods is not comprehensive, and given variability in the populations of squid targeted is not a definitive comparison. The use of a particular type of gear is a function of the licence held by the fisher and the fishing conditions. At certain times the squid will not take a jig, or they may come around a light when it is easier to dip-net or spear the animals. Dip-netting and spearing are primarily conducted at night, therefore the differences in population characteristics of animals using the beds day vs. night are different, and not a function of gear type. However, the differences in methods used on the south-east and east coast maybe further evidence that large spawning aggregations do not occur in the south-east, possibly a function of some feature of the habitat that is not conducive to aggregative spawning behaviour. This also means that state-wide restrictions on fishing methods and closures maybe difficult to implement.

We recommend that the density of newly deposited eggs may provide a fishery independent measure of recruitment potential that accommodates differences and changes in the size and fecundity of females in the population. Measures of egg production may provide the most direct assessment of future population size. Additionally, embryo mortality rates are typically c. 10%, and it is predicted that juvenile mortality rates will be low relative to fish. Therefore, egg deposition rates could potentially provide a reasonably accurate estimate of future recruitment. However, southern calamary appear to display inter-generational differences in aggregative behaviour associated with egg deposition, with spawning aggregations and egg production in the inshore areas of the east and south-east coast of Tasmania only occurring during the spring/early summer period (Chapter 1). Based on age estimates, the adults in these spawning aggregations are the product of spawning activity from the previous autumn/early winter. Therefore, either this spawning event is occurring in inshore waters but is non-aggregative, or spawning is occurring in areas that have not been surveyed. Anecdotal information from fishers suggests that eggs have been seen and trawled from deeper waters (ca 20 m), however the recent absence of trawling and dredge fishing operations in most of Tasmania makes it difficult to determine if spawning still occurs in deeper habitats.

Given the short lifespan of southern calamary there is the need to ensure successful production of offspring from every generation regardless of environmental conditions. To do this, populations need to maintain variability in biological characteristics so that some component of the population can survive the environmental conditions experienced. Regardless of the differences in life history strategies among southern calamary stocks there may be a need to provide protection from over-fishing for both stocks. However, given the differences it is also possible that regional management strategies based on the biological characteristics and the fishing methods employed may need to be implemented.

Chapter 7: Description and assessment of the Tasmanian southern calamary fishery

(Authors: JM Lyle and M Haddon)

Background

Southern calamary represent a significant component of the Tasmanian scalefish fishery, as well as being of importance to recreational fishers. Over the past five years commercial catches have fluctuated between c. 75-100 tonnes per annum with 2002/03 landings valued at around $0.8m, ranking it amongst the top three species (by value) taken in the scalefish fishery. Southern calamary also support significant commercial and recreational fisheries in South Australia (Triantafillos 1998) and Victoria (Anon 2002).

Management context

Management strategy

In Tasmania, southern calamary are managed under the Scalefish Fishery Management Plan, implemented in late 1998 (DPIF 1998) and subsequently reviewed in 2001. The management plan effectively defines the level of access to most scalefish species, including southern calamary, through a licensing system based on gear allocation for gillnets, hooks, and fish traps. Specialised fishing methods such as beach and purse seine are licensed separately while all holders of scalefish licences, along with Tasmanian Rock Lobster licence-holders, have access to squid jigs, dip nets, and spears.

A dramatic rise in southern calamary catches, from historic levels of < 20 tonnes to almost 100 tonnes in 1998/99, prompted a warning in August 1999 by the Minister for Primary Industries, Water and Environment that management arrangements for southern calamary were under review and future restrictions on catch, effort, and numbers of operators accessing the resource may need to be introduced. In addition, two 2-week-long closures of Great Oyster Bay to fishing for southern calamary were implemented during the peak spawning season between October and December 1999 as a precautionary measure to protect egg production. In 2000 the closures were extended to three 2-week closures and back to two in 2001. In 2002 closures two 2-week closures were continued and spatially extended to include adjacent fishing grounds in Mercury Passage.

Growing markets for the species, coupled with the increasing use of squid jigs by fishers, contributed to the expansion in the fishery. In effect, there are presently about 670 licence holders entitled to fish for southern calamary in Tasmania and, apart from a combined possession limit of 30 southern calamary and arrow squid for holders of Scalefish C licences[3] introduced in November 2001, there are no regulated restrictions on the size of the catch. The possession limit was introduced specifically to limit further expansion of the fishery. Also in November 2001 a daily bag for recreational fishers was introduced with a limit of 20 ‘squid’ (southern calamary and/or arrow squid) and a possession limit of 30 squid.

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[3] In Tasmania there are more than one type of scalefish fishing licence available (*viz* Classes A, B, and C), the most restrictive (in terms of gear allocation) and most numerous of these is the class C licence.

Performance Indicators

In the absence of more quantitatively rigorous stock assessments, the Scalefish Fishery Management Plan includes a number of performance indicators that are applied generically to the fishery and specifically at the species level. For southern calamary fishery performance is measured by reference to:

- variations in the total catch from year to year, or between seasons, regions, and sectors;
- trends in effort;
- trends in catch rates;
- changes in biological characteristics, such as a changes in size or age structure; and
- other indicators of fish stock stress, e.g. disease outbreaks.

As part of this strategy, trigger points have been defined as levels of, or rates of change, that are considered to be outside the normal variation of the stock(s) and the fishery. The trigger points provide a framework against which the performance of the fishery can be assessed and (if necessary) flag the need for management action. Trigger points for southern calamary are reached when one or more of the following criteria are met:

- commercial catch is outside of the 1990 to 1997 range, or, when total catch declines or increases in one year by more than 30% over the previous year;
- targeted fishing effort is at least 10% greater than the highest level for the period 1995 to 1997;
- catch per unit effort (CPUE) is less than 80% of the lowest annual value for the period 1995 to 1997;
- there is a significant change in the size composition of commercial catches or a significant change in the abundance of a year class, with particular importance on pre-recruit abundance;
- significant numbers of southern calamary are landed in a diseased or clearly unhealthy condition; or when,
- any other indication of fish stock stress is observed.

It is in this context that previous assessments for southern calamary in Tasmania have been undertaken (e.g. Lyle and Hodgson 2002). These performance indicators are applied generically for all scalefish species but they may not necessarily meaningful for calamary. For example, the fourth performance indicator speaks of year classes and pre-recruit abundance, which in a sub-annual species such as calamary is not useful. Being placed in a Management Plan, means, however, that revising them may not be a trivial matter.

Data sources

Commercial Fishery

Commercial catch and effort data are based on Tasmanian General Fishing Returns. Catch returns prior to 1995 provided monthly summaries of catches (landings), but were often incomplete or very limited in terms of providing effort information. Lennon (1998) discussed limitations of these catch returns in some detail and, in summary, noted that they provided only basic information about production levels and are of little value for effort and catch rate analyses.

During 1995, a revised General Fishing Return was introduced, replacing the monthly return with catch and effort information reported on a daily basis for each fishing method used. The revised returns provide greater detail about fishing operations, including more explicit specification of fishing method, greater spatial resolution (½ degree rather than 1 degree blocks), plus details about effort and depths fished. Recent amendments (1999) to the catch returns include provision for fishers to nominate target species. Notwithstanding these improvements, catch returns are not validated or verified against catch disposal records or processor returns.

Catch information from 1980 has been compiled for the purposes of this report while effort and catch rate analyses are restricted to data provided for the period July 1995 to February 2003[4]. A fishing year, from July to the following June has been defined for annual reporting, the primary justification being that this period reflects the seasonality of the fishery along with key biological processes, including the timing of the major spawning activity (Chapter 2).

Two measures of effort have been examined: (i) days fished (i.e. number of days on which southern calamary were caught); and (ii) for squid jigs, number of jig hours fished. Since catch rate data are typically log-normally distributed the arithmetic mean does not accurately describe the data (see Fig. 7.16). Thus, in generating catch rate statistics, the geometric mean of all valid individual daily catch records has been calculated. The geometric mean is calculated as the *n*th root of the product of the scores (y_i):

$$GM_{\bar{y}} = \sqrt[n]{\prod y_i}$$

This is equivalent to computing the arithmetic mean of the natural-logarithm transformed catch rate, and then back-transforming by taking the exponent:

$$GM_{\bar{y}} = \exp\left[\frac{1}{n}\left(\sum \ln\left(y_n\right)\right)\right]$$

It should be noted that catch rates calculated in this manner do differ slightly from the more simplistic approach of dividing total catch by total effort or using the arithmetic mean of all catch records.

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[4] All General Fishing returns available as at April 2003 have been incorporated into the analyses.

Recreational fishery

Estimates of recreational catch are based on the results of a national survey of recreational fishing that was undertaken during 2000/01 (Lyle *et al.* in press).

Catch, effort and catch rates

State-wide overview

During the latter half of the 1990s there was a marked expansion in the fishery for calamary in Tasmania, with catches rising from < 20 tonnes p.a. prior to 1995/96 to c. 90 tonnes in 1998/99, accompanied by a trebling of effort (Fig. 7.1). Subsequent catches have fluctuated between about 75 tonnes and a peak of 103 tonnes in 2001/02. Increased fishing effort has been the result of an expansion in the number of operators catching calamary, from around 30 in 1995/96 to over 70 since 1998/99 (Fig. 7.2). Furthermore, based on catches taken by the top ten operators (ranked on catch) in each year, it is evident that the quantities taken by this group more than doubled with the expansion of the fishery (Fig. 7.2). The fact that just ten operators have consistently taken a disproportionate share of the catch also indicates that many fishers participate in this fishery on a part-time or casual basis, either targeting the species opportunistically or taking incidental catches. As such, there would appear to be considerable latent effort amongst current participants, in addition to potential for new participants to enter the fishery (a consequence of the scalefish licensing system).

Southern calamary are taken by a variety of gear types including purse seine, beach seine, squid jig, spear, and dip net, with squid jigs the primary capture method in recent years (Fig. 7.3). In 2002/03 around 87% of the total catch was taken using jigs. Although some night fishing occurs, jig fishing is generally conducted during the day over shallow areas of seagrass and macro-algae to target squid concentrated on these beds.

Figure 7.1: Annual catch (tonnes) and effort (fisher days) for the Tasmania southern calamary fishery since 1980/81.

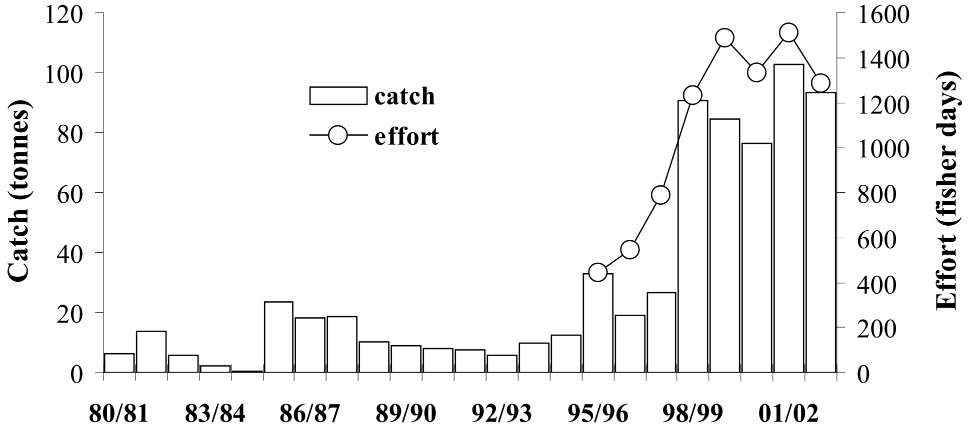
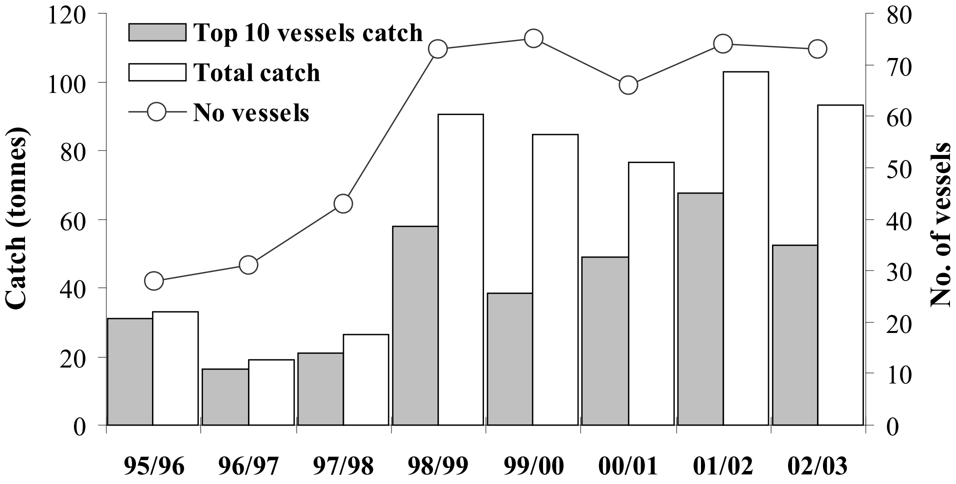


Figure 7.2: Number of vessels reporting southern calamary catches, catch taken by the top ten vessels (ranked on reported annual catches) and total catch by year for the period 1995/96 – 2002/03.



Since 1995/96, there has been a marked shift from seine nets to the use of jigs in the calamary fishery. Seine nets (principally purse seine) initially accounted for over two thirds of the catch but increased jig effort in 1998/99 produced the sharp rise in catches observed in that season (Fig. 7.3). Seine net catches gradually declined, from over 20 tonnes in 1995/96 to less than 10 tonnes in each year since 1999/2000. Purse seines currently account for only a minor proportion (< 40%) of the seine catch of calamary, the balance being mainly by-product taken in beach seines. The introduction of a limited entry purse seine fishery with the implementation of the Scalefish Management Plan, along with increased acceptance of jigs and competition on the fishing grounds has contributed to the decline in purse seine activity. Since 1998/99 jig catches have fluctuated between 55 and 81 tonnes p.a., representing over 70% of the total landings in each year.

Southern calamary are also taken by dip nets, generally as a by-product of fishing for garfish, or targeted with spears at night. Combined catches from these methods have ranged between about 5 - 14 tonnes p.a. since the mid-1990s.

The Tasmanian calamary fishery is highly seasonal, with greatest catches taken from late winter to early summer, with catches and catch rates peaking between September and November (Fig. 7.4). Fishing for calamary does continue throughout the remainder of the year but catches and catch rates tend to be low.

Figure 7.3: Annual catch of southern calamary in Tasmania by method for the period 1995/96 – 2000/03.

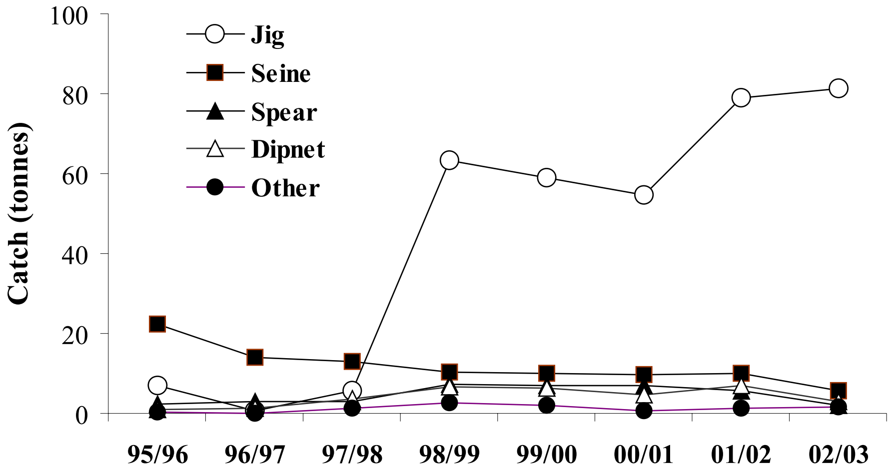
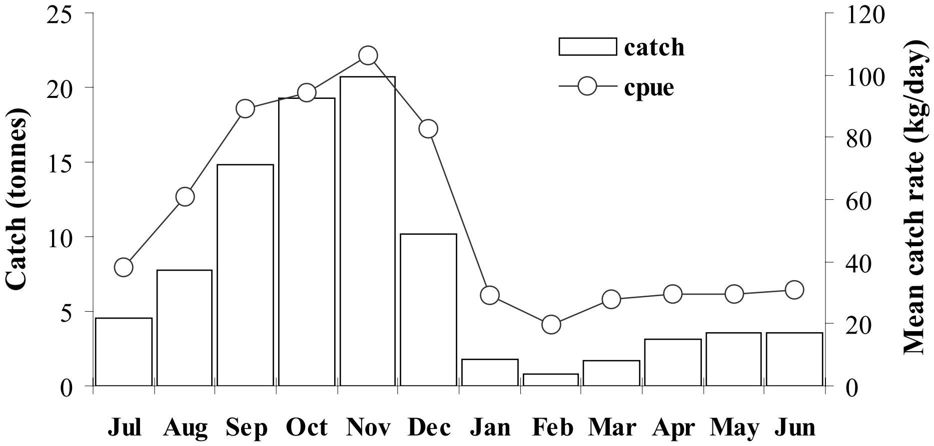


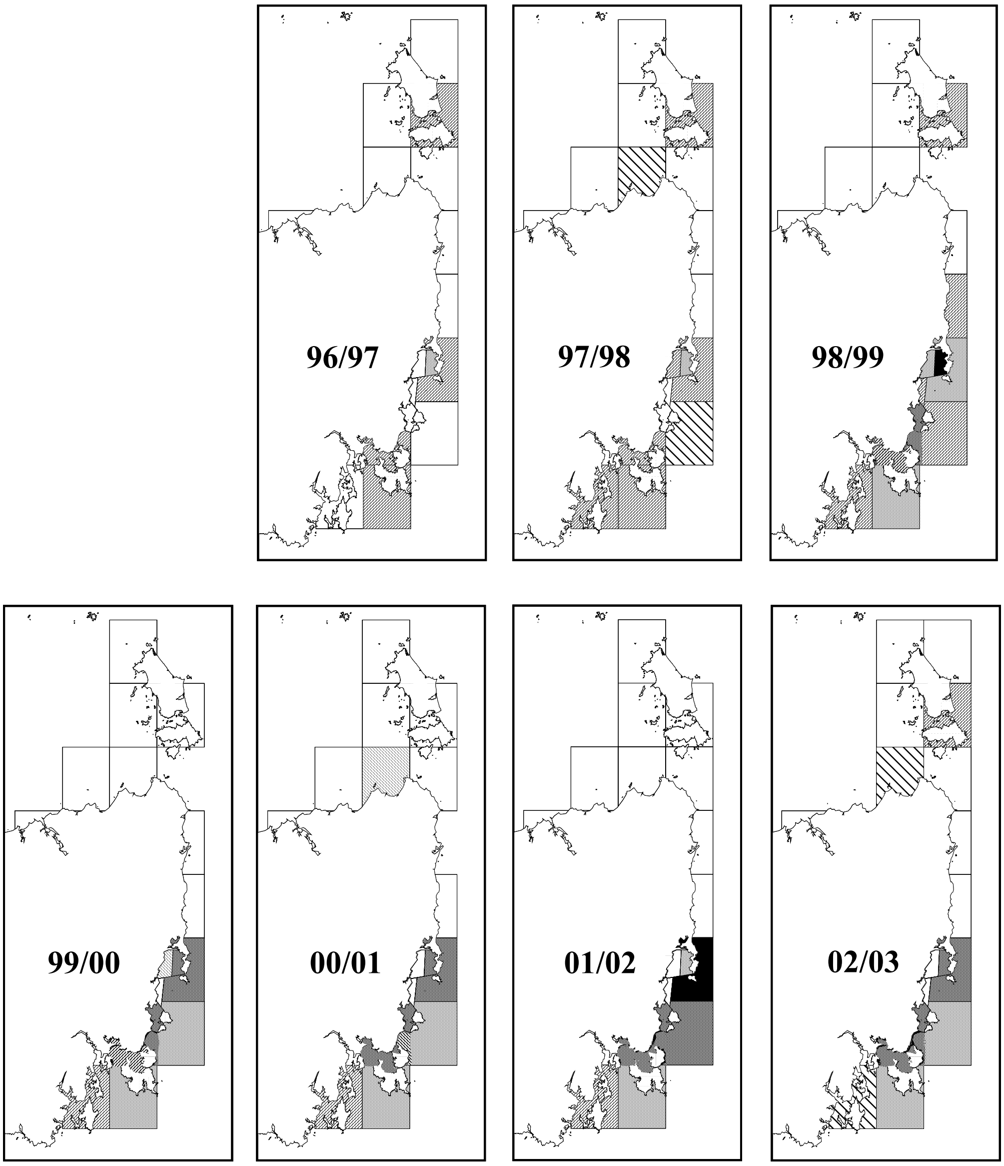
Figure 7.4: Mean monthly catch (tonnes) and mean monthly catch rate (kg per day) for southern calamary based on the period 1998/99- 2002/03.



Regional analyses

Southern calamary are taken commercially along the north and east coasts of Tasmania and off Flinders Island, with the catches concentrated off the east coast between Great Oyster Bay and the Tasman Peninsula, including Norfolk and Frederick Henry Bays. The development of the fishery is clearly evident in Fig. 7.5, with the initial expansion of catches in 1998/99 occurring in the eastern side of Great Oyster Bay (incorporating Coles Bay) and then subsequently expanding to other areas to the south.

Figure 7.5: Total catch of southern calamary by fishing year and grids for the period 1996/97 to 2002/03 (based on General Fishing Returns). Data are not shown where less than five boats reported catches.



Key

□ < 5 vessels

▧ < 1 tonne

▨ 1-5 tonnes

░ 5-10 tonnes

▒ 10-20 tonnes

■ > 20 tonnes

To facilitate spatial analyses, the main fishery off the east coast has been split into four major regions, North East Tasmania (NE), Great Oyster Bay (GOB), Mercury Passage (MP) and South East Tasmania (SE) (including Tasman Peninsula, Frederick Henry and Norfolk Bays) (Fig. 7.6).

The calamary fishery was centred initially in Great Oyster Bay, based on spawning aggregations, and up until 1998/99 this region accounted for over half of the state-wide catch (Fig. 7.7). As the fishery developed, catches in each of the main regions, apart from the North East, increased though since 1999/2000 the Great Oyster Bay fishery has stabilised at around 30 tonnes p.a. By contrast, Mercury Passage catches continued to rise, reaching an historic high of 40 tonnes in 2002/03. Catches from the South East rose steadily to about 23 tonnes in 2000/01 and again in 2001/02, but fell to just 13 tonnes in 2002/03. The introduction of short-term closures in Great Oyster Bay during the peak catching period each year since 1999 has been a significant factor in contributing to the stability in catches in that region whilst encouraging expansion into other areas such as Mercury Passage.

Figure 7.6: Map of the eastern half of Tasmania showing fishing regions used in data analysis. NE – North East Tasmania, GOB – Great Oyster Bay, MP – Mercury Passage, SE – South East Tasmania.

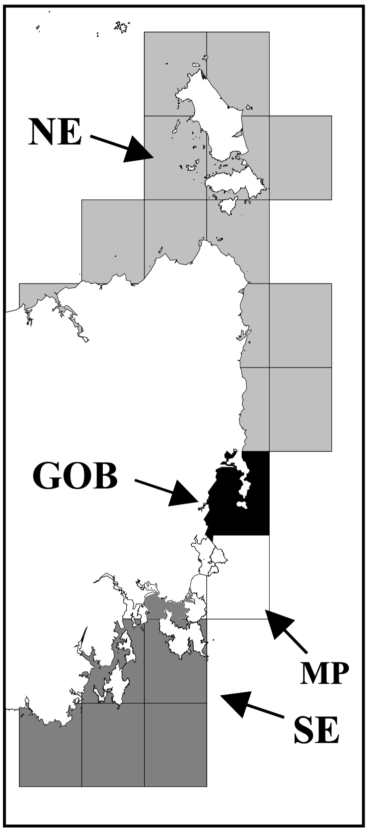
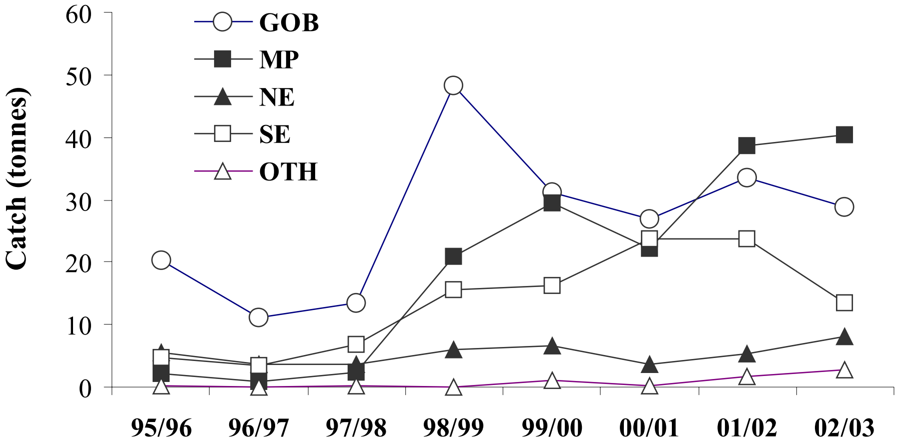
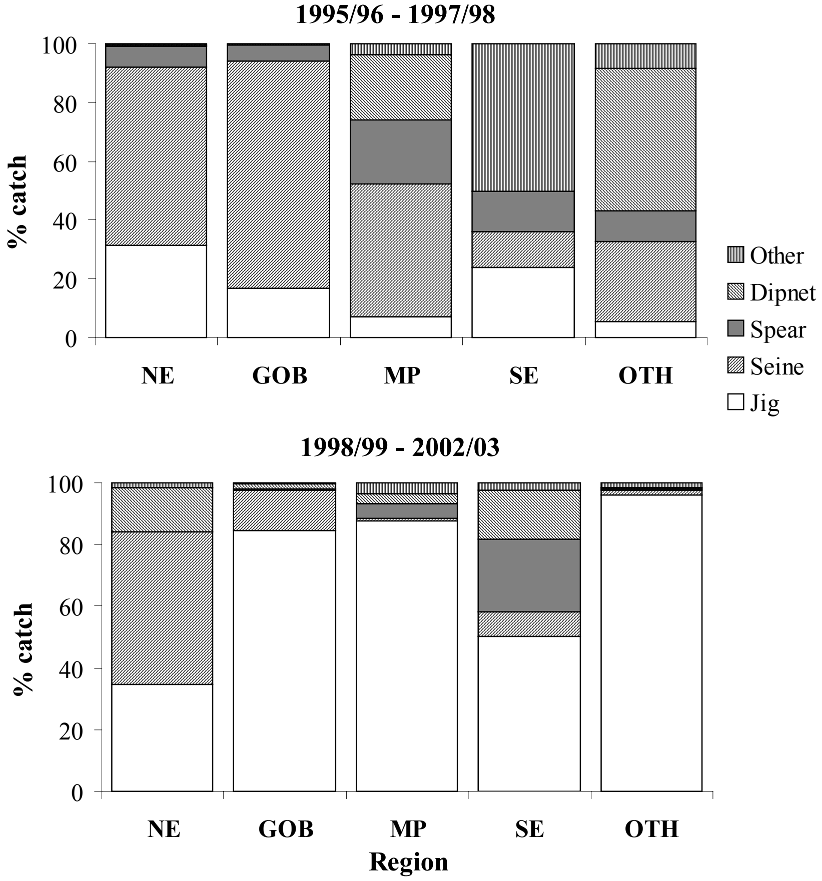


Figure 7.7: Annual catch of southern calamary by fishing year and fishing region. NE – North East Tasmania, GOB – Great Oyster Bay, MP – Mercury Passage, SE – South East Tasmania, OTH – elsewhere Tasmania.



Prior to the expansion of the fishery in 1998/99, seine methods, and to a lesser extent dip nets, were the dominant catching methods utilised by commercial fishers throughout Tasmania (Fig. 7.8). At the time jig catches represented a relatively minor component of the fishery. Since then the dominance of jig catches (> 80% of catch) is clearly evident regionally in Great Oyster Bay, Mercury Passage and elsewhere Tasmania (Fig. 7.8). In the South East, however, jigs account for just half of the catch and spear and dip nets the bulk of the remainder. Although a minor component of the fishery, the relative mix of methods in the North East has changed little over time. Seine nets continue to be the primary gear, with jigs of secondary importance. Such regional differences in the contributions of the various fishing methods reflect a range of factors including gear preferences of fishers, squid behaviour and availability, and levels of targeted fishing as opposed to incidental catches of calamary.

Figure 7.8: Relative catch composition, by fishing method and region, prior to significant expansion (1995/95–1997/98) and subsequent (1998/99-2002/03) to development of the calamary fishery. NE – North East Tasmania, GOB – Great Oyster Bay, MP – Mercury Passage, SE – South East Tasmania, OTH – elsewhere Tasmania.



Trends in jig catch, effort, and catch rates have been examined in more detail for the three main fishing regions: Great Oyster Bay, Mercury Passage and the South East (Fig. 7.9). Collectively, jig catches from these regions have accounted for 67-79% of state-wide catch of southern calamary in each year since 1998/99. Apart from being the major fishing method, the use of jigs represents targeted fishing activity for calamary thus uncertainties that arise when catches are the result of targeted and non-targeted effort are minimized.

After the initial expansion of the Great Oyster Bay fishery in 1998/99 effort more or less stabilized, no doubt influenced to some extent by the introduction of the short-term fishing closures in late 1999 and each year since (Fig. 7.9). These closures contributed to the shift in effort to the adjacent Mercury Passage region where, over the past two fishing years, catch and effort levels have exceeded those in Great Oyster Bay.

Catch rates (kg per jig hour) in both Great Oyster Bay and Mercury Passage have generally declined since 1998/99, such that in 2002/03 catch rates were less than half (46%

and 44%) of the respective 1998/99 levels and 74% and 53%, respectively, of 1999/2000 levels. Closures during periods of peak catch rates in Great Oyster Bay will have contributed to the observed decline (at least initially) but do not account for coincident declines in catch rates in Mercury Passage. In both regions daily catches fell sharply between 1998/99 and 2000/01, from over 100 kg to less that 70 kg per day, before recovering to a mean of about 80 kg per day.

Unlike the other regions, catch rates (kg per hour and kg per day) in the South East have tended to remain relatively stable but at levels consistently lower than for either Great Oyster Bay or Mercury Passage (Fig. 7.9). In 2002/03, however, catch rates (kg per hour) for Mercury Passage had fallen to levels comparable to those in the South East.

Catch rate data for Great Oyster Bay and Mercury Passage fisheries provide some insight into the dynamics of the fishery. It is evident that in the face of declining catch rates, fishers have effectively expended more jig hours of effort on a daily basis in order to maintain daily catch levels. Catch rate analyses do not, however, take account of searching time, that is visual searching for evidence of spawning activity (egg masses on spawning beds) and/or time spent ‘exploratory’ fishing[5]. Should search time have increased over the history of the fishery then the effective decline in catch rates will have been underestimated. Conversely, there is potential that with increased fishing effort/fisher interactions on the fishing grounds there will have been negative impacts on individual catch rates through gear saturation effects. The relative interactions of these factors, along with issues of data quality, cannot be assessed at this stage but do represent uncertainties in the interpretation of catch rate trends.

Of relevance to the catch rate analyses (and stock health) are the observation that during the summer of 2001/02 many calamary fishers reported 'yellowing, stinky and rotting' squid in their catch from Great Oyster Bay and areas further south. A telephone survey of all major calamary fishers in Tasmania followed, with most fishers from Great Oyster Bay reporting that 10-30% of their catch (on average) had been affected and was unsaleable. Muscle and skin samples from affected squid were found to have large quantities of small ciliated burrowing protozoans, probably resulting in secondary infections of mixed gram negative and filamentous gram-negative rods, mixed vibrio, and flavobacteria, and necrosis of surrounding tissues (Les Gabor, Fish Health Unit, TAFI, unpub data). The last report of diseased squid was February 2002. The effect of the disease on stock levels, or on reported catch and catch rate estimates over this period (i.e. some fishers reported catch and effort of diseased catch and others did not) is unknown. While the cause of this phenomenon is unclear, the impact of this disease in shaping the population structure or characteristics of survivors for 2001/02 is uncertain.

Recreational fishery

Recreational catch information was derived as part of the national recreational fishing survey and was based on a telephone/ diary survey methodology (Lyle *et al.* in press). Overall, for the twelve months between May 2000 and April 2001 an estimated 44,000 squid, of which around 30,000 were reported as southern calamary, 6,000 as arrow squid and 8,000 as unspecified squid were harvested by recreational fishers in Tasmania. As some of the unspecified squid are likely to have been calamary, an adjustment, based on

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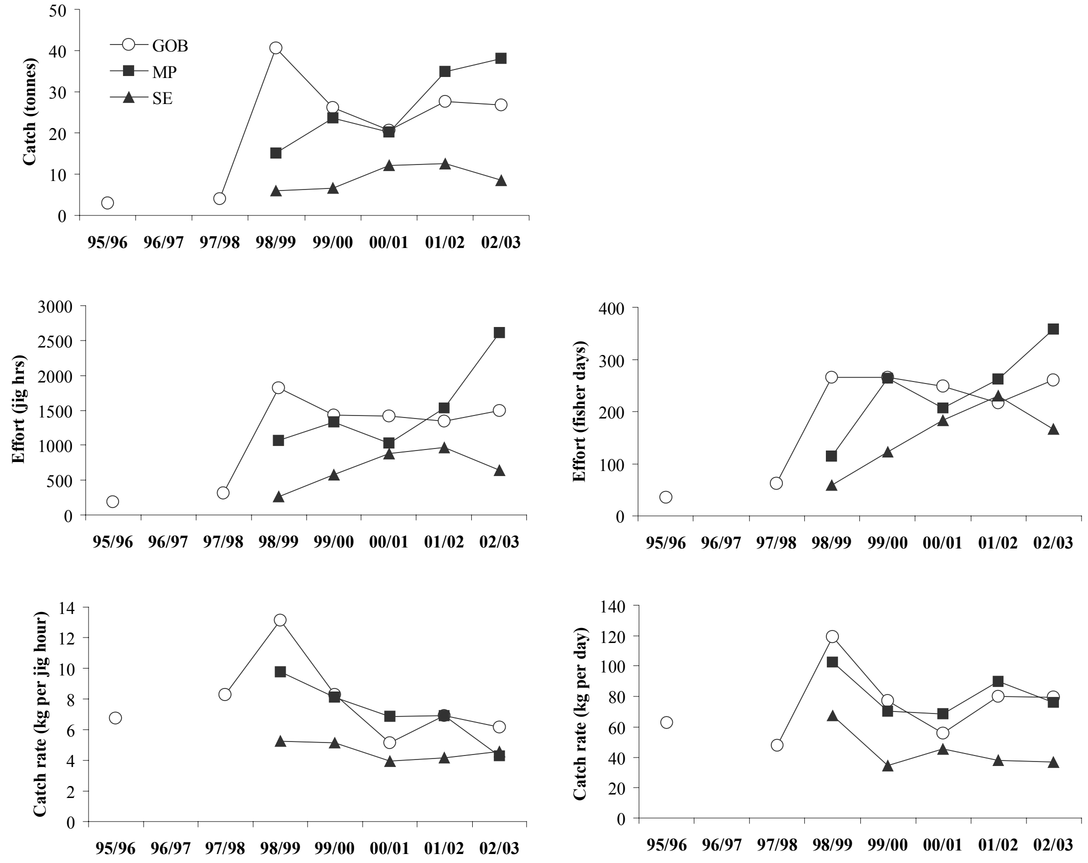
[5] Jig fishers generally test potential fishing sites with a short period of fishing, if catch rates are poor they move on to alternative sites until ‘acceptable’ quantities of squid are located.

the ratio of calamary to arrow squid by fishing location, has been applied to these unspecified squid catches to develop revised catch estimates. This analysis indicated that the recreational harvest was in the order of 37,000 calamary, equivalent to about 22 tonnes[6] or almost 30% of the 2000/01 commercial catch.

Regionally, about 27% of the harvest (numbers) was taken from Great Oyster Bay and Mercury Passage with a further 27% from South East Tasmania. The north coast accounted for 19% and D'Entrecasteaux Channel (an area closed to commercial calamary fishing) contributed a further 12% of the harvest. The majority (88%) of the calamary were caught using jigs with dip nets (10%) and spears (2%) also used by recreational fishers.

Figure 7.9: Squid jig catch, effort (jig hours and fisher days) and catch rates (kg per jig hour and kg per day) by fishing year for key fishing regions since 1995/96. GOB – Great Oyster Bay, MP – Mercury Passage, SE – South East Tasmania. No information is shown where less than five vessels reported catches.



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[6] A mean weight of 0.6 kg per individual has been assumed.

Modelling the southern calamary fishery

Modelling strategies

The expansion of the calamary fishery has given rise to the need to develop a method of assessing the status of the fished stocks. In turn the type of assessment possible will dictate what performance indicators can be used successfully in this fishery. Investigating performance indicators is equivalent to asking particular questions about a stock and its status. More complex stock assessment models have a greater chance of being able to answer complex questions about a fishery. Unfortunately, the data requirements for complex stock assessment models can be heavy and, obviously, it is best to limit the questions being asked of a formal assessment to those that can be answered by analysis of the available data.

In the case of southern calamary, there is a great deal of information available about a sub-set of the stock (Chapters 1, 4, 5 & 6). However, many biological properties varied greatly from year to year, including growth rates, mean size of animals, and the mean age of animals in the fishery. Under such rampant variability the data requirements for a model that attempts to describe the detailed dynamics of the calamary populations would be immense. Instead, such information becomes important in emphasizing, in a qualitative way, that any answers that are produced would be highly uncertain.

Despite the limitations, there are two possible forms of assessment model that could be used with calamary, these are the classic surplus production models (Schaeffer 1954, 1957; Haddon, 2001) and various within year depletion models (e.g. De Lury, 1947, 1951; Geaghan & Castilla, 1986; Agnew *et al.*, 1998). Both of these approaches have relatively simple data requirements and as a consequence are limited in what can be expected of them. The requirements are a listing of catches, effort, and catch rates through time. The surplus production models are generally applied to annual data while the depletion models are generally used within years. Only after an inspection of the available information can we determine which modelling approach may be viable.

Intra and inter-annual patterns in catch and catch rates

Commercial catch and effort data indicate that squid jigs now account for the bulk of the catch (Fig. 7.3) which has a number of fortunate aspects, not least being that the only species targeted with jigs are calamary (or arrow squid). Furthermore, catches and the use of jigs did not increase to significant levels until the 1998/99 fishing year.

The fishery is prosecuted in a number of different geographical areas (see Fig. 7.5) and, at least initially, we will consider the main areas separately and compare them. There are three major catching regions: Great Oyster Bay, Mercury Passage, and South East Tasmania (refer Figs 7.5 & 7.7).

The fisheries in Great Oyster Bay and Mercury Passage show many similarities of duration and intensity as indicated in the patterns of production within and between fishing years (Figs 7.10 & 7.11; Table 7.1). However, they differ markedly from the fishery in the South East, both in period of maximum intensity of activity (catches) and in duration of jig fishing (Figs 7.10 & 7.11; Table 7.1). The jig fishery in the South East peaked in activity slightly later than in the other two regions and lasted for a much shorter period. Furthermore, there were minor peaks of activity in the middle of the year (April through to

June), which did not appear to happen in Great Oyster Bay or Mercury Passage. The summary statistics obtained from fitting the series of normal distributions to the observed patterns of catches permit the different areas and seasons to be directly compared (Table 7.1). This analysis indicated that over time there has been a slight trend for the peak in fishing activity in Great Oyster Bay and Mercury Passage to occur a few weeks earlier in the calendar year and for the duration of peak fishing activity (represented by StDev and Duration in Table 7.1) to be longer.

Table 7.1: . The formal descriptions of activity patterns as represented by normal distributions fitted to each year's fishing catches for each region separately. Week is the week number within the calendar year in which the peak of activity occurs; StDev is literally the standard deviation in weeks of the normal curve fitted to the activity pattern; Duration is the 95% bounds of the normal curve in weeks; Amplitude is the relative size of the curve needed to cover each season; and BackGround is the constant level of catch that can be expected to occur outside of the main fishing season. Secondary (minor) peaks of activity in the middle of 2001 and 2002 in the South East are indicated (refer also Fig.7.10).

	98/99	**99/00**	**00/01**	**2001**	**01/02**	**2002**	**02/03**
Great Oyster Bay							
Week	44.55	43.56	41.80		43.01		41.52
StDev	6.1658	5.0585	6.2901		6.5987		4.6276
Duration	24.2	19.8	24.7		25.9		18.1
Amplitude	37295.5	25779.3	22010.6		24089.3		23579.6
BackGround	128.797						
Mercury Passage							
Week	46.67	44.04	43.59		43.82		43.82
StDev	3.7113	6.2555	6.28719		5.14256		8.6598
Duration	14.5	24.5	24.6		20.2		33.9
Amplitude	11531.8	20240.6	18273.5		31310.2		42974
BackGround	94.7164						
South East Tasmania							
Week	46.78	47.99	48.29	17.93	45.74	20.47	45.83
StDev	0.7703	1.8128	1.9301	2.6223	4.6439	2.7397	3.2709
Duration	3.0	7.1	7.6	10.3	18.2	10.7	12.8
Amplitude	3516.85	3349.82	8136.59	1182.47	8304.65	1562.06	5798.95
BackGround	78.4996						

Figure 7.10: Weekly catches (kg) by major fishing regions from the start of 1998. The smooth curve represents a set of normal distribution used to describe the background level of fishing plus the peak of activity in terms of week number and the duration of the season in weeks for each season (see Table 7.1). The effects of the fishing closures first introduced in the 1999/00 season are evident as the spiky pattern of catches visible each year.

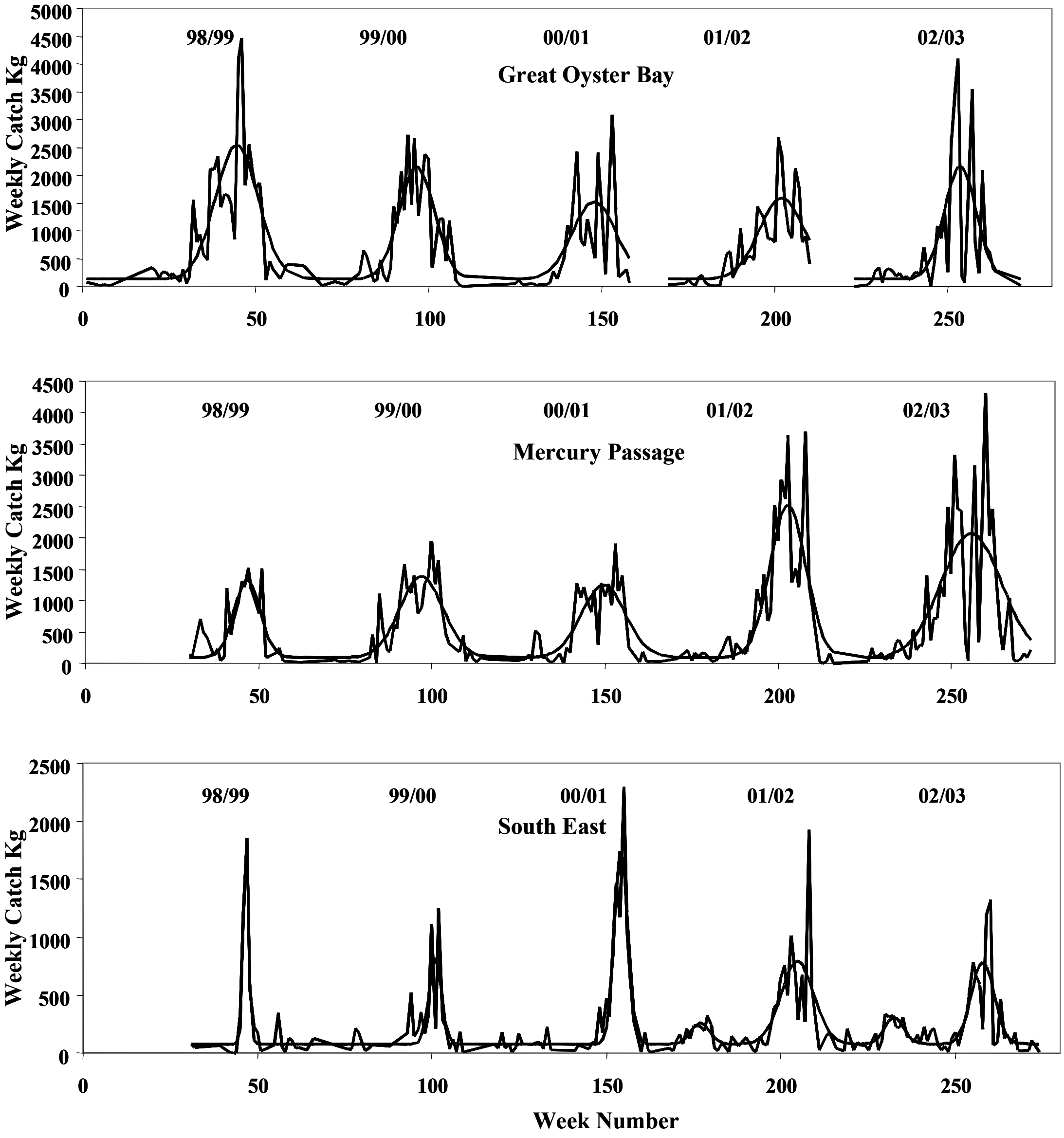
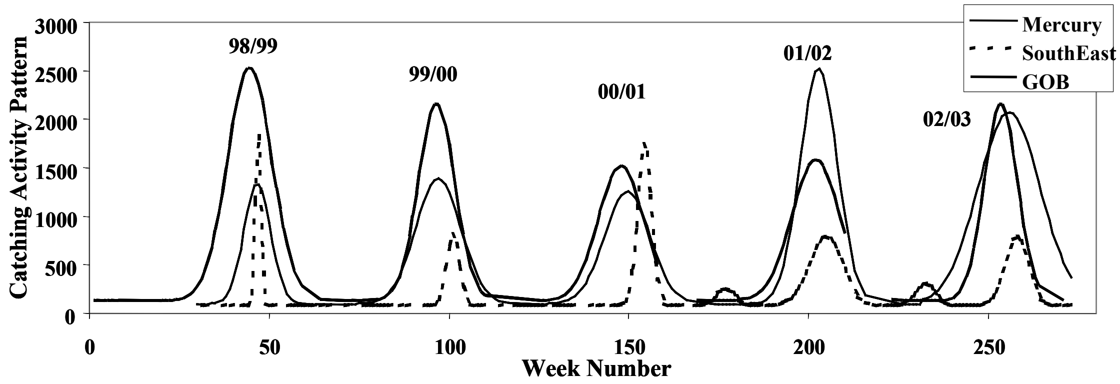


Figure 7.11: A compilation of the normal curves representing the relative catching activity in the three areas (see Table 7.1). Note that Mercury Passage (the fine solid line) was only developing as a fishery in 1998/99 hence it only lasted for a relatively short period. The similarity between Mercury Passage and Great Oyster Bay is clear.



In South East Tasmania a range of fishing methods are used (see Fig. 7.8), each with too little catch for useful modelling to be pursued. Thus, we will not attempt to model the fishery in the South East beyond the formal description already given (Figs 7.10 & 7.11; Table 7.1).

Apart from the obvious decline in mean weekly catch rates across the years in Great Oyster Bay there was no clear pattern apparent in catch rates within each season (Fig. 7.12). Similarly, there were no obvious within season patterns in catch rates for Mercury Passage, although in some years there was a hint of declining catch rates through the peak catching period (e.g. in 1998/99 and possibly 2000/01) (Fig. 7.12). Some lowering of catch rates during 2002/03 is perhaps evident in Mercury Passage.

In the following, because their pattern of catches are so similar, the fisheries in Great Oyster Bay and Mercury Passage have been assessed by combining the data from the two regions and treating them as a single fishery. This had the effect of increasing the number of observations available in each week (and season), which improved our confidence in the results derived from the data (Figs 7.13 & 7.14). Visually, the general trend is one of relatively steady decline in catch rates over the history of the fishery. Unfortunately, the depletion methods of estimating stock biomass within a year require the data to exhibit a general and monotonic decline in catch rates against cumulative catches. In none of the years observed has this pattern been exhibited. This is likely due to the rapid growth rates of the calamary such that at the beginning of the fishing season the biomass available continues to increase despite catches being removed. This means that depletion methods do not provide a useful avenue to pursue with southern calamary.

Agnew *et al*. (1998) successfully applied a DeLury depletion assessment method to squid data from the Falkland Islands by modifying the analysis to permit the inclusion of more than one cohort (which was why their data did not exhibit clear, monotonic declines through the peak catching period). With the southern calamary there may well be a wide range of different aged animals present on the fishing grounds but, unfortunately, they do not appear to be in distinct cohorts (Chapter 5).

Figure 7.12: Geometric mean catch rates by week since the start of 1998 for Great Oyster Bay and Mercury Passage.

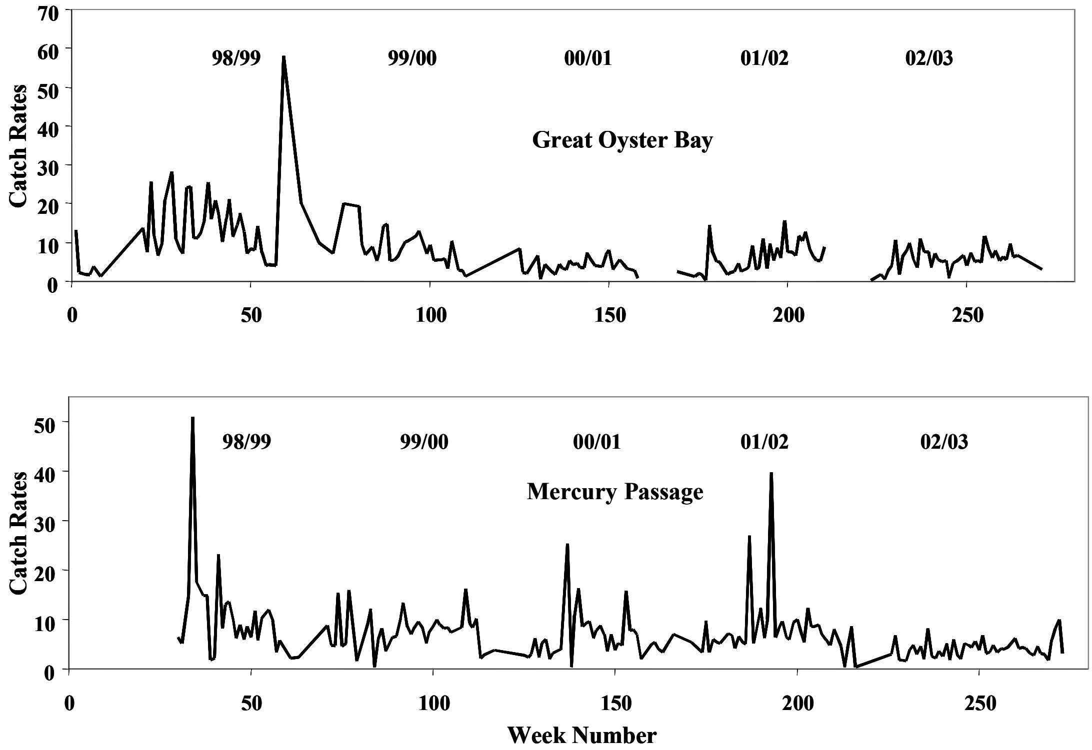


Figure 7.13: Combined weekly catches from Great Oyster Bay and Mercury Passage starting at the beginning of 1998. The influence of the two 2-week closures is clearly visible in 2002/03, when they applied to both Great Oyster Bay and Mercury Passage.

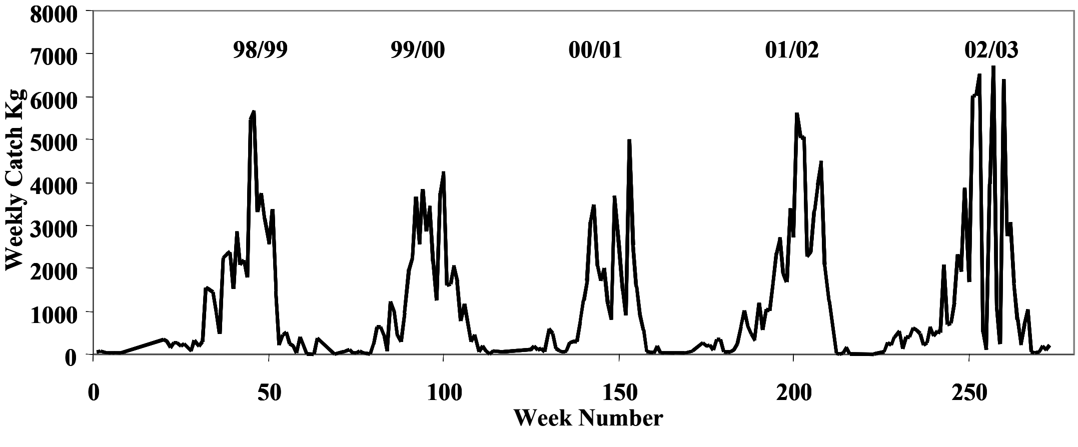
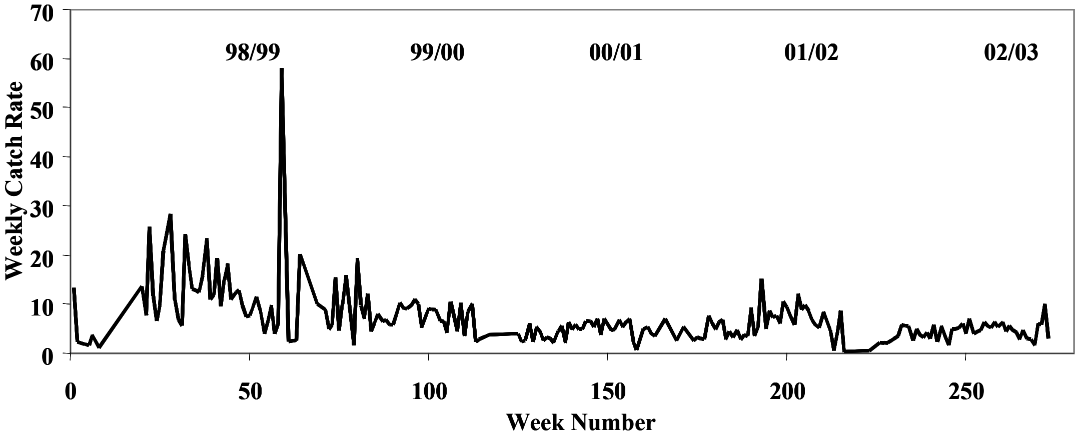


Figure 7.14: Weekly catch rate data for data combined from Great Oyster Bay and Mercury Passage.



Surplus Production Modelling

The basic idea behind a surplus production model is that it attempts to describe the catch through time in terms of biomass available and catch rates. We use the catch rate trend as the index of relative abundance needed to relate the catches to stock biomass. If the system dynamics are treated at an annual time-step then the patterns become clearer and the modelling is simplified (Fig. 7.15; Table 7.2). As there are only six years of catch rate data, it would be best to use only the simplest of models having the minimum number of parameters. A non-equilibrium version of the simplest model available (Schaefer, 1954, 1957; Haddon, 2001) can be described by the following equations with only two parameters. The basic stock dynamics are described by the delay-difference version of the standard logistic production model:

$$\begin{aligned} &B_0 = K \\ &B_{t+1} = rB_t\left(1 - \frac{B_t}{K}\right) - C_t \end{aligned} \qquad (1.1)$$

where r is a parameter depicting population growth rate and K represents the unfished equilibrium population size. B_t represents exploitable stock biomass in year t, and C_t represents the catch in year t. The first year of catch data is 1995/96, however, the model may only be fitted to catch rates from 1997/98 up to 2002/03 because of limitations in the available data. The model is fitted to the available catch rate data with the following:

$$\begin{aligned} &\frac{\hat{C}}{E} = qB_t \\ &SSQ = \left(Ln\left(\frac{C}{E}\right) - Ln\left(\frac{\hat{C}}{E}\right)\right)^2 \end{aligned} \qquad (1.2)$$

where *q* is the catchability coefficient, SSQ is the sum of squared residuals, and *Ln* refers to natural logs. This implies that log-normal residual errors are being used. The relative normality of the distribution of log-transformed catch rates (Fig. 7.16) confirms that the use of log-normal residual errors when fitting the model is justified.

An alternative model fitting criterion would be to use a maximum likelihood approach, which would entail minimizing the following negative log-likelihood (Haddon, 2001):

$$-LL = \frac{n}{2}\left(Ln\left(2\pi\right) + 2Ln\left(\hat{\sigma}\right) + 1\right) \tag{1.3}$$

where σ is:

$$\hat{\sigma} = \sqrt{\frac{\sum\left(Ln\left(I_t\right) - Ln\left(\hat{I}_t\right)\right)^2}{n}} \tag{1.4}$$

where the I_t are the respective observed and expected catch rates, and *n* is the number of years of observations. However, with log-normal errors the solutions obtained are identical to those from using the simple sum or squared residual errors. The estimation of the catchability coefficient can be made using a closed form version of the equation:

$$\hat{q} = e^{\frac{\sum Ln\left(\frac{I_t}{B_t}\right)}{n}} \tag{1.5}$$

While the model may only be fitted to the final six years of data it is apparent from the count of records that not all estimates of seasonal catch rate are estimated with equal precision or confidence (e.g. 1997/98 has only 32 data points). A solution to this heterogeneity is to use a weighted least squares approach which applies a weight equal to the square root of the number of observations contributing to that data point:

$$SSQ = \sqrt{N}\left(Ln\left(I_t\right) - Ln\left(I_t\right)\right)^2 \tag{1.6}$$

where *N* is the number of observations that contribute to the estimate of I_t. When this is done the optimum solution provides a reasonable match of predicted catch rates against observed (Fig. 7.17). The earliest data point has the worst fit but this is not weighted greatly in the analysis as only relatively few data records went into the estimate of observed jig catch rate in 1997/98.

Table 7.2: Summary statistics for each fishing season. The Catch Rates are the geometric mean catch rates of individual catch records. Records refers to the number of recorded jig days of effort in the database.

Fishing Season	Catch (tonnes)	Catch rate (kg per jig hour)	Records
1995/96	22.48		
1996/97	11.94		
1997/98	15.80	6.625	32
1998/99	69.10	11.439	390
1999/00	60.70	7.361	563
2000/01	49.00	5.068	501
2001/02	72.10	5.871	524
2002/03	69.00	4.772	641

Figure 7.15: Combined data from Great Oyster Bay and Mercury Passage, showing the jig catch rates (solid line) and the total catches by all methods (dotted line) from the combined area.

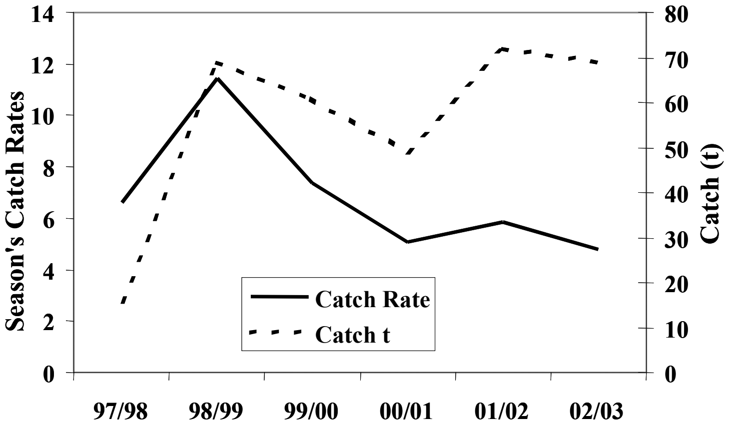


Figure 7.16: Histogram of the relative percent frequency of observations of log catch rates for calamary in the Great Oyster Bay and Mercury Passage regions.

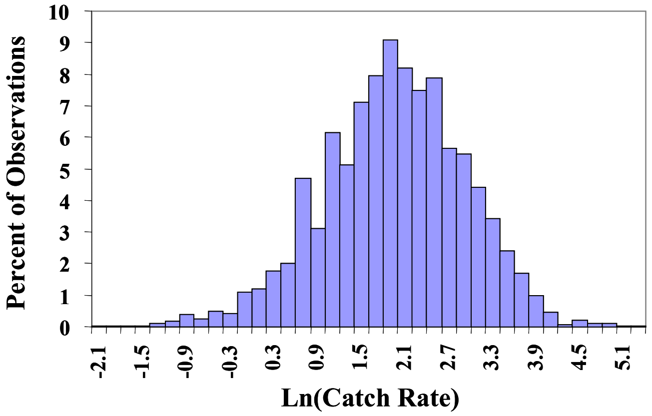
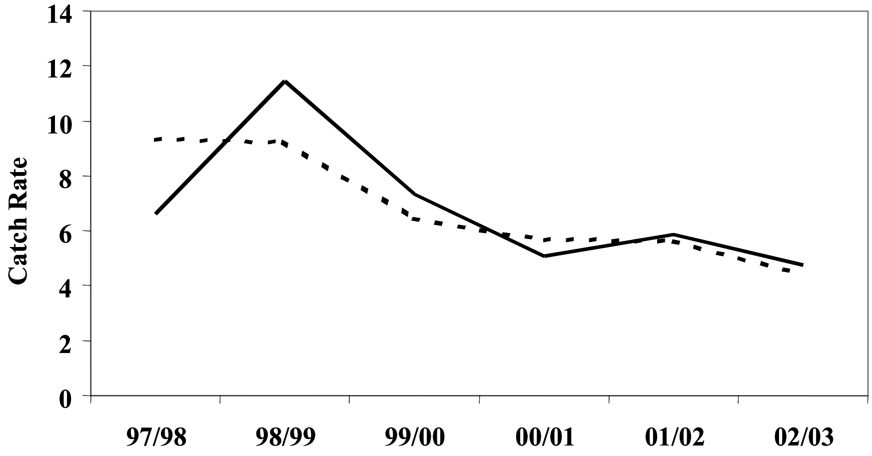


Figure 7.17: A comparison of catch rates from the observed (solid line) and the predicted (dotted line) catch rates.



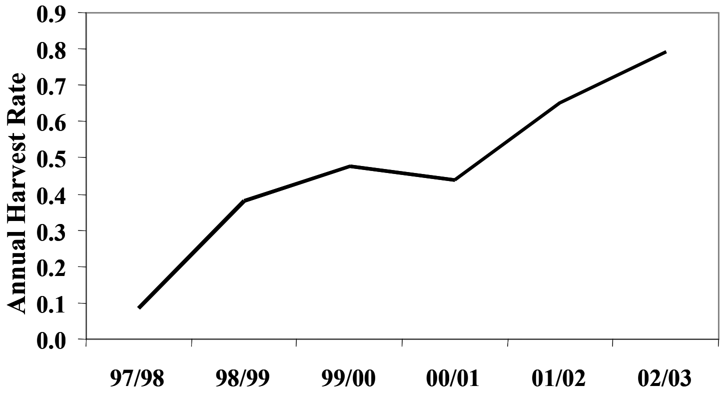
Model Fit

The optimum fit to the model is robust, in that it is not possible to force the model to accept alternative scenarios of productivity and biomass, i.e. there are no false minima even close to the optimum solution. The optimum solution implies a declining series of stock biomass levels, which relate directly to a steadily increasing harvest rate in the fishery (Table 7.3; Fig. 7.18). The most recent years are showing signs of fishing mortality levels that are typically unsustainable.

Table 7.3: Output from the surplus production model fitted to the calamary data from Great Oyster Bay and Mercury Passage combined. *r* and *K* are parameters of the model; *q* is the catchability; SSQ is the sum of weighted squared residuals; Sigma is σ from Eq. 1.4, and –LL is the negative log-likelihood; Biomass is the predicted exploitable stock size in the middle of the fishing season; Pred CE is the predicted catch rate; and H is the harvest rate or Catch/Exploitable Biomass. Recreational catches are added as a proportion of the commercial catch. Note the decline in productivity (*r*) and increase in unfished population size (*K*) as recreational proportion increases.

Recreational %	0.0	10.0	20.0			
r	0.988953	0.971467	0.957113			
K	198.0425	220.8902	243.7661			
q	0.050953	0.045475	0.041052			
SSQ	2.442008	2.481503	2.513561			
Sigma	0.637967					
-LL	7.165223					
Season	**Catch t**	**Catch Rate**	**Records**	**Biomass**	**Pred CE**	**H**
1995/96	22.48			198.0		
1996/97	11.94			175.6		
1997/98	15.80	6.625	32	183.3	9.34	0.086
1998/99	69.15	11.439	390	181.0	9.22	0.382
1999/00	60.70	7.361	563	127.3	6.48	0.477
2000/01	49.04	5.068	501	111.5	5.68	0.440
2001/02	72.14	5.871	524	110.7	5.64	0.652
2002/03	69.02	4.772	641	86.8	4.42	0.795

Figure 7.18: The annual harvest rate (as Catch/Exploitable Biomass) through the six seasons of the fishery being modelled.



Performance Indicators

The analysis suggests that the unfished, mid-season exploitable biomass in the Great Oyster Bay and Mercury Passage region was in the order of 200-245 tonnes but has been reduced to only about 90-107 t (depending on assumed level of recreational catch). With commercial catches in the order of 70 t this implies that the harvest rate is dangerously high. The predicted harvest rate reduces slightly if recreational catches are considered in the analysis. The primary analysis in Table 7.3 assumes a recreational take of zero. If the recreational take is assumed to be 10% of the total commercial catch in each year then the harvest rate in the final year declines slightly to 0.78, a recreational take of 20% of the total commercial catch takes the harvest rate down to 0.768[7]. Factoring in recreational catches has this small reducing effect on harvest rates, despite increasing the catches, because the increased catches imply that the stock is less productive than when there are no recreational catches, but has a higher starting biomass. Irrespective of the level of recreational catch, the current harvest rate would appear to be too high to be sustainable. The fact that the harvest rate has increased markedly over the past two years is also cause for great concern.

The current performance indicator relating to catch rates is not as sensitive as one based on these estimates of Harvest Rate. The harvest rate provides an indication of the escapement (the proportion of the available biomass not harvested). This could be used as an effective performance indicator, although what level of escapement to use would need to be decided. Typical escapement values used are approximately 40%, which is an arbitrary figure derived from experience with other squid fisheries around the world (Agnew *et al*. 1998). It should be noted that while this was the target in the Falkland squid fishery, that fishery still experienced collapse. What this implies is that we would not wish to see a harvest rate greater than 60%.

Alternative performance indicators are also available when using surplus production models. The old notion of Maximum Sustainable Yield can be interpreted as the maximum long-term yield possible if the dynamics described by the available data are representative or typical of the dynamics of the stock being considered. If this is the case then an estimate of this long term equilibrium yield can be obtained from:

$$LTY = \frac{rK}{4} \tag{1.7}$$

Given the range of recreational catch levels this implies that the Long Term Yield (LTY) for the Great Oyster Bay and Mercury Passage fishery is between 48 – 52 tonnes, although there is great uncertainty about this figure.

Uncertainty

Unfortunately, the precision of the assessment using the simplistic representation provided by the surplus production model is low. The uncertainty can be estimated by using a bootstrap procedure that generates a bootstrap sample of the log-normal residuals which are combined with the optimal fitting line to generate new bootstrap samples of catch rate time series, each of which are refitted providing new estimates of parameters and model outputs (Haddon, 2001). Bootstrap 95 percentile confidence intervals can thus be

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[7] Note, recreational catch estimates for 2000/01 for Great Oyster Bay and Mercury Passage were equivalent to about 12% of the commercial catch.

placed around the various model outputs (Figs 7.19 & 7.20). Clearly the precision of estimates is poor, especially the prediction of harvest rate. For instance in 2001/02 and 2002/03 the upper 95 percent limit on harvest rate reached of 1.0 (total harvest of all available biomass) whereas the lower limit was around 20%.

The high levels of uncertainty about this analysis mean that care must be taken if the results are to be used in a formal assessment of the Tasmanian stock. However, the increasing trend observed in the implied harvest rate is consistent with the observed decline in catch rates, the declining levels of estimated egg-production (Chapter 2), and the increasing levels of effort being imposed on this species.

Figure 7.19: The predicted catch rates (solid line; observed catch rates are here denoted by the dotted line) from the optimal fit (when recreational catches are set at 10% of commercial catches). The fine lines about the solid line represent the 95% bootstrap percentile confidence intervals.

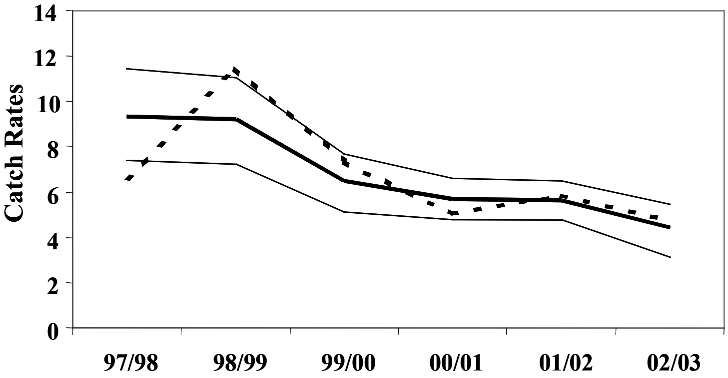
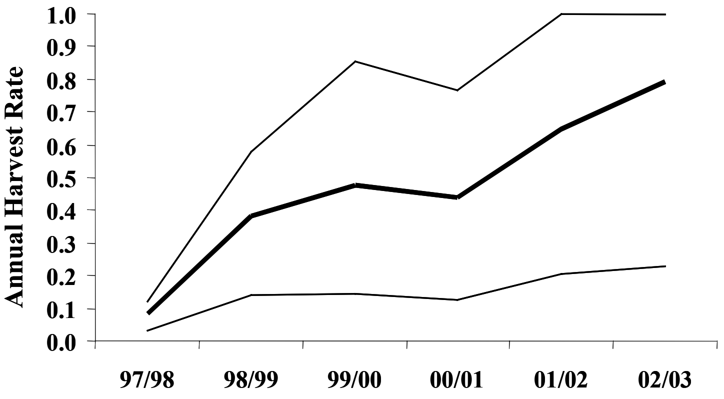


Figure 7.20: The predicted harvest rate from the optimal fit (when recreational catches are set at 10% of commercial catches). The fine lines represent the 95% bootstrap percentile confidence intervals.



Management Implications

Preliminary modelling of the Tasmanian calamary fishery suggests that harvest rates are very high within the main area of the fishery, implying that the fishery has impacted significantly on stocks and that current catch levels are not sustainable. This observation is set against the fact that there continues to be growing interest in the fishery and that there is substantial capacity within the Tasmanian scalefish industry to increase effort levels.

Currently there is limited information available on the stock structure of southern calamary in Tasmania and such information is required to assess the validity of current spatial management and regional analyses reported here. In particular, the relationships between calamary populations fished in Great Oyster Bay and Mercury Passage and other regions need to be investigated.

The observation that calamary have a life span of generally less than one year, with no accumulation of recruitment across a number of years, suggests considerable potential for inter-annual variability in abundance coupled with vulnerability to recruitment over-fishing, especially since the species can be targeted whilst aggregating to spawn. Given such vulnerability, the impact of fishing activities on the spawning behaviour of the aggregations needs to be addressed. Furthermore, since growth and reproductive characteristics of 'micro-cohorts' differ substantially, depending upon the timing of hatching and subsequent environmental conditions, environmental factors may prove as important as fishing mortality in driving the population dynamics and determining spatial patterns of abundance.

Although there is a high degree of uncertainty with the present assessment, key indicators do suggest that maintaining the status quo for the Tasmanian southern calamary fishery is a high-risk strategy. For the fishery to remain sustainable a more precautionary approach is required, including consideration of options that will effectively reduce harvest rates.

Benefits and Beneficiaries

This research has provided the biological basis for management decisions made by Tasmanian Department of Primary Industries, Water and the Environment, in particular:

- The timing and length of fishing closures have been based on information provided from this project. Specifically, the temporal and spatial patterns of egg deposition by southern calamary, including the identification of peak periods of spawning, quantification of egg loss, and the relationship between egg deposition rates and the biomass and reproductive status of the spawning population.

- The preliminary evidence from modelling has identified that harvest rates are very high. Based on this the recommendation, if taking a precautionary approach, is that managers and fishers seek management strategies that reduce effort and hence harvest rates.

- The recognition that the fishery is not based on a single cohort of individuals, but a series of micro-cohorts with different life history characteristics, i.e. growth, age and size at reproductive maturation. It is recommended that the range of micro-cohorts may need some protection from over-fishing.

Ultimately, commercial and recreational fishers will be the primary beneficiaries from this research in that it provides a basis for assessing the status of the calamary resource in the future and a framework for the on-going management of the fishery.

This project has also contributed to the wider scientific community, particularly in cephalopod biology, a quantification and analysis of population biology and dynamics. In particular, the assessment of short-term fishing closures as a management tool allows overseas fisheries to explore management options.

Further Developments

Over the course of this project and in meetings with managers and fishers a number of directions for further work have become evident, including:

- Determination and assessment of spawning sites outside the currently known shallow seagrass beds. In particular the need to follow up on anecdotal reports of deepwater (c. 20m) spawning sites.

- Identification of the movement patterns of adults along the coast and between spawning areas, the time spent by individuals on the spawning grounds, and the extent of dispersion of juveniles.

- Ecology of juveniles and sub-adults. Most of the research has focused on the adult population and the eggs; however, little is known about the early life history of these animals particularly survivorship rates.

- There is a need to continue assessments of egg deposition rates and using a long time series to determine whether relationships exits that will allow future biomass to be estimated from current egg production levels.

- There is a need to determine if the variability in life history characteristics is primarily a function of genetics or the environmental characteristics (eg food, temperature). This will then determine if management needs to consider protection of genetic subgroups.

- The impact of intensive fishing activity on the spawning behaviour of individuals needs to be determined. Southern calamary spawning behaviour is very complex, involving mate selection, pair spawning, and an aggregation is composed of many different components (sneaker, paired & bull males, and paired & single females).

- Southern calamary females are multiple spawners, however, estimates of individual fecundity and an assessment of the factors that affect fecundity, are unavailable as we currently have no information about spawning frequency or the number of batches deposited.

Planned Outcomes

1. The development of quantifiable biological indicators for inclusion in fisheries specific management plans.

The research provided a description of the reproductive ecology that allowed managers to make decisions on fishing closures during the spawning period. In addition we identified the potential suitability for egg production by squid to be a useful fishery independent indicator of biomass

2. An increased understanding of southern calamary and its relationship with ecology of inshore waters

In describing the inter-annual variability in abundance and the life history characteristics of southern calamary it was determined that these two elements were unrelated and simple environmental correlates not evident.

3. Quantification of the spatio-temporal variability in growth and population structure of southern calamary

Spatial and temporal variability in life history characteristics of calamary at a range of scales provided input into management decisions about the type and extent of fishing closures used to control harvest rates. Region specific patterns in population biology, fishing methods, and harvest rates suggest the potential of considering a region specific approach to management.

4. Recommendations on the optimal harvest strategy, taking into account fishing gear types

Modelling of the jig fishery indicates that to remain sustainable a more precautionary approach is required, including consideration of options that will effectively reduce harvest rates

Conclusions

Objective 1: Describe temporal and spatial variability in rates of growth, size and age distributions and reproductive status of populations of southern calamary.

On an inter-annual level this study identified two groups of years of similar abundance (eg: 1996/96 and 2000/01, and 1999/00 and 2001/02), but with very different population structure and characteristics. If we were generating environment-recruitment relationships these two populations would be considered equivalent. However, the factors responsible for generating a population consisting of smaller, slower growing squid with little sexual dimorphism and high levels of reproductive investment (eg 1996/97), are going to be very different to those factors resulting in a population of larger, faster growing squid with extreme sexual dimorphism in body size and low levels of reproductive investment (eg 2000/01 and 2001/02). In the search for environment-recruitment relationships for squid the 'spawning stock' is considered as a single uniform unit. However, seeking a relationship between abundance and environmental parameters at such a gross level will not shed light on the mechanisms that lead to any given level of abundance. Therefore, use of environmental-recruitment relationships as predictive management tools maybe limited.

Within each spawning season the reproductive status, abundance, and reproductive output of the stock declined from October to December. Size and size-at-age data indicates that younger individuals are continually entering the spawning aggregation throughout the October-December period. The presence of older squid, and preliminary tagging information, suggests that individuals stay in the aggregations for several months. Furthermore differences in the biological characteristics (growth rates, and somatic and reproductive condition) among months indicate variable growth rates and reproductive characteristics that are likely to be a function of genetic and environmental factors.

Large spatial scale differences were evident, with the populations in the south-east of the state appeared to be slower growing, with generally smaller and older individuals being caught. Interestingly this was a characteristic of summer caught individuals on the east coast. Given those individuals that hatch out in January and February were likely to have been from eggs deposited some six weeks earlier, animals from the south-east were approaching an annual lifecycle.

The eggs and embryos on the spawning beds are vulnerable to mortality processes, eg storms, and temperature and salinity fluctuations, which result in temporal variability in survivorship. Temporal variations in developmental rates of embryos can translate to differential hatch times, suggesting that an entire egg mass will hatch over a longer period when incubation temperatures change, compared to egg masses experiencing relatively stable temperatures. Understanding the effect of the environment on embryonic development and hatching success can reduce some of the variability encompassed within existing stock-recruitment relationships, which are currently based on spawner biomass/ parental stock sizes. Reducing variability within predictive stock-recruitment relationships will allow fisheries managers to make more informed and accurate decisions about the fishery.

Objective 2: Describe the spatial and temporal patterns of spawning activities and quantify the reproductive output of southern calamary populations.

There appears to be considerable spatial and temporal differences in the spawning activities of southern calamary. The inshore populations of southern calamary show a consistent spatial and temporal trend of high gono-somatic index, high levels of reproductive output and large body size during the spring and early summer. During the autumn and winter there was little evidence of high levels of reproductive activity, based on low GSI and few egg masses observed inshore. Therefore, spawning aggregations and egg production in the inshore areas of the east and south-east coast of Tasmania only occurred during the spring/early summer period. Based on age estimates, the adults in these spawning aggregations are the product of spawning activity from the previous autumn/early winter. Therefore, either this spawning event is occurring in inshore waters but is non-aggregative, or spawning is occurring in areas that have not been surveyed. Anecdotal information from fishers suggests that eggs have been seen and trawled from deeper waters (ca 20 m), however the recent absence of trawling and dredge fishing operations in most of Tasmania makes it difficult to determine if spawning still occurs in deeper habitats.

It appears that, unlike the eastern populations, animals in the south-east do not form large spawning aggregations, and instead there is isolated low density deposition of egg masses spread over broader areas. The management significance of this for the fishery means that concerns about targeting of spawning aggregations in the south-east may not be such an issue as off the east coast. However, given the differences it is also possible that regional management strategies based on the biological characteristics and the fishing methods employed may need to be implemented.

Objective 3: Determine the age, size, spawning condition and sex composition of the southern calamary caught by commercial fishers using different fishing gear.

Regional differences in the methods used to harvest southern calamary were evident between eastern and south-eastern Tasmania. As a result many of the contrasts were not possible due to the dramatic differences in catch methods and the dominance of certain catch methods. On the east coast most of the squid are landed by squid jigs, and in some cases this is 100% of the catch. As all squid during the spring/summer are mature, there is no scope for differences in spawning condition. There was no evidence of a difference in the average size or in the size frequency distribution of animals caught with jig, spear, and purse-seine. However, dip-netting catches on average larger squid. In two comparisons of sex ratios between the gear types, it was found that there was no difference between jigging and spearing. In many cases daily variation in sex ratios of individuals caught by the same catch methods was greater that difference among catch methods. Due to the variability in age insufficient data was available to determine any age selectivity occurring among catch methods.

Objective 4: Develop performance indicators to be used with southern calamary populations and other short-lived marine species.

Given that preliminary evidence from modelling has identified that harvest rates are very high and that managers and fishers seek a management strategy that reduces harvest rates, the use of closures appears to be a viable option to limit effort on spawning aggregations. Crucially, however, closures will need to allow for a balance between allowing time for the adults to spawn, and removal of these short-lived animals for commercial value prior to losses due to natural mortality.

Potentially the density of newly deposited eggs may provide a fishery independent measure of recruitment that accommodates differences and changes in the size and fecundity of females in the population. Measures of egg production may provide the most direct assessment of future population size. Additionally, embryo mortality rates are typically c. 10%, and it is predicted that juvenile mortality rates will be low relative to fish. Therefore, egg deposition rates could potentially provide a reasonably accurate estimate of future recruitment.

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Appendix 1: Intellectual Property

Not applicable

Appendix 2: Staff Involved

Dr Natalie Moltschaniwskyj, Tasmanian of Fisheries and Aquaculture Institute, University of Tasmania (School of Aquaculture)

Dr Jeremy Lyle, Tasmanian of Fisheries and Aquaculture Institute, University of Tasmania (Marine Research Laboratory)

Assoc. Prof. Malcolm Haddon, Tasmanian of Fisheries and Aquaculture Institute, University of Tasmania (Marine Research Laboratory)

Dr Gretta Pecl, (FRDC funded) Tasmanian of Fisheries and Aquaculture Institute, University of Tasmania (Marine Research Laboratory)

Mr Simon Willcox, Tasmanian of Fisheries and Aquaculture Institute, University of Tasmania (Marine Research Laboratory)

Mr Sean Tracey, Tasmanian of Fisheries and Aquaculture Institute, University of Tasmania (Marine Research Laboratory)

Mr Michael Steer (PhD student) Tasmanian of Fisheries and Aquaculture Institute, University of Tasmania (School of Aquaculture)

Dr Alan Jordan, Tasmanian of Fisheries and Aquaculture Institute, University of Tasmania (Marine Research Laboratory)