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Ecology of the Arrow Squid (*Nototodarus gouldi*) in Southeastern Australian Waters.

A Multi-Scale Investigation of Spatial and
Temporal Variability.

Kathryn Emily Stark, BSc.

Submitted in fulfilment of the
requirements for the Degree of Doctor of Philosophy
University of Tasmania May 2008

Declaration of Originality

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Ethics Approval

This project was approved by the University of Tasmania Animal Ethics Committee (Permit A0006997, 9/10/2002).

Statement of co-authorship

One chapter of this thesis (chapter 5) has already been published in a peer reviewed journal:

Stark, K.E., G.D. Jackson, J.M. Lyle (2005). Tracking arrow squid movements with an automated acoustic telemetry system. *Marine Ecology Progress Series* 299: 167-177.

The following people contributed to the publication of the work undertaken as part of this thesis:

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Jeremy Lyle 5%
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George Jackson contributed to the formation of the idea of the project and obtained the funding. He also assisted with the refinement and presentation of the research paper.

Jeremy Lyle provided logistical support for the project and assisted with the refinement and presentation of the research paper.

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Abstract

Phenotypic plasticity together with a short lifespan, rapid growth and the ability to move over considerable distances mean that squid populations are extremely responsive to changing environmental conditions, and this generates highly variable and complex patterns of population ecology. This study examined the population ecology of the ommastrephid squid *Nototodarus gouldi* in southern Australian waters; investigating how patterns of distribution and abundance vary in space and time, and the factors that may be driving these patterns.

Broad scale GIS and statistical (GAM and GLM) analyses of trawl fishery observer data identified clear ‘hotspots’ of *N. gouldi* abundance in southeastern Australian waters, which corresponded with areas of significant mesoscale oceanographic activity (i.e. strong shelf break fronts, convergence zones and upwelling). Abundance was seasonal, but this seasonality varied between locations. Remotely sensed sea surface temperature and chlorophyll-a concentration were unable to account for the spatio-temporal patterns in *N. gouldi* encounter and catch rates, possibly due to a temporal mismatch between local oceanographic activity and the evidence of its effect on *N. gouldi*.

Lagged relationships between local environmental conditions and *N. gouldi* abundance were then examined on an annual scale for one region- the Bonney Coast, a ‘hotspot’ area subject to seasonal upwelling activity. Local wind speed and ENSO were both strongly correlated with annual abundance, most likely due to their influence on mixing and upwelling activity, and thus prey availability. Cross validation of a linear model incorporating these environmental variables suggested reasonably good predictive ability. A negative correlation between jig and trawl derived indices of abundance however suggests that inter-annual variability is driven by distributional changes as well as recruitment variability, with the depth distribution of *N. gouldi* possibly changing in response to the position of the upwelling front.

Population structure and life history characteristics of *N. gouldi* on an inshore jig ground in southeastern Tasmania exhibited significant variability over four years, although patterns were not always consistent for the two sexes, particularly in relative levels of reproductive investment. Abundance was also highly variable over this four year period however there was no clear relationship between biological characteristics and available abundance. Squid in a year of extremely high abundance were a similar size and age to those sampled in years of low abundance; the change in biomass therefore attributed to changes in numbers of squid.

Nototodarus gouldi appear to undertake ontogenetic bathymetric migrations, with squid recruiting to the jig fishery as small juveniles, growing and maturing over the summer before moving away, most likely into deeper waters where large mature individuals are caught by trawlers. A change in sex ratio over the jig season also indicates that males may leave the jig grounds earlier than females. Tracking of *N. gouldi* using an automated acoustic telemetry array also showed that squid moved away from the inshore jig grounds, but this movement was not in any way synchronous, with individuals apparently leaving over an extended time period in the

season of the tracking study- a year of very low abundance. In contrast, the persistence of large mature *N. gouldi* on the jig ground when abundance was extremely high suggests the increased numbers of squid may be due to longer residency times and the accumulation of individuals.

Thus, the ecology of *N. gouldi*, like many other commercially exploited ommastrephid squid, appears to be closely linked to hydrography and ocean productivity. They are in greatest abundance where the shelf break is strongly defined or where other mesoscale oceanographic activity is present (e.g. upwelling), and variability in biomass cycles also appears to be related to the seasonality and nature of local mesoscale oceanography. Further investigations are needed to elucidate the finer-scale variability and detail of the mechanisms driving these patterns. In particular, investigation into the linkages between populations on jig and trawl fishery grounds and the relationship between ontogeny and depth distribution appear to be critical for understanding patterns of distribution and abundance, and for the development of appropriate fishery assessment models.

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Table of Contents

CHAPTER 1.....	1
General Introduction	
 CHAPTER 2.....	 11
Broad-scale spatio-temporal patterns of arrow squid (<i>Nototodarus gouldi</i>) abundance in southeastern Australia: investigation of environmental associations.	
 CHAPTER 3.....	 37
Inter-annual variability in arrow squid (<i>Nototodarus gouldi</i>) abundance in the Bonney upwelling, southern Australia: environmental correlations and predictive models.	
 CHAPTER 4.....	 63
Inter-annual variability in population structure and life history parameters of the arrow squid (<i>Nototodarus gouldi</i>) in southeastern Tasmania, Australia.	
 CHAPTER 5.....	 93
Tracking arrow squid movements with an automated acoustic telemetry system: <i>Nototodarus gouldi</i> in inshore Tasmanian waters	
 CHAPTER 6.....	 110
General Discussion	
 REFERENCES.....	 118
 APPENDIX A.1.....	 139
 APPENDIX A.2.....	 143

Chapter 1:

General Introduction

Life Cycles and Population Ecology of Squid

Although squid generally fill a similar ecological niche to teleost fish, their physiology and life cycle characteristics set them well apart, specifically their short lifespan, rapid growth and development, and phenotypic plasticity (Boyle & Boletzky 1996). Most squid species live for only a year or less (Jackson & O'Dor 2001) and thus the population is made up of new individuals each year. Squid growth is much faster than in similar sized teleost fish (Forsythe & Van Heukelem 1987, Lee 1994), and unlike fish, they do not reach an asymptotic size (Alford & Jackson 1993). This is evident at the cellular level, with squid growing over their entire lifespan by both hypertrophy (increased muscle size) and hyperplasia (addition of new muscle fibres, Moltschaniwskyj 1994, Pecl & Moltschaniwskyj 1999), while teleost fish generally cease hyperplasia with age (Jackson & O'Dor 2001). Squid have exceptionally high growth efficiency, with a protein-based metabolism that rapidly converts energy into growth rather than storage (O'Dor & Webber 1986, Lee 1994, Moltschaniwskyj & Semmens 2000). The metabolic and growth rates of squid are indeed higher than many poikilothermic vertebrates, including most teleost fish, and can in fact be as high as some mammals (Pörtner & Zielinski 1998, Zielinski & Pörtner 2000).

Although genetic variation is relatively low in squid populations, they show a high degree of phenotypic plasticity in all life history characteristics (Boyle & Boletzky 1996). Large intra-specific variability has been documented for egg size and rates of embryonic development (e.g. Steer et al. 2002, Steer et al. 2003a), hatchling size (e.g. Ikeda et al. 1999, Steer et al. 2003b, Pecl et al. 2004a), growth (e.g. Arkhipkin 1996, Pecl 2004, Jackson et al. 2005), age and size at maturity (e.g. Arkhipkin & Laptikhovsky 1994, Boyle et al. 1995, Jackson & Yeatman 1996, Arkhipkin et al. 2000) and reproductive investment (e.g. Pecl 2001, McGrath Steer & Jackson 2004, Smith et al. 2005). Phenotypic plasticity together with a short lifespan and rapid growth mean that squid at the individual, and ultimately population level are extremely responsive to changing environmental conditions. Coupled with the ability to move over considerable distances, these features contribute to the unpredictable and complex patterns of distribution and abundance evident for many squid species (Boyle & Boletzky 1996). Large seasonal, inter-annual and spatial variability in abundance are therefore characteristic features of most squid populations.

Although ageing studies show that many species spawn and hatch year-round (e.g. Arkhipkin et al. 2000, Jackson et al. 2005), biomass production is typically seasonal, with peaks on an annual or bi-annual scale. This may be due to differential survival and growth under seasonally changing environmental conditions, particularly during the early life history stages (O'Dor 1998, Grist & des Clers 1999). Squid hatched in different seasons can have very different biological characteristics (e.g. Jackson 1995, Dawe & Beck 1997, Arkhipkin et al. 2000, Jackson & Moltschaniwskyj 2001b, Pecl & Moltschaniwskyj 2006) and laboratory based experimental studies

have confirmed the importance of both temperature and food availability to rates of growth (Forsythe 1993, Forsythe et al. 2001, Jackson & Moltschaniwskyj 2001a). Later hatched cohorts can grow faster and ‘catch-up’ with the earlier hatched cohorts when exposed to better conditions during the important juvenile stages (e.g. Hatfield et al. 2001, Pecl 2004), ultimately influencing the seasonal timing and relative size of the biomass recruiting to the population (Grist & des Clers 1998, 1999, Reiss et al. 2004).

Without the stability of multiple year classes that longer lived fish populations possess, population size can also vary dramatically from year to year, sometimes by several orders of magnitude (Rodhouse 2001). Annual recruitment is strongly influenced by environmental variability, particularly at the time of hatching (Bakun & Csirke 1998), and environment-recruitment relationships have been described for a wide variety of commercially exploited species including *Illex argentinus* on the Patagonian shelf (Waluda et al. 1999, Waluda et al. 2001a), *I. illecebrosus* in the western Atlantic (Coelho & Rosenberg 1984, Dawe & Warren 1993, Dawe et al. 2000), *Todarodes pacificus* and *Thyanoteuthis rhombus* in the Sea of Japan (Sakurai et al. 2000, Kang et al. 2002, Miyahara et al. 2005), *Dosidicus gigas* in the eastern Pacific (Waluda et al. 2004, Waluda & Rodhouse 2006), *Loligo forbesi* and *L. vulgaris* in the English Channel and North Sea (Robin & Denis 1999, Pierce & Boyle 2003), and *L. gahi* in the southwest Atlantic (Agnew et al. 2000).

The mechanisms by which the environment may control temporal variability in recruitment are however, not always clear. The environmental variables most often examined are those which are most readily available, usually sea surface temperature (SST) and climatic indices such as the North Atlantic or Southern oscillation indices (NAO and SOI). While SST can exert a direct effect on embryonic development (Villanueva 2000a, Boyle et al. 2001, Villanueva et al. 2007) and post-hatching growth rates (Forsythe 1993, 2004), it may also act as a proxy for the productivity of the system or mesoscale dynamics such as the position of a current important for dispersal or prey concentration (e.g. Jackson & Domeier 2003, Roberts 2005, Waluda & Rodhouse 2006). Climatic indices most likely reflect the influence of broad-scale atmospheric circulation patterns on the oceanographic regime (e.g. Dawe et al. 2000, Dawe et al. 2007).

The nature of squid life cycles and their ability to respond rapidly and dramatically to environmental change thus promote considerable temporal variability in abundance, at both seasonal and annual scales. Life history characteristics and population structure have also been shown to vary significantly over geographic scales. For example, Moreno et al. (2005) found that *L. vulgaris* in the eastern Atlantic and Mediterranean varied between locations in mean and maximum length and weight, condition (weight-at-length), size-at-maturity, levels of reproductive investment and the seasonal timing of spawning and recruitment. These differences were attributed to latitudinal changes in temperature, as well as the timing of productivity cycles related to upwelling activity. *Illex coindetti* sampled in several locations in the European Atlantic and Mediterranean (Arvanitidis et al. 2002) and northwest Africa (Arkhipkin 1996) also varied between locations in size-at-recruitment, timing of recruitment, condition, growth rate, maximum size and age, size-at-maturity and maturity structure. Some of these biological indices were correlated with SST and/or chlorophyll-a concentration (Arvanitidis et al. 2002). The timing and magnitude of

squid biomass cycles may therefore also vary between locations in response to the specific local environmental conditions encountered.

Spatio-temporal patterns of biomass for many squid species are further complicated by ontogenetic migrations. Many ommastrephid species, particularly those associated with high energy western boundary current systems (O'Dor & Coelho 1993), undertake large scale migrations between spawning and feeding grounds, often over thousands of kilometres (e.g. *I. argentinus*, Haimovici et al. 1998; *I. illecebrosus*, O'Dor & Dawe 1998; *T. pacificus*, Takami & Suzu-Uchi 1993, Mokrin et al. 2002; *Ommastrephes bartramii*, Bower & Ichii 2005). Loliginid squid undertake smaller scale movements (in the order of a few hundred kilometres or less), usually between feeding grounds in deeper waters and inshore shelf waters where they form dense breeding aggregations (e.g. *L. gahi*, Hatfield et al 1990, Hatfield & Rodhouse 1994; *L. vulgaris reynaudii*, Sauer et al. 2000; *L. forbesi* and *L. vulgaris*, Waluda & Pierce 1998, Sims et al. 2001). These movements, coupled to the timing of the life cycle, dictate the seasonal location of biomass (Boyle & Boletzky 1996), and may vary in timing and nature depending on the local oceanography and environmental conditions. For example, *L. forbesi* in the English Channel migrate earlier in warmer years (Sims et al. 2001), perhaps in relation to precocious maturation (Pierce et al. 2005).

Squid may also display environmental preferences, influencing how the biomass is spatially distributed. For instance the distribution of *I. argentinus* in the southwest Atlantic has been linked to sea surface and bottom temperature and the presence of thermal gradients (Waluda et al. 2001b, Bazzino et al. 2005, Sacau et al. 2005), and for *Loligo* spp. in the North Sea and English Channel a suite of variables including water temperature, salinity, sea level pressure, solar flux and wind direction may be important (Pierce et al. 1998, Waluda & Pierce 1998, Bellido et al. 2001, Denis et al. 2002). Environmental change can influence patterns of distribution and abundance, with range expansions and contractions evident in response to changing SST (e.g. Chen et al. 2006, Zeidberg & Robison 2007). As with recruitment models, the environmental relationships may be indirect in nature, instead reflecting mesoscale activity and/or prey availability (e.g. Ichii et al. 2002), the distribution of different water masses (e.g. Mokrin et al. 2002, Arkhipkin et al. 2004a), or may correlate with a decline in predators (Zeidberg & Robison 2007).

The short lifespan, rapid growth and development, high levels of phenotypic plasticity and mobility of squid all contribute to complex patterns of population ecology. They allow squid to act as ecological opportunists, responding rapidly and dramatically to environmental change, and this has led to terrestrial analogies of desert locusts (Rodhouse 2001) and weeds (O'Dor 1998). However these characteristic features of squid also grossly “exaggerate the difficulties of establishing useful generalizations about populations” (Boyle & Boletzky 1996, p985). Population abundance fluctuates greatly in space and time and this makes the quantification of the role of squid as predators and prey in ecosystem studies and the development of useful assessment and management strategies for commercially exploited stocks extremely difficult.

Traditional stock assessment techniques developed for longer lived fish populations are not relevant to squid, severely limiting the options available for fishery

assessment and management. Understanding the role of squid in the ecosystem is also complicated by their spatio-temporal variability in abundance, although they are clearly an important source of prey to higher predators. The availability of squid can influence the breeding success (Xavier et al. 2003) and distribution patterns (Jaquet & Gendron 2002) of higher predators, and may have a substantial influence on rates of natural mortality and recruitment of prey populations, including many commercially exploited fish (eg. Ivanovic & Brunetti 1994, Boyle & Rodhouse 2005).

This study examines the population ecology of the arrow squid, *Nototodarus gouldi* in southern Australian waters; describing patterns of distribution and abundance and investigating the factors shaping these patterns. Commercial fishing statistics and surveys of *N. gouldi* (JAMARC 1978a, 1978b, 1979, Willcox et al. 2001, Lynch 2004) suggest highly variable spatial and temporal trends in abundance, and while recent investigations have shed light on the life cycle of *N. gouldi* and spatial and seasonal trends in its growth and reproductive strategies (Jackson et al. 2003, McGrath Steer & Jackson 2004, McGrath-Steer 2004, Jackson et al. 2005), little is understood of its ecology, specifically patterns of distribution and abundance. *Nototodarus gouldi* is a key component of the southern Australian continental shelf and slope ecosystem, and spatial and temporal variability in availability may have considerable impacts on both predator and prey populations. *Nototodarus gouldi* also support the largest commercial cephalopod fishery in Australian waters, although industry development and management have been hindered by a lack of understanding of patterns of distribution and abundance.

Review of the biology, ecology and fisheries of *Nototodarus gouldi*

The Indo-Pacific arrow squid genus *Nototodarus* has three species- *N. sloanii* (Gray, 1849) occurring around southern New Zealand; *N. hawaiiensis* (Berry, 1912) broadly distributed in the tropical Indo-Pacific; and *N. gouldi* (McCoy, 1888), the study species, present around northern New Zealand and southern Australia (Dunning & Förch 1998). In Australian waters the distribution of *N. gouldi* ranges from southern Queensland on the east coast and mid Western Australia on the west coast, encompassing all southern coastal waters, including Tasmania (Dunning 1998, Dunning & Förch 1998).

Life Cycle

Nototodarus gouldi appear to live for up to 12 months, with sampled squid having maximum ages of 360 days for females and 325 days for males (Jackson et al. 2005). Female *N. gouldi* are consistently larger in size, reaching a maximum of 393 mm dorsal mantle length (ML) and 1655 g total body weight (BW), while the largest males recorded are only 366 mm ML and 1057 g (Jackson et al. 2003). Mature males have been observed from around 200 mm ML, with most males greater than 280 mm ML fully mature (O'Sullivan & Cullen 1983). Females attain sexual maturity at larger sizes than males, from around 280 mm ML, with most females mature at mantle lengths greater than 320 mm (O'Sullivan & Cullen 1983, Willcox et al 2001). These sizes at maturity are similar to those found for the species in New Zealand waters, where mantle length was shown to be a better determinant of maturity than age (Uozumi 1998).

Ageing studies suggest that *N. gouldi* have a protracted spawning period with hatching taking place throughout the year (Uozumi 1998, Jackson et al. 2005). They appear to be multiple spawners with eggs released in small batches (McGrath & Jackson 2002). Females are mated before they are fully mature and sperm is stored in buccal pouches around the mouth (McGrath & Jackson 2002). Eggs are fertilised as they pass the buccal mass and are transferred to a large pelagic egg 'balloon' (O'Shea et al. 2004). The egg mass is a free floating gelatinous sphere of at least 1.5m in diameter and contains several thousand eggs (O'Shea et al. 2004).

Population ecology

Allozyme electrophoresis on samples of *N. gouldi* collected from 6 locations around southern Australia revealed no evidence of more than a single species (Triantafillos et al. 2004). Allele frequencies were similar for all sites (separated by up to 4300 km) and all polymorphic loci, however the study was somewhat limited by small sample sizes low numbers of genetic markers and alleles per marker. The possibility of some population sub-structuring on the east coast of Australia was suggested and further molecular investigation using microsatellite analysis and/or mitochondrial DNA sequence data are needed to clarify any fine-scale variability in population structure.

Large-scale ontogenetic migrations of many commercially exploited ommastrephid squid are well documented (e.g. *Todarodes pacificus*, Takami & Suzu-Uchi 1993, Mokrin et al. 2002; *I. illecebrosus*, O'Dor & Dawe 1998; *I. argentinus*, Haimovici et al. 1998). However, tag-recapture studies off southeastern Australia (Machida 1983) and western New Zealand (Sato 1985), and studies of population biology (Uozumi 1998, Jackson et al. 2005) provide no evidence of any similar migration by *N. gouldi*. Mature male and female *N. gouldi* have been found at all sampled locations in Australian waters, suggesting that spawning occurs across their entire range (Jackson et al. 2003, Jackson et al. 2005). *Nototodarus gouldi* paralarvae close to the probable size at hatching (0.8 to 1.0 mm ML) have also been collected over a broad area of the Australian continental shelf from southern Queensland to the western Great Australian Bight (Dunning 1985, Dunning & Förch 1998). Spawning in northern New Zealand waters also appears to occur across the entire geographic range of *N. gouldi* (Uozumi 1998).

Size and age structure of *N. gouldi* is complex and highly variable in space and time (Jackson et al. 2005). There is often a mix of several modal groups (Harrison 1979, Machida 1983, O'Sullivan & Cullen 1983), and hatch frequencies from monthly samples off western Victoria suggest up to four main cohorts within a year (Jackson et al. 2003). The southern NSW population appears unique from those sampled elsewhere in Australian waters, with individuals being generally smaller for a given age, and maturing earlier (Winstanley et al. 1983, Jackson et al. 2003).

Little is known of patterns of distribution and abundance except from fishery statistics. *Nototodarus gouldi* is available year round to demersal trawlers fishing in shelf and slope waters and also appear seasonally in shallow coastal waters, where they are targeted by commercial jig fisheries (Winstanley et al. 1983, Willcox et al. 2001). However the jig fisheries are highly localised and seasonal in nature and both catches and catch rates fluctuate greatly between locations and years. The timing of

availability on jig grounds also varies between different locations (Willcox et al. 2001, Lynch 2004, Sahlqvist 2007). Japanese surveys of *N. gouldi* in the 1970s and 1980s covered a much broader area of the shelf than the current jig fisheries, and also found a high level of spatial and temporal variability in availability (JAMARC 1978a, 1978b, 1979). It is not known what drives the variability in abundance of *N. gouldi*, but it is most likely related to oceanographic conditions and prey abundance given that these are important drivers of the distribution and abundance of other ommastrephid squid (Anderson & Rodhouse 2001). Growth rates are also highly variable among locations and seasons, and for female *N. gouldi*, correlated with ocean productivity (Jackson et al. 2003).

Prey & Predators

Stomach contents analyses have shown the diet of *N. gouldi* to consist of small planktonic crustaceans, fish and squids (Machida 1983, O'Sullivan & Cullen 1983, Smith 1983, Uozumi 1998). The relative contribution of crustaceans to the diet was negatively correlated with squid size, while the occurrence of cephalopod prey increased with size (O'Sullivan & Cullen 1983, Uozumi 1998). The fish component of the diet remained constant over all sizes of *N. gouldi* in one study (O'Sullivan & Cullen 1983), but increased in another (Uozumi 1998). The proportion of *N. gouldi* with empty stomachs also increased with size and maturity of both male and female squid (O'Sullivan & Cullen 1983, Uozumi 1998).

In southern Australian samples, pilchards (*Sardinops pilchardus*) and juvenile barracouta (*Leionura atun*) were the most common fish species identified in the diet of *N. gouldi* (Machida 1983, O'Sullivan & Cullen 1983). Crustaceans included *Leptochela sydeniensis* (a carid prawn), *Cirolana* sp. (an isopod), and other unidentified crabs (adults and megalopa larvae), isopods and amphipods. The cephalopod component of the diet was mostly ommastrephid squid and a few unidentified Octopuses. The majority of the squid prey appeared to be conspecifics of considerably smaller size than the predators, and this could not be attributed to post-capture cannibalism (O'Sullivan & Cullen 1983).

Stomach fullness of *N. gouldi* is greatest at night and dawn, and lowest at dusk (O'Sullivan & Cullen 1983, Uozumi 1998), suggesting that *N. gouldi* feed primarily at night. This is consistent with *N. gouldi* behaviour determined from an echo sounding and sonar study in which squid aggregated on the bottom during the day and then dispersed throughout the water column at night (Evans 1986). Jig fishing catch rates are also highest at night (Nowara & Walker 1998), although this is probably related to the use of lights as attractants. Vertical stratification of *N. gouldi* has been suggested, with smaller squid apparently feeding higher in the water column than larger squid (Nowara and Walker 1998), perhaps in response to prey distributions.

Nototodarus gouldi is a key prey species in southern Australia and is consumed in large numbers by many fish (Dunning et al. 1993, Young et al. 1997, Lansdell & Young 2007), birds (Hedd & Gales 2001) and marine mammals (Gales et al. 1993). The contribution of *N. gouldi* to the diet of these higher predators has been found to vary spatially, seasonally and inter-annually. For example, *N. gouldi* was more abundant in east coast swordfish (*Xiphias gladius*) and yellow-fin tuna (*Thunnus*

albacares) diets in winter compared to summer (Lansdell & Young 2007). In southern Australian waters however, Australian and New Zealand fur seals (*Arctocephalus pusillus doriferus* and *A. fosteri*) consumed relatively more *N. gouldi* during summer and autumn months (Gales et al. 1993, Page et al. 2005), although Littnan et al. (2007) found that such seasonal trends also varied between locations and years. Considerable inter-annual variability was also evident in the contribution of *N. gouldi* to the diet of Shy Albatross (*Thalassarche cauta*) during their breeding season off northwestern Tasmania (Hedd & Gales 2001). These spatial, seasonal and inter-annual patterns in the consumption of *N. gouldi* probably reflect the highly variable patterns of *N. gouldi* abundance as well as the foraging behaviour and preferences of the predators.

Commercial Fishery for N. gouldi in Australian waters

The commercial potential of squid resources in Australian waters was first recognised by the Japanese with the Golin Gyukuyo Fishing Company conducting surveys around Tasmania in 1969/70. Several feasibility surveys were then conducted by the Tasmanian Fisheries Division (Harrison 1979, Willcox et al. 2001) and the Japanese Marine Fishery Resources Research Centre (JAMARC 1978a, 1978b, 1979) during the 1970s and 80s. Commercial Japanese, Taiwanese and Korean squid jig vessels also fished Australian waters from 1977 to 1988 under joint venture partnerships with Australian companies, taking up to 8000 tonnes of *N. gouldi* each year from Tasmanian, Victorian and South Australian waters (Sahlqvist 2007). Domestic vessels first geared up for jig fishing in Tasmanian waters in 1972. However, interest levels quickly waned due to variable availability of squid, poor prices and limited market opportunities (Willcox et al. 2001).

The domestic jig fishery in Bass Strait began with just one vessel fishing in the 1986/87 season. Participation and annual catches through the early 1990s were low (a maximum of 17 vessels and 400 tonnes), primarily due to the seasonal and unpredictable availability of squid and relatively high running costs of light-equipped jig vessels (Sahlqvist 2007). A successful season in 1995 (over 1200 tonne) however, rekindled interest in the fishery and up to 40 vessels fished Bass Strait and western Victorian waters in the following two seasons. During the early and mid 1990s there was also small-scale jig fishing in Tasmanian State waters, with up to 17 local operators using hand-lines (Willcox et al. 2001). Following on from the expansion of the Bass Strait fishery in the mid 1990s, there was a rapid increase in the number of vessels fishing in Tasmanian State waters in 1998/99, with the entry of several new jig boats as well as boats usually based on the mainland. Participation in the jig fisheries has however, generally declined since the late 1990s, with less than 30 vessels active since 2000 (Sahlqvist 2007). This is due to the unpredictable nature of the fishery coupled with poor market prices and increasing competition with imported squid product.

All jig fishing for *N. gouldi* is conducted in shallow continental shelf waters, usually less than 150 m depth. There is little by-catch with less than 1% of the catch made up of squid species other than *N. gouldi* (most often *Todarodes filippovae* or *Ommastrephes bartramii*; Sahlqvist 2007). Very little effort is directed outside of the traditional fishing grounds off western Victoria, in Bass Strait and to a lesser degree southeast Tasmania, although reasonable catches are also taken occasionally from

waters off eastern Victoria (Willcox et al. 2001, Lynch 2004, Sahlqvist 2007). This concentration of effort over small discrete areas is unrelated to management restrictions, with the boundaries of the Commonwealth managed fishery (the Southern Squid Jig Fishery, SSJF) extending from southern Queensland (24°30'S) to the South Australian border with Western Australia (129°E), including Tasmanian waters beyond the 3 nautical mile State boundary. The Tasmanian State managed jig fishery has access to all Tasmanian waters within 3 nautical miles from the coastline.

The jig fisheries are highly seasonal with the majority of fishing occurring during the autumn months (February to June) in Bass Strait and western Victoria, and during summer (December to February) in southern Tasmania (Willcox et al. 2001, Lynch 2004, Sahlqvist 2007). Currently, most active jig vessels are based on the mainland where they can access the more reliable Bass Strait grounds, and only venture south to Tasmania when availability is particularly high. Although jig fishing occurs on several spatially (and temporally) discrete fishing grounds, this doesn't necessarily reflect any population structuring. Instead the location of jig fishing grounds has much to do with port locality and the presence of suitable jig ground (i.e. relatively flat and shallow sea floor). *Nototodarus gouldi* are also caught over much of southern Australia and year-round as a by-product by demersal trawl fisheries which operate on deep continental shelf and upper slope grounds, targeting more valuable finfish species (Lynch 2004, Sahlqvist 2007).

Catches of *N. gouldi* have fluctuated greatly from year to year in both the jig and trawl fisheries. Between 1995 and 2007 the Commonwealth managed jig fishery (SSJF) annual catches have fluctuated by a factor of almost 6- from 360 tonnes in 2000 to more than 2000 tonnes in 1997 (Sahlqvist 2007). In Tasmanian waters, jig catches have been even more sporadic, with low catches (0.8 - 12 tonnes) taken in most years, but large peaks occurred in 1999/00 (476 tonnes; Willcox et al. 2001) and more recently in 2006/07 (at least 690 tonnes; J. Lyle *pers. comm.*). Demersal trawl catch is slightly more stable than the jig catches, but has ranged from 315 to 1052 tonnes since 1986 (Sahlqvist 2007). The demersal trawl and jig fisheries do not appear to have any common trend in their annual catch trajectories.

Although the scale of the *N. gouldi* fisheries are small by global squid fishery standards, it is the most important commercially exploited cephalopod in Australia (in volume of catch), and has considerable potential for expansion, at least in terms of effort applied, with less than 30% of the allocated SSJF Statutory Fishing Rights assigned to active vessels in 2006 (J. Davis *pers comm.*).

THESIS STRUCTURE & PRESENTATION

The spatial and temporal variability evident in the availability of *N. gouldi* to commercial fisheries and higher predators in southern Australia prompts the questions: how does the abundance of *N. gouldi* vary in space and time, and what factors might be driving these patterns? This study approaches these questions within a hierarchical framework, investigating the ecology of *N. gouldi* at several spatial and temporal scales. Patterns of *N. gouldi* distribution and abundance are described and links to environmental conditions investigated, firstly over a broad spatial area, and then by focussing on inter-annual variability at a particularly productive location.

This thesis examines if large-scale spatial and seasonal patterns in abundance can be explained by environmental variability, and if annual abundance be predicted from pre-recruitment environmental conditions. Continuing investigations at a smaller spatial scale, this thesis then explores how population biology varies inter-annually and the relationship between population structure, life history characteristics and abundance- are changes in population biomass linked to the biological characteristics of the population? Finally, small-scale movement and activity patterns of *N. gouldi* are examined to provide insight into habitat utilisation and occupancy times in relation to the seasonal availability on an inshore jig ground.

There are four chapters in the body of this thesis, each briefly outlined below. Each chapter has been written as a free-standing research paper and can therefore be read independently without the need to refer back to other areas of the thesis for clarification. However, this has resulted in some repetition between the main chapters, particularly in the introductory sections.

Chapter 2:

Broad-scale spatio-temporal patterns of arrow squid (*Nototodarus gouldi*) abundance in southeastern Australia: investigation of environmental associations.

Little is known of the ecology of *N. gouldi*, so the first step was to describe spatial and seasonal patterns of distribution and abundance in southeastern Australia. Catch and effort data from a demersal trawl fishery were used to calculate the probability of *N. gouldi* (which is a non-targeted by-product) being present in a particular location at a particular time, and the relative abundance when present. Statistical models were used to determine if spatio-temporal patterns could be related to environmental variables. This chapter provided an important basis for the thesis and suggested the appropriate scale and scope for further work.

Chapter 3:

Inter-annual variability in arrow squid (*Nototodarus gouldi*) abundance in the Bonney upwelling, southern Australia: environmental correlations and predictive models.

This chapter builds on chapter 2, by examining inter-annual variability in abundance at one of the most productive locations for *N. gouldi* in southeastern Australia. The aim of this chapter was to investigate if predictive models of *N. gouldi* annual abundance could be developed using a suite of time-lagged environmental variables. As two different fisheries for *N. gouldi* operate in the area, there was the opportunity to compare indices of abundance derived from the two fisheries which generally operate at different depths, and consider the ecological implications of their relationship. This chapter provided important insight into the processes driving variability in available biomass and the potential application of predictive models for forecasting and managing squid fisheries.

Chapter 4:

Inter-annual variability in population structure and life history parameters of *Nototodarus gouldi* in southeastern Tasmania, Australia.

Changes in the available abundance of squid are often attributed to environmental influences and these can also impact on population structure and life history characteristics. This chapter examines inter-annual variability in the population biology of *N. gouldi* collected over 4 seasons (1999/00, 2000/01, 2002/03 and 2003/04) from the same location, and the relationship with annual available abundance which fluctuated greatly in the years sampled. Few studies have examined inter-annual variability in squid population structure and life history characteristics, although seasonal and latitudinal comparisons show that these parameters can vary greatly in response to environmental variability. This study also provides a description of the population biology of *N. gouldi* on an inshore jig fishing ground (in contrast to previous work from trawl caught squid) and discusses the possibility of ontogenetic migrations between jig grounds in shallow continental shelf waters and the trawl grounds in deeper shelf-break and upper slope waters.

Chapter 5:

Tracking arrow squid movements with an automated acoustic telemetry system: *Nototodarus gouldi* in inshore Tasmanian waters.

This study used an acoustic telemetry array to track *N. gouldi* movements and activity patterns in Storm Bay, southeastern Tasmania during the austral summer in 2002/03. The aim of this study was to gain insight into the behaviour of *N. gouldi* when in inshore aggregations, and in particular the movement dynamics of the population and the timing of emigration from the study area. This work contributes to understanding of the seasonal abundance of *N. gouldi* in inshore shelf waters.

Chapter 5 is presented as published:

Stark, K.E., G.D. Jackson, J.M. Lyle (2005). Tracking arrow squid movements with an automated acoustic telemetry system. *Marine Ecology Progress Series* 299: 167-177.

The relative contributions of each co-author are outlined in the Statement of co-authorship (page ii).

A brief overview of the general findings and conclusions of the thesis are provided in **Chapter 6**, along with a discussion of the implications of these findings to our understanding of squid population dynamics, and suggestions for future research.

Chapter 2:

Broad-scale spatio-temporal patterns of arrow squid (*Nototodarus gouldi*) abundance in southeastern Australia: investigation of environmental associations.

INTRODUCTION

Knowledge of spatial and temporal variability in the ecology of species is an important component of population dynamics modelling and thus resource and ecosystem management. In particular, how patterns of distribution and abundance relate to habitat or environmental conditions has long been examined (Andrewartha & Birch 1954, Cushing 1982) and used to generate hypotheses about the processes or mechanisms shaping these patterns (explanatory models), and also for predicting future patterns under changed conditions (predictive models, Guisan & Zimmermann 2000, Austin 2002). Predictive models are becoming increasingly important as issues of climate change and other human induced environmental degradation confront us. Although for forecasting purposes it is not necessary to understand the mechanisms driving such species-environment relationships, without some sound ecological basis we cannot be certain if or when the underlying ecological relationship may break down.

Squid are short-lived ecological opportunists with extreme plasticity in biological parameters and life histories (O'Dor 1998, Boyle & Rodhouse 2005). They display a high degree of responsiveness to environmental conditions, with rates of growth, maturity and reproductive strategies shown to be strongly influenced by spatial and seasonal variability in water temperature and food intake (Forsythe 1993, Villanueva 2000, Jackson & Moltschaniwskyj 2001a, 2001b, Moreno et al. 2005, Pierce et al. 2005, Pecl & Moltschaniwskyj 2006). Given the key role of squid in the marine ecosystem as prey for numerous species of marine mammals, birds and fish, and as a voracious predator of smaller fish and crustaceans, it is becoming increasingly important to understand how their ecological patterns may be affected by environmental change. For instance, the recent range expansion of the Humboldt squid, *Dosidicus gigas* in the eastern North Pacific is thought to be related to increasing water temperatures coupled with a decline in higher predators (Zeidberg & Robison 2007). The ecological impact of this expansion, particularly on other commercially exploited fish such as hake, is causing considerable concern. In contrast, the squid *Loligo forbesi* has disappeared from much of its range in association with increased sea surface temperatures throughout the 1990s (Chen et al. 2006).

Changes to a species distribution not only impact the other species with which they interact or compete, particularly those with longer life-spans and less capacity to respond to environmental change, but also the fishing industries which rely on them. Understanding the relationship between commercially exploited squid and environmental conditions is therefore critical to ecosystem based fishery management and industry development. If environmentally driven spatial or seasonal changes in availability can be predicted, then control measures (such as effort or

catch quotas, spatial and/or seasonal closures) and fishing practises can be adjusted appropriately, and impacts on other species modelled.

The arrow squid, *Nototodarus gouldi*, is the dominant squid species in southern Australian waters and an important prey for many larger fish, birds and marine mammals (Dunning et al. 1993, Gales et al. 1993, Young et al. 1997, Hedd & Gales 2001). They are also commercially exploited, being the target of Australia's largest squid jig fishery and an important by-product in the demersal trawl fishery (Sahlqvist 2007). However commercial and exploratory fishing statistics for *N. gouldi* suggest highly variable patterns of distribution and abundance in waters of southeastern Australia (Machida 1983, Willcox et al. 2001, Lynch 2004). The oceanography of this region is also quite complex with a number of different current systems and mesoscale activity in the form of shelf break fronts, upwelling and eddies.

The two dominant currents around southern Australia are the East Australian Current (EAC) and the Leeuwin Current (LC). The EAC is a western boundary current that brings warm, nutrient poor water poleward from the Coral Sea down the east coast of the Australian mainland and Tasmania. It has a strong seasonal cycle, flowing stronger and extending further south in summer (Ridgeway & Godfrey 1997). The LC is an anomalous poleward flowing eastern boundary current, also carrying warm, nutrient poor waters down the coast of Western Australia. During winter it extends east along the southern Australian coast (where it is sometimes called the South Australian current), and then south down the west coast of Tasmania (the Zeehan current), covering a total distance of 5500 km (Ridgeway & Condie 2004). In summer the flow off southern Australia reverses, and the Flinders Current (FC), a westward flowing northern boundary current, induces summer-autumn upwelling (Lewis 1981, Schahinger 1987, Middleton & Cirano 2002, Middleton & Platov 2003, Kampf et al. 2004). Variability in the direction, timing, spatial extent and intensity of these currents in southeastern Australia creates mesoscale variability in physical environmental parameters such as temperature and primary production. These oceanographic processes may be driving the spatial and seasonal variability in *N. gouldi* ecology, as shown for other ommastrephid squid in similar dynamic environments (Waluda et al. 2001b, Ichii et al. 2002, Bazzino et al. 2005, Sacau et al. 2005, Waluda & Rodhouse 2006).

Without a quantitative understanding of spatio-temporal patterns of *N. gouldi*, fishery development and management is increasingly hindered, and uncertainty regarding their ecosystem role increased. Indeed, one of the highest research priorities identified by the Southern Squid Jig Fishery Management Advisory Committee in 2007 is to understand spatial and temporal distribution patterns of squid populations (P. Domaschensz, *pers comm.*). The southeast region has also been identified as being one of the most vulnerable to climate change in Australia, with models predicting a large increase in sea surface temperature on the east coast as a consequence of increased EAC strength and southward flow, and changes to wind driven circulation, particularly upwelling (McInnes et al. 2003, Hobday et al. 2006a). A dramatic change to ocean stratification is also predicted, with less mixing leading to reduced nutrient supply and therefore declines in primary and secondary production.

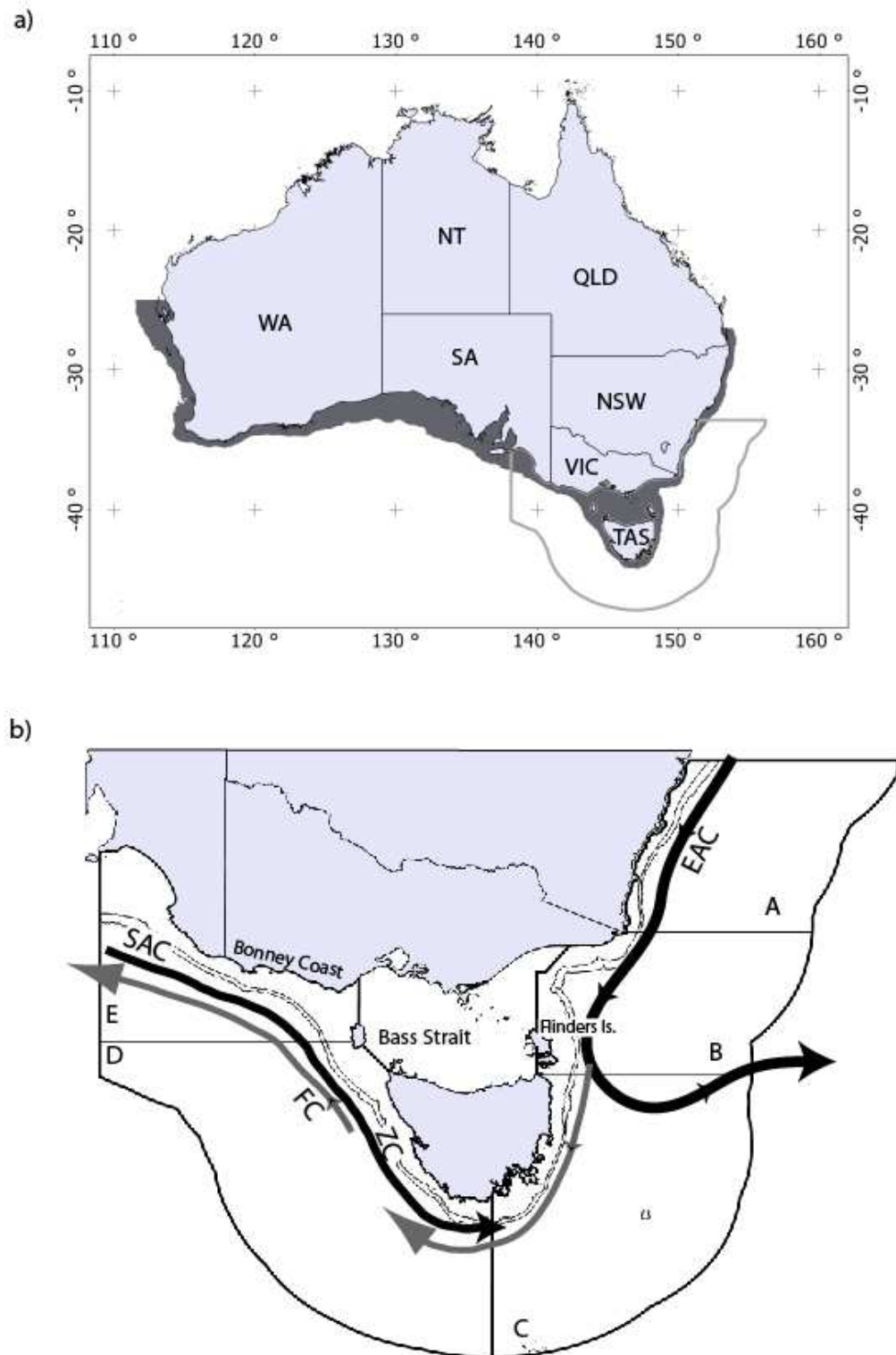


Figure 2.1. Maps of a) the range of *N. gouldi* (dark grey shaded area) in Australian waters, and the study area (outlined). The Australian States and Territories are shown: QLD, Queensland; NSW, New South Wales; VIC, Victoria; TAS, Tasmania; SA, South Australia; WA, Western Australia; NT, Northern Territory. The study area is enlarged in b) showing the trawl fishery boundaries by zone (where A, B & C are in the east region and D & E are in the west region for analyses). Major surface (black arrows) and subsurface currents (grey arrows): SAC is South Australian Current, FC is Flinders Current, ZC is Zeehan current (derived from Leeuwin current), and EAC is East Australian Current. 200 and 1000m depth contours are shown as thin grey lines.

In order to understand how squid might respond to future climate change, an understanding of their current ecology in relation to environmental parameters is required. This study therefore aims to quantitatively describe the spatial and temporal patterns of abundance of *N. gouldi* in southeastern Australian waters, and determine if there is any relationship to local environmental conditions, represented by remotely sensed sea surface temperature (SST) and chlorophyll-a concentration (CHL).

SST is the environmental parameter most often investigated in squid-environment studies as it is easily obtained, and squid have been shown to have strong physiological responses to temperature (e.g. Forsythe 1993, Forsythe et al. 2001). Although the temperature at the sea surface does not necessarily reflect the temperatures that the squid are directly exposed to, data on the conditions within the water column or at the sea bottom are not as readily available. SST is nonetheless an effective proxy for the local environmental conditions experienced by squid, and a useful indicator of mesoscale oceanographic processes (e.g. Waluda et al. 2001a, 2001b, Ichii et al. 2002, Roberts 2005, Waluda & Rodhouse 2006).

In addition to temperature, food availability may have a strong influence on patterns of distribution and abundance. Productivity of lower trophic levels may be an important predictor of squid ecology, especially given their high energy requirements (Wells & Clarke 1996, Webber et al. 2000, Jackson & O'Dor 2001). *Nototodarus gouldi* are opportunistic predators, feeding on a wide variety of fish and small crustaceans (O'Sullivan & Cullen 1983), making empirical data on the availability of prey difficult to obtain. However, remotely sensed surface CHL, as a proxy measure of surface phytoplankton or primary production, are available. Although the relationship between phytoplankton and squid is mediated through several levels of the food web, links between CHL and *N. gouldi* growth (Jackson et al. 2003) suggest it may be a useful parameter to examine.

MATERIALS AND METHODS

Fishery Observer Data

In the absence of fishery independent data on the distribution and abundance of *N. gouldi*, catch and effort data from a demersal trawl fishery observer program were used. Fishery catch-per-unit-effort (CPUE) is assumed to be linearly related to abundance by the classic equation:

$$CPUE = qN \quad (1)$$

where N is the population biomass or abundance, and q is the catchability coefficient and assumed constant.

The trawl sector of the Southern and Eastern Scalefish and Shark Fishery (<http://www.afma.gov.au/fisheries/sess/sess/>) is licensed to fish Commonwealth waters, from the 3 nm limit of State waters out to the 200 nm Exclusive Economic Zone, off southern NSW, Victoria, Tasmania, and eastern South Australia (Figure 2.1). The sector is primarily comprised of demersal otter trawlers, although Danish seining and

mid-water trawling also occur. The fishery targets a suite of valuable finfish species which are quota managed, but also harvests numerous non-quota by-product species, including squid (Tilzey 1994). The Integrated Scientific Monitoring Program (ISMP) is an observer program established by AFMA in 1997, continuing from its predecessor, the Scientific Monitoring Program (1992- 1996; Koopman et al. 2005). ISMP observers carry out on-board monitoring of vessels during normal fishing activities, collecting shot-by-shot details of the trawl position and depth, effort (trawl hours) and weights of all retained and discarded catch, where a shot is an individual trawl. Between 1 and 6 shots are usually undertaken by vessels during a days fishing. Latitude and longitude were used to indicate the specific location where catches occurred, however depth represents the distance to the seafloor, and not necessarily the depth at which the squid were caught as some catches may occur in the water column as the trawl is hauled in.

While the ISMP has less coverage than the full set of commercial fishing logbook data (approximately 2.5% of shots monitored), sampling intensity is still reasonable - between 657 and 957 shots were observed annually from 1998 to 2004. Observer data also has the considerable advantage in that by-catch and catch of non-quota by-product species such as squid are recorded. A much higher proportion of this catch is identified to the species level, and there is greater consistency in the reporting of operational data, such as effort, than in commercial logbooks. The ISMP also provides some level of geographical and seasonal stratification in its sampling design (Knuckey & Gason 2001). For this study ISMP data for demersal trawlers between 1998 and 2004 is used to match the availability of remotely sensed environmental data. This period also avoids potential issues associated with changes in fishing practises prior to and immediately following the introduction of an Individual Transferable Quota (ITQ) management system in 1992 (Baelde 2001).

Although considerably more squid catch is identified to the species level in the observer data (70%) compared to the fisher reported logbook data (22%), there are still a large number of records where squid catch is recorded as a general 'squid' category. The presence or absence of squid in a shot is an essential component of the abundance estimation and thus it is important to distinguish those shots for which *N. gouldi* were definitely absent. *Nototodarus gouldi* accounted for 96% of the identified ISMP squid catch (by weight) between 1998 and 2004, and most likely contributed to a significant component of the unspecified squid catch as well, since both categories were rarely reported in the same shot (only 7 records, <0.1%). As the degree of squid identification is likely to vary between observers, and thus between ports and years, it is not valid to simply disregard the shots with unspecified squid catch, as this could strongly bias estimates of encounter rates (the proportion of shots with *N. gouldi*). Therefore, both *N. gouldi* catch and unspecified squid catches are used for analysis in this study; it is assumed that *N. gouldi* dominate the unspecified squid catches. This introduces a degree of uncertainty in the analyses, and therefore the results generated by the combined *N. gouldi* and unspecified squid catch data were also compared with those from using the *N. gouldi* catch data only (Appendix A.1).

Initial investigations found that the proportion of *N. gouldi* in the total squid catch declined with depth. *Nototodarus gouldi* were not identified in any catches beyond 1000m depth, and the small number of squid catches that occurred in waters between

600 - 1000m were highly influential and resulted in complex multi-modal response functions. Although some of these records were identified as *N. gouldi* (in 20 of 658 shots in waters 600 – 1000m depth; 0.03%), it seems likely that these records may have been misidentifications, as *N. gouldi* is similar in appearance to the deep water inhabiting *Todarodes filippovae*. Data were therefore further restricted to observations in waters 600m or less in depth. Results incorporating the shots between 600 and 1000m depth are presented in Appendix A.2 for comparison.

This depth restriction removed zero catches which are simply outside the known distributional range of *N. gouldi* (the 'naughty naughts' of Austin & Meyers 1996), and reduced the influence of any unidentified deep-sea species within the general squid catches. It also reduced the complexity required in the GLMs. A small number of shots without location (latitude & longitude) or depth data were also excluded, as were any offshore fishing records (generally targeting orange roughy, *Hoplostethus atlanticus* around 250 km from nearest coast).

Due to confidentiality requirements, reporting of logbook information based upon aggregation of less than 5 vessels cannot be shown.

Environmental Data

AVHRR (Advanced Very High Resolution Radar) SST (°C) and SeaWiFS (Sea-Viewing Wide Field-of-view Sensor) sea surface CHL (mg.m⁻³) data were obtained from the CSIRO Marine & Atmospheric Research Remote Sensing Unit (<http://www.marine.csiro.au/remotesensing>), courtesy of Orbimage and the NASA SeaWiFS Project (<http://oceancolor.gsfc.nasa.gov/SeaWiFS>), and accessed via SDODE (Hobday et al. 2006b). SST and CHL data were available as 6 and 7.94 day composites respectively, and aggregated to 0.5 degree spatial resolution. This scale of extraction was selected arbitrarily as a compromise between maintaining fine scale spatial and temporal variation, and reducing noise and the number of missing values due to cloud cover.

Data Analysis

As the trawl fishery rarely targets squid, an approach that takes into account the large number of zero catch observations was necessary. Zero inflation is a common attribute of abundance data, reflecting the patchiness of the environment and/or the inherent heterogeneity of the species concerned (Fletcher et al. 2005). A number of methods are available for dealing with such data, however the simplest is the two-phase approach used here. While mixture models may lead to a better fit when some of the zeros arise from measurement error (Fletcher et al. 2005), the use of observer rather than fisher logbook data in this study should have minimised the recording of false zeros.

Spatial and seasonal trends in (i) the proportion of shots with squid present (encounter rates), (ii) the mean CPUE for shots where squid were present (catch rates), and (iii) the total abundance (calculated from i and ii, see below) were examined by 5 fishing zones (A- E; Figure 2.1), and at a finer 0.5 degree square spatial scale.

CPUE was calculated for each shot as the catch (kg) per hour fished. As catch is recorded in kilograms not numbers, abundance from herein is in reference to weight or biomass. The distribution of CPUE was highly skewed with multiplicative errors, so data were log-transformed prior to analysis. Mean log(CPUE) values were back-transformed after adding $s^2/2$ (where s^2 is the sample variance; Aitchison & Brown 1957).

Total abundance was estimated assuming a Δ -distribution (Aitchison & Brown 1957), taking into account both the log(CPUE) conditional on squid being present, and the probability of squid being caught. The minimum variance unbiased estimators of the mean of the total abundance c , and variance of the mean $\text{var}_{est}c$ were calculated after Pennington (1983, 1996):

$$c = \begin{cases} \frac{m}{n} \exp(\bar{y}) g_m(s^2/2), & m > 1 \\ \frac{x_1}{n}, & m = 1 \\ 0, & m = 0 \end{cases} \quad (2)$$

$$\text{var}_{est} c = \begin{cases} \frac{m}{n} \exp(2\bar{y}) \left\{ \frac{m}{n} g_m^2(s^2/2) - \left(\frac{m-1}{n-1} \right) g_m\left(\frac{m-2}{m-1} s^2\right) \right\}, & m > 1 \\ \left(\frac{x_1}{n} \right)^2, & m = 1 \\ 0, & m = 0 \end{cases} \quad (3)$$

where n is the number of observations, m is the number of non-zero observations, x_i = untransformed CPUE_{*i*}, $y_i = \log(\text{CPUE}_i)$, and \bar{y} and s^2 are the sample mean and variance of y , and $g_m(t)$ is a function of m and t (e.g. $t = s^2/2$ in Eq. 2), defined by:

$$g_m(t) = 1 + \frac{m-1}{m} t + \sum_{j=2}^{\infty} \frac{(m-1)^{2j-1}}{m^j (m+1)(m+3) \dots (m+2j-3)} \times \frac{t^j}{j!} \quad (4)$$

Data were imported into a GIS (Manifold 6.50) and exploratory maps created to examine fine scale (0.5 degree square) spatial patterns. Means were also examined by fishing zone. All CPUE calculations were repeated using *N. gouldi* catch data only for comparison (Appendix A.1). Maps of seasonal patterns cannot be shown at the 0.5 degree spatial scale due to confidentiality requirements, instead seasons were compared graphically between fishing zones only.

Statistical Models

Due to the very different geography (in particular the orientation of the coastline), all statistical analyses were conducted separately for the East and West regions of the fishery, where the East region includes zones A, B and C, and the West region includes zones D & E (Figure 2.1). This was to limit the need for complex non-linear or interaction terms in the description of spatial location using latitude and longitude. Splitting of the analysis by region was also useful for the environmental investigation, where SST and CHL are used as indicators of oceanographic processes. As the two regions are subject to distinct current systems and subsequently quite different mesoscale activity (Figure 2.1), the splitting of the analysis allows different regional response functions for SST and CHL.

Generalized Additive Models (GAMs, Hastie & Tibshirani 1990) and Generalized Linear Models (GLMs, Nelder & McCullagh 1989) were used to quantify relationships between squid and (i) spatial and seasonal covariates (latitude, longitude, depth and month), and (ii) environmental covariates (SST and CHL). As the environmental covariates inherently vary in both space and time, the objective was to determine if they could adequately describe, or account for the spatial and temporal variability in the data within a GAM or GLM framework. Although SST and CHL are surface measurements, they are used as proxies for the conditions the squid are exposed to, and potential indicators of mesoscale oceanographic activity.

The simplest form of a GLM is a linear least squares regression model (*i.e.* with normally distributed errors and identity link), but the GLM family also include models with alternative response distributions (such as gamma, Poisson, or binomial), and more general connections between the linear predictor and the mean response, as defined by the link function (Nelder & McCullagh 1989). GAMs are non-parametric extensions of GLMs (Hastie & Tibshirani 1990). The response variable is modelled as the sum of separate non-parametric functions of each of the predictor variables. While the individual functions of the predictor variables are linear in GLMs, in GAMs they may also be non-parametric smoothing functions, such as regression splines, allowing much more flexible response curves.

GAMs were used here primarily as an exploratory tool, to identify the form of relationships between response and predictor variables. The flexible and data-driven nature of GAMs makes them well suited for this purpose, as they are not constrained to fit predefined parametric shapes as in GLMs. Although this flexibility makes GAMs a popular choice for modelling species–environment relationships, they can often produce complex response functions, and with no retrievable model formula in the classic sense, they can be difficult to interpret ecologically. Parametric response functions in GLMs are often able to capture much of the same variation as a complex GAM function, with a more reasonable ecological explanation (Austin 2002).

A two stage analysis approach was taken with both GAMs and GLMs to account for the two types of data available: the presence/absence of squid and the catch-per-unit-effort of squid given they are present. First the probability of a positive observation, *i.e.* squid being present in a shot, was modelled as a logistic GAM (Eq. 5) or GLM (Eq. 6), with a binomial distribution and logit link function:

$$\ln\left(\frac{p_i}{1-p_i}\right) = \sum_{j=1}^N f_j(x_{ij}) \quad (5)$$

$$\ln\left(\frac{p_i}{1-p_i}\right) = \sum_{j=1}^N \beta_j x_{ij} \quad (6)$$

where p_i is the probability that squid are present in the i -th shot, and x_{ij} are the values of the explanatory variables for the i -th shot. In the GAM (Eq. 5), the f_j are smoothing functions, while for the GLM (Eq. 6) the β_j are the linear coefficients to be estimated. These models are referred to hereafter as the PA-GAM and PA-GLM models (after Presence-Absence).

The CPUE conditional on a positive catch of squid was then modelled with a normal GAM (Eq. 7) or GLM (Eq. 8) on log-transformed CPUE data:

$$\ln(CPUE_i) = \sum_{j=1}^N f_j(x_{ij}) \quad (7)$$

$$\ln(CPUE_i) = \sum_{j=1}^N \alpha_j x_{ij} \quad (8)$$

where $CPUE_i$ is the catch rate (kg.h^{-1}) for the i -th shot, x_{ij} are the values of the explanatory variables for the i -th shot. The f_j (Eq. 7) are smoothing functions, and the α_j (Eq. 8) are the linear coefficients to be estimated. These models are referred to hereafter as the CE-GAM and CE-GLM models (after Catch-per-unit-Effort). CPUE data were log transformed prior to analysis, rather than applying a log link function to the raw data, as errors were multiplicative. CE models were fitted to the combined squid dataset and also the *N. gouldi* dataset (Appendix A.1).

All GAMs and GLMs were done in R version 2.4.1 (R Development Core Team 2007), using penalized regression splines in the mgcv package for GAMs (Wood 2006, 2007). GAM plots were examined to identify the most appropriate parametric response function with which to parameterize GLMs, which were then fitted with the same spatial and seasonal, or environmental predictor variables as linear or second order polynomial terms. Two-way interactions only were allowed in the GLMs, as higher order interactions are difficult to interpret ecologically and their inclusion destabilized many of the models. Where strong correlations occurred between predictor variables, only the variable which provided the best ‘fit’ (see below) was included in models. CHL was log transformed (logCHL) prior to analysis due to a skewed distribution with a few extremely large values. In all models a ‘Year’ factor was included (or made available for selection) to account for potential differences in recruited biomass between years.

The Akaike Information Criterion (AIC, Akaike 1973 cited in Burnham & Anderson 1998) was used to assess model fit for different combinations of predictor variables. As it is rarely feasible to consider all possible covariate combinations (including interactions), some process of predictor variable selection is required. In this study predictor variables were selected via an automated stepwise selection process using

the StepAIC function from the MASS package (Venables & Ripley 2002). A base model with all potential main effects was initially fitted, and then stepwise backward elimination and/or forward selection of main effect and two-way interaction terms applied until an optimal model was reached, i.e. that with the lowest AIC. This selection process was chosen as initial investigations found that the optimal models from this process were more parsimonious (i.e. lower AIC) than those determined from a manual forward stepwise selection process starting with only an intercept term. This is because while some predictor variables could not reduce the AIC when included as a main effect, they could substantially lower the AIC when their interaction terms were considered. Goodness of fit is indicated in all models by the percentage of the null deviance explained by the covariates (Nelder & McCullagh 1989).

RESULTS

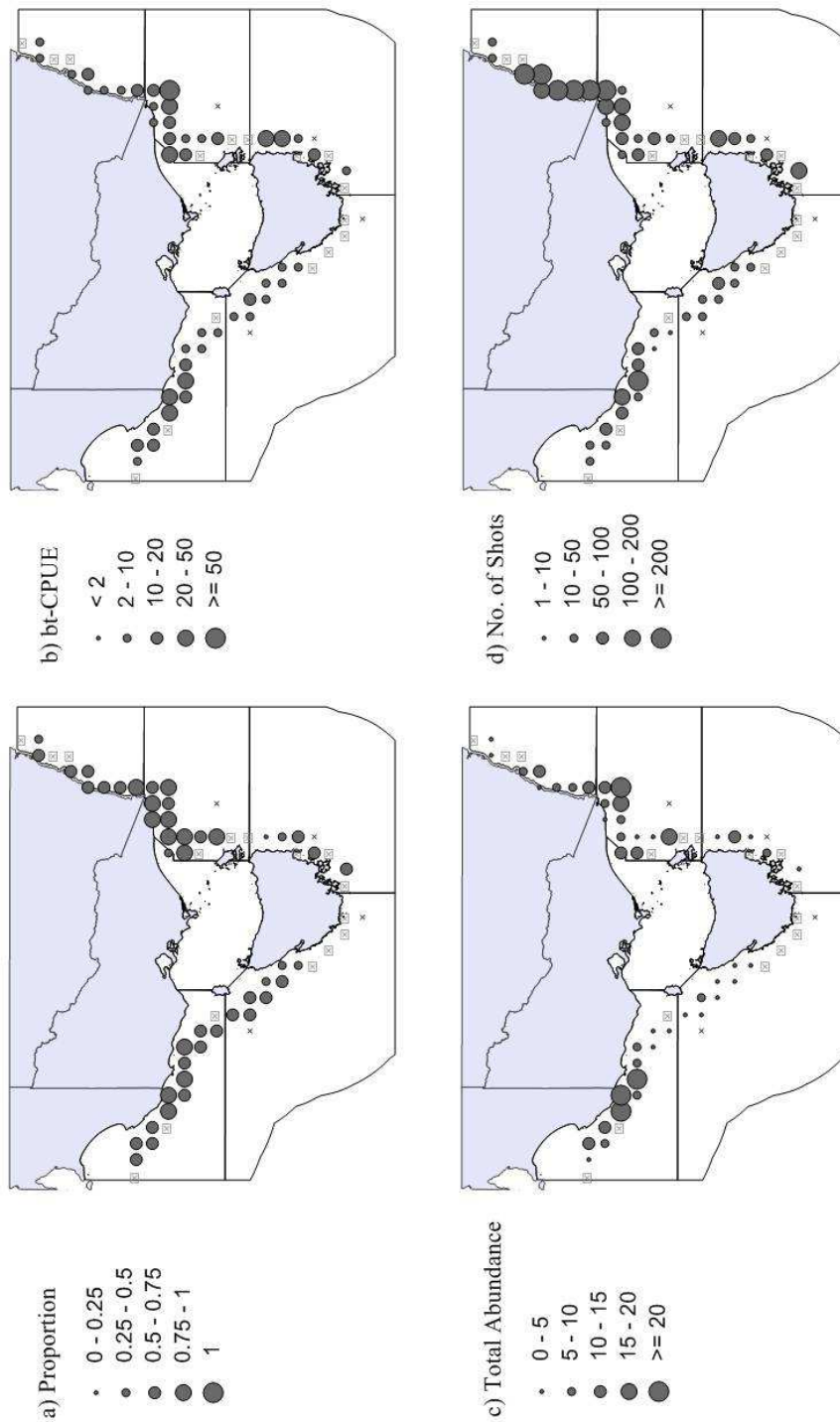
Spatial & seasonal patterns

Squid were present throughout southeast Australian waters, although there was considerable spatial variability in encounter rates (proportion of shots with squid present; Figure 2.2a), catch rates (CPUE when present; Figure 2.2b), total abundance estimates (Figure 2.2c) and sampling intensity (Figure 2.2d). Over all years (1998-2004), encounter rates, catch rates and thus total abundance estimates were highest in waters east and west of Bass Strait (i.e. in zones B & E; Figures 2.2 & 2.3). These areas had large numbers of observed shots (Figure 2.2d), being productive areas for more valuable finfish species and therefore subject to intensive fishing pressure (Larcombe et al. 2001, Prince 2001). Although encounter rates were similar for zones B and E (0.78 and 0.75 shot⁻¹; Figure 2.3a), the mean catch rate in zone E was much higher, particularly in waters near the Victorian and South Australian border (Figure 2.2b). The mean abundance estimate for zone E (18.6 kg.hr⁻¹) was therefore almost double that of zone B (9.8 kg.hr⁻¹, Figure 2.3b). No information is available on abundance of squid within Bass Strait (i.e. between zones B & E), as trawl effort was scarce, although jig fishing for squid does occur in this region (Lynch 2004).

Despite intensive sampling (Figure 2.2d), and a relatively high overall encounter rate (0.70 shot⁻¹), the abundance estimate for NSW waters (zone A; Figure 2.3), was reduced by low catch rates. In waters off eastern Tasmania (zone C) encounter rates were low (0.57 shot⁻¹; Figure 2.3a), however catch rates were quite high, particularly off the north-east coast (Figure 2.2), and the total abundance estimate similar to that for zone A (Figure 2.3b). In western Tasmanian waters (zone D), the encounter rate (0.53 shot⁻¹; Figure 2.3a) was similar to that for eastern Tasmania (zone C), but the mean catch rate was the lowest of all zones, leading to the low estimate of abundance (2.81 kg.hr⁻¹; Figure 2.3b).

There was strong seasonal variability in the distribution and abundance of *N. gouldi*, with a general decline occurring in all zones from autumn to spring, driven primarily by changes in catch rates (Figure 2.4). However the relative magnitude of abundance varied greatly between zones within seasons, with the autumn abundance estimate in zone E almost 3 times as great as that for east coast zones A and B, and 7 times that estimated for Tasmanian waters (zones C & D; Figure 2.4). Abundance during

Figure 2.2. Maps of
a) proportion of shots with squid; b) average CPUE where present (back-transformed; $\text{kg} \cdot \text{hr}^{-1}$); c) average abundance ($\text{kg} \cdot \text{hr}^{-1}$); based on delta distribution unbiased mean estimator, and d) number of shots. All are by 0.5° spatial squares.
☒ denotes data that cannot be shown due to confidentiality
x marks agreement; x marks where zero combined squid catch occurred. Note that scales for symbol size are not necessarily linear.



summer months varied between zones, being low and similar to spring estimates in zones A and E, but high in B and C/D (Figure 2.4). Summer encounter rates, catch rates and abundance estimates for Tasmania were the highest of all four seasons in these two regions (zones C & D; Figure 2.4e & f). This was driven primarily by observations taken on the east coast (zone C), with summer abundance on the west coast (zone D) lower than both autumn and winter (data not shown).

The availability of squid was much more variable in Tasmanian waters compared to other areas, with encounter rates ranging from 0.83 shot⁻¹ in summer to only 0.34 shot⁻¹ during winter (Figure 2.4e). The low winter encounter rates are however, balanced by increased catch rates, suggesting a change in the behaviour of *N. gouldi* in Tasmanian waters during winter.

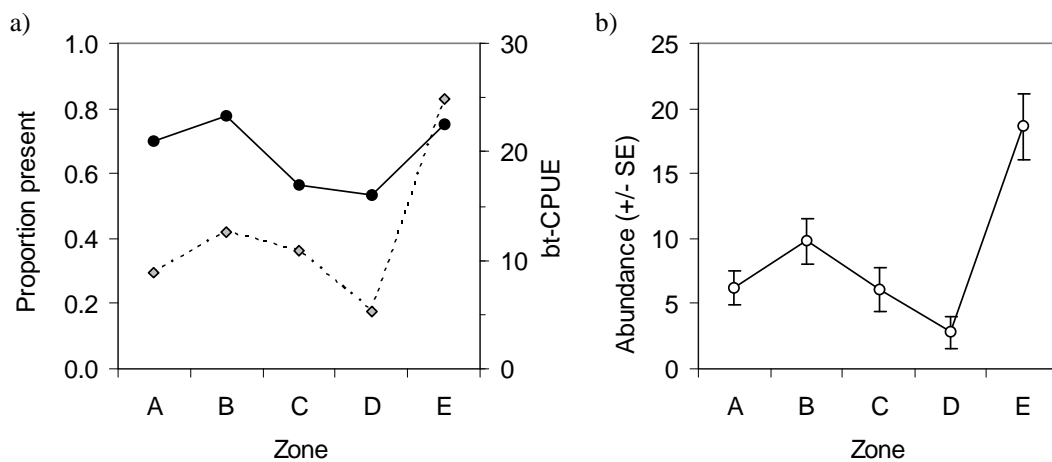


Figure 2.3. Squid abundance by zone: a) proportion of shots with squid present (black line and filled circles), and mean CPUE when present (kg.hr⁻¹) back-transformed from log scale (dashed line and grey diamonds), and b) total abundance of squid (kg.hr⁻¹) with standard error (based on delta distribution unbiased mean estimator). See Figure 2.1 for boundaries of each zone.

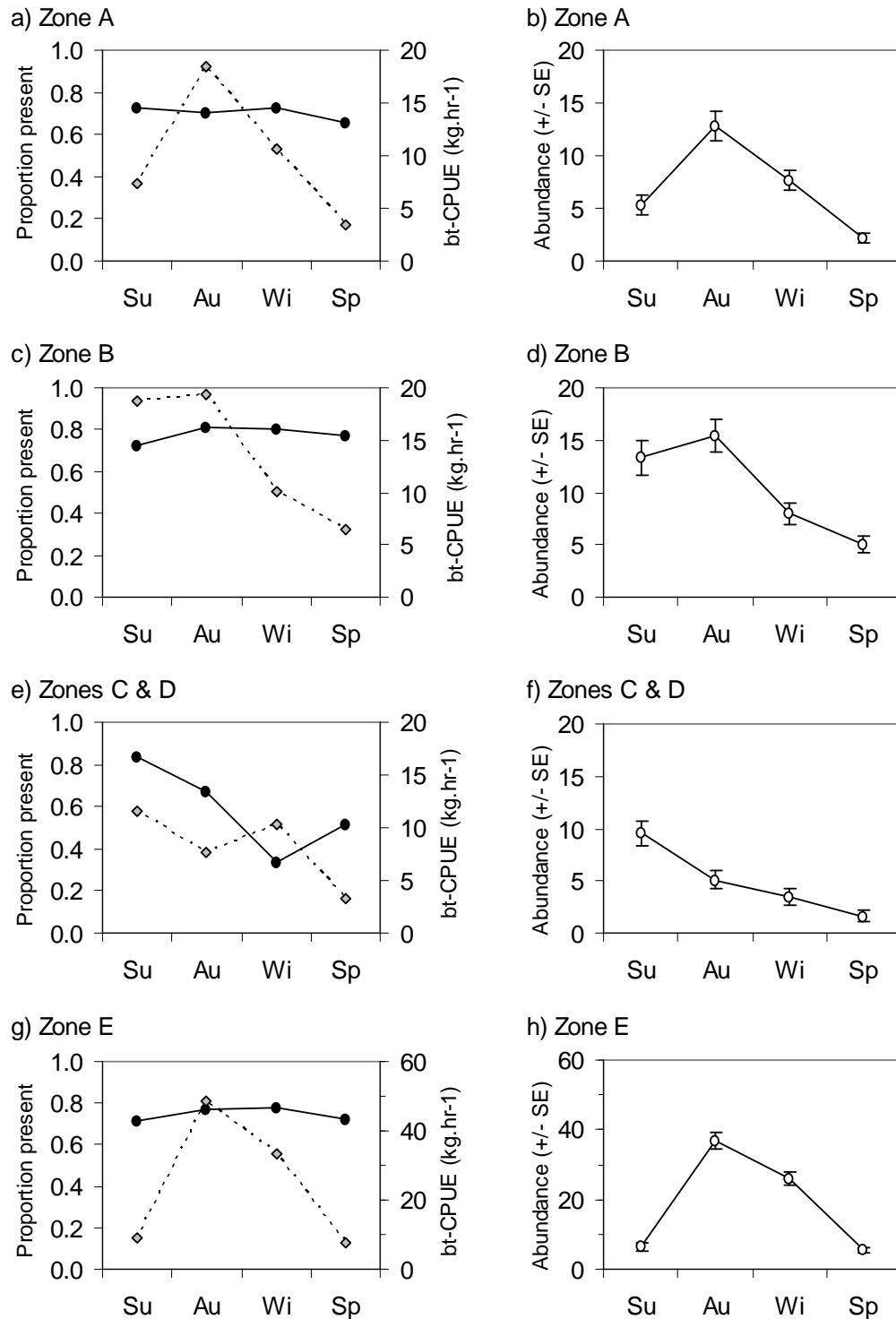


Figure 2.4. Proportion of shots with squid present (black line and filled circles; left graphs), mean CPUE when present (kg.hr⁻¹) back-transformed from log scale (dashed line and grey diamonds; left graphs), and Total Abundance (kg.hr⁻¹; based on delta distribution unbiased mean estimator) with standard error (right graphs), by Season (Su = Summer, Au = Autumn, Wi = Winter, Sp = Spring), and by Zone (a & b- Zone A; c & d- Zone B; e & f- Zones C & D combined due to confidentiality restrictions; g & h- Zone E). SE is standard error. See Figure 2.1 for boundaries of each zone. Note different y-axis scale on g & h.

a. Spatio-temporal Models

GAM plots display the relationship between each of the individual covariates and the response variable in the units of the link function, i.e. log odds for the PA-GAM (presence-absence) models, and log CPUE for the CE-GAM (catch-per-unit-effort) models. Spatio-temporal GAMs, including latitude or longitude, depth and month covariates and a year factor, explained 13.6% and 23.5% of the deviance in the squid PA data, and 27.3% and 58.4% of the deviance in the CE data, for the east and west regions respectively.

Latitude and longitude were highly correlated due to the orientation of the coastline ($r = 0.94$ and -0.96 for east and west regions respectively; $p < 0.001$ for both), and as such only one of the two terms was included in each model. The ‘best’ term (i.e. explaining the most deviance in the data) was latitude for the east region, but longitude for the west region, reflecting the direction of the greatest variability in the data. Both latitude and longitude GAM response functions were non-linear and displayed several small modes or peaks, which were generally consistent in location for the PA and CE-GAM plots, although variable in their relative effect, particularly in the east region (Figures 2.5 & 2.6).

These peaks occurred off the north east coast of Tasmania and Flinders Island ($40.0 - 42.5^\circ\text{S}$), the southeast corner of the mainland ($37.5 - 38.5^\circ\text{S}$), and along the Bonney coast ($140 - 142^\circ\text{E}$). PA and CE-GAM plots display declining encounter and catch rates at the latitudinal extremes of the fishery (Figures 2.5 & 2.6), reflecting the known range of *N. gouldi* (Winstanley et al. 1983, Dunning 1985, 1998), with the northern and southern boundaries of the fishery close to their distributional limits (Figure 2.1).

GAM response functions for depth in the east region were dome shaped, with encounter and catch rates peaking at around 250m (Figure 2.5). In the west region few shots were observed in waters less than 200m depth (only 56 shots; 5%) compared to the east region (2065 shots; 54%), and the west region PA-GAM showed a relatively linear (negative) response to depth (Figure 2.6). In contrast, the CE-GAM plot for the west region displayed a decline in catch rates at depths below around 275m (Figure 2.6), a trend also seen in the east region plots. The inconsistency in depth response functions for the west region PA- and CE- GLMs suggests that there may be a change in the spatial aggregation and/or behaviour of squid in waters less than 275m, although the small number of observations generates considerable uncertainty around this result.

The month covariate displayed very different response functions in the west and east region PA-GAM plots. In the east region, encounter rates varied widely with month, peaking in February and May, and low in March and November (Figure 2.5). The east region CE-GAM plot for month was similar to that for the PA data, with catch rates peaking in May-June, and low in October-November (Figure 2.5). However, the rapid decrease in encounter rates during March was evident as a small dip only in the catch rate response curve. In the west region encounter rates showed much less seasonal variability, declining slowly from January to December, while the CE-GAM

plots showed a small peak in catch rates around June, similar to that in the east region (Figure 2.6).

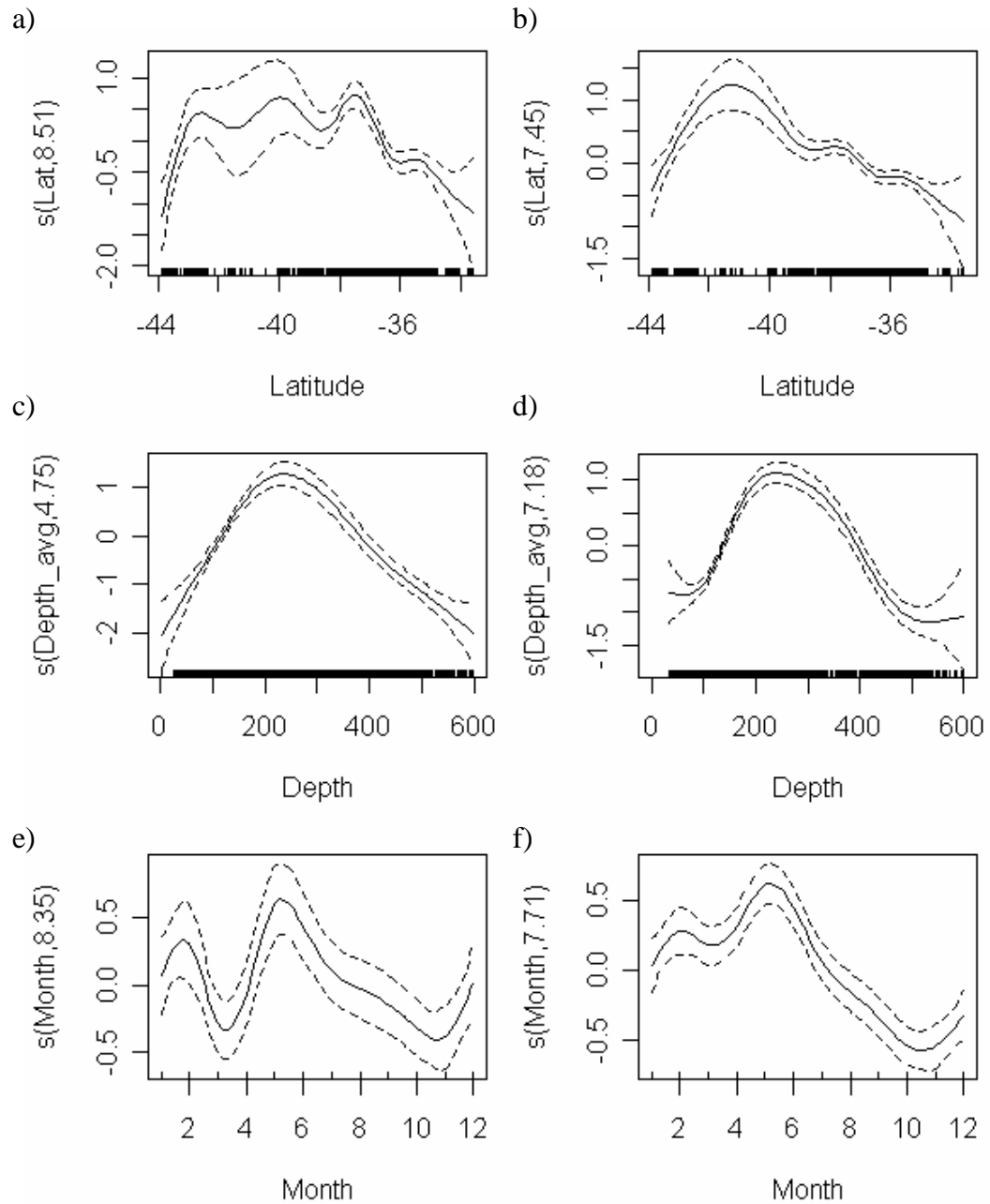


Figure 2.5. East region PA (presence-absence; Figs a, c & e) and CE (catch-per-unit-effort; Figs b, d & f) spatio-temporal GAM plots. Dashed lines are 95% pointwise confidence intervals. Y-axis label includes the approximate degrees of freedom for each covariate. Small markers along the x-axis (rug plot) indicate where observations occurred. Note the different y-axis scales.

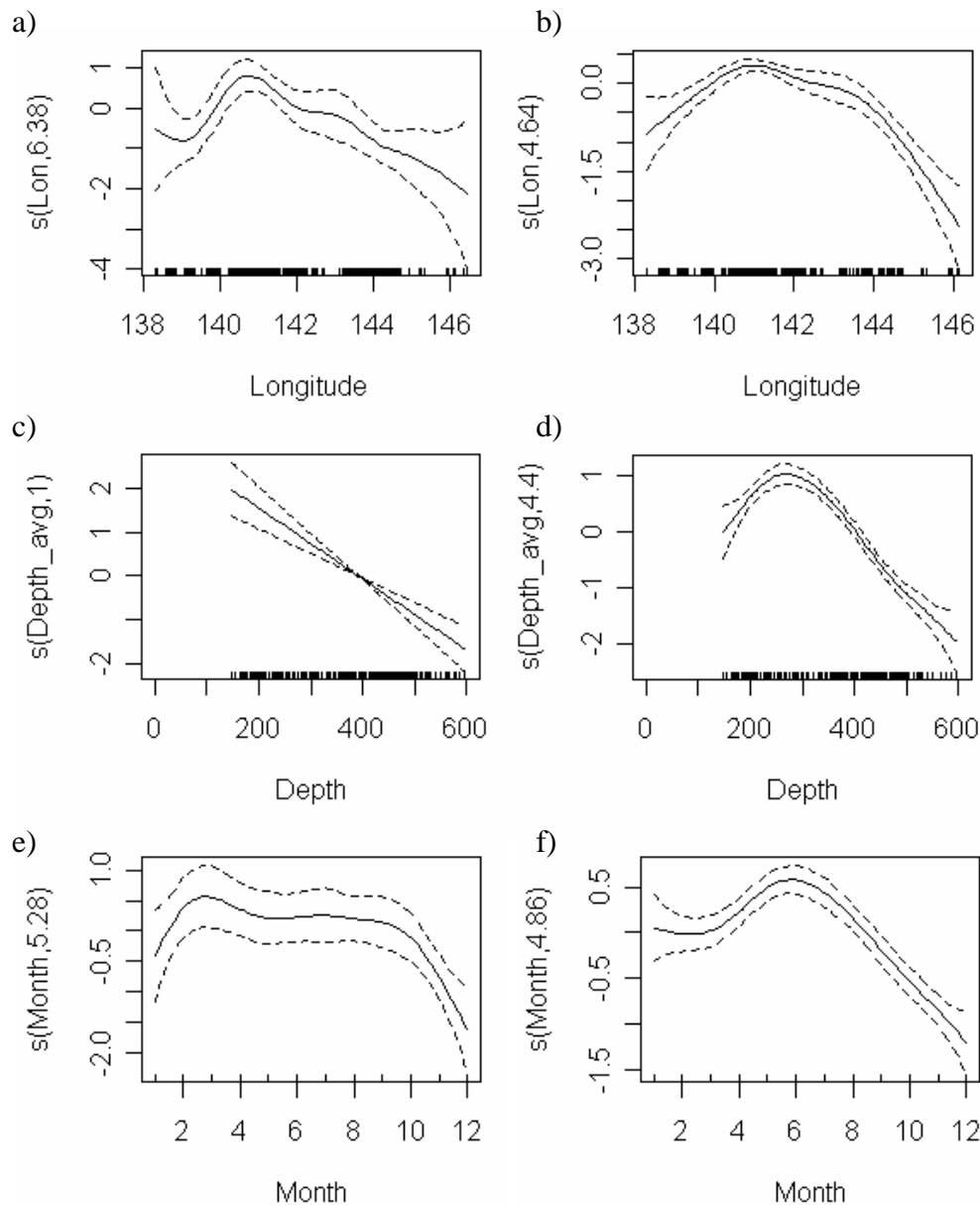


Figure 2.6. West region PA (presence-absence; Figs a, c & e) and CE (catch-per-unit-effort; Figs b, d & f) spatio-temporal GAM plots. Dashed lines are 95% pointwise confidence intervals. Y-axis label includes the approximate degrees of freedom for each covariate. Small markers along the x-axis (rug plot) indicate where observations occurred. Note the different y-axis scales.

b. Environmental models

Environmental predictors could only explain very small amounts of the deviance in the data despite the flexible GAM framework. Only 0.9 and 2.3% of the deviance for the east region PA- and CE-GAMs, and 9.0 and 14.2% for the west region PA- and CE-GAMs respectively were explained by the environmental covariates SST and logCHL. Small peaks in the CE-GAM plots for SST were inconsistent between regions, and PA-GAM plots for SST showed linear effects in opposite directions (Figures 2.7 & 2.8). GAM plots for logCHL were also inconsistent in shape between regions and response variables, however all showed a decline (albeit with large confidence intervals) at large values of logCHL (Figures 2.7 & 2.8).

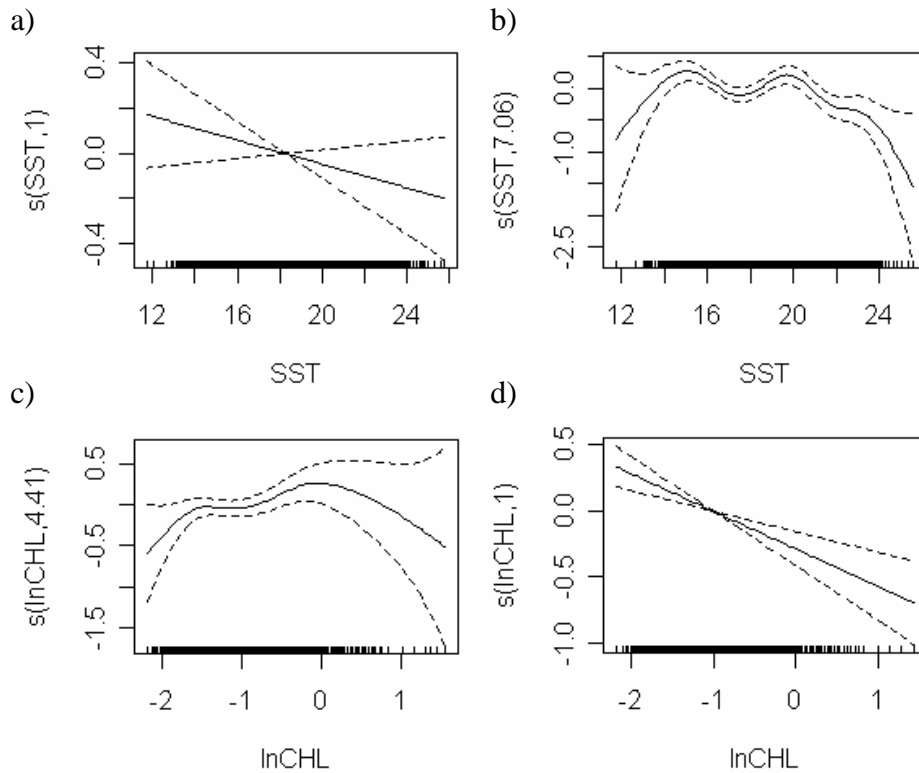


Figure 2.7. East region PA (presence-absence; Figs a & c) and CE (catch-per-unit-effort; Figs b & d) environmental GAM plots. Dashed lines are 95% pointwise confidence intervals. Y-axis label includes the approximate degrees of freedom for each covariate. Small markers along the x-axis (rug plot) indicate where observations occurred. Note the different x and y-axis scales.

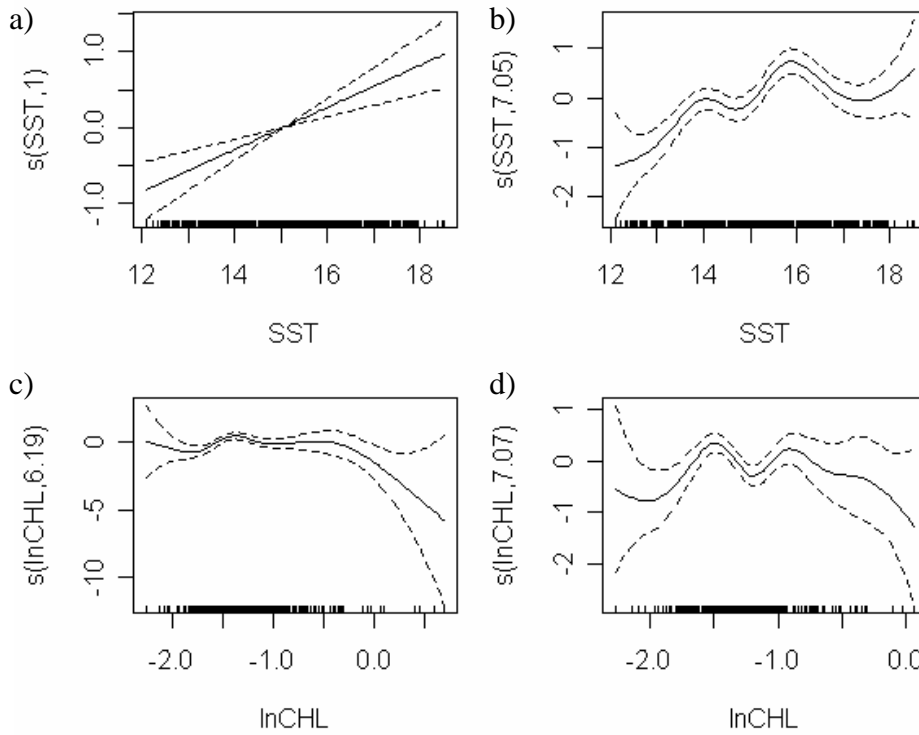


Figure 2.8. West region PA (presence-absence; Figs a & c) and CE (catch-per-unit-effort; Figs b & d) environmental GAM plots. Dashed lines are 95% pointwise confidence intervals. Y-axis label includes the approximate degrees of freedom for each covariate. Small lines along the x-axis (rug plot) indicate where observations occurred. Note the different x and y-axis scales.

GLMs

a. Spatio-temporal Models

All available predictor covariates and all possible two-way interactions were selected for inclusion in the spatio-temporal models by AIC, except in the west region PA-GLM where the only interactions present were those with the year factor (Table 2.1). Latitude, longitude and depth were fitted in all spatio-temporal GLMs as second order polynomial terms, except in the west region PA-GLM where depth was a linear term. Month and Year were modelled as categorical variables.

West region GLMs explained a greater percentage of the deviance than the east region models, and within both regions the CE models explained more than the PA models, however the total null deviance was lower in west region and CE models (Table 2.1). The relative contributions of the spatial and temporal covariates to explaining the deviance varied between the two regions and response variables. In all models interaction terms were important (Table 2.1), reflecting the complex response functions displayed in some GAM plots (Figures 2.5 & 2.6).

Combined spatial covariates (latitude/longitude, depth, and their interaction) generally explained more deviance (11 - 40%) than temporal (year and month and their interaction) covariates (5 - 23%; Table 2.1). Depth was the most important predictor in all spatio-temporal GLMs, its main effect and interactions accounting for

between 14 and 43% of the explained deviance in all models (including depth interactions; Table 2.1). In both regions the month factor and its interactions were more important in the CE models compared to corresponding PA models (Table 2.1). The Year factor explained very little of the deviance as a main effect, but was included as its interactions were important, suggesting that spatial and especially seasonal trends in abundance are changing from year to year (Table 2.1).

b. Environmental Models

SST and logCHL were both entered as second order polynomials, except for logCHL in the east region CE model, and SST in the west region PA-GLM. Only small percentages of deviance were explained by SST and logCHL in the environmental GLMs (Table 2.2), much less than that described by the spatio-temporal GLMs (Table 2.1). Less than 1.5% of the deviance was explained by SST and logCHL in the east region models, with SST not even selected for inclusion in the east region PA-GLM. In the west region slightly more deviance was explained by SST and logCHL, a total of 5.2 and 8.5% for the PA- and CE-GLMs respectively (Table 2.2), however the models still explained considerably less deviance than the spatio-temporal models (Table 2.1).

Table 2.1. Spatio-temporal GLM results for a) east region PA, b) west region PA, c) east region CE, and d) west region CE. In all models depth and latitude/longitude were entered as 2nd order polynomials, except in b) where depth is a linear term. Month and year are categorical variables. Predictors are shown in the order that they were added to the model. See text for explanation of variable selection process.

	Region	Model	Predictor	Df	Deviance	% Deviance Explained		Region	Model	Predictor	Df	Deviance	% Deviance Explained
a)	East	PA	<i>Null Model</i>	3603	4165.7		b)	West	PA	<i>Null Model</i>	914	966.0	
			Depth	2	315.9	7.6				Depth	1	128.9	13.3
			Latitude	2	98.1	2.4				Longitude	2	33.2	3.4
			Month	11	46.4	1.1				Month	11	31.7	3.3
			Year	6	21.4	0.5				Year	6	25.9	2.7
			Depth:Month	22	127.5	3.1				Month:Year	52	116.1	12.0
			Depth:Latitude	4	67.2	1.6				Depth:Year	6	12.6	1.3
			Depth:Year	12	67.7	1.6				<i>Full Model</i>	836	617.7	36.1
			Latitude:Month	22	83.4	2.0							
			Month:Year	64	147.5	3.5							
			Latitude:Year	12	39.9	1.0							
			<i>Full Model</i>	3446	3150.7	24.4							
c)	East	CE	<i>Null Model</i>	2649	6764.1		d)	West	CE	<i>Null Model</i>	712	1712.5	
			Depth	2	983.5	14.5				Depth	2	606.8	35.4
			Latitude	2	177.8	2.6				Longitude	2	60.2	3.5
			Month	11	407.7	6.0				Month	11	194.0	11.3
			Year	6	23.1	0.3				Year	6	105.0	6.1
			Month:Year	64	513.1	7.6				Depth:Month	22	91.2	5.3
			Depth:Year	12	168.4	2.5				Longitude:Month	22	63.8	3.7
			Depth:Latitude	4	85.1	1.3				Month:Year	51	101.9	6.0
			Latitude:Month	22	132.0	2.0				Longitude:Year	12	35.0	2.0
			Depth:Month	22	114.0	1.7				Depth:Longitude	4	11.2	0.7
			Latitude:Year	12	54.7	0.8				Depth:Year	12	19.8	1.2
			<i>Full Model</i>	2492	4104.8	39.3				<i>Full Model</i>	568	423.7	75.3

Table 2.2. Environmental GLM results for a) east region PA, b) west region PA, c) east region CE, and d) west region CE. Predictors are shown in the order that they were added to the model. See text for explanation of variable selection process. 2nd order polynomial terms are indicated by p subscript. Year is a categorical variable (indicated by f subscript).

	Region	Model	Predictor	Df	Deviance	% Deviance Explained		Region	Model	Predictor	Df	Deviance	% Deviance Explained
a)	East	PA	<i>Null Model</i>	3603	4165.7		b)	West	PA	<i>Null Model</i>	914	966.0	
			logCHL _{p}	2	12.8	0.3				SST	1	25.9	2.7
			Year _{f}	6	17.8	0.4				logCHL _{p}	2	19.0	2.0
			<i>Full Model</i>	3595	4135.1	0.7				Year _{f}	6	26.6	2.8
										SST:logCHL _{p}	2	5.7	0.6
										<i>Full Model</i>	903	888.8	8.0
c)	East	CE	<i>Null Model</i>	2649	6764.1		d)	West	CE	<i>Null Model</i>	712	1712.5	
			SST _{p}	2	15.6	0.2				SST _{p}	2	76.3	4.5
			logCHL	1	50.5	0.7				logCHL _{p}	2	10.9	0.6
			SST _{p} :logCHL	2	29.6	0.4				Year _{f}	6	57.8	3.4
			<i>Full Model</i>	2644	6668.5	1.4				SST _{p} :logCHL _{p}	4	58.9	3.4
										<i>Full Model</i>	698	1508.5	11.9

DISCUSSION

Nototodarus gouldi show complex spatial and temporal patterns in abundance, yet very little of this variability could be attributed to environmental conditions, indicated here by SST and CHL. This result was unexpected, as many other squid species show patterns of distribution and abundance closely tied to environmental conditions, including *Illex argentinus* (Waluda et al. 2001b, Bazzino et al. 2005, Sacau et al. 2005), *Dosidicus gigas* (Ichii et al. 2002) and *Loligo* spp. (Pierce et al. 1998, Waluda & Pierce 1998, Bellido et al. 2001, Denis et al. 2002). Either SST and CHL are poor indicators of the variables that drive the spatio-temporal patterns of *N. gouldi* abundance in southeastern Australia, or their influence could not be detected at the broad scale examined using the fishery data and modelling framework applied in this study. In all models spatial and seasonal terms were able to explain considerable amounts of the deviance in the data (from 24 to 75%), however the processes involved in shaping these patterns are not clear.

Applying data from a commercial fishery to ecological analyses should always come with some caveats. The use of CPUE assumes that it is linearly related to abundance and that catchability is constant, yet there are many examples in the literature where this assumption does not hold (e.g. Hilborn & Walters 1987, Harley et al. 2001). There are two main reasons for assuming constant catchability, and hence that CPUE is a reasonable index of abundance in this study. Firstly, the data were from a multi-species fishery that very rarely targets *N. gouldi*, and secondly, analyses have been limited to a subset of years over which management and fishing practises have remained relatively stable (Baelde 2001). It was however, not possible to standardise for differences in catchability between vessels (due to factors such as vessel power, capacity and technology), as the necessary information is not available. Standardising for vessels as a whole (Punt et al. 2000, Maunder & Punt 2004) was not feasible; different vessels tend to fish primarily from one port and thus vessel effects were confounded with spatial effects.

Another potential limitation of the use of fishery dependent data was the poor level of squid species identification, although using observer rather than fisher logbook data greatly increased the proportion identified. The majority of the squid catch that was identified was *N. gouldi* and it was assumed that the species also contributed to the vast majority of the unidentified squid catch. Comparison of the CE-GAM and GLM results with those derived using the subset of identified *N. gouldi* catch data showed very little difference, providing support for this assumption.

Modelling the two components of the catch and effort data separately allows a comparison of covariate effects on the two response functions (i.e. PA and CE), and therefore can provide greater insight into the processes shaping patterns of distribution and abundance. For example, latitudinal peaks evident in the east region GAM plots varied in relative size between presence data and abundance data. While the probability of catching squid was similar for shots at 42°S (eastern Tasmania) and 38°S (eastern Victoria), the catch rate (when present) was considerably greater off Tasmania. The population (size and age) structure of trawl caught *N. gouldi* sampled in two years and seasons from Lakes Entrance (eastern Bass Strait) and Tasmania did not differ greatly in size, age or maturity status (Jackson et al. 2003);

instead spatial arrangement (i.e. tendency to school/aggregate) may explain the difference in catch rates between the two locations. Level of aggregation may vary in response to fine scale abiotic and biotic conditions, in particular the local availability and dispersion of suitable prey.

Effects of month also varied for the two response variables, particularly in the east region for which there was a dramatic decline in encounter rates during March and April, which was not matched in the catch rate response curves. It is unclear what might be responsible for this pattern; it does not appear to correspond to any significant spawning period or other life history event which could affect availability of squid. Fisher behaviour may be responsible for this pattern, but the detail of any such changes is not clear. The effect of month also varied between the two regions, although catch rates peaked in May/June in both CE-GAM plots. This increase in abundance (biomass) during the colder winter months is also reflected in the diet of a major predator- the swordfish (*Xiphias gladius*) caught off the east coast of Australia between approximately 22 and 38°S (Lansdell & Young 2007). Examination of *N. gouldi* abundance by zone however, suggests the nature of seasonal patterns vary over finer spatial scales, and this is accounted for in the GLMs by significant interactions between spatial and month terms.

There was considerable variability in the spatial distribution of *N. gouldi*, with latitude, longitude and depth all important predictors of squid presence and abundance. Depth was the most important spatial predictor in all GLMs, and abundance of *N. gouldi* in both regions peaked near the shelf-break. The shelf-break is a frontal zone, the transition area between the waters of the shelf and the open sea, and usually associated with high biological productivity (Mann & Lazier 1996). Wind forcing can influence the position of the shelf break front, and this may explain the depth by year and month interactions in the GLMs.

The increased encounter and catch rates of *N. gouldi* near the shelf break, coupled with latitudinal and longitudinal trends, suggest that mesoscale oceanographic features play an important role in the ecology of *N. gouldi*. Many marine species have been found to be associated with both coastal and oceanic frontal waters, including cetaceans (Davis et al. 2002, Doniol-Valcroze et al. 2007), turtles (Polovina et al. 2000, 2001), tunas (Royer et al. 2004, Schick et al. 2004), anchovies and sardines (Hansen et al. 2001, Valavanis et al. 2004), and squid (Waluda et al. 2001b, Valavanis et al. 2004). The three areas with highest *N. gouldi* abundance were waters off (i) the Bonney coast (140- 142°E), (ii) far east Victoria (37.5 – 38.5°S) and (iii) northeastern Tasmania and Flinders Island (40 – 42°S), and are all subject to notable mesoscale frontal activity.

In the waters off the Bonney coast, from western Victoria to eastern SA, summer and autumn upwelling events occur, introducing nutrient rich deep water to the shelf (Lewis 1981, Schahinger 1987). Nitrate concentration increases from background levels of 0.1 - 0.9 mmol.m⁻³ up to between 6 and 7 mmol.m⁻³ during upwelling (Lewis 1981). Although the Bonney upwelling does not produce nutrient concentrations of the scale seen in other upwelling systems around the world, it is a highly productive area amongst the typically oligotrophic waters of southern Australia.

In waters east of Bass Strait, a persistent shelf-break front occurs where cool and dense Bass Strait water meets the warmer water of the Tasman Sea and ‘cascades’ down the continental slope (Godfrey et al. 1980, Tomczak 1985, Gibbs et al. 1986, Tomczak Jr 1987, Gibbs et al. 1991). This shelf-break front is a year-round feature, but is most prominent in winter and spring (Tomczak & Tanner 1989, Belkin & Cornillon 2003). Winter concentrations of nitrate in surface waters increase from less than 1 mmol.m⁻³ in Bass Strait, to more than 5 mmol.m⁻³ at the shelf break, and derive from the mixing of deep nutrient rich waters of Sub-Antarctic origin (Gibbs et al. 1986). The process of nutrient enrichment in this area may be driven by the Bass Strait cascade, however the mechanism has not yet been demonstrated conclusively (Gibbs et al. 1991). Summer upwelling has also been described for eastern Victorian waters (Rochford 1979), although satellite images of SST and CHL suggest it is not a consistent feature like the Bonney coast upwelling.

Waters off the east coast of Tasmania are a complex mix of subantarctic and subtropical (EAC) water masses (Harris et al. 1987). The boundary of the two water masses, the subtropical convergence, is a strong frontal zone and its position varies seasonally between northeast and southeast Tasmania (Harris et al. 1987). Off the east coast of Tasmania (ca. 42.5°S), CTD profiles have also indicated the winter presence of a strong shelf break front (perhaps associated with the subtropical convergence) and upwelling was suggested by high nitrate, phosphate and fluorescence levels (Young et al. 1996).

Seasonal and sometimes sporadic jig fisheries for *N. gouldi* (Lynch 2004) also occur in all three of these areas which have been identified as fish production (and hence trawl effort) ‘hotspots’ (Larcombe et al. 2001, Prince 2001).

Mean SST and CHL however, appear to be unable to account for the increased *N. gouldi* encounter and catch rates in these areas. Measures of gradients in SST have been used elsewhere to identify and associate frontal activity with species distributions (Waluda et al. 2001b, Schick et al. 2004, Valavanis et al. 2005), and it is probable that mean SST as examined here is not a useful indicator of this frontal activity. However, the increased productivity generated by the mesoscale activity in these areas should be evident in the CHL data. The lack of a statistical relationship may be primarily attributed to a temporal mismatch, with the timing of peak frontal activity in these hotspots (leading to elevated CHL), not corresponding with the peak seasonal abundance of *N. gouldi* in the same areas. *Nototodarus gouldi* hatch and recruit to the fishery year-round (Jackson et al. 2003, Jackson et al. 2005), however strong month effects and significant interactions with spatial variables in the CE-GLMs indicate that seasonal trends in abundance are regionally specific, as indeed are the seasonal patterns in frontal activity (as described above). This suggests that the processes driving patterns of distribution and abundance may be lagged behind the physical oceanographic changes, or they may be acting on the pre-recruitment life history stages.

For instance, in the California upwelling system a delay of several months has been found between the phytoplankton peak and the ensuing increase in the biomass of zooplankton (Hayward & Venrick 1998). The arrival of large predators (blue whales, *Balaenoptera musculus*) to forage in the region is also delayed to coincide with the zooplankton peak (Croll et al. 2005). As *N. gouldi* feed on a variety of small fish,

crustaceans, and cephalopods, including conspecifics (O'Sullivan & Cullen 1983), it is possible that the mismatch between squid abundance and environmental conditions may be a result of delayed responses by the lower trophic levels which ultimately link *N. gouldi* to the frontal activity. Alternatively this mismatch may be related to environmental influences on the vulnerable pre-recruit life-history stages. Rates of growth and survival during paralarvae and juvenile (pre-recruit) stages are critical determinants of the biomass recruiting to the fishery, and correlations between environmental conditions experienced during these early life stages and the biomass of adult squid have been found for a wide variety of squid species (Robin & Denis 1999, Agnew et al. 2000, Dawe et al. 2000, Waluda et al. 2001a, Georgakarakos et al. 2002, Pierce & Boyle 2003, Waluda et al. 2004, Miyahara et al. 2005).

Frontal activity may not only increase the availability of suitable prey, but also be an important factor in dispersal and transport of the paralarvae and juvenile squid (Bakun & Csirke 1998). *Nototodarus gouldi* that recruit during the peak season off eastern Victoria are hatched over the preceding winter and early spring (June - September, Jackson et al. 2003), and this hatch period coincides with the strongest definition of the Bass Strait front which extends down northeastern Tasmania (Tomczak & Tanner 1989, Belkin & Cornillon 2003). The convergent flow at fronts tend to aggregate phytoplankton and zooplankton (Bakun & Csirke 1998) and are associated with high concentrations of fish larvae (Bjorkstedt et al. 2002, Munk et al. 2003) and squid paralarvae (Leta 1992, Bower et al. 1999, Vecchione 1999, Zeidberg & Hamner 2002, Watanabe et al. 2004). Therefore those squid that hatch during periods of strong frontal activity may subsequently recruit with a greater biomass than those micro-cohorts that hatch at other times of the year, due to the retention of paralarvae and increased availability of food. However, in upwelling systems in particular, there may be a trade-off between the benefits of increased biological productivity and feeding opportunities, as eggs and paralarvae in these high energy zones may be transported offshore, away from preferred waters (Bakun & Csirke 1998), or the physical conditions optimal for growth and development may be compromised (e.g. by the cold water associated with upwelling). This might explain why the main cohort recruiting to the Bonney coast area hatches several months prior to the start of the upwelling season (winter - spring, Jackson et al. 2005).

In all models there were significant spatial and/or seasonal interactions with year. As the oceanographic processes influencing *N. gouldi* ecology vary from year to year in nature and strength, so too will the shape of the response function for the spatial and temporal variables representing those processes. Given the regional variability in the seasonal patterns of *N. gouldi* abundance, and in the timing of mesoscale oceanographic activity, future studies examining lagged environmental relationships on regional scales should provide more insight into the processes driving abundance and at what life history stages these processes are most important.

Chapter 3:

Inter-annual variability in arrow squid (*Nototodarus gouldi*) abundance in the Bonney upwelling, southern Australia: environmental correlations and predictive models.

INTRODUCTION

Squid are an important component of the marine ecosystem; they are voracious predators and a major source of prey for many marine mammals, seabirds, sharks and fish. Squid are also an increasingly important focus of commercial fisheries, with worldwide catches rising significantly in the last few decades relative to more traditional finfish species (Caddy & Rodhouse 1998). However, squid populations often fluctuate greatly in size from year-to-year, showing little evidence of any stock-recruitment relationship (Boyle & Boletzky 1996, Bakun & Csirke 1998). This variability in abundance limits the options for fishery management (Rodhouse 2001), and can lead to significant ecosystem effects. The availability of squid can influence the breeding success (Xavier et al. 2003) and distribution patterns (Jaquet & Gendron 2002) of higher predators, and may have a substantial influence on rates of natural mortality and recruitment of prey populations, including many commercially exploited fish (eg. Ivanovic & Brunetti 1994, Boyle & Rodhouse 2005).

Fluctuations in squid abundance are frequently attributed to the environmental conditions they are exposed to during their life, particularly during the early life history stages. The flexibility inherent in squid life histories allows dramatic individual level responses to environmental conditions. Factors such as ambient temperature and food availability may influence the timing, nature and success of spawning, hatching, growth and reproductive maturity (eg. Forsythe 1993, Jackson & Moltschaniwskyj 2001a, 2001b, Steer et al. 2004). These effects are manifested at the population level as dramatically variable recruitment. Without overlapping generations to dampen effects, annual recruitment determines the abundance of squid resources available to higher predators and fisheries.

Quantifying links between environmental conditions and recruitment can be extremely useful for assessment and management of squid resources, particularly where relationships are lagged and can be utilised in a predictive manner (Agnew et al. 2000, Rodhouse 2001, Agnew et al. 2002). While such relationships are difficult to ascertain in fish because of their long lifespan and the presence of many overlapping generations, tight relationships have been found for many squid species. Abundance has been shown to be closely related to sea surface temperature for a wide range of squid species including *Illex argentinus* on the Patagonian shelf (Waluda et al. 1999, Waluda et al. 2001a), *I. illecebrosus* on the Scotian shelf (Coelho & Rosenberg 1984), *Todarodes pacificus* and *Thyanoteuthis rhombus* in the Sea of Japan (Sakurai et al. 2000, Kang et al. 2002, Miyahara et al. 2005), *Loligo forbesi* and *L. vulgaris* in the English Channel and North Sea (Robin & Denis 1999, Pierce & Boyle 2003), and *L. gahi* in the southwest Atlantic (Agnew et al. 2000). El Niño - Southern Oscillation (ENSO) parameters are also important predictors of squid abundance (Roberts & Sauer 1994, Waluda et al. 1999, Dawe et al. 2000,

Taipe et al. 2001, Ichii et al. 2002, Pierce & Boyle 2003, Waluda et al. 2004, Waluda & Rodhouse 2006), most likely through teleconnections with the local environment. These relationships, although not necessarily providing any understanding of the mechanisms affecting recruitment, are nevertheless useful for management purposes, provided the relationships are maintained over time.

This study aims to investigate the relationship between environmental conditions and temporal patterns of abundance of the arrow squid *Nototodarus gouldi* in Australian waters. *Nototodarus gouldi* is widespread in southern Australian waters from southern Queensland to mid Western Australia. It is one of the most valuable commercially exploited cephalopod species in Australia and an important prey for many fish, birds and marine mammals (Dunning 1993, Gales et al. 1993, Young et al. 1997, Hedd & Gales 2001). *Nototodarus gouldi* has an annual life-cycle and is a multiple spawner with hatching occurring year-round (McGrath & Jackson 2002, Jackson et al. 2003). Large spatial and temporal variability in *N. gouldi* biological parameters has been described, possibly linked to environmental variability (Jackson et al. 2003, McGrath Steer & Jackson 2004, Jackson et al. 2005).

Nototodarus gouldi are distributed over the continental shelf and slope and are genetically well mixed over their range (Triantafillos et al. 2004). No spatial associations with environmental variables have been found, but their abundance is greatest in areas of strong mesoscale frontal activity (Chapter 2) - in waters off eastern Victoria where there is a persistent shelf-break front (Godfrey et al. 1980, Tomczak 1985, Gibbs et al. 1986, Tomczak Jr 1987, Gibbs et al. 1991), and along the Bonney Coast (from western Victoria to eastern South Australia), where austral summer-autumn upwelling events occur (Lewis 1981, Schahinger 1987).

Nototodarus gouldi do not appear to undertake large scale migrations unlike many other ommastrephid squid, but do make seasonal incursions into shallow inshore waters where they are targeted by jig boats (Willcox et al. 2001). In Australian waters, the main jig fishing ground for *N. gouldi*, in terms of the consistency and size of catches, is along the eastern end of the Bonney Coast, and is managed as part of the Southern Squid Jig Fishery (SSJF). *Nototodarus gouldi* are also an important by-product of a demersal trawl fishery (the South Eastern Trawl Fishery; SETF), working the shelf and slope year-round. In both fisheries the annual catches and catch rates fluctuate greatly from year to year (Sahlqvist 2007).

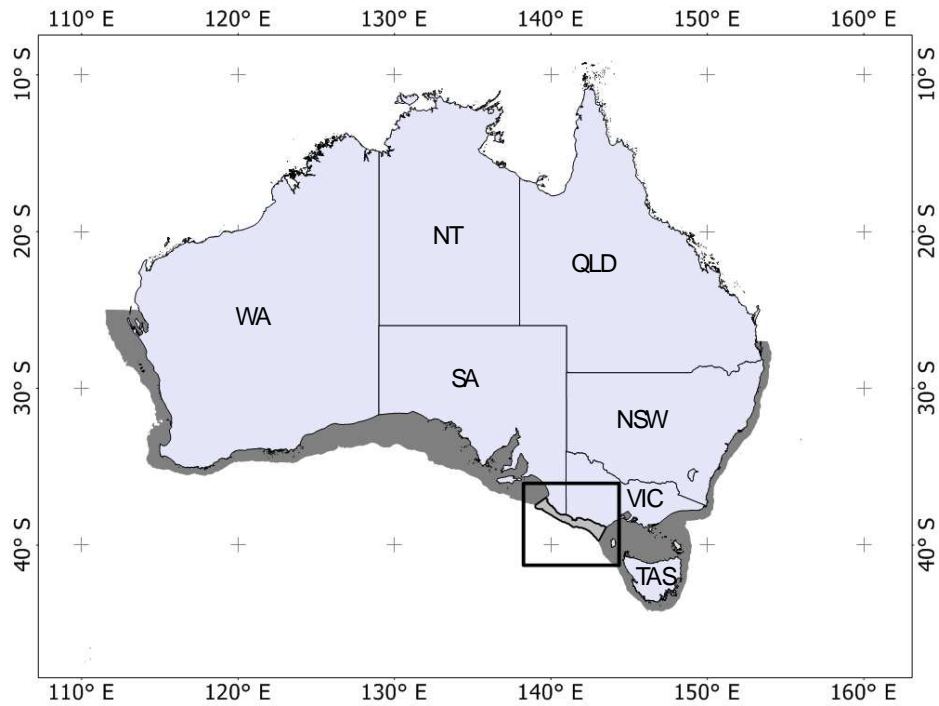
The objective of this study is therefore to explore the relationship between *N. gouldi* abundance and time-lagged environmental variables, and the potential development of predictive models based on these relationships. The Bonney Coast was selected as the focus for this study as it covers the main fishing ground of the jig fishery (Lynch 2004), and also accounts for a significant proportion of the total demersal trawl squid catch (SETF; Chapter 2). Development of predictive models which would give some indication of the relative size of the next year's recruitment would be of great benefit to both industry and managers of the fishery, as well as for use in ecosystem models given *N. gouldi*'s role as an important prey and predator species.

The Bonney coast is an area of dynamic oceanography, subject to seasonal upwelling (Schahinger 1987), which can be highly variable in timing and strength depending on patterns of local wind-forcing. Although the Bonney upwelling does not produce nutrient concentrations of the scale seen in other upwelling systems around the

world, it is a highly productive area amongst the typically oligotrophic waters of southern Australia - a 'hotspot' for commercial fisheries (Prince 2001) and an important feeding ground for higher predators including blue whales (Gill 2002, 2004).

Fishing effort has occurred consistently and at quite high levels in the Bonney Coast area over the history of both the jig and trawl fisheries, and thus provides an opportunity to compare predictive models developed from two independent time series of abundance, where abundance is inferred from fishery catch and effort data. While there is some spatial overlap of the two fisheries, they primarily operate over different depth ranges: jig vessels in shelf waters 50 - 150m depth, and demersal trawlers largely over the shelf edge and slope (greater than 200m depth). Other regions of southeastern Australia are subject to relatively low and irregular activity by the jig fishery in particular, and could not provide such useful time series of abundance estimates. In any case, the stock structure of *N. gouldi* in southeastern Australian waters is uncertain (Triantafillos et al. 2004), and larger scale spatio-temporal models of *N. gouldi* abundance (derived from trawl fishery data) around southeastern Australia (Chapter 2), show that seasonal (intra-) and inter-annual patterns are dependent on spatial location. It is thus appropriate to examine temporal trends on a smaller spatial scale as done here, rather than over the entire fishery area.

a)



b)

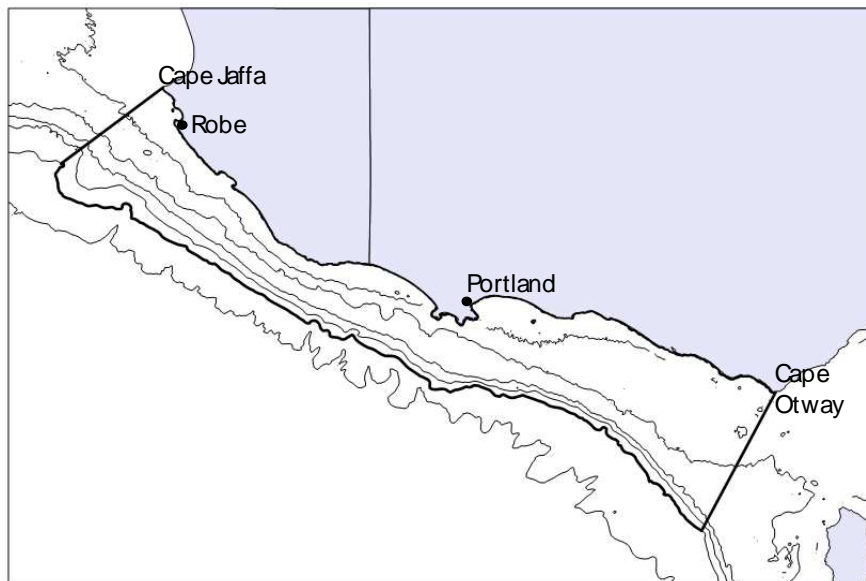


Figure 3.1. Maps of a) the range of *N. gouldi* (grey shaded area) in Australian waters, and the study area (Bonney coast; light grey area). The Australian States and Territories are shown: QLD, Queensland; NSW, New South Wales; VIC, Victoria; TAS, Tasmania; SA, South Australia; WA, Western Australia; NT, Northern Territory. The boxed area is enlarged in b) showing the study site boundaries, and the 50, 100, 200, 500, 1000 and 2000m depth contours as thin grey lines.

MATERIALS AND METHODS

Study Area

The Bonney coast is defined as that extending from Cape Jaffa to Cape Otway in southern Australia (Figure 3.1). The boundaries used to define the study area were based on the geography of the area and the distribution of fishing effort (see below), and are roughly perpendicular to the coastline and depth contours.

Fishery data

Commercial logbook data from the Southern Squid Jig Fishery (SSJF) and the trawl sector of the Southern and Eastern Scalefish and Shark Fishery (SETF) were provided by the Australian Fisheries Management Authority (AFMA) Data Section. Fishers are required to fill in daily logbooks providing details of their catch weight and composition, effort (hours fished), and the location of fishing (latitude & longitude). Data were extracted for the Bonney Coast study area only (Figure 3.1), and were available from 1996 to 2005 for the jig fishery, and from 1986 to 2005 for the trawl fishery. Only records where ‘normal fishing activity’ occurred were used. Records were excluded if effort was not recorded or greater than 24 hours. In the jig fishery a small number of zero catch records (~1%) were also excluded from all analyses as they had virtually no influence on the annual mean CPUE and their exclusion allowed a simpler standardisation model (see below). Zero catch records were however retained in the trawl dataset as squid are a by-catch in this fishery and the probability of squid being caught is an important component of the abundance estimation. For both fisheries CPUE was calculated as the catch (kg) per hour fished.

In the trawl fishery logbooks a significant component of the squid catch is unidentified and recorded only as ‘squid’. Examination of the species composition of squid catches in observer data (Koopman et al. 2005, Chapter 2) suggests that *N. gouldi* accounts for the vast majority of squid catches in the Bonney Coast area. Thus the total squid catch for each record was taken as that recorded as either arrow squid or a general (unspecified) squid category. If catches were recorded for both categories in a single record, only those specifically for arrow squid were included.

Due to the seasonality of the fishery, jig data were restricted to between February and July. Very little jig activity occurs on the Bonney coast outside this period and any catches are likely to be opportunistic and unlikely to be representative of true abundance. Considerable effort is however expended year round by demersal trawl operators in the Bonney Coast region, and catches of squid, although relatively low, do occur outside the February to July period. Thus standardised total abundance for the trawl fishery was calculated using data from all months of the year. Trawl standardisation models based on February to July only, as for the jig fishery, did not fit well, but indices were highly correlated with those from the full-data models (see below).

Environmental data

Two measures of ENSO activity were investigated. The Southern Oscillation Index (SOI) measures the atmospheric component of ENSO activity and is the standardized

pressure difference between Tahiti and Darwin. Sustained negative values of the SOI often indicate El Niño episodes, which usually occur every 2 - 7 years. Sustained positive values of the SOI are known as La Niña episodes. The Niño3.4 index (NINO) is an oceanic based measure of El Niño/La Niña activity and is the sea surface temperature anomaly for the tropical Pacific region between 5°N - 5°S and 120°W - 179°W. A sustained positive anomaly indicates an El Niño episode. The mean monthly and annual values of the SOI and the Niño3.4 index were obtained from the Climate Prediction Centre (<http://www.cpc.ncep.noaa.gov>).

Remotely sensed sea surface temperature (SST; °C) data were obtained from the NOAA-CIRES Climate Diagnostics Center (<http://www.cdc.noaa.gov>, Reynolds et al. 2002). Monthly SST (1982- 2006) values were obtained for all 1° grid squares which overlapped the Bonney coast study area. The proportion of the study area covered by each grid square was calculated in a GIS and weighted mean monthly and annual SST anomalies for the whole area calculated.

SeaWiFs (Sea-Viewing Wide Field-of-view Sensor) sea surface chlorophyll-a concentration (CHL; mg/m³) data were obtained from the CSIRO Marine and Atmospheric Research Remote Sensing Unit (www.marine.csiro.au/remotesensing), courtesy of Orbimage and the NASA SeaWiFS Project (<http://oceancolor.gsfc.nasa.gov/SeaWiFS>), and accessed via SDODE (Hobday et al. 2006b). CHL data were extracted as 7.94 day composites, averaged over the Bonney coast study area (Figure 3.1), and were available for every 6-12 day period from September 1997 only. Composites were converted to daily values and mean monthly and annual anomalies were calculated using 1998 - 2005 as the base period. For days where no composite was available, values were interpolated by taking the average of the two closest days where composites were available.

Water mass circulation along the Bonney coast is primarily the result of wind forcing (Middleton & Platov 2003, Cirano & Middleton 2004), so several wind parameters were also examined as potential predictors of *N. gouldi* abundance. Sea level is tightly linked to circulation and currents and may also be a useful indicator of upwelling activity. Monthly sea level (SL) data at Portland, and daily wind speed and direction data for Robe and Portland (Cashmore airport) were obtained from the Bureau of Meteorology (www.bom.gov.au). Sea level data were available from July 1991, and wind data from January 1985. Monthly and annual anomalies were calculated using 1992- 2005 as the base period. Wind data from both sites were used as they were not strongly correlated.

Moon phase data, as fraction of the moon illuminated, were obtained for every SSJF fishing day from the Astronomical Applications Department of the US Naval Observatory (<http://aa.usno.navy.mil/>) for use in standardisation models.

Standardisation of CPUE

In the absence of any fishery-independent data on the abundance of *N. gouldi*, commercial catch rates (catch-per-unit-effort, CPUE) were used. As catch is recorded in kilograms not numbers, reference to abundance hereafter relates to weight.

CPUE is assumed to be linearly related to abundance by the classic equation:

$$CPUE = qN \quad (1)$$

where N is the population biomass or abundance, and q is the catchability coefficient- a fixed constant of proportionality which is related to fishing efficiency. If q is constant through time (or known), CPUE is theoretically a useful measure of N . Catchability, however, usually varies through time, primarily as a result of variable fishing practises: changes in when, where, how and who fishes. Standardisation of CPUE using generalised linear models (GLMs) attempts to remove some of the variability in q (i.e. that variability in the CPUE series which is not a consequence of changes in population size), and produce a more meaningful index of abundance (Maunder & Punt 2004). By including variables which influence catchability in the statistical model, we are able to remove their influence and extract a more reliable annual (or monthly, bi-annual etc) index of abundance.

a. Model Structure

As squid are rarely targeted in the trawl fishery, there are a large number of records with zero squid catch. To incorporate this information into the abundance estimates a two stage or ‘delta’ GLM approach was used (Lo et al. 1992, Stefansson 1996). First the probability of a positive observation, i.e. squid being present in a shot, was modelled as a binomial GLM with a logit link function:

$$\ln\left(\frac{p_i}{1-p_i}\right) = \sum_{j=1}^N \beta_j x_{ij} \quad (2)$$

where p_i is the probability that squid are present in the i -th shot, and x_{ij} are the values of the explanatory variables for the i -th shot and the β_j are the coefficients to be estimated. This trawl presence-absence model is referred to hereafter as the T-PA model.

Secondly, the CPUE conditioned on a positive catch of squid, was modelled with a normal GLM on log-transformed CPUE data:

$$\ln(CPUE_i) = \sum_{j=1}^N \alpha_j x_{ij} \quad (3)$$

where $CPUE_i$ is the catch rate (kg/h) for the i -th shot, x_{ij} are the values of the explanatory variables for the i -th shot and the α_j are the coefficients to be estimated. The log-transformation of CPUE was required as data were highly skewed with many small values and few extremely large values. This trawl catch-per-unit-effort model is referred to hereafter as the T-CE model.

The standardised overall year effect for the trawl fishery (std-trawl), as a proxy for the annual total abundance, was calculated from the product of the Year coefficients from the two GLMs (T-PA and T-CE) transformed back onto the original scale. For back-transformation all other predictor variables were set to zero, indicating ‘average’ levels, as all continuous predictors in the standardisation models were

centred, and an ‘average’ vessel (based on effort) used as the reference level of the Vessel factor (see below). The expected probability (back-transformed from logit) of a non-zero catch in year t is therefore

$$E(p_t) = \frac{\exp(\beta_0 + \gamma_t)}{1 + \exp(\beta_0 + \gamma_t)} \quad (4)$$

where p_t is the probability of a non-zero catch in year t , β_0 is the intercept and γ_t is the Year coefficient for year t .

For the lognormal model the expected back-transformed year effect is simply

$$E(CPUE_t) = \exp(\gamma_t + \sigma_t^2 / 2) \quad (5)$$

where γ_t is the Year coefficient for year t and σ_t its standard error.

Total standardised trawl fishery derived abundance (std-trawl) for year t is therefore calculated as $p_t \cdot CPUE_t$.

For the jig fishery the small number of zero catch records (~1%) were excluded from analysis and only the CPUE data for positive catches were used to obtain an index of abundance. Examination of model diagnostics (Nelder & McCullagh 1989, Ortiz & Arocha 2004) suggested a GLM with a gamma error distribution and log link on untransformed CPUE data was more suitable than the normal GLM on log transformed data as used for the T-CE model. The back-transformed annual abundance series (std-jig) was simply the exponential of the year coefficients (i.e. $\exp(\gamma_t)$).

All standardisations were done in R version 2.4.1 using the glm function (R Development Core Team 2007).

b. Predictor Variables

The variables examined for inclusion in the standardisation models were: month, vessel, moon phase, several spatial co-ordinates and effort. Month was entered as a continuous covariate to account for any seasonal changes in fishing behaviour from year to year. Spatial co-ordinates were included as either latitude and longitude or the principal components of these two variables. Latitude and longitude were highly correlated in their raw state due to the orientation of the coastline. Therefore the first principal component represents the position along the coastline, while the second is the position out from, or perpendicular to the coast. Moon is the fraction of the moon illuminated, a continuous variable to account for potential catchability changes with moon phase in the jig fishery. As jig vessels rely on artificial lighting to attract squid, it is hypothesized that catchability would be lower during periods of high illumination (e.g. full moon), but higher around a new moon. Effort (hours fished) was also included as a potential explanatory variable in the T-PA models.

Vessel is a unique vessel identification code, and used as a proxy for all potential vessel effects. It accounts for differences in catchability between vessels, due to

variability in characteristics such as size, hold capacity, engine power, technology (including lighting) and amount of fishing gear, as well as skipper skill and experience. Sixty-four separate jig vessels have fished in the Bonney coast region during the 10 years of available logbook data, and 86 vessels over 20 years in the trawl fishery. To reduce variation in the CPUE time series due to inexperienced and opportunistic fishers, and to avoid over-parameterization of regression models, the datasets used for analysis were restricted to certain ‘indicative’ vessels only (e.g. Punt et al 2000). Vessel selection for the jig fishery was based on the number of years in which the vessel recorded a catch in the Bonney coast region (≥ 3 years), the total number of catch records in the region of interest (≥ 50), and the median number of catch records (days fishing) per year (≥ 18). This resulted in 31 vessels being selected for the jig analysis. For the trawl analysis only vessels which had fished on the Bonney Coast for 5 or more of the 20 years were used: 38 vessels. This substantially reduced the number of Vessel parameters required in the regression models, without sacrificing much information: the ‘indicator’ vessels still accounted for 84% and 94% of the total Bonney coast catch in the jig and trawl fisheries respectively, and exclusion of the other vessels made very little difference to the CPUE series.

c. Model Fitting & Selection

Predictor variables were added manually in a forward stepwise manner and model fits compared using both the Akaike Information Criterion (AIC, Akaike 1973 cited in Burnham & Anderson 1998) and the magnitude of change in residual deviance (relative to the null deviance). Explanatory variables were therefore included if they reduced AIC *and* reduced relative residual deviance by 1% or more, as with large datasets such as these, the AIC on its own has a tendency to overfit. AIC weights (AIC_w , Burnham & Anderson 2002) were used as a measure of the relative support for each of the models fit to the data. The AIC_w of all models examined sums to 1, and thus can be interpreted as the weight of evidence for each model being the best from the set of models tested. All continuous variables were centred around their mean before analysis. Second order polynomials were allowed for continuous variables where they provided a better fit. A Year factor was also necessary in all models in order to obtain the annual coefficients of abundance.

Links between trawl and jig fishery derived time series of total abundance.

Pearson correlation coefficients were calculated for the two standardised abundance time series, std-trawl and std-jig. 95% confidence intervals on the correlation coefficients were calculated with the boot library in R using the adjusted bootstrap percentile (BCa) method (Davison & Hinkley 1997).

*Links between *N. gouldi* abundance and environmental variables.*

The std-trawl and std-jig time series were correlated with the environmental conditions of the previous year. Analyses were conducted using both annual and monthly mean environmental parameters (Table 3.1). Bootstrap 95% confidence intervals were calculated for all correlation coefficients to determine the significance of the relationships. Simple linear regression models were then built (in R with the lm function) only allowing environmental variables which were significantly

correlated with the standardised abundance time series as potential predictor variables.

Auto-correlation in the residuals was examined using full and partial auto-correlation function (ACF and PACF) plots. Where residual correlation was significant, autoregressive models were applied using the `gls` function from the `nlme` library in R (Pinheiro et al. 2007). First-order autoregressive (AR(1)) models were found to be the most suitable. These models are of the same form as a normal linear regression model, except for the structure of the error term which follows a first order autoregressive process, i.e.

$$Y_t = \beta_0 + \sum_{k=1}^{p-1} \beta_k X_{kt} + \varepsilon_t \quad \text{where } \varepsilon_t = \rho \varepsilon_{t-1} + \mu_t \quad (6)$$

Each error term, ε_t , consists of a fraction of the previous error term plus a new disturbance term, μ_t . The parameter ρ is called the autocorrelation parameter. Only the μ_t are independent with $N(0, \sigma^2)$. AR(1) models were fitted using restricted maximum likelihood (REML). AIC and likelihood ratio tests were used to evaluate the addition of the autoregressive error term.

For the linear models with normal random errors, the predictive ability of the models was assessed by comparing the mean squared prediction error (MSPR) from a leave-one-out cross-validation procedure with the residual mean square error (MSE). A MSPR much greater than the MSE suggests poor predictive ability (Neter et al. 1996). Both partial and full (Francis 2006) leave-one-out cross-validations were examined. In partial cross-validation the same model structure is applied for each new prediction, only the coefficients differ. The MSPR_p (i.e. partial MSPR) is calculated as:

$$\text{MSPR}_p = \frac{\sum_{i=1}^n (d_i)^2}{n} \quad (7)$$

where n is the number of observations, d_i is the difference between the observed value for the i -th case and that predicted from a model fitted with all observations except i . This can be calculated more simply using an algebraically equivalent form where d_i is defined as:

$$d_i = \frac{e_i}{1 - h_{ii}} \quad (8)$$

where e_i is the ordinary residual for the i -th case and h_{ii} is the i -th diagonal element of the hat matrix (Neter et al. 1996).

Partial cross-validation has however been criticized (Francis 2006), as it leaves out the process of predictor screening. The full cross-validation mean square prediction error, MSPR_f , is therefore calculated as Equation 7 but where predictor screening is included at each step, i.e. each time the data is sub-divided and a new model fit (Francis 2006).

The predictive ability of models with correlated errors was not assessed as internal cross-validation is not particularly meaningful given the serial correlation in the data. Alternative methods of assessing predictive ability such as external cross validation (using new data) were not suitable due to the short time series available.

Table 3.1. Environmental variables: acronyms used in text and descriptions.

Abbreviation	Description
SOI	Southern Oscillation Index
NINO	Nino3.4 index
SST	Sea surface temperature
rSP	Wind speed at Robe
rDIR	Wind direction at Robe
pSP	Wind speed at Portland
pDIR	Wind direction at Portland
SL	Sea level at Portland
CHL	Surface chlorophyll-a concentration

RESULTS

The Fishery

Up to 2000 tonnes of squid was caught annually in the jig fishery from 1996 - 2005, but catches fluctuated from year to year, with as little as 350 tonnes taken in 2000 (Figure 3.2a). In most years more than half of the total annual catch was taken from the Bonney Coast, in 2002 it was 95%. By contrast in 2000, the poorest year for squid jig catch, only 17% of the catch came from the Bonney Coast, as catch rates were low and fishers searched elsewhere. Between 280 and 850 tonnes of squid were taken in the trawl fishery annually, and up to 53% of this was from the Bonney Coast (Figure 3.2b). Trawl catches of squid on the Bonney coast exceeded 200 tonnes per annum in 2001 and 2002, and peaked at 443 tonne in 2003 (Figure 3.2b).

Catches on the Bonney coast have fluctuated greatly between years, with the smallest annual catch (22 tonnes in 1989 for trawl; 59 tonnes in 2000 for jig) being less than 5% of the largest catch (443 tonnes in 2003 for trawl; 1780 tonnes in 1997 for jig) in both fisheries. There is strong seasonality evident with catches peaking in May (late austral autumn) in both the jig and trawl fisheries (Figure 3.2c & d). Although catches of squid are taken year round by trawlers on the Bonney Coast, the jig fishery is almost entirely confined to the February to July period.

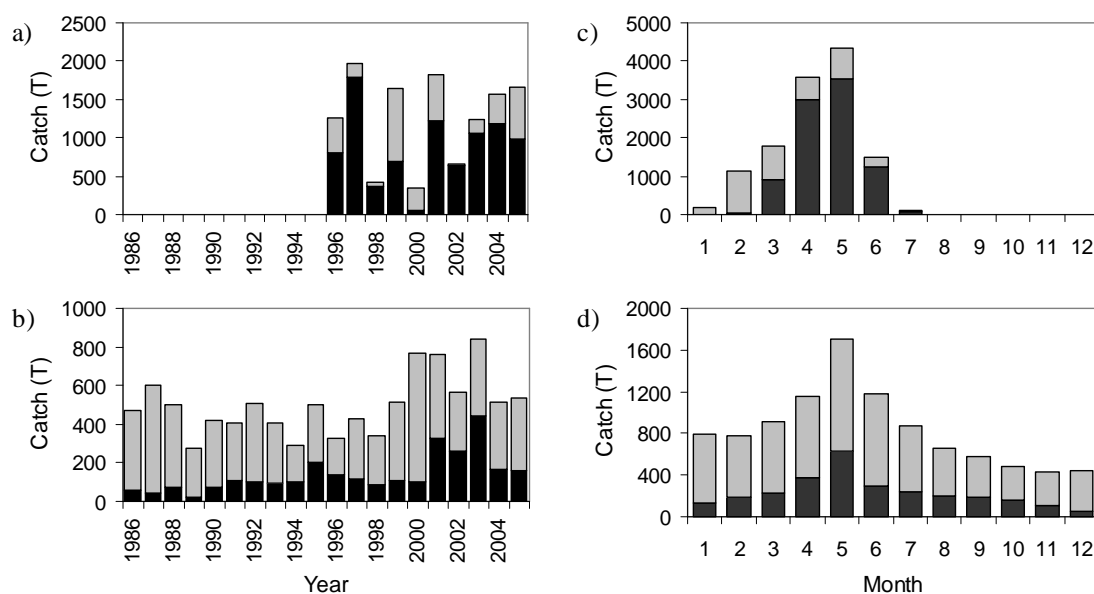


Figure 3.2. Total annual catch (tonnes; a & b) and monthly catch (c & d) across all years for the jig fishery (top row) and trawl fishery (bottom row). Values are shown for the Bonney Coast study area (dark grey bars), and for the rest of the fishery area (light grey bars).

Standardisation of CPUE

a. Jig Fishery

The best fit CPUE standardisation model for the jig fishery included a Vessel factor and a spatial covariate: the 1st principal component from a PCA on latitude and longitude (Table 3.2). Principal component analysis shifted the axes of the spatial coordinates (latitude and longitude) so that they were more meaningful with regard to the orientation of the coastline. The first principal component (PC-1) accounted for the majority of the variability in latitude and longitude (92.5%), providing a measure of spatial location parallel to the shore line (i.e. from north-west to south-east), and was entered as a second order polynomial in the jig standardisation model.

The jig standardisation model accounted for 36.7% of the residual deviance in the CPUE data. Vessel and PC-1 contributed 12 and 1% respectively to the total deviance explained (Table 3.2). All other variables examined (Month, Moon and PC2) could only contribute 0.5% or less to the deviance explained, despite lowering the AIC. As such, inclusion of these extra parameters made very little difference to the Year coefficients.

Table 3.2. Significant factors in the jig standardisation model. Response variable is log(CPUE). Predictors are shown in the order that they were added to the model. See Methods section for explanation of model structure and variable selection process. Df is degrees of freedom.

Predictor	Response Function	Df	Deviance	% Deviance Explained
<i>Null Model</i>		4167	3478.0	
Year	Factor	9	821.0	23.6
Vessel	Factor	30	418.0	12.0
PC-1	Polynomial- 2nd	2	35.8	1.0
<i>Full Model</i>		4126	2203.2	36.7

The main effect of the inclusion of the Vessel and PC-1 predictor variables was to reduce the value of the back-transformed Year coefficients relative to 1996, particularly in the later years (Figure 3.3). Thus the high catch rates from 2001 onwards appear to have been driven to some extent by changes in catchability q (due to changes in the combination of vessels fishing and to a lesser extent, their spatial location within the Bonney Coast study area), in addition to changes in population size N . The general shape of the standardised CPUE (std-jig) trajectory however remained similar to that based on a model containing a Year factor only (base model, Figure 3.3). There was no significant autocorrelation detected for the short std-jig total abundance time series ($r = 0.29$).

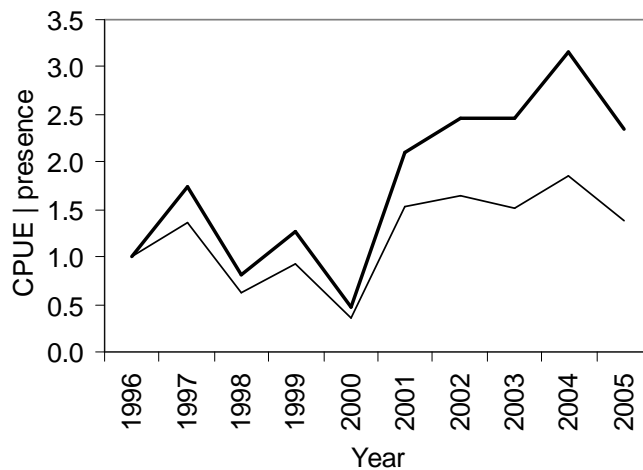


Figure 3.3. Annual standardised jig CPUE (back-transformed) for base model: $\log(\text{CPUE}) \sim \text{Year}$ (thick line), and the optimum standardisation model: $\log(\text{CPUE}) \sim \text{Year} + \text{Vessel} + \text{PC1} + \text{PC1}^2$ (thin line).

b. Trawl Fishery

Standardisation models account for 27 and 29% of the deviance in the trawl presence-absence and CPUE data respectively (Table 3.3). Depth and Vessel terms were included in both the T-PA and T-CE models. Depth in particular explains a large proportion, 19.4%, of the deviance in the presence-absence data (T-PA model), showing that the probability of catching squid in a particular shot is highly dependent on the depth being fished. Longitude was the only other spatial coordinate included (selected ahead of the spatial principal components), explaining ~2% of the deviance in the T-PA model. The Vessel factor was important in both models, but explained slightly more of the deviance in the CPUE data (i.e. T-CE model) showing that the combined vessel effects had more influence on catch rates than the probability of encountering squid. This may be due to the specifics of the gear being used and methods of fishing. Month was included in the T-CE model only, where it was the most important predictor variable (explaining 10% of the deviance). Thus, while the probability of catching squid remains relatively constant over the course of a year, the CPUE of squid, when present, is highly seasonal.

Table 3.3. Results of the trawl standardisation models. The T-PA model was a logistic GLM with presence or absence of squid in a shot as the response variable. The T-CE model was a Gaussian GLM on log-transformed CPUE data. Predictors are shown in the order that they were added to the models. See Methods Section for explanation of variable selection process. Df is degrees of freedom.

Model	Predictor	Response Function	Df	Deviance	% Deviance Explained
T-PA	<i>Null Model</i>		67822	89947.0	
	Year	Factor	19	2013.0	2.2
	Depth	Continuous	1	17464.0	19.4
	Vessel	Factor	37	3250.0	3.6
	Longitude	Polynomial- 2nd	2	1695.0	1.9
	<i>Full Model</i>		67763	65526.0	27.2
T-CE	<i>Null Model</i>		25559	31033.0	
	Year	Factor	19	1178.5	3.8
	Month	Polynomial- 2nd	2	3145.3	10.1
	Depth	Continuous	1	2428.3	7.8
	Vessel	Factor	37	2302.9	7.4
	<i>Full Model</i>		25500	21978.0	29.2

The back-transformed Year coefficients of the T-PA model show a substantial increase in the probability of catching squid during the 1990s (Figure 3.4a). This increase is not seen in the base model (with Year as the only factor) and is driven primarily by a change in the depths fished, possibly linked to management changes (introduction of ITQs) in the early 1990s and shifts in the species targeted by the trawlers. The T-CE model shows that annual CPUE (conditional on presence) oscillates between years, but also increases in the 1990s above the base model (Figure 3.4b).

The standardised index of total abundance (i.e. $p_t.CPUE_t$; std-trawl), is therefore substantially different from the base model estimates (Figure 3.4c), being much higher in the 1990s and lower in the 2000s, but still with considerable inter-annual variability.

Both the T-PA and T-AB standardisation models, and hence the combined total index of abundance (std-trawl), showed significant positive auto-correlation at a variety of lags ranging from 1-9 years. Partial ACFs show that correlations between consecutive years are driving this pattern (Table 3.4). Residuals from the base standardisation models (i.e. with Year as the only predictor variable) were not auto-correlated.

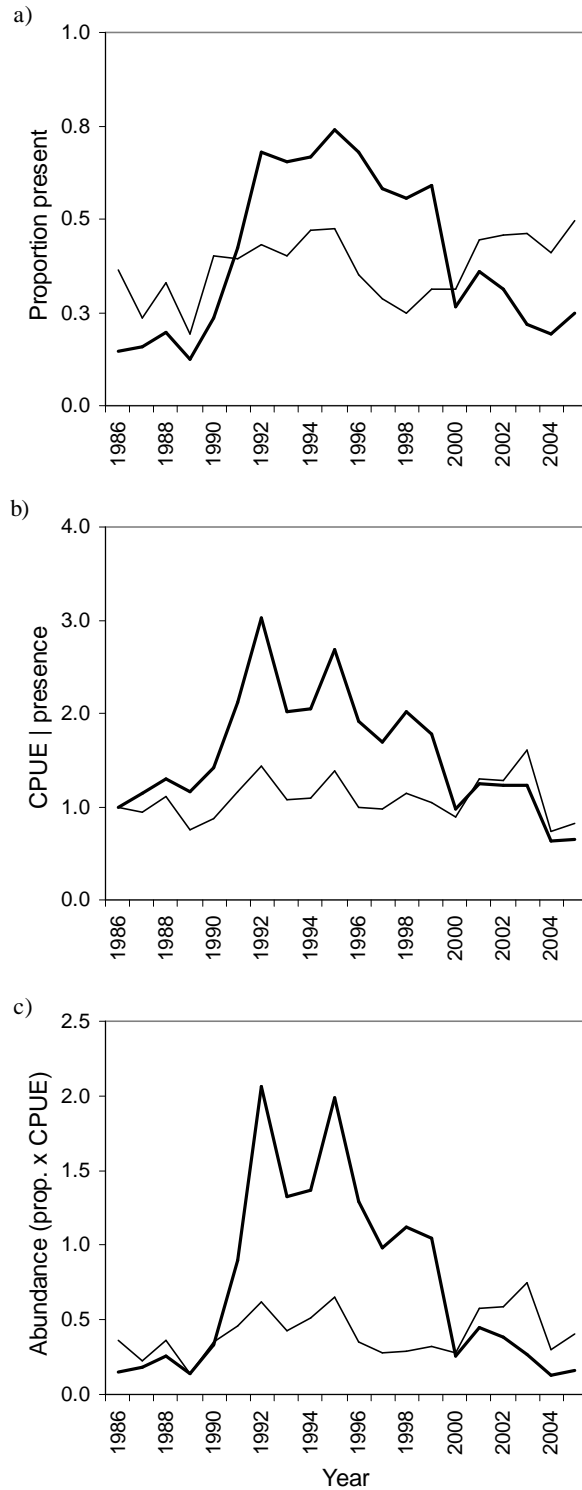


Figure 3.4. Back-transformed Year coefficients from (a) the T-PA model, (b) T-CE model, and (c) the combined index of total abundance (Proportion x CPUE | presence). Thin lines are for the base model (i.e. Year as the only explanatory variable), and thick black lines for the optimal standardisation models (see Table 3.2 for details). Note different scales for y-axes.

Table 3.4. Auto-correlations for trawl standardised annual time series. Lag is in years t . All correlations are statistically significant (*; based on BCa 95% confidence intervals: lower CL and upper CL).

Lag	Variable	r		lower CL	upper CL
1	T-PA $t, t+1$	0.84	*	0.55	0.94
1	T-AB $t, t+1$	0.66	*	0.45	0.81
1	T-total $t, t+1$	0.72	*	0.45	0.86

Links between Jig and Trawl standardised time series

Annual std-jig was negatively correlated with the std-trawl total abundance ($r = -0.44$), although this correlation was not significantly different from zero (95% bootstrap confidence interval: -0.91 to 0.37), primarily due to the year 2000 which was a strong outlier with low abundance for both fisheries. Excluding the year 2000 results in a large and significant correlation between the std-trawl and std-jig ($r = -0.83$, 95% bootstrap confidence interval: -0.94 to -0.16; Figure 3.5).

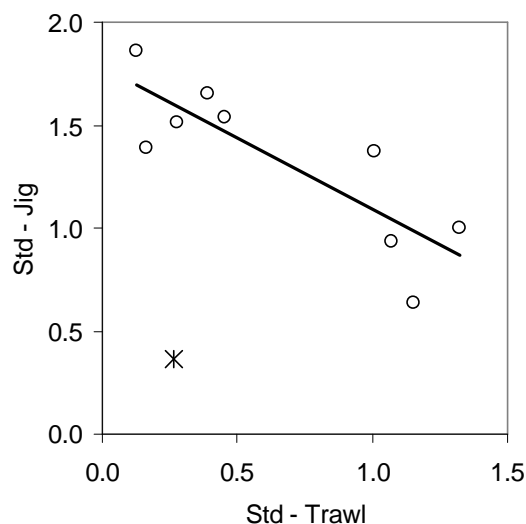


Figure 3.5. Relationship between std-jig and std-trawl annual time series, no time lag. Line is simple linear regression through the points, excluding that for the year 2000, marked by asterisk ($y = -0.692x + 1.780$, $r^2 = 0.69$, 7df).

*Correlations between *N. gouldi* abundance and environmental conditions*

a. Annual Environmental Parameters

The std-jig total abundance time series was not significantly correlated with any of the annual environmental variables (Figure 3.6a). The strongest correlations were with SL ($r=0.46$) and CHL ($r=-0.48$), however in all cases the bootstrap 95% confidence intervals were extremely wide. The std-trawl total abundance time series was significantly correlated with the previous years SOI ($r=-0.51$), rSP ($r=0.49$), pSP ($r=0.54$), pDIR ($r=0.63$) and SL ($r=-0.46$; Figure 3.6b). NINO and rDIR also showed strong positive correlations which were close to significant levels, but the lower boundary of both bootstrap 95% confidence intervals were just below zero.

b. Monthly Environmental Parameters

Correlations using monthly environmental variables were also examined, as the annual means may mask important inter-annual variability occurring in particular months. Other studies (e.g. Waluda et al. 1999, Agnew et al. 2000, Yatsu et al. 2000, Waluda et al. 2004) have found that conditions during the months of hatching may be the most important for predicting abundance of the fished population. Lagged correlations were extended back to May of the previous year only, as hatch-date distributions for squid caught in the Portland area (Jackson et al. 2003) showed that May 2000 was the earliest hatch month recorded for trawl-caught squid in 2001. The peak hatching period (derived from hatch-date frequencies in Jackson et al. (2003) weighted by total trawl catch) was between August and November.

Eighty-one correlation coefficients were calculated for each fishery, and given an alpha of 0.05, four or fewer significant relationships would be expected to occur due to chance alone. Fourteen significant relationships were found with the std-trawl, but only three with std-jig (Table 3.5). No further jig analysis was undertaken.

Wind conditions in August and November were significantly correlated with annual std-trawl abundance, with August pSP showing the largest absolute coefficient ($r = 0.71$; Table 3.5). SL in June and SOI in October also had strong negative correlations with the following year's std-trawl abundance (Table 3.5).

Wind and ENSO variables therefore appear to be the best potential predictors of squid abundance derived from trawl catch and effort data. Std-trawl abundance was not significantly correlated with SST or CHL at either monthly or annual scales (Figure 3.6b, Table 3.5). The most important months in terms of wind speed were August and November of the previous year.

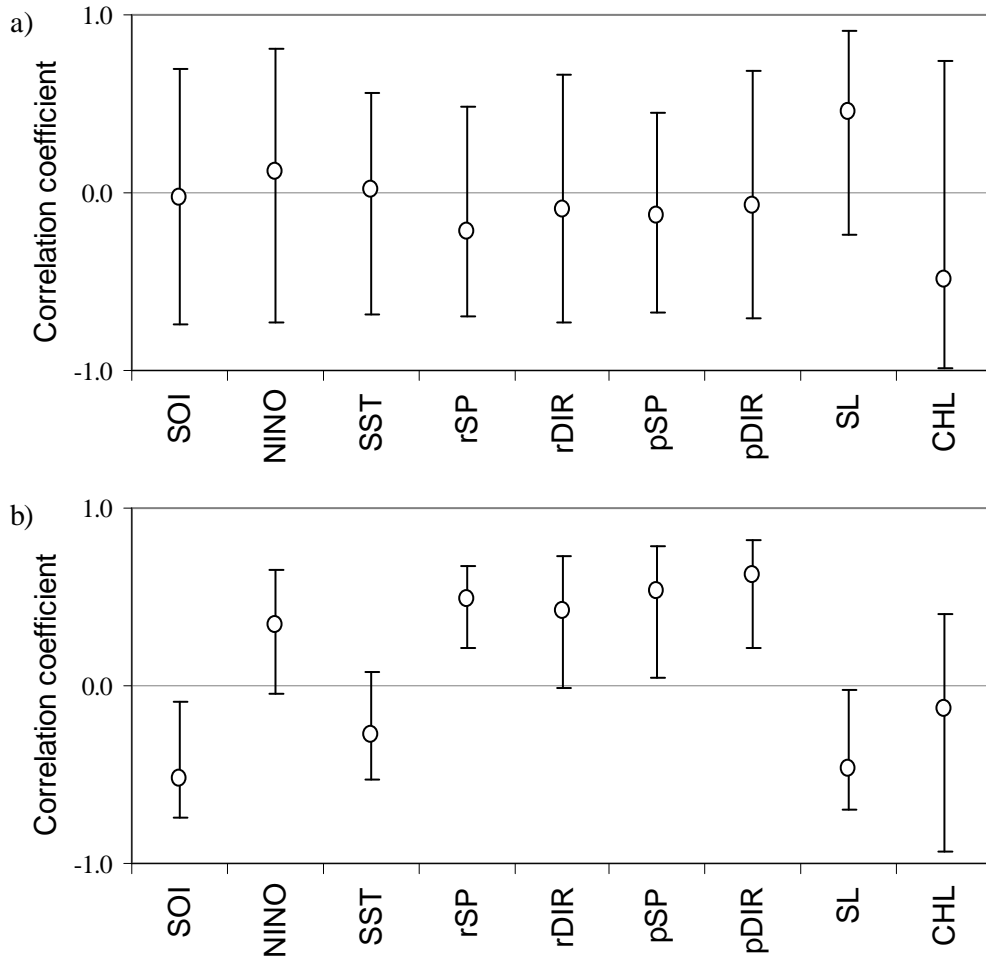


Figure 3.6. Correlation coefficients with BCa bootstrap 95% confidence limits (error bars) for standardised annual total squid abundance derived from a) std-jig, and b) std-trawl, and environmental variables of the previous year. Std-jig correlations were calculated over 10 years of data except for CHL which was only 7 years. Std-trawl correlations were calculated over 20 years of data except for SL which was over 13 years, and CHL which was only 7 years. Explanation of acronyms in Table 3.1.

Table 3.5. Lagged monthly correlation coefficients between environmental variables and std-trawl (std-jig). Only statistically significant correlations (based on bootstrap BCa 95% confidence intervals) are shown.

Month _t	Dec _{t-1}	Nov _{t-1}	Oct _{t-1}	Sep _{t-1}	Aug _{t-1}	Jul _{t-1}	Jun _{t-1}	May _{t-1}
SOI			-0.57					
NINO							0.55	
SST								
rSP	0.40	0.63			0.61			(-0.70)
rDIR		0.43			0.50		-0.47	
pSP	0.42 (-0.68)	0.55			0.71			
pDIR		0.56				0.46		
SL							-0.66	
CHL				(0.55)				

Regression Models

Regression models were built for the std-trawl data only, as the std-jig time series is very short and correlates with few environmental variables (Figure 3.6a, Table 3.5). The strong negative correlation between the std-trawl and std-jig time series (Table 3.5, Figure 3.5) suggests however, that models built using standardised trawl data, may also be useful for predicting jig abundance. A longer time series is required however to fully assess the relationship between the two fisheries.

Annual and monthly SL and CHL were not made available for selection as predictor variables in the regression models due to missing values in the early years.

a. Annual Models

Using annual mean environmental parameters as predictor variables did not remove the autocorrelation in the std-trawl time series, so AR(1) models were fitted, allowing for autocorrelation in the residuals. According to AIC, the best-fit AR(1) model contained no environmental predictors (Model A1; Table 3.6), although the 95% confidence interval around ρ was quite large (0.11- 0.97). AIC weights were however low for models with and without environmental predictors, suggesting that there was no clear optimal model from those examined. Models with pSP and/or SOI were the best-fit models with environmental predictors (Models A2-4; Table 3.6). All other annual environmental predictor models examined (20 in total) had AIC weights less than 0.10.

Table 3.6. Comparison of AR(1) models. Only the null model and the next three best-fit models are shown. ρ is the autocorrelation parameter.

Model	Predictors	ρ	MSE	AIC	AICw
A1	~ 1	0.81	0.583	30.07	0.20
A2	~ pSP	0.79	0.501	30.34	0.17
A3	~ pSP + SOI	0.81	0.432	30.42	0.17
A4	~ SOI	0.81	0.480	31.03	0.12

Annual pSP had a positive relationship with std-trawl abundance, although the coefficient was not significant (Table 3.7). SOI was significant when included, and had a negative effect on std-trawl abundance.

Table 3.7. Results for the four best-fit AR(1) regression models. * denotes significant at the 0.05 alpha level.

Model	Coefficients	Estimate	Std. Error	t-value	p-value	
A1	(Intercept)	0.57	0.44	1.29	0.212	.
A2	(Intercept)	0.60	0.40	1.50	0.150	.
	pSP	0.49	0.34	1.44	0.167	.
A3	(Intercept)	0.59	0.38	1.54	0.143	.
	pSP	0.55	0.30	1.81	0.088	.
	SOI	-0.17	0.07	-2.45	0.025	*
A4	(Intercept)	0.58	0.40	1.45	0.164	.
	SOI	-0.16	0.07	-2.18	0.043	*

b. Monthly Models

Residuals were not auto-correlated in any of the monthly predictor models examined, so time series regression was not necessary, and cross-validation prediction error could be calculated for all models.

AIC weights were also low for all monthly scale models examined, with the best-fit model having a weight of only 0.17 (Table 3.8). The low weights are probably due to strong correlations between the candidate monthly environmental predictor variables, thus many combinations of predictor variables produce similar fits. The best fit model according to AIC was model M4, and included August pSP, November rSP and October SOI as predictors. The $MSPR_p$ for this model was only slightly higher than the MSE (Table 3.8), suggesting good predictive ability. However, inclusion of SOI in the optimal model selected by AIC added only 0.04 to the total r^2 and reduced the AIC by only 0.2 (Table 3.8). The model without SOI (model M3) had almost the same AIC_w as the 3 parameter (M4) model, and the $MSPR_p$ was the lowest of all models examined (Table 3.8). Therefore the model M3 with August pSP and November rSP only as predictors, appears the most parsimonious for predictive purposes (Table 3.8).

Table 3.8. Comparison of monthly environmental regression models. Only the null and four best-fit models are shown. The lowest $MSPR_p$, AIC and highest AIC_w are underlined.

Model	Predictors	df	r^2	MSE	$MSPR_p$	AIC	AIC_w
M1	~ 1	19, 20		0.41	0.43	42.1	0.00
M2	~ Aug_pSP	18, 20	0.51	0.21	0.22	29.9	0.02
M3	~ Aug_pSP + Nov_rSP	17, 20	0.63	0.17	<u>0.20</u>	26.1	0.15
M4	~ Aug_pSP + Nov_rSP + Oct_SOI	16, 20	0.67	0.16	0.21	<u>26.0</u>	<u>0.17</u>
M5	~ Aug_pSP + Nov_rSP + Oct_SOI + Aug_rSP	15, 20	0.68	0.16	0.28	27.0	0.10

August pSP and November rSP both had a positive effect on the std-trawl (Table 3.9). The fitted values follow the observed values reasonably well, following the increase in the early 1990s, but underestimating values in the late 1990s, and overestimating std-trawl in the late 1980s (Figure 3.7). The partial cross-validated

predicted values were very close to the fitted values for model M3, and were strongly correlated ($r = 0.99$).

Table 3.9. Results for the linear regression model M3: std-trawl ~ August pSP + November rSP.

Coefficients	Estimate	Std. Error	t-value	p-value	
(Intercept)	0.76	0.09	8.20	0.000	***
Aug_pSP	0.28	0.08	3.31	0.004	**
Nov_rSP	0.24	0.10	2.37	0.030	*

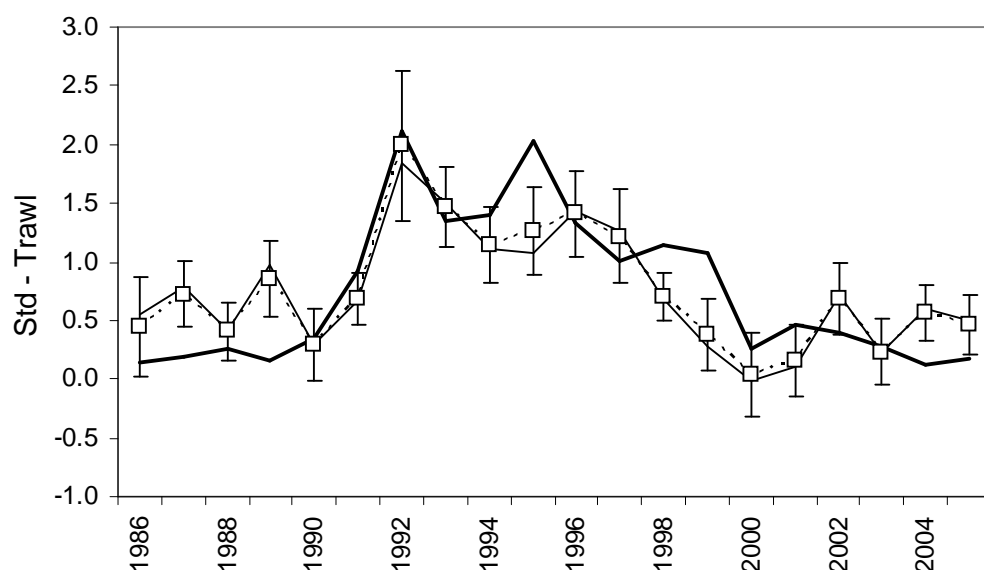


Figure 3.7. Observed (thick line), fitted (dashed line with \square) and partial leave-one-out cross validation predicted (thin line) std-trawl values. Fitted and predicted values are for model M3. Error bars on fitted values are 95% confidence intervals.

An objective selection criterion is necessary for automating the full cross-validation procedure, and in this case it was AIC. The $MSPR_f$ (0.427) was considerably greater than the MSE of both the 2 and 3 parameter monthly environmental models (0.17 and 0.16 for model M3 and M4 respectively; Table 3.8). Twenty models with ten different structures (combinations of predictor variables) were fitted and compared using AIC during the full cross validation. August pSP and November rSP were present in 19 and 17 of the 20 models respectively, and SOI in 12. Other environmental variables occurred in only 1 or 2 models. Predicted values from the full cross-validation did not fit the observed std-trawl data well (Figure 3.8), however as seen above (Table 3.8), AIC does not necessarily pick the best model structure for predictive purposes.

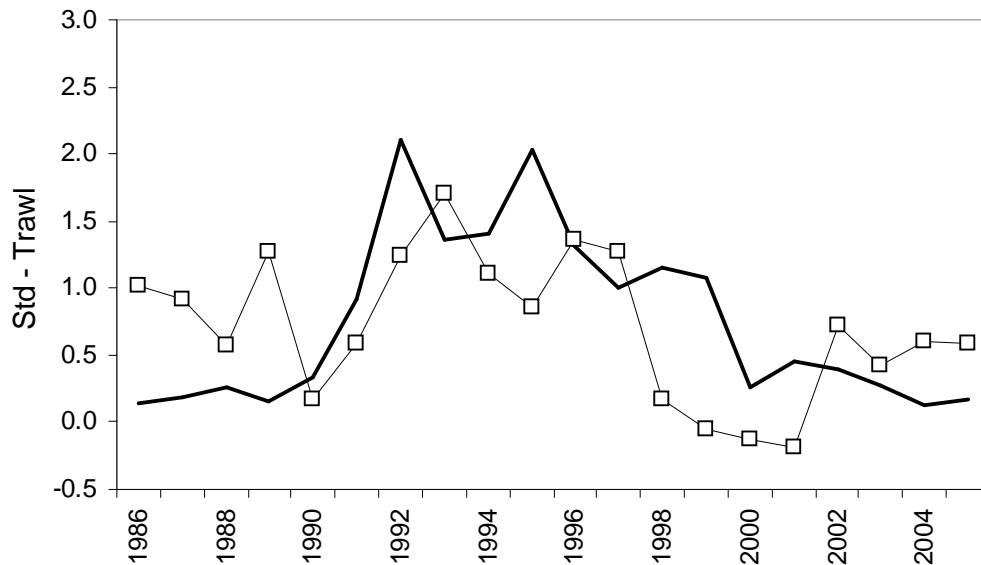


Figure 3.8. Observed (thick line) and full leave-one-out cross-validation predicted (thin line with □) std-trawl values.

DISCUSSION

The jig and trawl fisheries for *N. gouldi* in southern Australian waters are characterised by extreme year-to-year variability. This study shows that annual *N. gouldi* abundance derived from Bonney coast trawl fishery data is related to local and global (ENSO) environmental parameters, at both annual and monthly time scales. This finding has important implications for management and development of *N. gouldi* fisheries in Australian waters. With further validation, these lagged environmental relationships may be employed for short-term forecasts of annual abundance, or for longer-term predictions such as the consequences of climate change on *N. gouldi*, its natural predators, and the fishing industry. No significant relationships were found between the shorter jig fishery derived time series of abundance and environmental variables; although there was a negative correlation between the abundance of *N. gouldi* available to the two fisheries, suggesting shifts in the spatial distribution from year to year.

The best-fit model (selected by AIC) for describing annual trawl derived abundance included wind speed for the previous August and November, and the October SOI. Monthly environmental variables led to better predictive models than those built with annual environmental variables, as they were able to account for the auto-correlation in the standardised trawl abundance data. Empirical models for other fisheries have used SST to predict squid abundance (e.g. Robin & Denis 1999, Ueta et al. 1999, Waluda et al. 1999, Agnew et al. 2000, Pierce & Boyle 2003, Waluda et al. 2004). However, neither annual nor monthly mean SST was correlated with trawl or jig fishery derived *N. gouldi* abundance in this study. This suggests that quite different processes may be driving the inter-annual variability of *N. gouldi* in the Bonney upwelling area of southern Australia. Unlike SST, wind speed and the SOI cannot affect squid abundance directly, but instead may drive the oceanographic conditions the squid are exposed to, influencing patterns of movement and dispersal (especially paralarvae), and the availability of suitable prey and larger predators.

August and November, the months for which wind speed was most important, correspond to the main hatching period for trawl-caught squid sampled in 2001 (Jackson et al. 2003), and the start of summer upwelling events on the Bonney Coast (Gill 2004). Back-calculations from statolith based ageing found that almost 50% of trawl-caught *N. gouldi* hatched in the previous August and September (when monthly hatch distributions from Jackson et al. (2003) are weighted by fishery catch). This finding is consistent with other studies of squid-environment relationships, where correlations are typically strongest when the environmental variables considered relate to the time of hatching (Waluda et al. 1999, Agnew et al. 2000, Yatsu et al. 2000, Waluda et al. 2004). The mechanisms by which stronger winds in August may lead to higher abundance the following year are not known, but may be related to the dispersal of paralarvae and/or food availability for the juvenile squid (Bakun & Csirke 1998). August winds over Portland are predominantly westerly, and water circulation over the southern shelf is an eastward flowing extension of the Leeuwin current, which then turns south down the west coast of Tasmania (Ridgeway & Condie 2004). During winter the warm oligotrophic waters of the Leeuwin current cool as they travel eastwards, and downwelling and mixing occurs along the southern shelf (Godfrey et al. 1986, Cirano & Middleton 2004). Wind-driven turbulence intensifies this process, deepening the mixed layer and bringing more nutrients into the euphotic zone. The depth of the mixed layer in late-winter may subsequently influence the nature of the spring bloom, and therefore the availability of prey to the juvenile *N. gouldi*.

November wind speed over Robe was the second parameter selected for inclusion in the monthly environmental model. Winds are primarily south-easterly over Robe in November, and instigate summer upwelling events (Lewis 1981, Schahinger 1987), particularly along the western end of the Bonney Coast. The positive influence of November wind speed on squid abundance the following year is probably mediated through the behaviour of the upwelling and the subsequent productivity of the waters; with November wind conditions potentially a biologically relevant indicator of the intensity and nature of the upwelling over the entire summer.

The SOI was also included in the AIC-selected monthly environmental model. ENSO events are important to the strength of the Leeuwin current, being weaker in El Niño years, particularly during winter (Feng et al. 2003). ENSO may also influence the Bonney upwelling, with El Niño conditions (low SOI, high NINO) in this study associated with stronger wind speeds, lower sea level and lower sea surface temperatures along the Bonney Coast at 0 to 1 year lags (results not shown). This pattern is in the reverse of that found in North and South America, where El Niño conditions diminish upwelling activity (Mann & Lazier 1996). The inclusion of SOI may therefore also reflect the summer upwelling activity and represent a suite of associated local environmental parameters, including SL and/or CHL which were not considered as candidate variables in the regression models due to missing values for the early years.

These results suggest that food availability during the early juvenile and pre-recruit stages may therefore be the most important driver of *N. gouldi* abundance on the Bonney coast, as found for *Loligo opalescens* (Zeidberg & Hamner 2002, Jackson & Domeier 2003), and *Dosidicus gigas* (Ichii et al. 2002, Waluda & Rodhouse 2006), also in upwelling areas. However, the jig-derived time series of *N. gouldi* abundance

was negatively correlated with that derived from the trawl fishery, suggesting that the spatial distribution of squid along the Bonney Coast is also shifting from year to year (between the jig and trawl grounds).

The behaviour of the upwelling, represented in these models by November wind speed and October SOI, may not only influence the survival and growth of *N. gouldi* during the vulnerable early juvenile and pre-recruit stages (by controlling the availability of suitable prey), but may also influence the post-recruitment spatial distribution and patterns of aggregation of *N. gouldi*, in particular the relative abundance between the shallow jig grounds and the deeper shelf-break and slope regions fished by demersal trawlers. The intensity and nature of the wind-driven upwelling determines the location and strength of the upwelling front (the interface between the cool nutrient rich upwelled waters and the warmer stratified offshore waters), and to what degree any upwelled nutrients and subsequent primary and secondary production may be transported off the shelf through Eckman transport (Mann & Lazier 1996). Phytoplankton biomass and abundance of higher predators such as tunas, tend to be highest in the vicinity of upwelling fronts (Mann & Lazier 1996). Shifts in the location and dispersion of the upwelling production front from year to year may be the cause of the negative relationship between jig and trawl derived indices of abundance. In years of poor recruitment however, the abundance of squid will be low on both jig and trawl grounds, as seen in 2000. Thus the abundance of *N. gouldi* appears to be a complex interplay of environmental influences affecting rates of growth and survival during the pre-recruit stages, and spatial distribution post-recruitment.

While the possible mechanisms responsible for the relationships discussed above are uncertain, an exact understanding of the processes is not critical for predictive modelling purposes (Agnew et al. 2000). However, some form of validation of the models predictive ability is required. Unfortunately applying the model to new data was not feasible in this study due to the short time series of data available, instead leave-one-out cross-validation was used. Partial cross-validation suggests that the predictive ability of the optimal squid abundance-environment model is good, but can be improved by reducing the model to 2 environmental parameters by excluding SOI. In particular, the peak in 1992 was poorly predicted when SOI was included as an independent variable in the model. The full cross-validation which includes the uncertainty of predictor selection, in contrast suggests poor predictive ability. Francis (2006) showed through simulation that relying on partial cross-validation only can lead to the identification of chance correlations, or overestimate the reliability of useful environmental predictors. However, the selection of predictor variables at each step of the full cross-validation process requires an objective decision rule, usually AIC as used here and by Francis (2006), and it has already been demonstrated above that model structures selected by AIC are not necessarily the best models for predictive purposes. The full cross-validation could perform better with a decision rule based on the prediction error rather than the AIC.

Predictive ability may be compromised by indirect relationships between the environmental variables and squid abundance. If wind and ENSO parameters are proxies for productivity as discussed above, then models would perform better with primary and secondary productivity parameters as the explanatory variables. CHL was examined in this study as a proxy for primary production, but the time series of

data available was very short (7 years) and no significant relationship with squid abundance was found. Secondary and tertiary production, more relevant to *N. gouldi* which feed on small crustaceans and fish (O'Sullivan & Cullen 1983), are not always linearly related to primary production. More flexible curvilinear (e.g. GLMs with polynomial predictors) and non-linear model structures (e.g. Generalized Additive Models or Artificial Neural Networks) were not examined in this study, although they may perform better in investigating such environmental relationships (Megrey et al. 2005), particularly if longer time series of data are available. However, scatterplots of standardised *N. gouldi* abundance versus environmental variables did not suggest that curvilinear or non-linear models were appropriate here. Straight-line model forms have proven suitable for squid-environment relationships elsewhere, and given the short time-series of data available, alternative model structures were not pursued. Considerable caution should be used before increasing the flexibility of models in what is essentially a 'data-dredging' exercise, unless a specific mechanism generating non-linear or curvilinear relationships is being examined.

The magnitude of correlation coefficients calculated between trawl fishery abundance and environmental variables were comparable to those published elsewhere for other squid species (eg. Waluda et al. 1999, Pierce & Boyle 2003), and the best-fit model with three environmental predictors had a reasonably high coefficient of determination (0.67). However, the environmental models described here are highly dependent on the assumption that the standardized CPUE time series are suitable indicators of population abundance, or specifically the abundance of the population *available* to the fishery. The standardisation models are only able to explain relatively low proportions of the deviance (0.27 and 0.29 for the trawl fishery; 0.37 for the jig fishery), and this is in part due to an inability to include all potential influences on catchability, as the data to do this are simply not available. Factors such as skipper or crew experience, 'learning' behaviour, and advances in fishing technology change over time, and a time-averaged vessel factor cannot account for this. Changes in targeting practises, brought about by management restrictions or market preferences may not be reflected in spatial or seasonal variables, and can also influence fishery derived indices of abundance. Similarly, the behaviour of the fleet or dynamics of the fished population may cause non-linear relationships between catchability and abundance (eg. Rose & Kulka 1999). For *Nototodarus gouldi* in New Zealand waters there was no relationship between fishery CPUE and SST or SOI (Waluda et al. 2004). However unlike the Australian trawl fishery, in New Zealand squid are targeted and this can cause hyperstability in catch rates (Harley et al. 2001).

Jig fishery CPUE may too be less useful as an indicator of abundance, despite being standardised, due to the nature of the fishing: squid are targeted in large aggregations attracted to the fishing vessels by lights (Evans 1986). The catch rates for this fishery may also have an upper limit, based on what the gear and crew on the fishing vessels can handle (*pers obs.*). All these factors may add to hyperstability in the jig CPUE data, which cannot be removed by standardisation. It is possible that CPUE data from commercial jig fishing of *N. gouldi* is an unsuitable indicator of the available abundance. So while standardisation is an improvement on the use of raw fishery-dependent data, it is important to emphasize that the assumption of catch rates being proportional to abundance is not always upheld (Maunder & Punt 2004). However, in the absence of fishery independent survey data, standardised CPUE remains the

best available option. Without standardisation, we would have very different time series of abundance, particularly for the trawl fishery, and it would be impossible to know if correlations with environmental variables were reflecting changes in abundance, or catchability.

Conclusions

Although SST is the variable most often used as a predictor of fishery derived squid abundance, it was not important for *N. gouldi* in the Bonney Coast region of southern Australia. In this study, the environmental variables most useful for predicting trends in squid abundance were wind speed and ENSO conditions, but only for trawl fishery derived indices of abundance. It is hypothesized that these variables may directly influence local productivity and thus prey availability. However, by comparing two time series of *N. gouldi* abundance derived from different fisheries, this study suggests that abundance does not appear to be driven predominantly by pre-recruit processes, as found for other squid species. Instead *N. gouldi* abundance along the Bonney coast appears to be a complex interplay between environmental influences on the success of the pre-recruit stages as well as the spatial distribution of post-recruit squid. Comparing the population structure and life history strategies of *N. gouldi* between years of varying abundance and environmental conditions may provide insight into the relative contribution of these processes, particularly important for predictions over longer time scales such as responses to global climate change. Global warming is predicted to have significant impacts on wind conditions over southern Australia (McInnes et al. 2003, Hobday et al. 2006a) and could have considerable ramifications for populations of *N. gouldi* and the fishing industry that relies on them. Future work should therefore focus on understanding how wind speed in particular might influence *N. gouldi*, with particular emphasis on upwelling behaviour, ocean productivity and prey availability.

Chapter 4:

Inter-annual variability in population structure and life history parameters of the arrow squid (*Nototodarus gouldi*) in southeastern Tasmania, Australia.

INTRODUCTION

Many squid populations fluctuate greatly in size from year to year, with exploited species often varying in biomass by several orders of magnitude. For a number of species, annual biomass is strongly correlated with environmental variables, particularly the conditions experienced during the early life history stages (Robin & Denis 1999, Waluda et al. 2001a, Pierce & Boyle 2003, Chapter 3). It is often hypothesized that changes in biomass are mediated to some degree by environmental controls on biological parameters, particularly growth. Squid show a high degree of phenotypic plasticity in response to environmental variability, with growth rates, size at maturation, and reproductive investment shown to vary greatly between seasons of hatching (Jackson 1995, Arkhipkin et al. 2000, Pecl 2004, Pecl & Moltschaniwskyj 2006) and between squid in different geographic regions (Arkhipkin 1996, Jackson & Moltschaniwskyj 2001b, Jackson & Moltschaniwskyj 2002, Olyott et al. 2006). Controlled laboratory studies have confirmed the significance of both water temperature and food availability on squid growth (Forsythe 1993, Hatfield et al. 2001, Jackson & Moltschaniwskyj 2001a). As relative growth rates are highest during juvenile phases, the eventual size of adult squid is highly dependent on the early ontogenetic stages, and environmental variability during juvenile stages can therefore greatly influence the subsequent adult biomass (i.e. recruitment) from year to year.

A few studies have empirically examined the role of life history processes (particularly growth) in linking the environment to the abundance or biomass of recruited squid. In the upwelling system of the California coast, environmental (ENSO) influences on the recruitment (adult biomass) of *Loligo opalescens* have been shown to be mediated, at least in part, by changes to life history parameters. The biomass, size and growth rates of *L. opalescens* were all considerably greater during La Niña years (Jackson & Domeier 2003, Reiss et al. 2004), presumably due to increased food availability brought about by enhanced upwelling activity (Hayward & Venrick 1998, Zeidberg & Hamner 2002). However the underlying mechanisms linking the environment to recruitment are likely to be far more complicated in many other cases. In contrast to *L. opalescens*, a negative relationship has been described between levels of recruitment and growth of *L. forbesi* in the English Channel (Challier et al. 2005), suggesting intra-generation density dependent processes were important, such as competition for space and/or prey. Pierce et al. (2005) examined a much longer time series of data on the condition and maturation strategies of *L. forbesi* in Scottish waters, and found a complex interplay between environmental conditions and abundance. There were no straight forward trends like those seen in the studies described above (i.e. Jackson & Domeier 2003, Reiss et al. 2004, Challier et al. 2005) however, strong links between consecutive generations of *L. forbesi* were noted (e.g. high summer abundance leads to poor condition in squid

the following year). Pecl et al. (2004b) also found complex inter-annual patterns in the life history characteristics of the loliginid *Sepioteuthis australis*. In particular, population structure from years of similar abundance (recruitment) varied greatly, as did individual life history characteristics.

The mechanisms linking environmental conditions to recruitment are, therefore, not always straight forward, at least for loliginid squid. Pecl et al. (2004b) stressed the need for rigorous working hypotheses explaining fluctuations in squid abundance. In particular multi-year studies examining changes in population structure and individual life history characteristics of wild populations are needed. Few studies however, have examined inter-annual variability in population structure and life history characteristics of squid populations, particularly for ommastrephid species. Coehlo et al. (1994) examined size structure of *Illex illecebrosus* sampled over 20 years in relation to total annual catch in order to determine which seasonal cohorts were the most important to annual fishery production. Arkhipkin and Laptikhovsky (1994) examined growth of *I. argentinus* over 5 years, and Villanueva (1992) examined *Todarodes angolensis* growth over 3 years. In both these studies size at age was greater in years with cooler water temperatures.

The arrow squid, *Nototodarus gouldi* is widespread in southern Australian waters, from southern Queensland to mid Western Australia. *Nototodarus gouldi* is typically most abundant near the shelf break (Chapter 2), where it is caught by trawl fisheries and, although rarely targeted, is a valuable by-catch. It also occurs in inshore shelf waters where it is the exclusive target of Australia's largest squid jig fishery which occurs seasonally over a small number of fishing grounds generally less than 100m depth (Winstanley et al. 1983, Lynch 2004). Analysis of commercial trawl fishery data showed that the available biomass of *N. gouldi* in southeastern Australia varies seasonally and inter-annually, and not always consistently among locations (Chapters 2 & 3).

Temporal variability in abundance of *N. gouldi* is particularly pronounced off southeastern Tasmania, which is towards the species southern range limit. Occasional jig fishery catches occur in shallow shelf waters from autumn to spring, however the main recruitment period appears to be summer, and fishing effort peaks between December and February each season (Willcox et al. 2001). This is in contrast to elsewhere in southeastern Australia, where greatest availability of *N. gouldi* to both jig and trawl vessels is during autumn, and summer abundances are in fact very low in waters off New South Wales and western Victoria (Lynch 2004, Chapters 2 & 3). The Tasmanian jig fishery is comprised primarily of interstate based vessels, and operates somewhat irregularly, depending on the biomass available from year to year. While *N. gouldi* appear to be available during summer months in shelf waters right around the southeast coast (*pers obs.*), and possibly the west coast as well, fishing occurs mostly in Storm Bay, due to its close proximity to the port of Hobart (Figure 4.1).

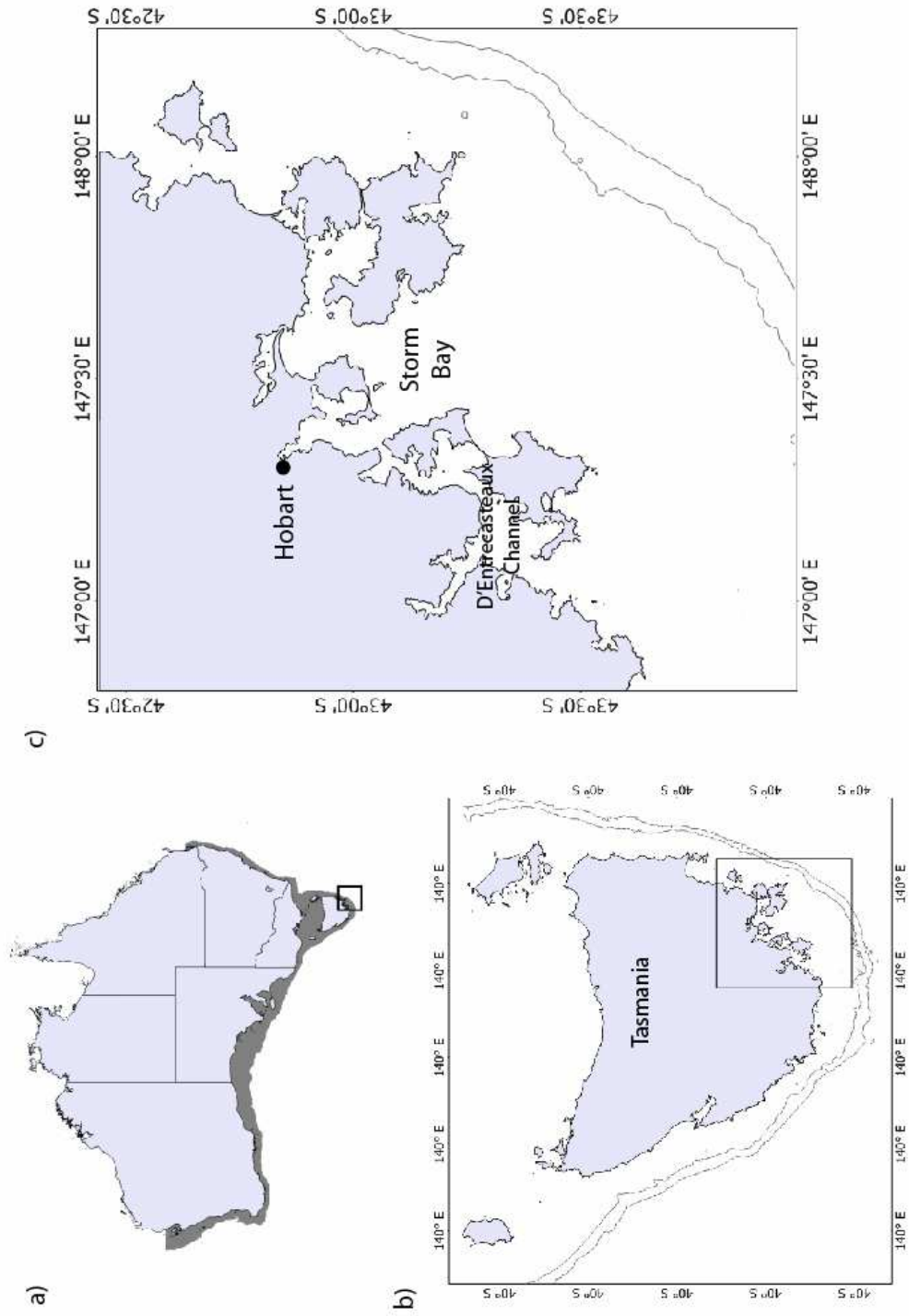
Nototodarus gouldi shows considerable phenotypic plasticity, with population structure, growth rates, condition, and reproductive investment varying greatly between seasons and locations, and with little consistency (Jackson et al. 2003, McGrath Steer & Jackson 2004, Jackson et al. 2005). Large inter-annual variability was also evident over two years of sampling, particularly in growth rates which

varied consistently between years over all locations and seasons. This result was unexpected, with interannual differences usually considered to be far smaller in magnitude than seasonal within-year variability (e.g. Arkhipkin & Laptikhovsky 1994). The collection of samples of *N. gouldi* from commercial fishers working in Storm Bay over four summer seasons (1999/00, 2000/01, 2002/03, 2003/04) allows a more in-depth investigation of inter-annual variability in population structure and life history parameters. Although only a short time series, these samples encompass seasons of record high and extremely low available biomass, and provide the opportunity to examine the relationship between biomass and population biology of an ommastrephid squid; to obtain insight into why recruitment might be so variable.

Growth is tightly linked to reproductive processes, which are also highly variable in *N. gouldi* (McGrath Steer & Jackson 2004, McGrath-Steer 2004). Factors influencing growth, such as temperature (e.g. Forsythe 1993), may also affect timing of maturation and strategies for allocation of energy for reproduction (Arkhipkin et al. 2000, Pecl & Moltschaniwskyj 2006). Therefore, in this study patterns of size-at-maturity and the relationship between somatic and reproductive investment are examined in addition to comparisons of population structure (i.e. sex, size, and age structure), rates of growth and condition.

While other studies of *N. gouldi* have examined spatial and seasonal patterns in biology using trawl fishery caught samples (Jackson & McGrath Steer 2004), this study provides an account of the population structure and life history characteristics of squid from the inshore jig grounds. The aims of this study are therefore to (1) provide a detailed description of the population structure and life history parameters of *N. gouldi* in inshore southern Tasmanian waters, (2) to compare the structure and life history parameters between populations sampled in four of five consecutive years, and (3) to determine if fluctuations in available biomass correlate with changes in population structure and/or life history parameters.

Figure 4.1. Map of a) the range of *N. gouldi* (dark grey shaded area) in Australian waters; b) Tasmania enlarged, with location of study area highlighted (box); c) Storm Bay study area enlarged. 200m and 1000m depth contours are shown as thin grey lines.



MATERIALS AND METHODS

Sample collection & processing

Nototodarus gouldi samples were collected from Storm Bay (Figure 4.1) in four austral summer seasons (1999/00, 2000/01, 2002/03 and 2003/04; Table 4.1) over 5 years (2001/02 was not sampled). Most samples were obtained from commercial jig vessels fishing in Storm Bay, although some squid in December 1999 and January 2000 were hand-jigged by researchers in the D'Entrecasteaux Channel and its associated bays (Figure 4.1). All squid were frozen prior to processing. Some squid from 1999/00 were initially collected as part of another study (Mitchell 2000), but were re-processed for this study after being stored frozen. Biological data (other than ages) for all 2000/01 samples is from Willcox et al. (2001), although these squid were also re-processed to obtain statoliths. Note that due to the seasonality of the fishery (over the austral summer), all references to 'year' or 'annual' values hereafter are with respect to the fishing year, e.g. 1999/00.

Defrosted squid were measured for dorsal mantle length (ML; to the nearest mm) and total body weight (BW; to the nearest 0.1g), sexed and assigned one of five maturity stages (after McGrath & Jackson 2002). Of the 1903 squid collected, 1771 had these basic measurements recorded (*nA*, Table 4.1). No BW was recorded for 122 squid in the January 2000 sample, and small numbers of squid (4 or less per sample) were missing at least one basic measurement, usually due to the specimen being damaged. Mantle and fin weights, and reproductive weight (gonad and accessory organs), measured to the nearest 0.1g, were taken for most squid except those sampled in the 2000/01 season (*nB*, Table 4.1).

Statoliths were removed from squid during the initial dissections, or at a later date after being refrozen (2000/01 samples). They were rinsed with 70% ethanol and stored dry. A representative sub-sample for ageing was chosen from those available by random selection within size classes. Unfortunately a large number of statoliths, primarily from January samples were unavailable for analysis after being lost during couriering to another laboratory.

Table 4.1. Sample information: days of month (sampling days) and methods of collection, and sample size. AJ is auto-jig, HJ is hand-jig. *n* = number of individuals in sample; *nA* is the number of individuals for which basic biological measurements were taken (ML, BW, sex, maturity stage); *nB* is number of individuals for which extra biological measurements were taken (mantle & fin weights, gonad & accessory reproductive weights); *nAged* is the number of individuals which were aged using statoliths.

Year	Month	Sampling days	Method	<i>n</i>	<i>nA</i>	<i>nB</i>	<i>nAged</i>
1999/00	December	2, 9, 23	HJ & AJ	168	166	153	80
	January	2, 7, 10, 13, 15, 31	HJ & AJ	220	98	97	-
	February	15	AJ	75	74	60	-
2000/01	December	5, 18	AJ	425	424	-	74
	January	4, 18	AJ	390	390	-	-
2002/03	December	25	AJ	45	44	40	41
	January	29	AJ	186	185	156	-
	February	6	AJ	230	226	191	99
2003/04	January	10	AJ	164	164	133	80

Ageing

The method used to prepare statoliths was modified from that of Arkhipkin (1993). Statoliths were embedded in thermoplastic cement (Crystal Bond[®]) with the posterior side parallel to the glass microscope slide. The statolith was ground with lapping film until the edge of the dorsal dome was reached. The extent and intensity of grinding was monitored continuously under a binocular light microscope (x40 magnification). The ground surface was then fixed onto a glass slide with Crystal Bond[®] and ground down to obtain a section thin enough for examination. Sections were viewed under a compound microscope at x400 magnification, and increments counted from the natal ring to the margin of the dorsal dome. A minimum of three counts was made for each statolith. When the three counts differed by less than 5%, their mean was used as an estimate of the number of increments. If the difference was greater, further counts were made until a satisfactory estimate was obtained, or the statolith was rejected.

The total number of statolith increments was assumed to be the age of the squid in days. No direct validation of the rate of ring deposition has been conducted due to difficulties in maintaining *N. gouldi* in captivity for sufficient periods of time (Jackson et al. 2005), and poor numbers of returns in tag-recapture studies (JAMARC 1978a, 1979). However there is some support for daily periodicity of statolith increments in *N. gouldi* (Jackson et al. 2005), and for the congener *N. sloanii* in New Zealand (Uozumi 1998).

Fishery Data

Commercial fishery catch and effort data were obtained from mandatory fishing logbooks for vessels operating in the study area (Figure 4.1) between 1995 and 2006. Catch-per-unit-effort (CPUE; kg/hr) was used to indicate abundance. As CPUE data were lognormally distributed, means were calculated on log transformed data and then back transformed after adding $\sigma_t^2 / 2$ where σ_t is the standard error for year t . Due to the seasonality of the fishery, annual means were calculated between September and August of the following year.

Analysis

Sex ratios (female/male) were calculated for each month and year, and 95% confidence intervals estimated by the adjusted bootstrap percentile (BCa) method (Davison & Hinkley 1997). Size (dorsal mantle length; ML) and age frequency histograms, and the proportion of *N. gouldi* at each of 5 maturity stages were plotted by sex, sample month and season.

A finite normal mixture model was fitted to the size frequencies using the mclust library (Fraley & Raftery 2007) in R. Each size-cohort is assumed to be normally distributed, with the overall distribution being a mixture of each of the normal components. Parameter estimation is via the EM algorithm and model selection based on the Bayesian Information Criterion. Mean age was compared between sexes, sample months and years using ANOVA. As ages were not available for the same months within all years (Table 4.1), each sample- a unique combination of year and month (YM), was used as a blocking factor. Type III Sums of Squares

(contrasts) were used for testing of main effects as the data were unbalanced between groups.

Separate lines regression was used to investigate inter-annual differences in size-at-age (i.e. growth), and total body weight-at-length (i.e. condition), somatic and reproductive weight-at-length (i.e. reproductive and somatic investment). Growth in both length (ML) and weight (BW) with age were examined. ML was log transformed, so the underlying growth model is of an exponential form. BW and age were both log-transformed i.e. a power form. Overall condition (BW-at-ML) was also modelled as a power function. Somatic and reproductive investment by mature animals (stages 4 and 5) were modelled as linear functions of ML. Somatic weight (SW) was the sum of mantle and fin weights, and reproductive weight (RW) the weight of all reproductive material, i.e. gonad plus nidamental glands, ovaries and oviducts for females, and gonad plus spermatophoric complex for males.

Homogeneity of slopes was examined by testing the significance of covariate-factor interaction terms, which were dropped from models when not significant (i.e. where $p \geq 0.05$). Where interaction terms were significant, slopes were compared between years using pairwise comparisons computed using the logical constraints method of Westfall et al. (1999) in the multcomp package for R (Bretz et al. 2004). In the presence of interactions, differences in the response variable (ML, BW, SW or RW) between years were examined by pairwise comparisons at defined levels of the covariate (age or ML).

In the absence of interaction effects, the null hypothesis that there is no effect of year on the response variable was tested with ANCOVA using Type III Sums of Squares (contrasts) due to the unbalanced structure of the data. Pairwise comparisons of main effect means were then performed using the multcomp package for R. In order to investigate the relationship between somatic and reproductive condition in mature squid, correlation coefficients were calculated for somatic and reproductive condition regression model residuals. Confidence intervals were estimated using the adjusted bootstrap percentile method (Davison & Hinkley 1997).

The probability of squid being mature (i.e. stage 4 or 5) at size (ML) was modelled as a binomial (binary) response using logistic regression. Chi-square tests were used to test the significance of the year factor and interaction terms. Pairwise comparisons of slopes and means were conducted as described above. Size at 10, 50 and 90% maturity was calculated for each year and sex using the delta method (Faraway 2006), with the p.dose function in the MASS library (Venables & Ripley 2002).

A repro-somatic index (RSI, %) was calculated for mature (stage 4 and 5) animals as the total RW (i.e. gonad plus nidamental glands, ovaries and oviducts for females, and gonad plus spermatophoric complex for males) divided by the total BW and multiplied by 100.

All linear models were analysed using lm or glm functions in R 2.4.1 (R Development Core Team 2007). Diagnostic plots were examined for outliers and to assess the suitability of each model structure. In all models the covariate (ML or age) was centred around its mean, to reduce potential collinearity between main effect and interaction terms.

RESULTS

Fishery based estimates of biomass

The total catch of *N. gouldi* each fishing year (i.e. between September and August, 1995/96 to 2005/06) by jig vessels in Tasmanian State waters ranged from less than 0.75 to almost 500 tonnes (Figure 4.2). Up to 95% of this catch was taken each year from Storm Bay between November and March (i.e. during the austral summer and in the study area; Figure 4.2). Catch rates fluctuated widely, with the highest mean CPUE in Storm Bay more than 30 times that of the lowest year. The year of highest catch, 401.9 tonnes in 1999/00 also had the highest catch rates (Figure 4.2). Of the other seasons sampled in this study, catch rates in 2000/01 were moderate, while in 2002/03 and 2003/04 catch and CPUE were all very low. Effort was also very low in the latter two years, so CPUE may not be a reliable or particularly quantitative indicator for comparison between years. The influx of large auto-jig vessels with experienced skippers and crew in 1999/2000 when squid were available in large quantities, and then again the following year (2000/01), may also have inflated CPUE-based estimates of abundance in comparison to the latter two years. CPUE comparisons are therefore best viewed as semi-quantitative; although there is little doubt that available abundance in 1999/00 was much greater than any of the other years.

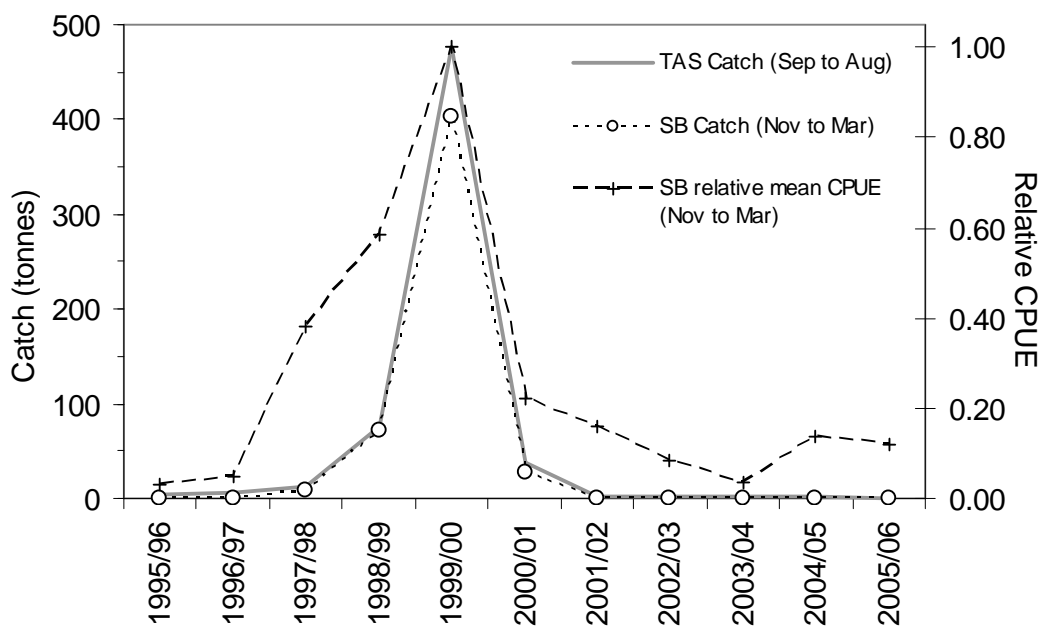


Figure 4.2. Annual (September to August) catch from Tasmanian (TAS) State waters (grey line), and from Storm Bay (SB) between November and March (short dashed line with white filled circles). Annual mean CPUE (back transformed from log scale) for Storm Bay between November and March is shown relative to 1999/00 (long dashed line with crosses).

Sex ratio

The ratio of females to males was significantly greater than 1 in all January and February samples, but not December (where significance is indicated by non-overlapping 95% bootstrap confidence intervals; Figure 4.3). The sex ratio increased progressively between December and February in all seasons sampled, suggesting

that sex-specific changes in availability were occurring over the summer season. There were no significant differences between years compared within months (Figure 4.3).

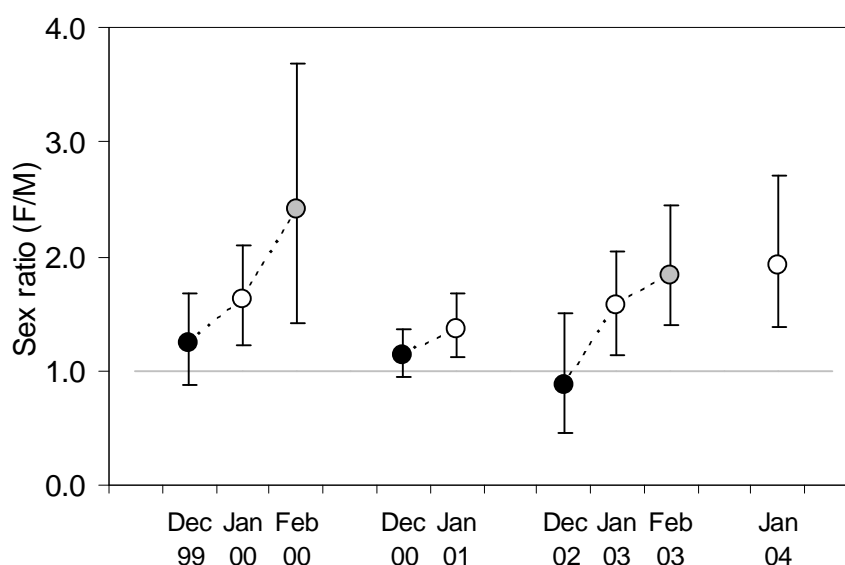


Figure 4.3. Sex ratio (female/male) by month and year. Error bars are BCa 95% confidence intervals. Grey horizontal line identifies a ratio of 1:1.

Size structure

Sampled *N. gouldi* ranged in size from 11.8 to 37.6 cm ML, however the larger animals were mostly females, with the largest male only 31.5 cm ML (Figure 4.4). One or two size cohorts were identified in each sample by normal mixture models (Table 4.2, Figure 4.5). The number of size-cohorts did not differ between males and females from the same samples, except for February samples where there were 2 female cohorts, but only one male cohort. In most samples the mean size of each male cohort was slightly less than that for the corresponding female cohort (except in December 2000; Table 4.2).

Size-frequency distributions from December 1999 and January 2000 were different from other years, as only a very small range of sizes occurred in a single distinct cohort (Figure 4.4). Apparent growth (in ML) of male and female size-cohorts was easily tracked over the 1999/2000 season (Figure 4.5). In February 2000 a new cohort was also evident, but it consisted of females only and accounted for less than 10% of the females sampled (Table 4.2). In all other years 2 cohorts were present for both males and females in most samples. Where only 1 size-cohort was identified (January 2003, January 2004 for both sexes, and February 2003 for males), there was much more within cohort variability than in those from the 1999/00 season (Figure 4.5).

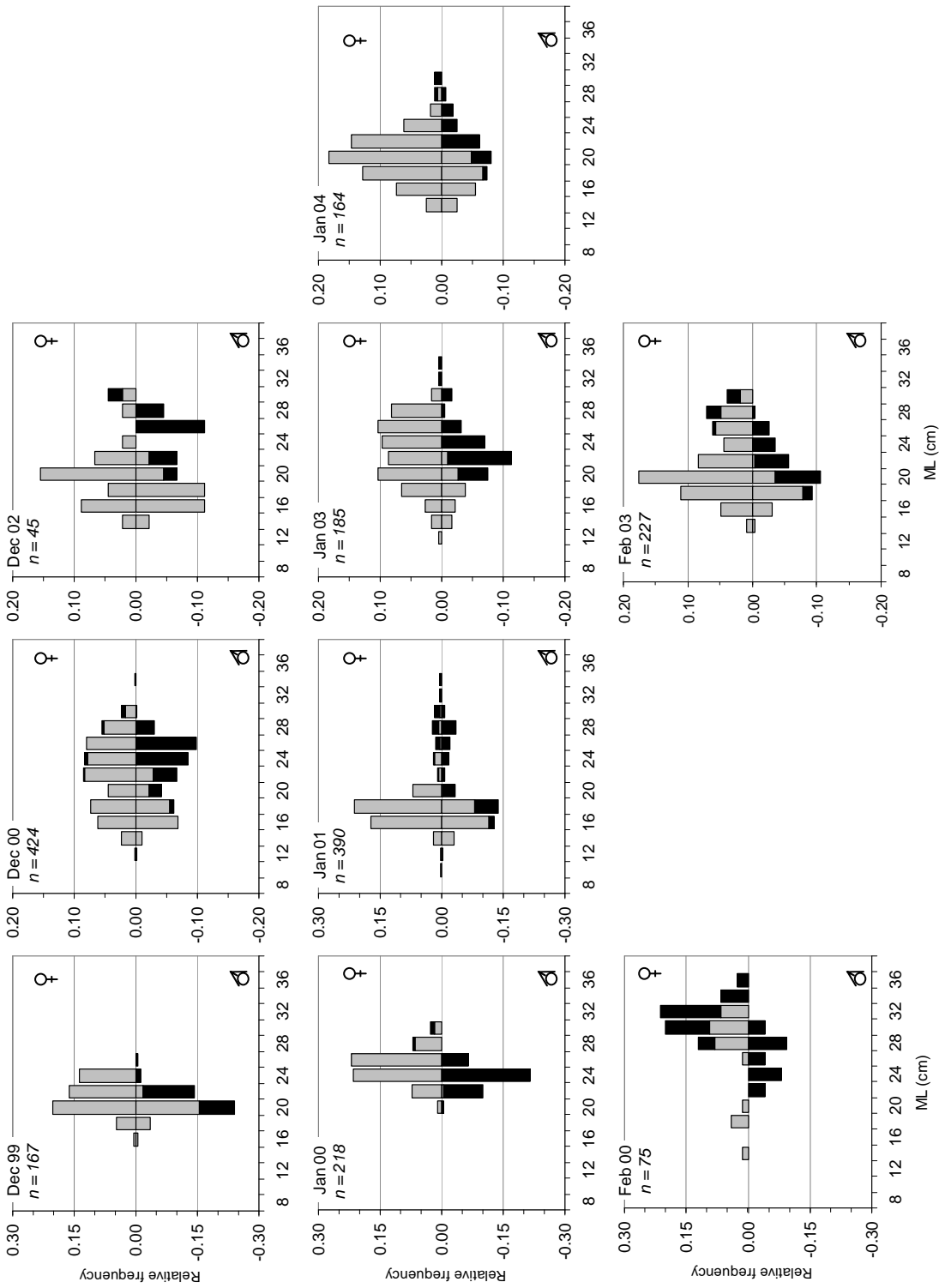


Figure 4.4. Relative size (ML) frequency histograms for *N. gouldi* by month and year. Positive y-axis displays females, negative y-axis displays males. Black bars are mature animals (stages 4 and 5), grey bars are immature animals (stages 1, 2 and 3). Note different y-axis scales.

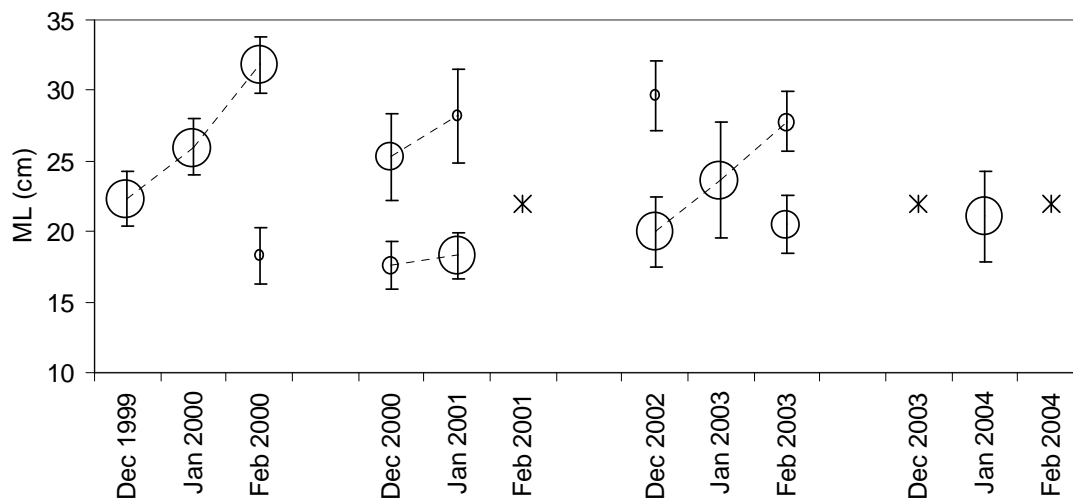
Apparent growth of individual size-cohorts in 2000/01, 2002/03 and 2003/04 were not as easily tracked within each season compared to in 1999/00. In 2000/01 the larger male and female cohorts increased in mean size from December to January (Figure 4.5), however the smaller female cohort showed only a very minor increase in mean size and the smaller male cohort decreased in mean size. Patterns in 2002/03 were similar to 1999/00 with clear growth of the main female size cohort over the season and evidence of new recruitment in February (Figure 4.5). However, for males the pattern broke down in February with only one intermediate male size-cohort identified, possibly a mix of those squid present in the previous month, and new recruits.

Comparisons of mean cohort size between years is complicated by the varying numbers of cohorts present, however some variability between years within months was evident. For example, in January, there were single size-cohorts evident in 2000, 2003 and 2004 for both sexes (Table 4.2, Figure 4.4), and mean cohort size (ML) was greatest in 2000, and smallest in 2003. In January 2001 however, there were two cohorts apparent, one greater than and one smaller than the mean cohort size in the other years.

Table 4.2. Mean ML (cm), and standard deviation (SD) of size cohorts identified by normal mixture models by sex, month and year. Prob is the mixing probability of each cohort for each sample and sex.

Month-Year	Size cohort	Female			Male		
		Mean	SD	Prob.	Mean	SD	Prob.
Dec-99	1	22.3	1.9	1	21.6	1.5	1
Jan-00	1	26.0	2.0	1	24.7	1.2	1
Feb-00	1	18.3	2.0	0.09	-	-	-
	2	31.8	2.0	0.91	27.0	2.4	1
Dec-00	1	17.6	1.7	0.30	18.3	2.1	0.38
	2	25.3	3.1	0.70	25.4	2.1	0.62
Jan-01	1	18.3	1.6	0.83	18.0	1.7	0.80
	2	28.2	3.3	0.17	27.5	1.7	0.20
Dec-02	1	20.0	2.5	0.84	19.1	2.2	0.71
	2	29.6	2.5	0.16	27.1	0.8	0.29
Jan-03	1	23.7	4.1	1	22.5	3.5	1
Feb-03	1	20.5	2.1	0.69	21.1	2.9	1
	2	28.0	2.1	0.31	-	-	-
Jan-04	1	21.1	3.2	1	20.5	3.1	1

a) Females



b) Males

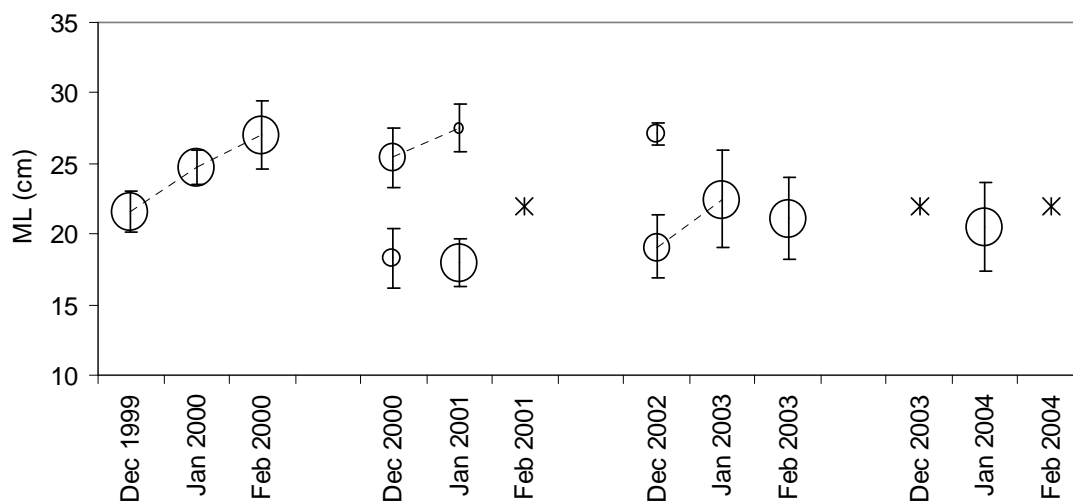


Figure 4.5. Size-cohorts for a) females and b) males. Each circle represents a size cohort, as identified by the mixture model. The size of the circle roughly represents the proportion of squid from each sample in that size cohort (Table 4.2). Dashed lines show where growth of size-cohorts is apparent. Error bars are one standard deviation. Asterisks mark where samples were not collected.

Age structure

Sampled *N. gouldi* were between 147 and 303 days old (Figure 4.6), with back-calculated hatch-dates falling between March and August. ANOVA was used to compare mean age between sexes and sample (where each sample is a unique combination of year and month; YM). The YM *Sex interaction term was not significant ($F_{4,364} = 0.59$, $p = 0.67$) and dropped from the model. The age of *N. gouldi* did not vary significantly between samples (YM), but did vary significantly between males and females (Table 4.3). Male *N. gouldi* were on average 14.5 (standard error: 2.8) days older than female *N. gouldi*. The mean hatch date (day-month) for sampled female *N. gouldi* was 8th June, while that for males was 24th May. The only year with ages available from more than one month (sample) was 2002/03, and *N. gouldi* caught in December 2002 were on average 7.5 days younger than those caught in February 2003, but this difference was not significant ($t_{1,373} = 1.52$, $p = 0.13$).

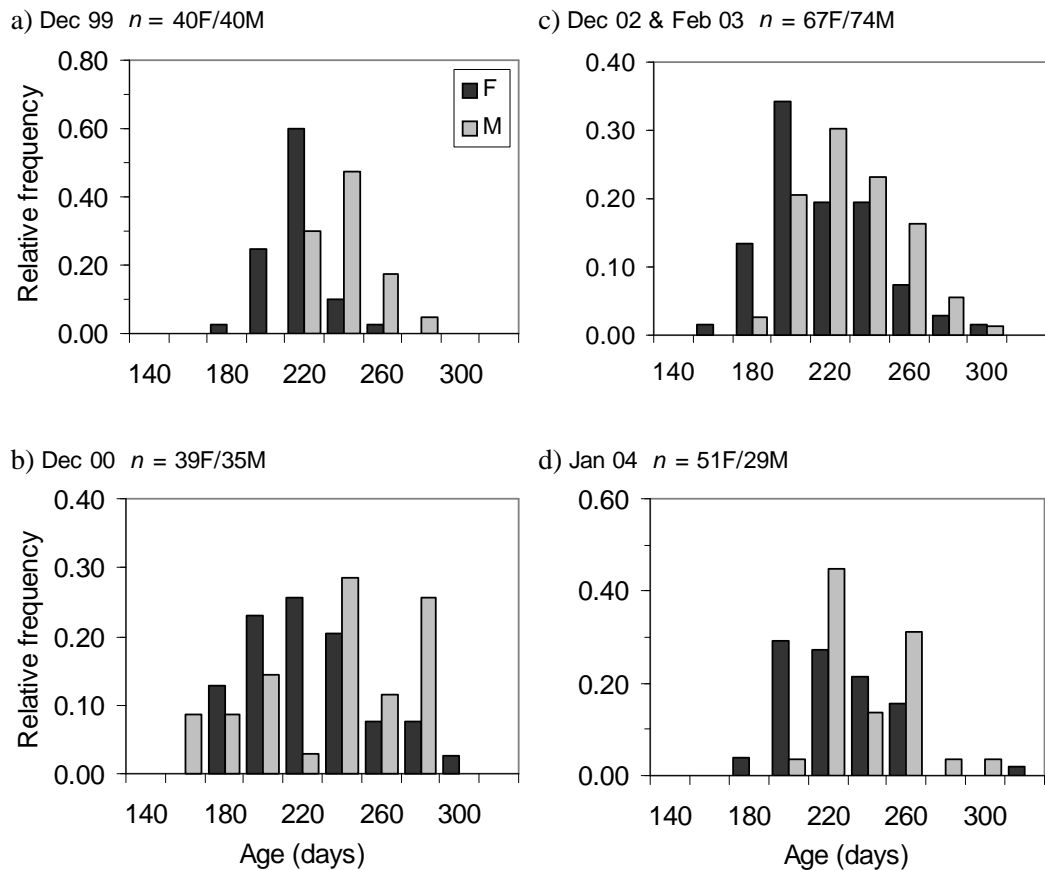


Figure 4.6. Relative age frequencies for *N. Gouldi* in a) December 1999, b) December 2000, c) December 2002 and February 2003 combined, and d) January 2004. Dark bars are for females, light bars are for males. Sample size shown (n = female/male).

Table 4.3. ANOVA comparing age between years and sex. The YM factor is a unique year-month combination. SSQ is sums of squares; MSQ is mean squares; RSS is residual sums of squares; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Response: Age	Df	SSQ	MSQ	F value	p value	
YM	4	4110	1028	1.45	0.22	
Sex	1	21951	21951	31.05	0.00	***
Residuals	368	260148	707			
Type III comparisons	Df	SSQ	RSS	F value	p value	
YM	4	6394	266543	2.26	0.06	.
Sex	1	21951	282100	31.05	0.00	***

Size at age (ML and BW)

Size-at-age did not vary between December 2002 and February 2003 (ML: $F_{1,136} = 0.00$, $p = 0.98$; BW: $F_{1,136} = 0.36$, $p = 0.55$), so the data for the two months were pooled to represent the 2002/03 season. Analyses were done separately for the two sexes so that effects of maturity on size at age could be examined for males. Few mature females were sampled and aged (9 only) and when maturity was included as a factor in the female models, they were destabilized by high collinearity (indicated by extremely large variance inflation factors). Female size-at-age results are therefore for immature squid only.

ANCOVA found a significant age by year interaction for all four models (male and female, ML and BW), however pairwise comparisons indicated that this interaction was in all cases driven by the 1999/00 season, which had a significantly lower slope (i.e. slower rate of growth) compared to the other three years which did not differ from each other. As the age and size range of *N. gouldi* sampled in 1999/00 was very limited (Figure 4.7), the analyses were repeated without an age by year interaction term, thereby forcing the growth rates (slopes) to be the same for all four years (Table 4.4).

Male *N. gouldi* were smaller than females in length (ML; Figure 4.7) and body weight (BW) over the range of ages sampled. ML-at-age of both sexes was significantly smaller in 2003/04 than in the other 3 years, whereas for BW-at-age, both sexes were significantly heavier in 2000/01 (Figure 4.8). These findings suggest that condition (i.e. BW-at-ML) was variable between years. As growth rates (i.e. regression slopes) were not different between years for either sex over the range of ages sampled, pre-recruit processes presumably accounted for the differences between years in size-at-age (i.e. regression intercepts). There was no significant interaction between maturity and age in the male models, although maturity was significant as a main effect (Table 4.4). Thus mature squid were larger than immature squid at the same age, but growth rates did not differ between mature and immature individuals.

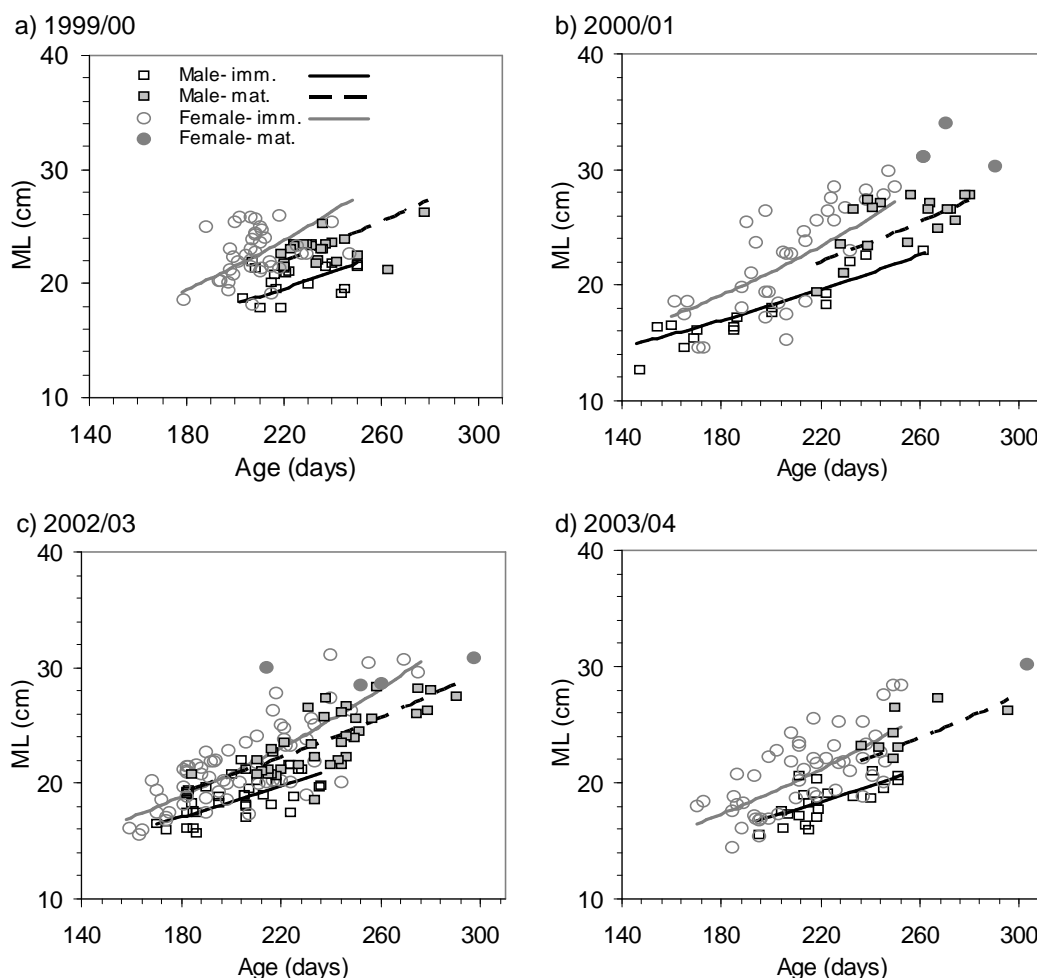


Figure 4.7. Observed values and fitted exponential curves for *N. gouldi* size (ML, cm)-at-age (days) for females (grey circles and dashed line) and males (black squares and thin solid line), by year.

Table 4.4. Analysis of covariance for size-at-age models. Male models (a & c) include a maturity factor, female models (b & d) are based on immature females only. Df is degrees of freedom; Age_c is centred Age. SSQ is sums of squares; MSQ is mean square; RSS is residual sums of squares; * p < 0.05; ** p < 0.01; *** p < 0.001.

a)	<i>Male</i>	<i>Response: log(ML)</i>	Df	SSQ	MSQ	F value	<i>p</i> value	
		Age _c	1	157.0	157.0	29560.7	0.000	***
		Year	4	1486.8	371.7	69966.4	0.000	***
		Mature	1	0.4	0.4	69.3	0.000	***
		Residuals	171	0.9	0.0			
		<i>Type III comparison</i>	Df	SSQ	RSS	F value	<i>p</i> value	
		Age _c	1	1.1	2.0	200.6	0.000	***
		Year	4	755.5	756.4	35551.9	0.000	***
		Mature	1	0.4	1.3	69.3	0.000	***
b)	<i>Female</i>	<i>Response: log(ML)</i>	Df	SSQ	MSQ	F value	<i>p</i> value	
		Age _c	1	231.8	231.8	17927.0	0.000	***
		Year	4	1527.7	381.9	29536.0	0.000	***
		Residuals	182	2.4	0.0			
		<i>Type III comparison</i>	Df	SSQ	RSS	F value	<i>p</i> value	
		Age _c	1	2.3	4.7	180.4	0.000	***
		Year	4	1527.7	1530.1	29536.1	0.000	***
c)	<i>Male</i>	<i>Response: log(BW)</i>	Df	SSQ	MSQ	F value	<i>p</i> value	
		log(Age) _c	1	627.0	627.0	9218.2	0.000	***
		Year	4	4527.7	1131.9	16640.8	0.000	***
		Mature	1	5.8	5.8	85.3	0.000	***
		Residuals	170	11.6	0.1			
		<i>Type III comparison</i>	Df	SSQ	RSS	F value	<i>p</i> value	
		log(Age) _c	1	9.5	21.1	140.1	0.000	***
		Year	4	1707.8	1719.4	6276.7	0.000	***
		Mature	1	5.8	17.4	85.3	0.000	***
d)	<i>Female</i>	<i>Response: log(BW)</i>	Df	SSQ	MSQ	F value	<i>p</i> value	
		log(Age) _c	1	502.0	502.0	3939.0	0.000	***
		Year	4	4935.8	1233.9	9682.8	0.000	***
		Residuals	181	23.1	0.1			
		<i>Type III comparison</i>	Df	SSQ	RSS	F value	<i>p</i> value	
		log(Age) _c	1	25.7	48.8	201.9	0.000	***
		Year	4	4935.8	4958.9	9682.8	0.000	***

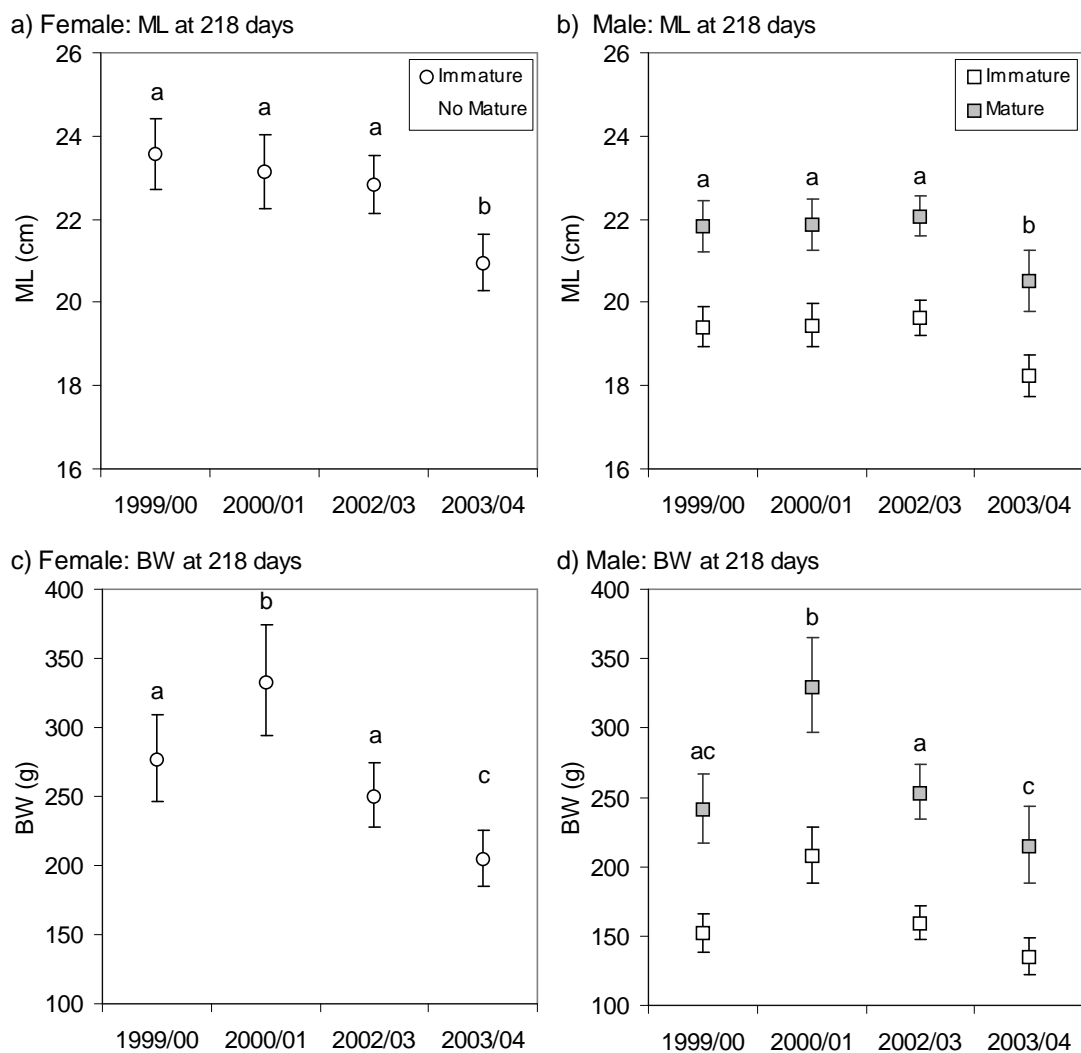


Figure 4.8. Fitted ML (a & b) and BW (c & d) at age = 218 days with 95% confidence intervals. Letters denote grouping according to post-hoc pairwise comparisons. Note that for b & d the groupings are the same for both immature and mature squid so letters only shown next to mature points.

Overall condition- total body weight at length

The effect of year and maturity on condition (BW adjusted for ML) were examined by separate ANCOVAs for males and females. The slope of the $\log(\text{BW})$ by $\log(\text{ML})$ relationship varied between years, as indicated by the significant interaction terms in both male and female ANCOVA tables (Table 4.5). For males the slope was significantly steeper in 1999/00 and 2002/03 compared to 2000/01 and 2003/04, while for females, slopes were steepest in 2002/03 and lowest in 2000/01 (Table 4.6). There was also a significant $\log(\text{ML})$ by maturity interaction in the male ANCOVA (Table 4.5), with mature male squid increasing in BW with size (ML) at a much faster rate than immature individuals (Table 4.6).

The overall condition of male and female *N. gouldi* was significantly greater in 2000/01 compared to all other years, except for very large mature females (34cm ML) which were still heaviest at size in 2000/01, but not significantly different from those in 2002/03 (Figure 4.9). Female condition was poor in 1999/00 for most sizes examined, although not significantly different from 2003/04. Small immature

females (16 cm ML) were in poorest condition in 2002/03, although condition in 1999/00 was also low (Figure 4.9). Male condition was also poorest in 1999/00 for immature and mature males at 22cm ML. Large mature males (28 cm ML) and small immature males (14 cm ML) were in poorest condition in 2002/03 and 2003/04 respectively, although neither of these years were significantly different from 1999/00 which was also low (Figure 4.9).

Table 4.5. ANCOVA results and for (a) female, and (b) male *N. gouldi* condition. Non-significant interactions were dropped from the model. Df is degrees of freedom; SSQ is sums of squares; MSQ is mean squares; RSS is residual sums of squares; log(ML)_c is centred log-transformed ML (cm). * p <0.05; ** p <0.01; *** p <0.001.

a)	<i>Female</i>	<i>Response: log(BW)</i>	Df	SSQ	MSQ	F value	p value	
		log(ML) _c	1	417.1	417.1	36622.5	0.000	***
		Year	3	6.7	2.2	194.6	0.000	***
		Maturity	1	0.1	0.1	5.0	0.025	*
		log(ML) _c : Year	3	0.7	0.2	18.9	0.000	***
		Residuals	1032	11.8	0.0			
		<i>Type III comparison</i>	Df	SSQ	RSS	F value	p value	
		Maturity	1	0.0	11.8	4.1	0.044	*
		log(ML) _c : Year	3	0.6	12.4	18.9	0.000	***
b)	<i>Male</i>	<i>Response: log(BW)</i>	Df	SSQ	MSQ	F value	p value	
		log(ML) _c	1	250.3	250.3	24566.9	0.000	***
		Year	3	5.2	1.7	168.9	0.000	***
		Maturity	1	0.4	0.4	35.1	0.000	***
		log(ML) _c : Year	3	1.0	0.3	32.4	0.000	***
		log(ML) _c :Maturity	1	0.1	0.1	12.3	0.000	***
		Residuals	695	7.1	0.0			
		<i>Type III comparison</i>	Df	SSQ	RSS	F value	p value	
		log(ML) _c : Year	3	0.9	7.9	28.2	0.000	***
		log(ML) _c :Maturity	1	0.1	7.2	12.3	0.000	***

Table 4.6. Comparison of condition (BW-at-ML) model slopes (i.e. coefficients of the log(ML)*Year interactions), for a) females, b) immature males and c) mature males. Letters denote grouping according to post hoc pairwise comparisons of slopes between years.

	Sex	Maturity	Year	Slope	Std. Error	
a)	Female	Combined	1999/00	3.31	0.05	a
		immature & mature	2000/01	3.15	0.03	b
			2002/03	3.47	0.04	c
			2003/04	3.20	0.07	ab
b)	Male	Immature	1999/00	3.49	0.11	a
			2000/01	3.02	0.06	b
			2002/03	3.48	0.07	a
			2003/04	3.03	0.10	b
c)	Male	Mature	1999/00	3.72	0.09	a
			2000/01	3.27	0.04	b
			2002/03	3.73	0.06	a
			2003/04	3.27	0.10	b

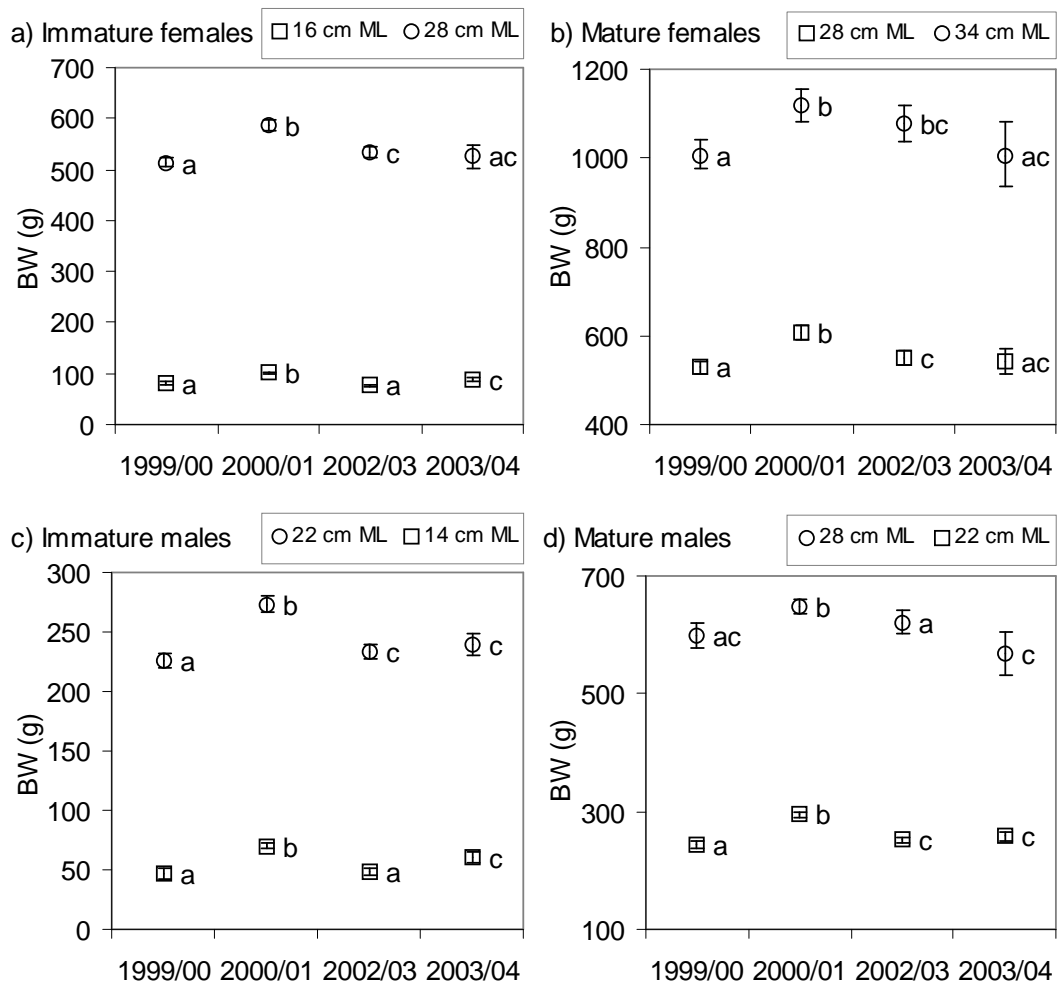


Figure 4.9. Fitted BW at various ML with 95% confidence intervals for a) immature females, b) mature females, c) immature males, and d) mature males. Letters denote grouping according to post hoc pairwise comparisons.

Maturity

In all months and years there was a greater proportion of mature (stage 4 and 5) males present than females (Figure 4.4, Figure 4.10). Between 40 and 100% of males were mature in all samples, and while 55% of females were mature in February 2000, in all other months mature females contributed less than 9%.

In 1999/00 the proportion of mature males and females increased over the three sampled months, as the single size-cohort present grew and matured. The small number of immature (stage 1 & 2) females in February (Figure 4.10) indicates the appearance of a new cohort (Figure 4.4). In all other years, there was no clear progression in the proportion of the population mature (Figure 4.10) due to the regular influx of cohorts of small immature individuals (as evidenced by the multi-modal length frequencies, Figure 4.4).

Only 3 of the 4 years could be used to investigate female maturity-size relationships; 2003/04 was excluded as only 3 mature females were sampled and logistic model fits were poor. Due to missing cells in the full model structure, separate analyses were done for the two sexes. This also reduced the complexity of models as size at

maturity was very different between the two sexes, with males mature from just 16.6 cm ML, while the smallest mature female sampled was 23.0 cm ML (Figure 4.4).

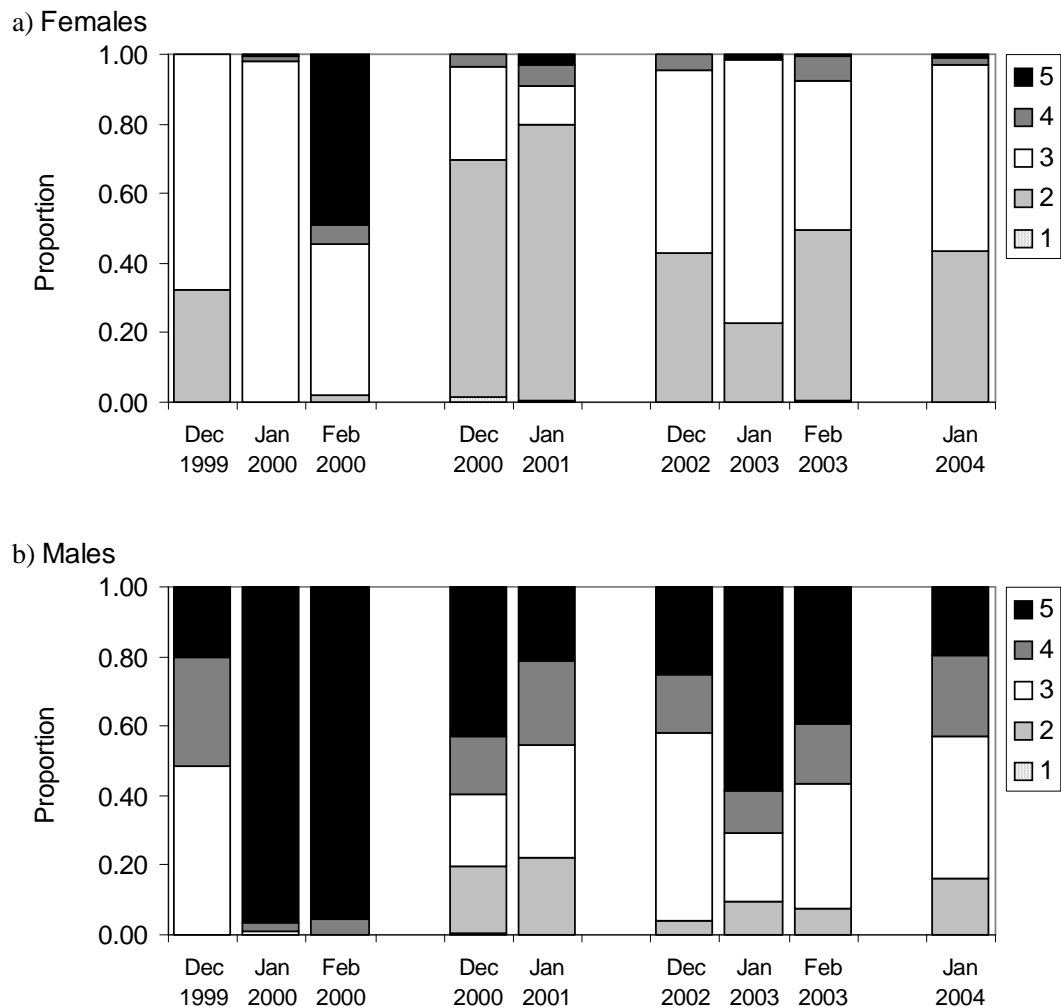


Figure 4.10. Proportion of a) females and b) males classified to each of 5 maturity categories by month and year. Stages 1, 2 and 3 are immature, 4 and 5 mature for both males and females.

Diagnostic plots confirmed the linear relationship between ML and maturity in a logistic model (i.e. when probability of being mature is logit transformed). The slope of the linear relationship which represents the mean rate of increase in the log-odds of being mature with size, was steeper for males than females (Table 4.7). Males therefore not only begin maturing at smaller sizes than females, but mature over a smaller size range; with the mean difference (weighted by year) between ML at 10 and 90% maturity 3.9 cm for males, and 5.9 cm for females.

The slope of the linear relationship also varied between years for both sexes; indicated by significant ML by year interactions in the analysis of deviance tables (Table 4.7). The slope was lowest in 2000/01 for both males and females (Figure 4.11), and pairwise comparisons show it was significantly lower than 1999/00 and 2002/03 for males, and significantly lower than 1999/00 only for females (Table 4.8). Despite differences being large, the slope in 2000/01 was not significantly different from 2003/04 for males, or 2002/03 for females, due to large variability around the

slope estimates in these years (Table 4.8). The difference between mean size at 10 and 90% maturity is therefore considerably greater in 2000/01 compared to the other years sampled.

Both males and females started maturing at considerably smaller sizes in 2000/01 compared to the other sampled years, with 10% mature at 17.0 cm ML for males and 26.6 cm ML for females (Figure 4.11 & 4.12). Size at 10% maturity was greatest in 1999/00 (Figure 4.12). Size at 50% maturity ranged between 30.6 and 31.4 cm for females, and 20.5 to 21.5 for males, and was greatest in 1999/00 for both sexes. Size at 90% maturity was greatest for both males and females in 2000/01 (Figure 4.12).

Table 4.7. Analysis of deviance table for a) female and b) male maturity logistic GLMs. Df is degrees of freedom; ML_c is centred ML. * p <0.05; ** p <0.01; *** p <0.001.

a) Female	Response: log odds maturity	Df	Deviance	Residual Df	Residual Deviance	p value	
	NULL			1010	534.5		
	ML _c	1	265.5	1009	268.9	0.000	***
	Year	2	7.0	1007	261.9	0.030	*
	ML _c : Year	2	9.1	1005	252.8	0.010	*
b) Male	Response: log odds maturity	Df	Deviance	Residual Df	Residual Deviance	p value	
	NULL			774	1042.4		
	ML _c	1	560.0	773	482.3	0.000	***
	Year	3	5.4	770	477.0	0.150	.
	ML _c : Year	3	34.3	767	442.7	0.000	***

Table 4.8. Comparisons of slopes (i.e. ML_c * Year coefficients) from logistic maturity-at-size model for a) females and b) males. Slope is the change in log-odds of being mature with a unit increase in size (ML, cm). 2003/04 was not analysed for females due to a paucity of mature specimens. Letters indicate statistical differences.

	Sex	Year	Estimate	Std. Error	
a)	Female	99/00	0.92	0.16	a
		00/01	0.51	0.08	b
		02/03	1.03	0.26	ab
		03/04	-	-	
b)	Male	99/00	1.78	0.33	a
		00/01	0.62	0.06	bc
		02/03	1.21	0.19	a
		03/04	1.81	0.62	ac

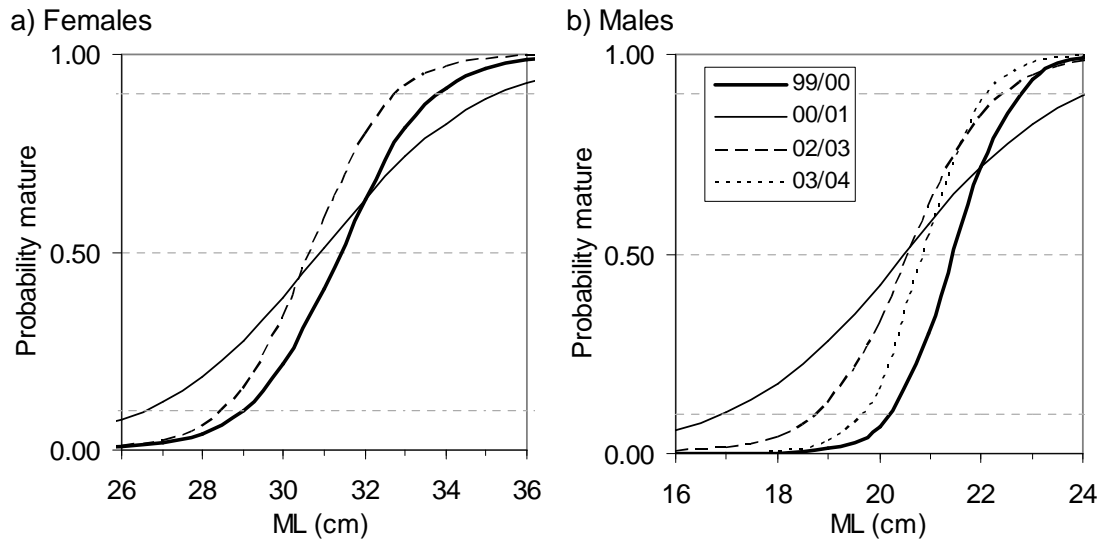


Figure 4.11. Fitted logistic curves for *N. gouldi* maturity at size (ML) by year for a) females and b) males. No model was fitted for females in 2003/04. Horizontal grey dashed lines indicate 10, 50 and 90% maturity. Note different scales on x-axes.

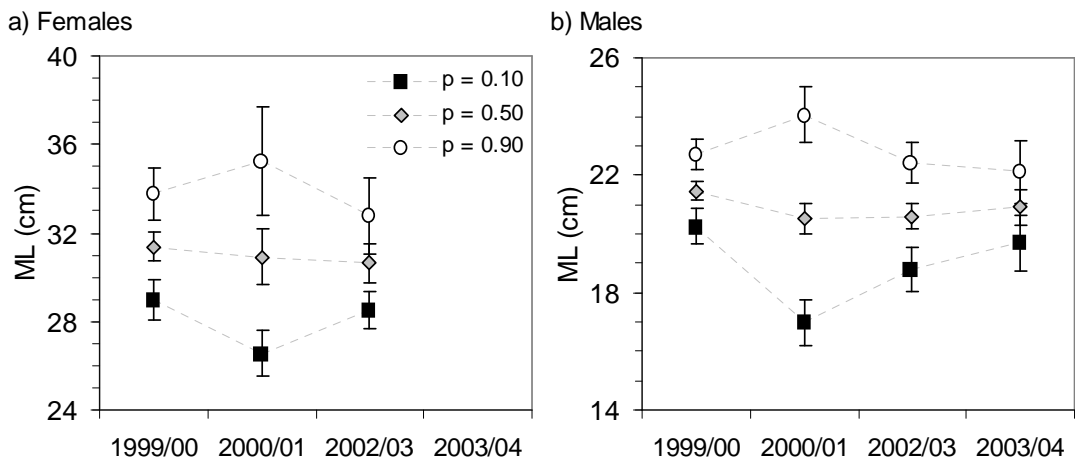


Figure 4.12. Mean size (ML) at 0.10, 0.50 and 0.90 probability of being mature by year for a) females, and b) males. Error bars are 95% confidence intervals. Note different scales for y-axes.

Somatic vs. reproductive condition

Mean reproductive investment in mature squid was quite low. Mature female RSI ranged from 1 to 14% (Table 4.9), although when only stage 5 squid are considered the minimum was increased to 5.2%. Female RSI was greatest in 1999/00 and lowest in 2002/03. Males showed greatest mean RSI in 2002/03 and lowest in 2003/04, with individual values ranging from less than 1% (1.6% for stage 5 only) to more than 5% (Table 4.9).

Somatic and reproductive weights adjusted for size (ML) were compared between years for mature squid of each sex. For females data were available for 1999/00 and 2002/03 only, while for males 2003/04 data were also available (only 3 mature females were present in 2003/04). For the female analyses, interaction terms were not significant and dropped from models (Table 4.10). Size adjusted SW for females

was significantly greater in 2002/03 compared to 1999/00, while the reverse applied to RW, with 2002/03 was significantly *less* than 1999/00 (Table 4.10, Figure 4.13).

Table 4.9. Repro-somatic index (RSI; %) for mature a) female and b) male *N. gouldi* (where stage 4 and 5 squid are considered mature). Note that separate somatic and reproductive weights were not collected for 2000/01 sampled squid.

	Sex	Year	Mean	SD	<i>n</i>	Min	Max
a)	Females	1999/00	8.42	2.46	28	4.08	13.95
		2000/01	-	-	-	-	-
		2002/03	4.18	3.26	14	1.01	11.32
		2003/04	6.08	4.81	3	2.96	11.63
b)	Males	1999/00	2.56	0.85	83	1.13	5.34
		2000/01	-	-	-	-	-
		2002/03	2.61	0.77	101	0.82	4.40
		2003/04	2.37	0.82	24	1.23	4.20

Table 4.10. ANCOVA results for female a) somatic weight (SW) and b) reproductive weight (RW) adjusted by size (ML). Non-significant interactions were dropped from the model. Df is degrees of freedom; SSQ is sums of squares; MSQ is mean square; RSS is residual sums of squares; log(ML)_c is centred log-transformed ML (cm). * *p* < 0.05; ** *p* < 0.01; *** *p* < 0.001.

a)	Female	<i>Response: SW</i>	Df	SSQ	MSQ	F value	<i>p</i> value	
		ML _c	1	124551	124551	214.00	0.000	***
		Year	1	3383	3383	5.81	0.021	*
		Residuals	38	22117	582			
		<i>Type III comparison</i>	Df	SSQ	RSS	F value	<i>p</i> value	
		ML _c	1	118942	141059	204.36	0.000	***
		Year	1	3383	25499	5.81	0.021	*
b)	Female	<i>Response: RW</i>	Df	SSQ	MSQ	F value	<i>p</i> value	
		ML _c	1	29594	29594	76.00	0.000	***
		Year	1	3429	3429	8.81	0.005	**
		Residuals	38	14797	389			
		<i>Type III comparison</i>	Df	SSQ	RSS	F value	<i>p</i> value	
		ML _c	1	17359	32156	44.58	0.000	***
		Year	1	3429	18225	8.81	0.005	**
c)	Male	<i>Response: SW</i>	Df	SSQ	MSQ	F value	<i>p</i> value	
		ML _c	1	656302	656302	2654.72	0.000	***
		Year	2	342	171	0.69	0.502	
		ML _c :Year	2	2813	1407	5.69	0.004	**
		Residuals	201	49691	247			
d)	Male	<i>Response: RW</i>	Df	SSQ	MSQ	F value	<i>p</i> value	
		ML _c	1	6075	6075	755.06	0.000	***
		Year	2	63	32	3.91	0.022	*
		Residuals	203	1633	8			
		<i>Type III comparison</i>	Df	SSQ	RSS	F value	<i>p</i> value	
		ML _c	1	6050	7684	752.04	0.000	***
		Year	2	63	1696	3.91	0.022	*

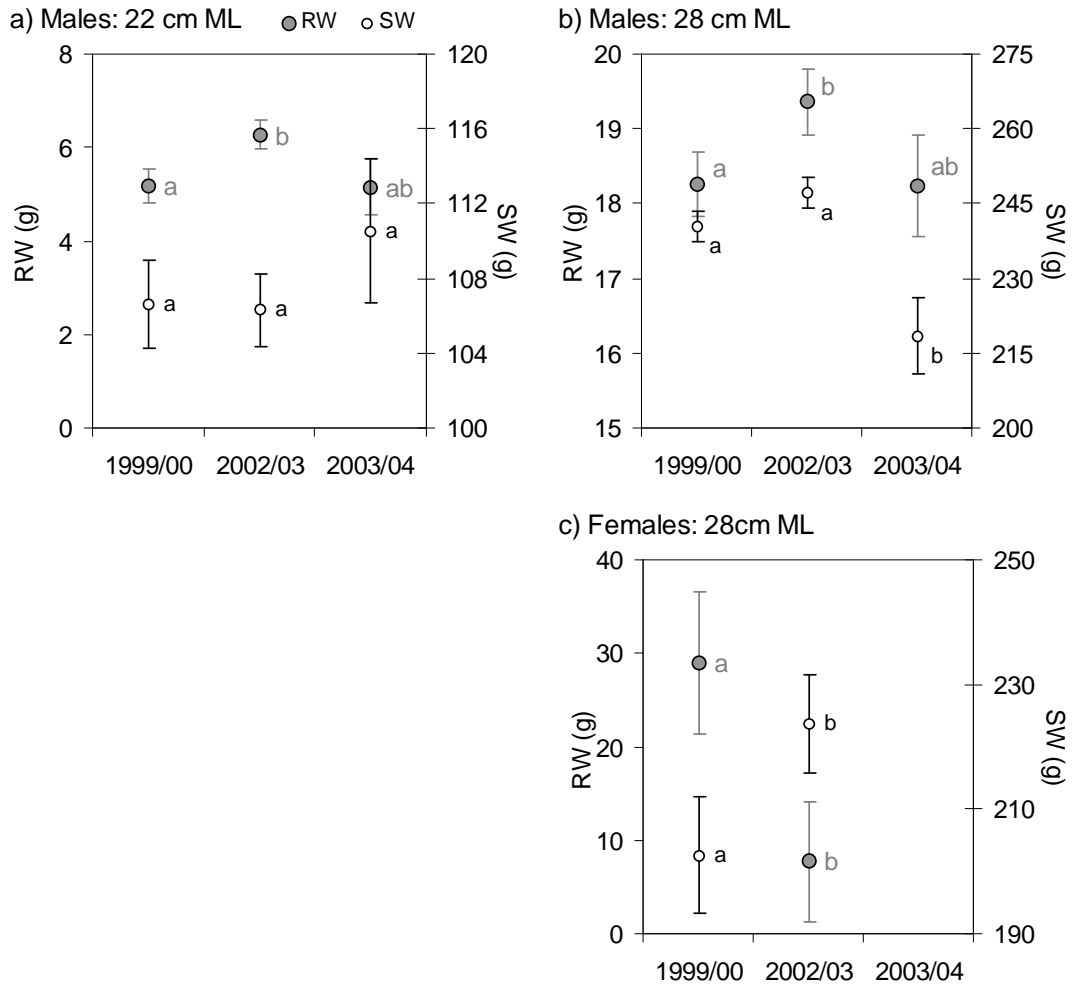


Figure 4.13. Fitted SW and RW (with standard error) by year for a) mature males at 22 cm ML, b) mature males at 28 cm ML and c) mature females at 28 cm ML. Error bars are standard errors. Letters denote grouping according to post hoc pairwise comparisons; solid circles and grey letters are for RW comparisons, open circles and smaller black letters are for SW comparisons. Male results only are shown at two ML sizes as there was a significant ML * SW interaction (Table 4.10).

For males a significant ML by year interaction was present (Table 4.10). The slope of the SW-ML relationship for male *N. gouldi* was significantly smaller in 2003/04 compared to 1999/00 ($t = -2.57$, $p = 0.011$) and 2002/03 ($t = -3.34$, $p = 0.003$), hence the different trends between years at different ML (Figure 4.13). There were no significant differences between years in SW for mature males at 22cm ML, however at 28 cm ML, SW was significantly lower in 2003/04 (Figure 4.13). Mature male RW did however, vary significantly between years (Table 4.10), with RW-at-size significantly greater in 2002/03 compared to 1999/00 but not 2003/04 (Figure 4.13). This RW trend is the opposite of what was found for females in 1999/00 and 2002/03.

Size adjusted SW and RW residuals were significantly correlated for females in 1999/00, and for males in 2002/03 and 2003/04 (Table 4.11, Figure 4.14). Correlation coefficients were negative for females in both years, suggesting a trade off between somatic and reproductive investment, while all male correlation coefficients were positive, suggesting a fixed proportion of investment between the different tissues.

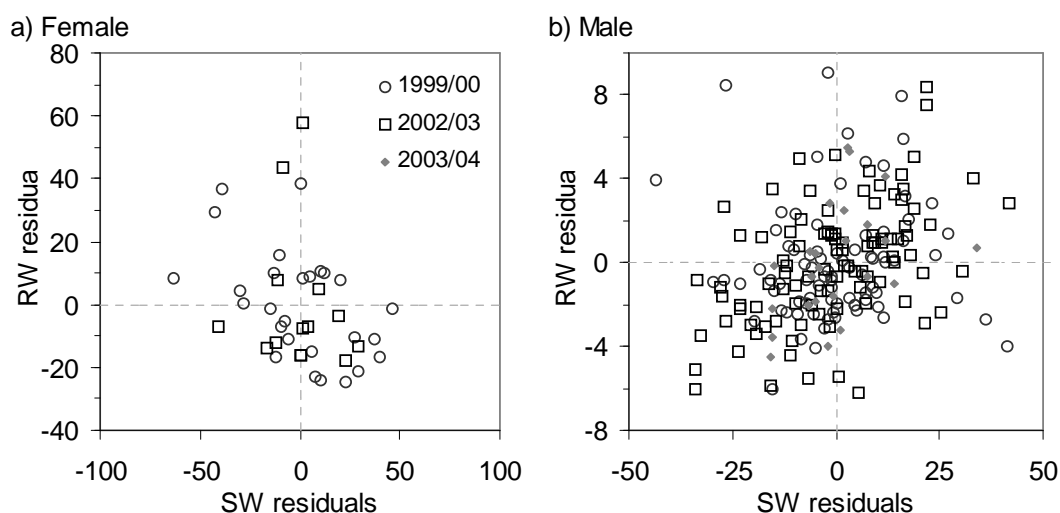


Figure 4.14. Size adjusted residuals from a) female and b) male SW and RW regression models.

Table 4.11. Correlation coefficients (r) and BCa 95% confidence intervals for a) female, and b) male SW and RW regression residuals. n is the sample size. * $p < 0.05$; ** $p < 0.01$.

	Sex	Year	n	r	95% CI		
a)	Female	1999/00	27	-0.50	-0.70	-0.24	**
		2002/03	14	-0.11	-0.49	+0.23	ns
b)	Male	1999/00	83	0.03	-0.24	+0.26	ns
		2002/03	100	0.45	+0.27	+0.60	*
		2003/04	24	0.38	+0.11	+0.65	*

DISCUSSION

Nototodarus gouldi, like so many other squid species, shows significant plasticity in population structure and life history characteristics. Considerable spatial and seasonal variability has already been described for this species (Jackson et al. 2003, McGrath Steer & Jackson 2004, Jackson et al. 2005), and this study shows that there is also substantial interannual variability. Size and maturity structure, size-at-age, size-at-maturity, condition and levels of reproductive and somatic investment differed between years at varying degrees. Results were often different between the two sexes, in particular inter-annual trends in reproductive investment varied dramatically between mature males and females. The population structure of *N. gouldi* on the inshore jig grounds was quite different to those sampled from trawl grounds in other studies, and varied within each fishing season, providing new insights into the dynamics of *N. gouldi* populations. The four years sampled in this study encompassed extremes in available biomass and therefore also provided the opportunity to examine the relationship between abundance, population structure and life history characteristics. However, like previous studies on loliginid squid (Pecl et al. 2004b, Pierce et al. 2005), relationships were not straight forward.

Population Structure

Nototodarus gouldi sampled from the inshore southeast Tasmanian jig fishery ranged from 147 to 303 days in age, and from 11.8 to 37.6 cm ML. For both males and females the age and size range in this study was slightly wider than previously published values from Tasmanian waters (171 – 283 days, 13.2 – 36.6 cm ML, Jackson et al. 2005), although frequency distributions were generally similar. *Nototodarus gouldi* recruit to the jig fishery as immature juveniles, but while males reach reproductive maturity during the jig season, most females sampled were classified as immature (stage 2) or preparatory (stage 3). Very few mature females were present in any samples, except in February 2000. Catches and catch rates in the Tasmanian jig fishery declined rapidly from February (Willcox et al 2001), and acoustic tracking work suggests that this may be due to squid moving away from the Storm Bay jig fishing grounds (Chapter 5).

In comparison to *N. gouldi* sampled from the Tasmanian jig fishery, samples collected from trawlers working the shelf edge and upper-slope in waters off southwestern Tasmania (unpublished data) and western Victoria (Jackson et al. 2003) were considerably larger (up to 40.5 cm ML), and predominantly mature (81 and 99% mature, females and males respectively in Tasmanian samples). The aged squid from western Victorian trawl samples were also generally older (up to 360 days). Many squid undertake ontogenetic migrations between feeding and spawning locations and ommastrephid squid are typically associated with large scale along-shelf migrations (e.g. *I. argentinus*, Haimovici et al. 1998; *I. illecebrosus*, O'Dor & Dawe 1998; *Ommastrephes bartramii*, Bower & Ichii 2005; *T. pacificus*, Takami & Suzu-Uchi 1993, Mokrin et al. 2002), although cross-shelf movements between inshore and offshore waters have also been documented (e.g. *I. argentinus*, Arkhipkin 2000; *I. coindetti*, Sanchez et al. 1998; *I. illecebrosus*, Dawe & Beck 1997, Hendrickson 2004; *Todarodes sagittatus*, Quetglas et al. 1998, Arkhipkin et al. 2001, Lordan et al. 2001). The distribution of *N. gouldi* may also vary with ontogeny, with larger and older squid found in deeper waters, and juveniles and sub-adults distributed over the shelf. Although these patterns may be biased by differential selectivity of trawl and jig fishing methods, an analysis of stomach contents of southern bluefin tuna (*Thunnus maccoyii*, Young et al. 1997) found that tuna foraging in shelf waters ate smaller *N. gouldi* than those in offshore waters. A bathymetric ontogenetic distribution has also been suggested for the congener *N. sloanii* in New Zealand waters (Uozumi 1998). Such a distribution may be an adaptation to reduce the impact of cannibalism (which can be significant in *N. gouldi*, O'Sullivan & Cullen 1983), or may be related to energy requirements and the distribution of suitable prey for the different ontogenetic stages.

The rapid growth and development of squid require levels of energy intake to be high. *Nototodarus gouldi* may utilise the shelf waters during juvenile stages to maximise their energy intake for reproductive development. The east coast shelf of Tasmania is generally dominated by productive subantarctic waters (SAW, Harris et al. 1987, Harris et al. 1991a) and has a greater abundance of zooplankton and micronekton compared to offshore waters (Young et al. 1996). This contrast is particularly pronounced in the summer when the oligotrophic waters of the East Australian Current (EAC) extend down the east coast of Tasmania (Harris et al. 1987, Harris et al. 1991a), and indeed tuna in EAC waters have been found to have

considerably less *N. gouldi* in their diet than those caught in SAW (Young et al. 1997). Current research is comparing the population structure of (shallow) jig and (deeper) trawl caught squid off Portland, western Victoria (G.D. Jackson *pers comm.*) and should provide further insight into possible ontogenetic patterns in the distribution of *N. gouldi*.

The most notable change in population structure within each fishing season was in sex ratio, with the proportion of females in the inshore population increasing from close to 0.5 in December to more than 0.65 in February. Males may leave the inshore feeding grounds earlier than females, having less intensive energy requirements and reaching reproductive maturity earlier. Sexual segregation in timing and pathways of migration has been documented for other ommastrephid squid. For example, male *I. argentinus*, were found to leave their shallow feeding grounds several weeks before females (Arkhipkin 1993), and male *O. bartramii* begin their spawning migration up to two months earlier than females (Bower & Ichii 2005), moving in different schools and even following different routes (Murakami et al. 1981 cited in Arkhipkin & Middleton 2002). A similar process may account for the change in *N. gouldi* sex ratio on the southeast Tasmanian jig grounds. Acoustic tracking of *N. gouldi* (Chapter 5) suggests that the population in Storm Bay is highly dynamic, with movement out of the area evident throughout the season. Unfortunately results were inconclusive with respect to sex specific patterns as few squid were tracked and not all were sexed.

The change in sex ratio may alternatively be related to behavioural changes affecting the vulnerability of the squid to the fishing gear (e.g. Hibberd & Pecl 2007). The RSI of female *N. gouldi* was almost three times as great as that for males on average, with females investing much more energy into reproductive development. Late preparatory stage females in particular, may feed more voraciously than males (e.g. Quetglas et al. 2001) to obtain sufficient energy for the maturation process, and this may increase their jig catchability, particularly towards the end of each fishing season as females get closer to size at reproductive maturity. In contrast, the catchability of males may decline later in the season as their focus shifts from feeding to mating. Female *N. gouldi* are often mated by males before they reach reproductive maturity (McGrath & Jackson 2002, McGrath Steer & Jackson 2004), with sperm stored in buccal pouches until required. Although in this study evidence of mating was not noted consistently, Mitchell (2000) found that mated females first appeared in Storm Bay samples in mid-January and the proportion mated continued to increase over the latter half of the summer season. It is possible that mature males would be less inclined to feed as mating begins, instead concentrating on maximising their reproductive success. Future work using a combination of dietary analysis and acoustic tracking could determine which of these hypotheses (emigration vs. catchability) may be most likely.

The number of size-cohorts present (between one and three), the mean size of these cohorts, and their variance changed from year-to-year. The ability to track the size-cohorts within seasons (i.e. from December to February) was also variable; while in some samples distinct cohorts were obvious (e.g. 1999/00), in others micro-cohort structure was difficult to discern (e.g. January 2003). Natural size modes in multi-cohort squid populations are notoriously difficult to track over time (Caddy 1991) due to the high degree of individual level variability in size-at-age, and/or relatively

continuous recruitment to the population. Waves of recruitment were evident in size-frequency distributions from southeast Tasmanian waters in the late 1970s (JAMARC 1978b, Harrison 1979), and in this study recruitment of *N. gouldi* also appears to be periodic with pulses of new size recruits separated by approximately 2 months in 1999/00 and 2002/03. However, in some samples (e.g. 2000/01) micro-cohort structure was less clear and suggested more continuous recruitment of individuals to the population. This could reflect a change in spawning strategy by the parent generations (McGrath Steer & Jackson 2004), or the influence of post-spawning environmental conditions on survival and growth rates. Timing of sampling can also strongly influence the apparent recruited population structure, in particular size frequencies that suggest periodic batch spawning may be generated when in actual fact the spawning and hatching is continuous through time (Boyle & Boletzky 1996). However, in this study the tightest size cohorts (1999/00) were derived from a much larger number of samples than the more variable size cohorts in other years. Unfortunately the availability of statoliths for ageing in this study was limited, and age structure could not be examined over the same temporal scale as size structure to infer spawning strategies and recruitment modes.

Life history characteristics

Nototodarus gouldi populations sampled from the Storm Bay jig fishery displayed considerable plasticity in all life history characteristics examined, consistent with observations over a wider spatial scale and finer seasonal scale (Jackson et al. 2003, McGrath Steer & Jackson 2004, McGrath-Steer 2004, Jackson et al. 2005). There was significant variability between years, but trends were not always consistent for the different characteristics examined, suggesting quite different life history strategies from year to year and also between sexes.

Rate of growth (i.e. the slope of the size-at-age relationship) did not vary between 2000/01, 2002/03 or 2003/04, therefore the significant differences between these years in size-at-age must have been shaped by pre-recruitment processes. Rates of growth may have instead varied during the early life-history stages, when squid are much more vulnerable to abiotic and biotic variability. Alternatively the different intercepts may be due to inter-annual differences in size at hatching (Pecl et al. 2004a) or size-specific mortality during the embryonic or juvenile stages (Steer et al. 2003b). Growth rates from the power curve fit to BW-at-age data were comparable with those reported previously for *N. gouldi* sampled in Tasmanian waters (Jackson et al. 2003). For immature females in this study, the slope of the log(BW)-log(Age) relationship (3.47 ± 0.24 s.e.) was well within the range (2.81 – 4.77) of slopes reported by Jackson et al. (2003), although for males (immature & mature) the slope fitted here (2.37 ± 0.20 s.e.) was at the lower end of the range of values reported previously (2.08 – 4.10; Jackson et al. 2003).

Rates of growth in 1999/00 were difficult to compare with other seasons due to the limited size and age range of animals with statoliths available for ageing. As there were no significant differences between the other three years, the same mean rate was assumed to apply to 1999/00. However, if slopes of the size-at-age models were allowed to vary freely between years, the fitted growth rate for 1999/00 was much smaller than the other three years (1.95 ± 0.49 s.e. for females, and 1.21 ± 0.49 s.e. for males) and well below previous reported values (Jackson et al. 2003).

Unfortunately, the limited availability of statoliths prevented a more accurate determination of growth rate in this year.

Size-at-maturity, condition and relative levels of repro-somatic investment in mature squid also varied between years. In particular, the transition from immature to mature occurred over a much greater size range in 2000/01. Good overall condition may account for the maturation of individuals at smaller lengths (ML) in 2000/01 compared to other years, but it is not clear why some immature animals persisted at large sizes (thereby increasing the size at 90% maturity). There may have been more than one underlying size-at-maturity trajectory due to other variables not considered. External factors such as temperature, photoperiod and food availability can all affect maturation rates (Mangold 1987), and may have generated greater variability in size-at-maturity during 2000/01.

Levels of reproductive and somatic investment by mature *N. gouldi* vary seasonally and spatially (McGrath Steer & Jackson 2004, McGrath-Steer 2004), and this study found significant inter-annual variability too. Unfortunately data on reproductive and somatic investment were not available for 2000/01, the year that *N. gouldi* were in the best overall condition, and few mature females in 2003/04 meant it was also excluded from analyses. However, it is clear that *N. gouldi* may vary greatly in their strategies of energy investment from year to year, and that male and female squid can respond differently under the same conditions; while reproductive investment by females was significantly greater in 1999/00 compared to 2002/03, for males the reverse trend was seen. Sex specific differences in reproductive investment were also found by McGrath Steer and Jackson (2004), although females appeared to lag behind males in their response to seasonal changes rather than showing an opposing trend as found here.

Relative levels of energy investment between reproductive and somatic tissues were also sex-specific and varied between years. There was no evidence at the population level of any trade-off between somatic and reproductive tissues for male *N. gouldi*, as found for many other ommastrephid species (e.g. *I. argentinus*, Clarke et al. 1994; *I. coindetti*, Rosa et al. 2005; *Moroteuthis ingens*, Jackson et al. 2004; *Sthenoteuthis oualaniensis*, Harman et al. 1989; *Todaropsis eblanae*, Rosa et al. 2005). However, there was considerable individual level variability in energy investment strategies by males in 1999/00, perhaps suggesting more variable resource availability. In contrast, the substantial reproductive investment by females in 1999/00 was clearly at the cost of somatic growth. Such a trade-off must be driven by either a preferential diversion of energy away from somatic growth (e.g. Hatfield et al. 1992, Ho et al. 2004), or utilisation of somatic tissue as an energy source (e.g. Laptikhovsky & Nigmatullin 1993, Jackson et al. 2004). In 2002/03, there was no clear relationship between levels of reproductive and somatic investment across the female population, suggesting greater individual level variability, and this is consistent with previous reports for mature females in Tasmanian waters (McGrath & Jackson 2002, McGrath-Steer 2004).

McGrath-Steer (2004) suggests that changes in energy investment strategies may be related to environmental conditions, with females more likely to trade-off during less favourable conditions (and indeed overall condition of *N. gouldi* was poor in 1999/00). However it is unclear why female reproductive investment should have

therefore been so much higher in 1999/00 compared to in 2002/03 when no trade-off was evident. The relationship between repro-somatic investment and abiotic and/or biotic conditions are further complicated by the contrasting trends for male *N. gouldi*. Again, it is not clear why male and female *N. gouldi* would respond differently in the same season, presumably under the same environmental conditions, although it may relate to the very different levels of energy investment required by the two sexes for reproductive processes, and their relative responses to different environmental parameters. Unfortunately 2-3 years of data is insufficient and a longer time series is necessary for understanding the different trends in repro-somatic investment under varying environmental conditions.

Relationship with population biomass

Jig catches and catch rates of *N. gouldi* in Tasmanian waters reached record highs in 1999/00, and it was hypothesized that population structure and life history characteristics would also be different from the following years. *Nototodarus gouldi* in 1999/00 however, were not generally different in size or age to squid sampled in the other three years. Growth rates, as discussed earlier, were difficult to determine for 1999/00, however assuming a rate common to all years, neither length- nor weight-at-age in 1999/00 stood out from the other years. If growth rates (regression slopes) were allowed to vary between years then growth was in fact significantly slower in 1999/00 compared to other years. The large biomass in 1999/00 must therefore be attributed to increased numbers, and not size of *N. gouldi*.

The number of available *N. gouldi* may be related to the persistence and accumulation of individuals on the Storm Bay jig grounds. Individual *N. gouldi* appeared to remain inshore longer in 1999/00 compared to the other years, with a substantial proportion of both male and female squid sampled in February 2000 large in size and fully mature. Acoustic tracking of *N. gouldi* movements in 2002/03 (Chapter 5) and 2003/04 (unpublished data) however, suggest that the population was constantly shifting in Storm Bay during these low abundance years, with squid leaving the area over an extended period. It is not known what factors control residency times on the Storm Bay jig grounds, but its likely that both environmental conditions and biological characteristics play a role. Further work is needed to examine inter-annual variability over a longer time period in relation to oceanographic and environmental conditions.

Just as individual life histories can collectively influence population size and structure, so too can population level processes affect individual life histories (De Roos et al. 2003), and in a resource limited environment density dependent effects should be evident. Challier et al. (2006) described density dependence in *L. forbesi* from the English Channel with growth rates lower in years with larger recruitment. While comparisons of *N. gouldi* growth were inconclusive, condition (BW-at-ML) of *N. gouldi* was poor in years of both small (2002/03 and 2003/04) and large (1999/00) squid biomass, but not in 2000/01, a season with a moderate abundance. This suggests that the carrying capacity of the ecosystem may change between years, and indeed the relative influence of the oligotrophic EAC and the cooler, more productive subantarctic waters on the southeastern Tasmanian jig grounds varies greatly depending on the strength and southerly extent of the EAC (Harris et al. 1987, Harris et al. 1991b). In highly productive systems, such as the California

upwelling, the carrying capacity may rarely be reached, and this may explain the clear relationship between mean size and growth rates of individual squid, and abundance of the population (Jackson & Domeier 2003, Reiss et al. 2004). This may also be the case for *N. gouldi* in the Bonney upwelling off western Victoria which is a persistent seasonal feature. Future work comparing the life history characteristics of squid from western Victoria and southeast Tasmania over years with varying biomass levels could provide useful insight into *N. gouldi* population ecology.

Chapter 5:

Tracking arrow squid movements with an automated acoustic telemetry system: *Nototodarus gouldi* in inshore Tasmanian waters¹

INTRODUCTION

The arrow squid *Nototodarus gouldi* is widespread across southern Australia and in northern New Zealand. Recent biological studies have shown that in Australian waters *N. gouldi* are genetically well mixed (Triantafillos et al. 2004), live for less than one year and are multiple spawners with hatching occurring year-round (McGrath & Jackson 2002, Jackson et al. 2003). The species is a valuable by-catch of shelf and slope trawl fisheries and is the exclusive target of Australia's largest squid jig fishery, which occurs seasonally in waters off Victoria (Winstanley et al. 1983, Lynch 2004). There is also a sporadic jig fishery in inshore Tasmanian waters during the summer months, concentrated primarily off the southeast coast. Samples from this fishery have shown that female *N. gouldi* are mostly immature when they first move into coastal waters, but mature progressively throughout the Tasmanian summer (Willcox et al. 2001, Chapter 4). The inshore movement in southeastern Tasmania is most likely related to feeding as females of this species must meet the cost of maturation with increased food consumption rather than through energy re-allocation (McGrath & Jackson 2002). Similar feeding migrations are well documented for other ommastrephid squid (Haimovici et al. 1998, Perez & O'Dor 1998, Mokrin et al. 2002, Nigmatullin et al. 2002, Watanabe et al. 2004).

Nototodarus gouldi is the most important cephalopod resource in Australian waters, yet little is known of its ecology and nothing of its movement patterns. The biomass (based on fishery production) of *N. gouldi* in southeastern Tasmania varies greatly, both within and between years (Willcox et al. 2001), and movement, possibly in response to environmental conditions, is thought to play a key role in shaping these patterns. Despite this, we have no understanding of the timing and nature of movement between inshore and offshore areas, how *N. gouldi* utilise the inshore environment, and how they behave with regard to schooling and activity patterns. Such issues can now be addressed with fewer logistical constraints with the development of electronic tagging systems.

Use of acoustic tracking systems and archival data loggers has provided valuable insights into migration patterns (e.g. Block et al. 2001, Comeau et al. 2002b), gene flow and dispersion (e.g. Moran et al. 2003), habitat preferences and home ranges (e.g. Parsons et al. 2003), and responses to physical and biological variability (e.g. Brill et al. 2002, Heupel & Hueter 2002). However, few studies using this technology have been conducted on cephalopods. Most have focussed on behaviour and energetics over small spatial and temporal scales, employing radio-acoustic

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positioning and telemetry systems (RAPT, O'Dor et al. 1994, Sauer et al. 1997, Aitken et al. 2005). Larger scale movement and migration patterns are known to be important processes in cephalopod populations, but are usually implied from analyses of distribution, abundance and biological patterns (e.g. Hatfield & Rodhouse 1994b, Arkhipkin 2000). There has been very limited tag-recapture work (Nagasawa et al. 1993, Sauer et al. 2000, Markaida et al. 2005), active tracking (Nakamura 1993) or use of archival and pop-up satellite tags (TOPP; www.toppcensus.org).

The aims of this study were to investigate and describe the movement patterns of *N. gouldi* in southeastern Tasmania using an automated underwater acoustic tracking system (Vemco Ltd, Shad Bay, Nova Scotia Canada). The system comprises compact acoustic receivers, each containing a hydrophone and data recorder, and small tags that transmit a unique acoustic signal (Klimley et al. 1998, Voegeli et al. 1998). Receivers moored at specific locations will continuously record the presence of any tag that moves into its detection radius, and thus movement pathways and spatial usage patterns can be derived.

MATERIALS AND METHODS

Study Site

The study was carried out in Storm Bay and its associated bays, inlets and estuaries (Figure 5.1). Storm Bay is a large shallow basin in southeast Tasmania, between 43°04'- 43°15' S and 147°23'- 147°42' E. It has an area of more than 500 km² and a maximum depth of 85 m (Clementson et al. 1989). The waters are mostly less than 50m in depth and the bottom primarily sand, with occasional small patches of rocky reef.

Acoustic Receivers

Sixty-four VR2 acoustic receivers (Vemco Ltd, Shad Bay, Nova Scotia Canada) were deployed within the study area. Each receiver was fastened to a vertical steel pole on a concrete mooring, approximately 1 metre above the sea floor. Acoustic release mechanisms (Sub Sea Sonics, San Diego USA) were attached to receivers deployed in deep water (>20m); otherwise divers were used for retrieval. Receivers were aligned equidistantly into 'curtains' across the entrances to several water bodies in the study area (curtains B, C, D, E, F, G, H and I; Figure 5.1). Receivers at L were not aligned in a single curtain but as 3 short lines perpendicular to the coastline (Figure 5.1) and are referred to as 'array' L. These receivers were originally deployed as part of another study, but are included here as arrow squid detections were recorded on them.

The depths of receivers ranged from 2 to 55 m, and were placed on sand, silt or seagrass, although one receiver (E1) was on low profile reef. Receivers were spaced between 725 and 930m apart within each curtain. Although not range-tested, a detection radius of between 365 and 465 m was required for full curtain coverage.

The receiver network was deployed in October 2002, but due to a lack of availability squid were not tagged until January 2003. Most receivers were retrieved in early April 2003 although one receiver in curtain H was removed earlier (21st March) after becoming entangled in a fishing net. The receivers in array L were not retrieved until May 2003 and a receiver in curtain G was not retrieved until July 2003 due to difficulties in relocating it.

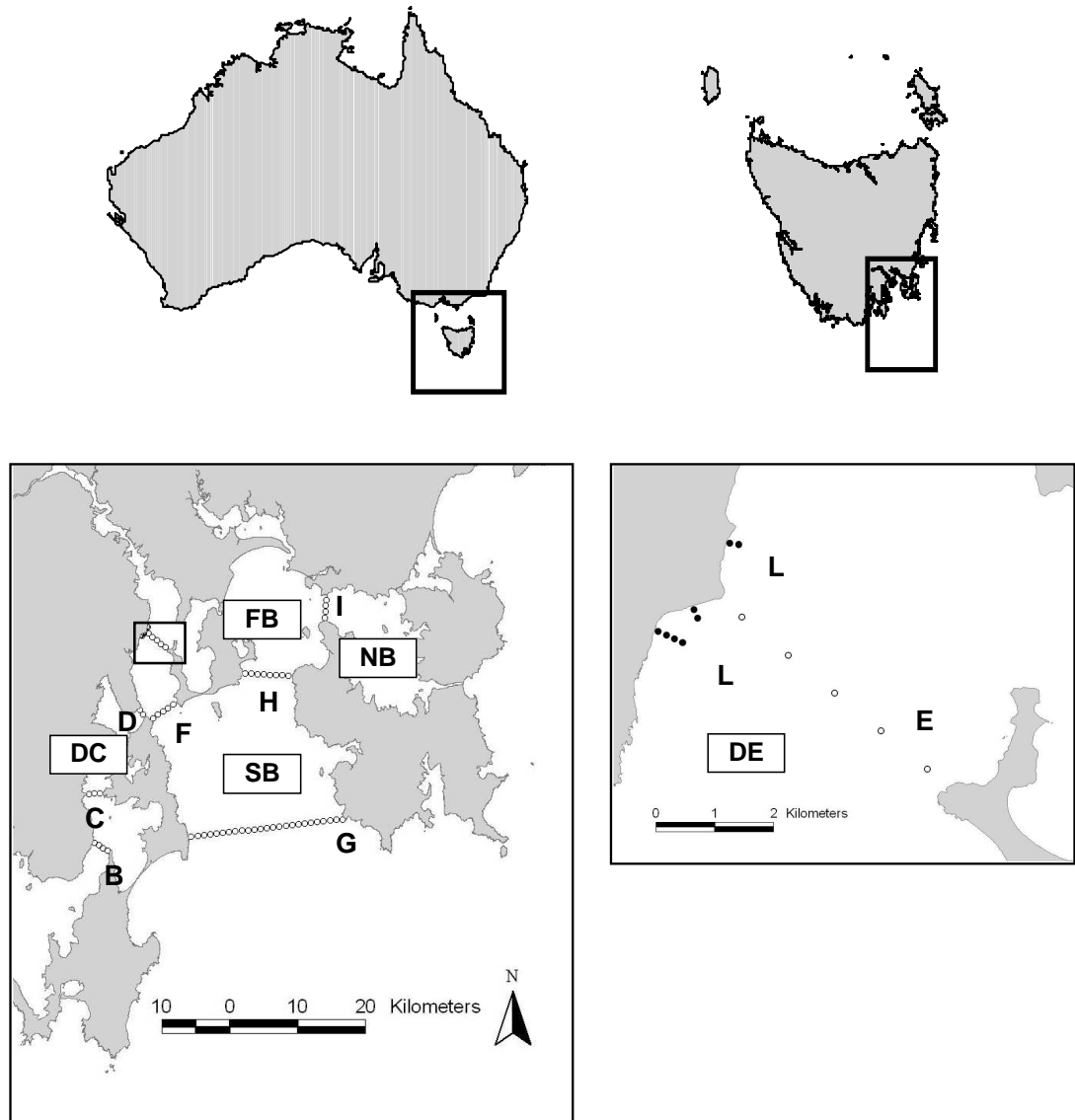


Figure 5.1. Study area in southeast Tasmania, Australia. FB Frederick Henry Bay; NB Norfolk Bay; DC D'Entrecasteaux Channel; SB Storm Bay; DE Derwent Estuary. Each unfilled circle represents one VR2 receiver. Receivers were aligned into 'curtains', which are labelled B to I, and 'array' L. The boxed area is shown at greater resolution, displaying the arrangement of Curtains E (filled circles) and L (unfilled circles).

Acoustic Transmitters

The transmitters used to tag arrow squid were V8SC-2H coded pingers (Vemco Ltd, Shad Bay, Nova Scotia Canada). The cylindrical transmitters are 30mm in length, 9mm in diameter, and weigh 3.1g in water. They each transmit a unique pinging sequence at 69 kHz frequency which is repeated after a random delay of between 20 and 60 seconds. Battery life was rated at 87 days. Transmitters were activated by soldering together the two activation wires and prepared for tagging by gluing a fine 1.10 x 38 mm needle across the top of the transmitter. Squid were tagged with the transmitters 2 to 25 days after activation; the delay for some transmitters being due to unexpected difficulty in obtaining squid for tagging. *Nototodarus gouldi* were scarce and patchy during the 2002/3 summer; individuals were rarely captured at the same location and time as each other (Table 5.1). Thus transmitter batteries were due to expire between 62 and 85 days after actual deployment.

Table 5.1. Details of tagged squid. Asterisk indicates tags that were detected during the study. ML is mantle length (cm); Sex is male (M), female (F), or not determined (U). Brackets indicate squid tagged and released together (similar time and location).

Tag No.		Date & Time	ML (cm)	Sex
78	*	11/01/2003 8:45	21	U
75	*	11/01/2003 8:56	22	U
88		11/01/2003 10:28	22	U
[69	*	16/01/2003 5:59	25	M
63	*	16/01/2003 6:50	20	F
65		28/01/2003 22:31	20	U
84	*	28/01/2003 23:25	22	F
[86		29/01/2003 1:23	18	F
68		29/01/2003 1:32	23	F
62	*	29/01/2003 2:55	24	F
81	*	29/01/2003 4:15	19	F
[67		03/02/2003 8:16	19	M
87	*	03/02/2003 8:34	25	F
[71	*	03/02/2003 9:02	23	M
76		03/02/2003 9:03	19	U
72		03/02/2003 9:40	20	F
77		03/02/2003 9:41	20	U
70		03/02/2003 9:42	21	M
66		03/02/2003 9:45	20	M
79	*	03/02/2003 9:47	20	U
64	*	03/02/2003 9:54	21	M
[73	*	03/02/2003 9:59	20	M
90		03/02/2003 10:29	20	M

Nototodarus gouldi were caught using jigs on hand lines and immediately placed in a tagging cradle. Dorsal mantle length (ML) was measured to the nearest centimetre and individuals were sexed where possible by noting presence of hectocotylisation

on arm IV. A minimum tagging size of 18 cm ML was set, ensuring the transmitter was less than 2.5% of the total body weight in all individuals (Willcox et al. 2001).

The transmitter was placed just inside the ventral mantle of the squid, the needle piercing through the mantle to the outside where it was crimped in place and cut off. Silicon washers were used to prevent the transmitter and crimp from abrading the squids mantle (after O'Dor et al. 1994). After tagging, squid were injected at the base of the arms with one to two millilitres of the antibiotic tetracycline, dissolved to saturation in seawater (approx. 6 mg/ml). Squid were held gently in the water and released when deemed to have recovered sufficiently (when jetting water strongly). Squid were out of the water during the tagging process for less than one minute.

Analyses

Data were downloaded as text files from the VR2's and then transferred to an MS-Access database. Individual movement tracks were plotted in ArcView 3.2 using the Animal Movement extension point-to-polyline tool (Hooge et al. 2001). Spatial usage was examined by comparing detection data between receivers and curtains. No statistical tests were conducted due to the spatial autocorrelation of the data. The coverage of each curtain was calculated as the proportion of a straight line running along a curtain (through each receiver) that was within detection range, assuming receiver detection radii of 400m. This is probably a conservative estimate given that detection ranges have been found to be at least 400m over a range of depths and habitats (Arendt et al. 2001, Heupel & Hueter 2001, Comeau et al. 2002b, Welch et al. 2002).

Activity patterns were inferred by the number of visit events. A visit event for a particular transmitter was defined as a continuous string of observations at a curtain, where there was no more than 30 minutes between consecutive observations. Thus a single visit event could comprise only one observation at one receiver, or a large number of observations at several receivers within a curtain. Visit event duration was the time between the first and last detection of a visit event, plus one minute. This ensured that visit events of just one observation had a duration of one minute, the maximum possible time between pulse transmissions. The distribution of visit event durations was highly skewed and could not be normalised by transformation, so the median and median absolute deviation (MAD, Quinn & Keough 2002), were used as location and spread descriptors.

Time, distance and speed (rate of movement) were calculated for movements recorded between non-adjacent receivers. Time was that between the last detection at one receiver and the first detection at the next non-adjacent receiver. Distance was measured between the positions of the two relevant receivers, in both kilometres (km) and mantle lengths (ML) specific to the squid in question.

Associations between tagged squid were investigated by arranging all observations into time intervals of (i) 20, and (ii) 60 minutes. Squid were considered to be associated with one-another if detected at the same location within the same time interval (i.e. a paired or group detection).

RESULTS

Acoustic Receivers and Transmitters

Twenty-three *N. gouldi* were tagged with transmitters and released over a four-week period between mid January and early February 2003 (Table 5.1). All squid were released within the northern part of Storm Bay (between curtains F, G & H), except for two that were released near the mouth of the Derwent River, north of curtain F. Of the tagged squid, eight were female, eight were male, and sex was not determined for seven. They ranged in size between 18 and 25 cm ML and all appeared to recover rapidly from the tagging procedure.

Two of the receivers in curtain E, and one in array L were not recovered, due to detachment from their moorings. Another receiver, in curtain G, was recovered but had been irretrievably damaged, so effectively a maximum of 60 receivers were present at any stage during the study and this number declined as the study progressed (Figure 5.2). One receiver had a memory failure while deployed (curtain F), and for two others the data did not download completely after retrieval (curtain G). Thus the end date for these three receivers is not the retrieval date, but rather the date of the last recorded detection (F: Jan 23rd, G: Jan 22nd and Feb 25th).

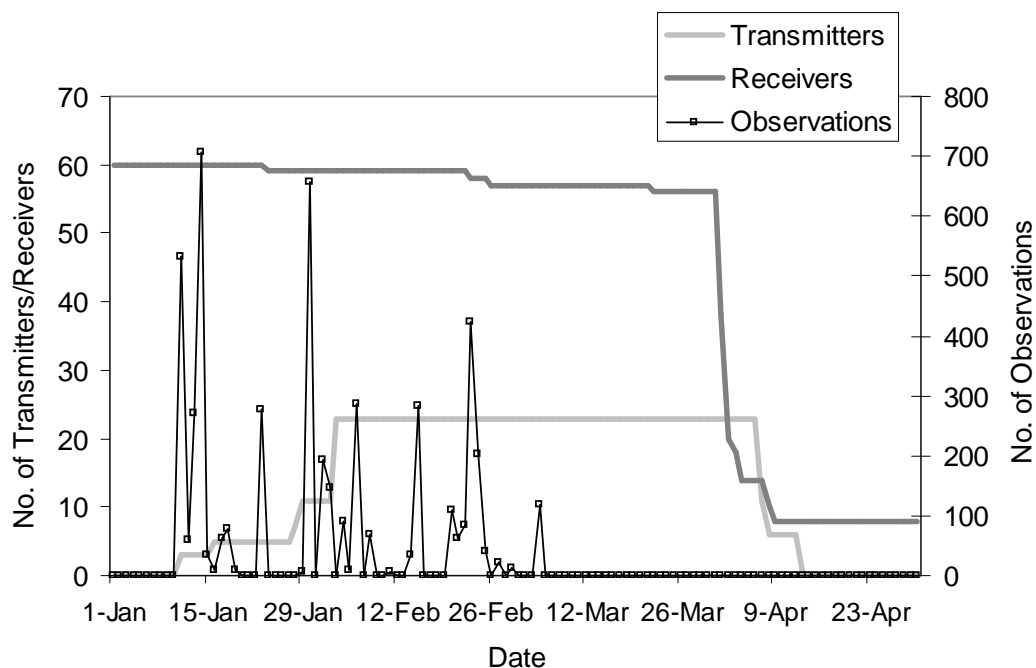


Figure 5.2. Number of active receivers and transmitters, and number of observations recorded by date.

Overlap of receiver ranges was evident for curtains F, G and H, as some transmitter signals were detected at the same time at adjacent receivers within these curtains. Despite this, the loss and failure of receivers in curtains E, F and G means they could not have full coverage for at least some of the study duration.

Detections

Twelve of the tagged squid (52%) were detected at least once during the study (Table 5.2). This group comprised five females, four males and three of unknown sex. They ranged in size from 19 to 25 cm, thus reflecting the size structure and sex ratio of the tagged sample (see Table 5.1). Neither the release date nor the location of release appeared to have any bearing on whether a squid was detected or not.

Each of the twelve detected squid accounted for between 23 and 1832 observations (Table 5.2), representing between 1 and 24 visit events. Squid were first detected either on the day they were released or up to 17 days later (Table 5.2). The number of separate days on which individual squid were detected ranged between 1 and 11 days, over periods of 2 to 37 days (i.e. from date of release to date of last detection). There were no detections recorded after the 5th March 2003 (Figure 5.2), despite the fact more than 50 receivers were present in the study area until the end of March and transmitter batteries should not have expired until early April.

Table 5.2. Details of detected transmitters: the number of days between release and 1st detection; the number of actual days on which each squid was detected; the number of days from release to last detection; the number of observations recorded; the number of curtains visited; and the number of receivers visited.

Transmitter	Days to 1st detection	Days Detected	Period (days) Detected	No. of Observations	No. of Curtains	No. of Receivers
78	0	6	13	1832	3	12
75	0	7	9	132	1	1
69	16	2	24	242	2	4
63	2	1	3	71	1	1
84	2	11	37	1219	3	15
62	7	7	32	138	3	4
81	0	2	2	593	2	6
87	17	1	18	23	1	1
71	12	1	13	284	1	2
79	1	1	2	54	1	4
64	1	1	2	36	1	2
73	3	1	4	265	1	2
<i>Mean</i>	<i>5.1</i>	<i>3.4</i>	<i>13.3</i>	<i>407.4</i>	<i>1.7</i>	<i>4.5</i>
<i>Total</i>		<i>30</i>		<i>4889</i>	<i>6</i>	<i>35</i>

General movement patterns

Eight of the twelve tracked squid were detected at least once at curtain G, at the entrance to Storm Bay, and for each of these squid curtain G was also the site of their final detection (Table 5.3, Figure 5.3). There was no consistent pattern of movement by squid prior to their final detection at G. Five of the squid detected at curtain G did not visit any other curtain (transmitters 63, 64, 71, 79 and 87; Figure 5.3). After being tagged these five squid took between 1 and 17 days to travel to curtain G, where they were detected on one day only, and not detected again. The other three squid detected at G (transmitters 62, 69 and 84) first spent time around curtains D, E,

and F, arriving at curtain G between 23 and 36 days after being tagged and released (Table 5.3). The date of final detection at curtain G varied widely, ranging from the 18th January to the 5th March (Table 5.3).

Four transmitters were not detected at curtain G at any stage; instead these squid moved further inshore/upstream from their tag and release point. Only one of these squid (transmitter 81) did not at any stage move into Storm Bay, instead all detections were recorded within the Derwent Estuary. Transmitter 73 was detected for the first and last time at curtain H, and transmitters 75 and 78 at curtain F (Table 5.3, Figure 5.3).

Only one squid (transmitter 62) was detected at the entrance to the D'Entrecasteaux Channel (curtain D). It was detected later that same day at curtain F, suggesting that if it indeed had moved into the Channel, it did not travel far or spend long there. A squid detected at curtain H (transmitter 73) was there for approximately 3.5 hours, but as it was not detected again it is impossible to determine if it continued into Frederick Henry Bay or moved back into Storm Bay.

Spatial usage

Tagged squid were detected at six of the nine curtains (Table 5.4). There were no observations recorded at curtains B, C or I, indicating that the tagged squid did not move down the D'Entrecasteaux Channel, or into Norfolk Bay. The three most visited curtains, in terms of number of tagged squid and number of observations, were G, F and E, which were also the curtains with the poorest coverage due to missing or failed receivers (Table 5.4). Most squid visited few receivers within a curtain (Table 5.2), however, the particular receivers visited varied among squid and thus transmitters were detected at at-least two-thirds of the active receivers within each curtain (excluding curtains D and H which only detected one transmitter each; Table 5.4). Observations were recorded at receivers covering a wide range of depths (2 to > 50 m) and distances from the shoreline (0.6 to > 10 km).

Receivers that recorded observations were generally spread across the curtains, however, the number of observations recorded and transmitters detected varied greatly among receivers within curtains. Two adjacent receivers in both curtain E and F recorded the most observations of all receivers, and several squid returned to these same receivers after spending time elsewhere (Figure 5.3). The other active receivers in these curtains had comparatively few or no observations. There were no particular receivers that dominated curtain G in terms of the number of observations recorded, although squid were not detected at the receivers closest to the shore of the Tasman Peninsula and Bruny Island.

Table 5.3 Curtains at which each squid was detected, by date. Shading indicates day of tag and release, * denotes last detection, - marks days between detections.

Month	Day	Transmitter												
		78	75	69	63	84	62	81	87	71	79	64	73	
Jan	10													
	11	F	F											
	12	F	-											
	13	L	F											
	14	E, L	F											
	15	-	F											
	16	E	-											
	17	-	F	-	-									
	18	-	F	-	G*									
	19	-	F*	-	.									
	20	-	.	-	.									
	21	-	.	-	.									
	22	-	.	-	.									
	23	F*	.	-	.									
	24	.	.	-	.									
	25	.	.	-	.									
	26	.	.	-	.									
	27	.	.	-	.									
	28	.	.	-	.									
	29	.	.	-	.	-		L						
	30	.	.	-	.	F	-	E,L*						
	31	.	.	-	.	-	-	.						
	Feb	1	.	.	F	.	E	-	.					
		2	.	.	-	.	F	-	.					
		3	.	.	-	.	-	-	.					
		4	.	.	-	.	-	-	.	-	-	G*	G*	-
		5	.	.	-	.	-	F	.	-	-	.	.	-
		6	.	.	-	.	-	F	.	-	-	.	.	H*
7		-	-	.	-	-	.	.	.	
8		.	.	G*	.	-	-	.	-	-	.	.	.	
9		-	-	.	-	-	.	.	.	
10		-	-	.	-	-	.	.	.	
11		-	F	.	-	-	.	.	.	
12		-	-	.	-	-	.	.	.	
13		-	-	.	-	-	.	.	.	
14		G	-	.	-	-	.	.	.	
15		-	-	.	-	G*	.	.	.	
16		-	-	.	-	
17		-	-	.	-	
18		-	-	.	-	
19		-	-	.	-	
20		G	-	G*	
21		G	-	
22		G	-	
23		G	-	
24		G	D, F	
25		G	F	
26		-	-	
27		-	F	
28		-	-	
Mar	1	-	G*	
	2	-	
	3	-	
	4	-	
	5	G*	
	6	

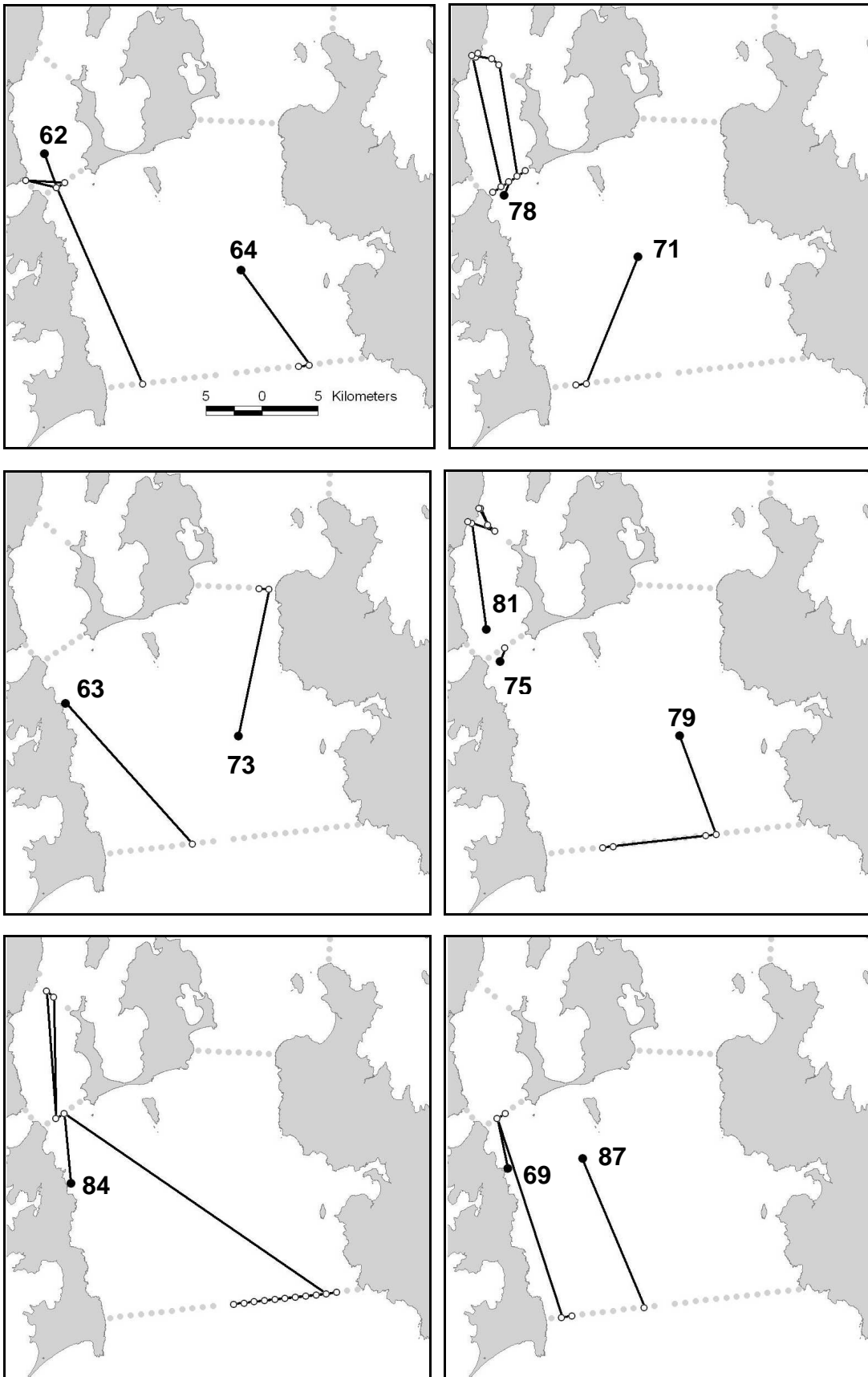


Figure 5.3. Movement tracks for the 12 detected squid. Black filled circle denotes point of tag and release, and number refers to the transmitter number. Open circles denote receivers where the animal was detected, and black lines the straight-line track between receivers. Shaded circles are all active receivers.

Table 5.4. For each curtain, the number of tagged squid (i.e. transmitters) detected, observations recorded, the number of receivers with observations / the maximum number of active receivers, the proportion of coverage by the curtain (assuming 400m detection radius), the number of visit events and median visit duration in hours, with median absolute deviation (MAD) in brackets. The coverage for curtains F and G is a range as some receivers did not function for the full duration of the study.

Curtain	# of squid	# of observations	# of receivers	% Coverage	# of visit events	Median visit event duration
B	0	0	0 / 4	1.00	0	-
C	0	0	0 / 3	1.00	0	-
D	1	18	1 / 2	1.00	2	0.28 (0.26)
E	3	880	2 / 3	0.62	11	0.18 (0.16)
F	5	1491	5 / 5	0.75 – 0.91	46	0.30 (0.28)
G	8	1534	18 / 24	0.76 - 0.83	30	0.53 (0.52)
H	1	265	2 / 8	0.87	1	3.54
I	0	0	0 / 4	0.91	0	-
L	2	701	7 / 7	n/a	7	0.58 (0.49)

Activity patterns

The duration of visit events was highly skewed, with 30% of visit events only one minute in length (the minimum possible visit event duration by definition), and 70% less than 1 hour. This suggests that squid were either often near the detection limit of receivers, or that they were passing through a narrow area of overlap. The longest visit event was transmitter 78 at curtain F for 8.7 hours. Curtains G and array L both had a similar median visit event duration of just over 30 minutes, while the median for curtains D and F was only around 17 minutes. Curtain E had a median of just 10.5 minutes, and for curtain H there was only one visit event (transmitter 73), 3.5 hours long (Table 5.4).

Over all receivers in all curtains except G, eighty-seven percent of visit events occurred in the first 10 days after an individual was tagged and released (Table 5.4). At curtain G however, the majority of transmitters were detected after at least 10 days at liberty, and these detections tended to be towards the end of the study regardless of the date of tag and release (Table 5.3). Eighty percent of visit events at curtain G occurred more than 30 days after the start of the study.

The number of visit events detected varied throughout the day without any clear pattern associated with photoperiod. The median duration per visit event however, was highly variable after sunset and before sunrise (2100 till 0600) and relatively low during daylight hours (Figure 5.4).

There were 19 trips between non-adjacent receivers by six of the detected squid. The longest distance travelled between consecutive receiver detections was 28.6 km, although half of the distances travelled were less than 3.5 km (Table 5.5). Sixty-eight percent of the trips were less than 2 days in time, although they ranged up to 12.3 days. There was large variability in the calculated speed of straight-line travel, from 0.003 to 1.489 m.s⁻¹, or 0.01 to 7.84 ML.s⁻¹. Shorter distances had more variable

speeds, while trips of 10 km or more were never more than 0.12 m.s^{-1} or 0.5 ML.s^{-1} (Table 5.5).

Only two transmitters were detected at the same receiver within the same 20-minute time interval. Transmitters 75 and 78 were both detected over a 2-hour period at curtain F, less than an hour after being tagged. They both remained in the general area of curtains E, F and array L for a further 8 days, however the only time during this period that they were both detected within the same 20-minute time interval, they were detected at different curtains, at least 10 km apart (Table 5.3). No other pairs or groups of transmitters were detected at the same receiver in the same time interval, even when the time interval was increased to 60 minutes. However, transmitters 64 and 79 were detected at different receivers in curtain G on February 4th, the day after they were both tagged (Table 5.3). These two pairs of squid (transmitters 75 & 78, and 64 & 79) were the only squid detected together throughout the study. In both cases they were squid tagged and released together. Other groups of squid were tagged and released together but they were not detected during the study (e.g. transmitters 68 & 86, Table 5.1).

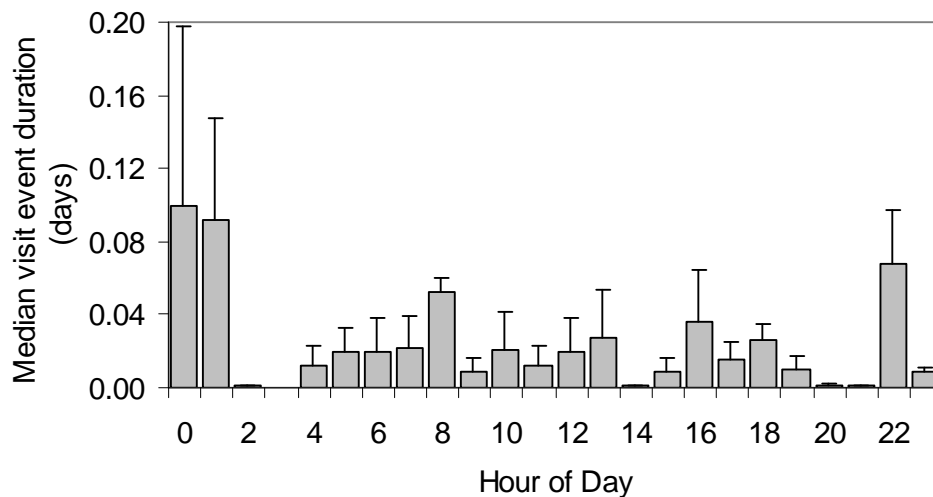


Figure 5.4. The median visit event duration (plus median absolute deviation), by hour of day.

Table 5.5. The distance (km & mantle length, ML), time (min) and speed (m/min & ML/min) of travel recorded between non-adjacent receivers.

Transmitter	Date Start	Curtain		Distance (km)	Time (min)	Speed (m.s ⁻¹)	Distance (ML x 10 ⁴)	Speed (ML.s ⁻¹)
		Start	End					
62	05-Feb	F	D	2.8	294.4	0.003	1.16	0.01
62	24-Feb	D	F	3.4	9.2	0.104	1.43	0.43
62	27-Feb	F	G	19.2	44.0	0.121	8.00	0.50
69	01-Feb	F	G	18.7	164.6	0.032	7.50	0.13
78	12-Jan	F	L	12.0	35.7	0.094	5.73	0.45
78	14-Jan	L	E	1.8	0.5	1.001	0.86	4.77
78	16-Jan	E	F	10.1	155.3	0.018	4.80	0.09
79	04-Feb	G	G	9.3	3.5	0.732	4.66	3.66
81	29-Jan	L	E	2.6	2.6	0.277	1.34	1.46
81	30-Jan	E	L	1.7	2.4	0.196	0.90	1.03
81	30-Jan	E	L	1.7	0.8	0.604	0.90	3.18
81	30-Jan	L	E	1.6	0.3	1.489	0.87	7.84
84	30-Jan	F	E	11.5	36.6	0.087	5.21	0.40
84	01-Feb	E	F	10.9	26.5	0.114	4.96	0.52
84	02-Feb	F	G	28.6	284.5	0.028	13.00	0.13
84	14-Feb	G	G	2.8	137.7	0.006	1.27	0.03
84	22-Feb	G	G	1.9	27.3	0.019	0.85	0.09
84	23-Feb	G	G	1.9	1.9	0.269	0.85	1.22
84	25-Feb	G	G	8.4	185.0	0.013	3.81	0.06

DISCUSSION

A significant finding of this research relates to the implied movement of individuals away from the study area. Two-thirds of the tracked squid were last detected at curtain G, across the entrance to Storm Bay. Although the design of the receiver network precludes determination of the movement direction (see below), the fact that receivers and transmitters were active for an extensive period after the final detections at G supports the notion that the squid moved out of the study area to other coastal or deeper shelf waters. It is possible that other tagged squid may have moved out of the study area without being detected. Three receivers failed while deployed within curtain G and it is possible gaps may have existed elsewhere. Without extensive range testing we cannot be certain of the precise level of curtain coverage during the study. However, with an assumed detection range of 500m, extrapolation of the numbers of squid observed moving through curtain G to that expected with complete coverage would account for just one or two of the undetected squid. Those squid that were never detected most likely remained within the confines of Storm Bay, never moving into the detection range of curtains F, H or G, or were subject to post-tagging mortality or tag loss.

It is difficult to interpret the relationship between individual movements out of the study area and the dynamics of the whole population as the year of the study was a poor one for *N. gouldi* in southern Tasmania. The available biomass was very low, and as such there was little commercial fishing, with catches of just 2 tonne taken in 2002/03, the lowest catch in ten years (Lyle 2003). Without commercial fishery or

survey data we cannot relate the observed movement patterns to the distribution and persistence of the population in Storm Bay over the study period. However, the timing of movement out of Storm Bay seen in this study is consistent with that evidenced by the fishery in previous years (1998/99, 1999/00, 2000/01), for which considerable data is available (Willcox et al. 2001). In general, commercial catches declined through February, and were very small by March. The movement of tagged squid in our study suggests that this decline in catch may be consistent with squid leaving the Storm Bay area, with most tagged individuals moving to the outer curtain (G) during February.

Movement out of the study area was not in any way synchronous, with individuals apparently leaving over an extended time period, suggesting a dynamic population whose composition changes throughout the inshore summer season. Although the movement dynamics may differ during periods of high abundance (as the variables influencing the abundance may also affect the population level patterns of residency), the patterns seen during this study have important implications from a fishery and ecosystem management perspective as it suggests that the decline in commercial catches in late summer is not entirely due to localised fishing effects, but is influenced by emigration too. The complexity of separating the effects of migration from the effects of commercial catches adds to the difficulty of assessing the resource (Basson et al. 1996).

There was no evidence of tagged squid moving from Storm Bay or the Derwent Estuary into the D'Entrecasteaux Channel. *Nototodarus gouldi* are known to utilise the Channel, having been caught in large numbers by recreational fishers in previous years (e.g. 1999/00; pers obs.), and the connectivity of these areas is of particular interest as the Channel is closed to commercial fishing and perceived as a 'refuge' area, particularly in years of high fishing intensity. Our data suggest that either there was limited mixing of *N. gouldi* between the Channel and its adjacent waters (the Derwent Estuary and Storm Bay), or that the mixing was primarily uni-directional, with the Channel acting as a passageway for squid into the adjacent inshore waters, but not vice versa. Alternatively, *N. gouldi* may not have utilised the Channel at all during the study. Unfortunately we have no information on the availability of *N. gouldi* in the D'Entrecasteaux Channel during the study period, nor the connectivity of these water bodies in years when the biomass was high. Again, it is feasible that factors influencing the low inshore biomass may have also affected the patterns of residency in the study area. The environmental and/or prey conditions may have been only suitable in some areas, and not in the Channel during the study. Alternatively, it may be simply that sample sizes were insufficient to detect movement into all areas.

Nototodarus gouldi made use of a large part of the remaining study area, with several individuals moving extensively between curtains in the Derwent Estuary and Storm Bay. Some individual receivers in the lower Derwent Estuary region had notably more detections from more tagged squid, implying that they may have been within a passageway or frequently used route between the Derwent River and Storm Bay, or may have been desirable areas for other reasons, such as concentration of prey. These observations may have been influenced by the tag and release position, though it was noted that several individuals returned to these same receivers on multiple occasions. Further research coupling *N. gouldi* movement and spatial usage to small-scale environmental conditions, particularly prey density (e.g. Reid & Hindell 2000,

Heupel & Hueter 2002) would be of value, particularly if conducted over seasons of contrasting abundances.

Rates of movement varied greatly, particularly over short distances. Half the trips measured were at less than 0.5 ML.s^{-1} and approximately 80% were less than 1.5 ML.s^{-1} . In general, speeds greater than this (including the maximum calculated, 7.8 ML.s^{-1}) were between receivers placed less than 2 km apart and therefore greatly influenced by the fact the calculations do not take into account the detection radius of each receiver. If the detection radius is for example, 500m, the difference in the distance between the transmitters when detected and that estimated by receiver placements could be up to 1km, and this has significant influence on straight-line speeds calculated over short distances.

Rates of movement calculated over 10 km or more ranged from 0.09 to 0.52 ML.s^{-1} , however, there was one instance of an average speed of 3.6 ML.s^{-1} over 9.3 km by transmitter 79 moving between receivers G10 and G20. This movement was clearly not straight-line as the squid was not detected at the receivers in-between, and is therefore a minimum. While maximum speeds of another ommastrephid squid, *Ommastrephes bartramii*, determined by active tracking, were only 0.5 ML.s^{-1} while on spawning grounds (Nakamura 1993) and 0.8 ML.s^{-1} when migrating to the spawning grounds (Yoshida et al. 1990), tag recapture studies of *Todarodes pacificus* recorded travelling at speeds of up to 2.14 m.s^{-1} (Araya, 1967 cited in Nagasawa et al. 1993). Assuming a maximum ML of 50 cm (Roper et al. 1984), this is equivalent to 4.3 ML.s^{-1} . High-speed travel is clearly feasible for squids, although actual swimming speed may be quite different to observed movement rates due to the influence of water movements (e.g. currents). We also cannot rule out that tagged squid may have been predated on, and the observed speeds were those of a larger predator not the squid.

Sonar and echo sounding surveys of *N. gouldi* have shown that they form dense aggregations close to the sea floor during the day and disperse throughout the water column at night (Evans 1986). However, on only one occasion in this study were more than two individuals caught at the same time and place. Either our catchability was extremely poor, or the squid were not forming large daytime aggregations in the study area; it may be that the numbers of *N. gouldi* during the study was below some 'threshold' for schooling behaviour. There was little evidence of positive association among individuals tagged and released together. Only a small number of individuals released in 'groups' were subsequently detected, and it was rarely together, except shortly after release. There was no evidence that they remained together further into the study. A lack of group fidelity throughout the study may be due to new aggregations being formed each day after night time dispersion. So while it seems likely that squid might be found in the same region at the same time in response to external variables such as prey concentration, we would not necessarily expect them to move together over the course of the study. Sample sizes were simply too small and this study not designed to maximise information regarding such behavioural patterns, however the potential of the automated VR2 system for elucidating school structure and behaviour is recognized.

There was no clear relationship between photoperiod (time of day) and activity inferred by the number of visit events, though the duration of visits was generally

greater and far more variable during the evening than during the day. Research suggests that *N. gouldi* are more active and feed more during the night compared to day (O'Sullivan & Cullen 1983, Nowara & Walker 1998). However, these results are confounded by the use of commercial jig boats with light attractants to obtain samples. Diurnal feeding behaviour is variable among other ommastrephid species, but it appears they are active hunters in both the day and night with several feeding peaks, depending on the diurnal behaviour of the prey (Haimovici et al. 1998, Laptikhovsky 2002, Quetglas & Morales-Nin 2004). Variability in the duration of evening visits in this study might be explained by a combination of periods of low activity as individuals remain in an area to feed or rest, set against short visit durations indicative of active movement into and out of the range of receivers, perhaps as the squid search for prey.

The use of the automated acoustic tracking system has provided new insight into the movement and activity dynamics of the inshore *N. gouldi* population in southeastern Tasmania. Future research could benefit from larger samples sizes (feasible given the relatively low cost of transmitters compared to other electronic tag types), and being able to couple the individual movement data to population distribution and abundance data. The design of the receiver network in this study made it difficult to determine direction of movement, or indeed whether the tagged animal actually crossed through a curtain, unless it was subsequently detected at another curtain. In future studies where understanding directionality is important, it could be more suitable to have double curtains, or at least stagger the placement of receivers in a zigzag design along the line of the curtain. This would have the added benefit of reducing the size of gaps created by lost or failed receivers.

Chapter 6:

General Discussion

Conclusions, implications & directions for future research

The objective of this research was to investigate how the abundance of *N. gouldi* varies in space and time, and what factors might be driving these patterns. This was approached through a hierarchical examination of the ecology, biology and behaviour of *N. gouldi* using a variety of data sources and methods, from statistical modelling of commercial fishery data to field based methods using novel technology.

The most significant specific findings of this study were:

- *Nototodarus gouldi* were shown to be distributed right around southeastern Australia, and were in highest abundance (by weight) near the continental shelf break. Clear ‘hotspots’ of abundance were identified in regions of significant mesoscale oceanographic activity (e.g. strong shelf-break fronts and upwelling).
- Abundance of *N. gouldi* was seasonal, but this seasonality varied considerably between locations, as did the timing and type of mesoscale oceanographic activity.
- Sea surface temperature and chlorophyll-a concentration (derived from sea colour) were unable to account for the spatio-temporal patterns in *N. gouldi* encounter rates and catch rates, possibly due to a mismatch between the timing of local oceanographic activity and evidence of its effect on *N. gouldi*.
- Annual abundance derived from Bonney coast trawl fishery data could be predicted with reasonably good ability from time-lagged local (wind speed) and global (ENSO) environmental parameters, most likely due to their influence on mixing and upwelling activity, and thus productivity and prey availability.
- A negative correlation between jig and trawl derived indices of abundance indicates that the depth distribution of *N. gouldi* may shift from year to year, possibly in relation to the location and dispersion of the upwelling front. In 2000 however, abundance was unusually low on both fishing grounds, suggesting poor recruitment overall to the Bonney coast region.
- *Nototodarus gouldi* recruit to the inshore jig fishery in southeast Tasmania as small juveniles, growing and maturing over the summer. Apparent timing of recruitment varied between years from relatively continuous to periodic- with pulses of recruits separated by up to 2 months.
- Large, mature squid which typically dominate trawl catches were rarely caught on the jig grounds of southeast Tasmania, suggesting that *N. gouldi* move into deeper waters after reaching sexual maturity. A clear change in sex ratio over the summer was evident and may be due to males maturing earlier and leaving the jig grounds before females, or sex-specific changes in catchability related to reproductive development and mating behaviour.

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- Population structure and life history characteristics of *N. gouldi* on the inshore jig ground varied significantly between years. Patterns were not always consistent between sexes, in particular reproductive investment strategies varied dramatically between mature males and females.
 - There was no clear relationship between population structure and annual abundance, with squid in a year of extremely high available abundance of similar size and age to those sampled in years of low abundance.
 - The large biomass in southeast Tasmania in 1999/00 was attributed to increased numbers (not size) of *N. gouldi*. The persistence of larger mature *N. gouldi* on the jig grounds in this year, a phenomenon not observed in the other years, suggests that inshore conditions were perhaps more favourable than elsewhere leading to aggregation and accumulation of squid biomass on the inshore jig grounds.
 - Acoustic tracking of *N. gouldi* in southeastern Tasmania found that squid moved away from the Storm Bay jig ground to other coastal or deeper shelf waters, between 1 and 36 days after tagging. However this movement was not synchronous, with individuals apparently leaving over an extended time period.
 - *Nototodarus gouldi* were active throughout the study area, however no squid were detected moving into the D'Entrecasteaux Channel, which is closed to commercial fishing and perceived as a 'refuge' area. Squid were regularly detected close to north Bruny Island suggesting a frequently used route between Storm Bay and the lower Derwent Estuary, or the area may be desirable for other reasons such as concentration of prey.
 - Rates of movement calculated over 10 km or more ranged from 0.09 to 0.52 ML.s⁻¹, although actual swimming speed is uncertain due to the unknown influence of water movements (e.g. currents).

Ecology and the oceanographic environment: how does N. gouldi compare to other ommastrephid squid?

Phenotypic plasticity together with a short lifespan and rapid growth mean that squid populations are very responsive to changing environmental conditions (Boyle & Boletzky 1996). These features, coupled with the ability to move over considerable distances, result in an ecology that is closely tied to the behaviour of the oceanographic systems in which the squid live (O'Dor 1992, Anderson & Rodhouse 2001). However, while most commercially exploited squid are associated with *one* of several large marine ecosystems (i.e. high velocity oceanic current systems, coastal upwelling systems or continental shelves; O'Dor 1992, Anderson & Rodhouse 2001, Boyle & Rodhouse 2005), the oceanographic environment of *N. gouldi* is quite complex. In Australian waters *N. gouldi* is influenced by separate eastern, western and northern boundary currents, and its range encompasses a variety of distinct mesoscale features including the Bonney upwelling, the Bass Strait cascade, and the subtropical convergence between the East Australian Current (EAC) and subantarctic waters. The complex oceanographic environment *N. gouldi* inhabits appears to have generated ecological patterns quite different to the general ommastrephid models described for less diverse systems (e.g. O'Dor 1992, Anderson & Rodhouse 2001).

A notable feature of many ommastrephid species, particularly those found in western boundary currents, is that they undertake large scale seasonal migrations, utilising the high velocity currents for transport between feeding and spawning grounds (e.g. Takami & Suzu-Uchi 1993, Haimovici et al. 1998, O'Dor & Dawe 1998, Mokrin et al. 2002, Bower & Ichii 2005). This migratory strategy allows squid to exploit regions of high productivity, but also maximise their reproductive success by spawning in warmer waters which may be separated from the feeding grounds over large latitudinal ranges (O'Dor 1992). Although *N. gouldi* is also associated with a western boundary current, it is only over part of its range, and the EAC is relatively weak and highly seasonal in nature (Ridgeway & Godfrey 1997). Spatial and seasonal trends in *N. gouldi* biomass (Chapter 2), population structure (Jackson et al. 2003), and the results of tag-recapture studies (Machida 1983, Sato 1985) do *not* suggest any large scale migrations. Australian waters are generally low in nutrients and it is also possible that *N. gouldi* have not evolved a migratory lifestyle as they are unable to fuel such energy demanding large scale travel (Clarke et al. 1994, Wells & Clarke 1996). *Nototodarus gouldi* instead maximises the range of environmental conditions available over its short life-span by inhabiting waters with highly seasonal oceanographic features and by undertaking seasonal (and possibly ontogenetic) shifts in depth distribution (Chapters 4 & 5). However, in the absence of large-scale current assisted migrations, the range of environmental conditions that can be exploited by individual *N. gouldi* are limited, and this may account for its relatively low fishery production compared to other western boundary current inhabiting squid (O'Dor & Coelho 1993).

Consistent with its non-migratory life history, *N. gouldi* also does not appear to utilise spatially distinct spawning grounds. Mature females (Jackson et al. 2003) and paralarvae (Dunning 1985, Dunning & Förch 1998) are widespread in southern Australian waters, suggesting that it is able to complete its entire life cycle over much, if not all, of its range. However, the seasonality of *N. gouldi* biomass production varies at regional scales (Chapter 2). This appears to be a response to the nature and seasonal activity of local oceanographic features, with *N. gouldi* life cycles probably timed to synchronise with the local environmental conditions that will optimise growth, development and reproduction (e.g. Arvanitidis et al. 2002, Moreno et al. 2005). In this respect, the ecology of *N. gouldi* is more similar to that typical for loliginid species (Boyle & Rodhouse 2005) than the traditional ommastrephid models (e.g. O'Dor 1992, Anderson & Rodhouse 2001). However the ecological niche of *N. gouldi* is by no means unique among ommastrephids, with other species showing similar ecology and life history strategies (e.g. *Illex coindetti*, Sanchez et al. 1998; and *Todarodes sagittatus*, Quetglas et al. 1998, Arkhipkin et al. 2001, Lordan et al. 2001).

Variability in abundance of N. gouldi over multiple scales.

Large scale variability in *N. gouldi* abundance appears to be tied to the distribution and seasonal activity of regional oceanographic features (Chapter 2). Although abundance could not be correlated to environmental variables (SST and CHL), this is possibly a function of scale, as the nature of any relationships between squid and environmental parameters are likely to vary between different types of oceanographic systems (Anderson & Rodhouse 2001). Species such as *N. gouldi* which inhabit complex oceanographic environments, may respond differently to the

same environmental parameters in different parts of their range. Relationships between environmental parameters and *N. gouldi* ecology are also likely to be lagged over time, and these lags may vary in length between regions depending on the specific local oceanographic features (e.g. Chapter 3). Further work into stock structure of *N. gouldi* in Australian waters is also needed to determine if regional scale variability (Chapter 2) is accompanied by genetic differentiation (e.g. Shaw et al. 1999) or simply reflects the inherent flexibility in life history characteristics and thus a population level response to environmental variability (e.g. Shaw et al. 2004).

Seasonal (possibly ontogenetic) shifts in depth distribution (Chapters 4 & 5) generate smaller scale variability in abundance of *N. gouldi*. In southeast Tasmania, the cross-shelf distribution of *N. gouldi* appears to be related to ontogeny with squid recruiting to the inshore jig fishery as small immature animals and moving offshore into deeper waters once sexually mature (Chapters 4 & 5). Other ommastrephid species normally associated with deeper shelf-break or slope waters are also seasonally found inshore (e.g. *I. argentinus*, Arkhipkin 2000; *I. illecebrosus*, Dawe & Beck 1997, Hendrickson 2004; *I. coindetti*, Sanchez et al. 1998; and *T. sagittatus*, Borges & Wallace 1993, Quetglas et al. 1998, Arkhipkin et al. 2001, Lordan et al. 2001).

The presence of ommastrephid squid in shallow shelf waters is thought to be related to prey availability (Boyle & Rodhouse 2005). Diet composition varies with the size of many squid species, including *N. gouldi* (O'Sullivan & Cullen 1983, Uozumi 1998), and the distribution of the preferred prey species may account for the apparent change in depth distribution with ontogeny. In Tasmania, the main prey of juvenile *N. gouldi* are small planktonic crustaceans (O'Sullivan & Cullen 1983) which tend to be in highest concentrations in shelf waters (Young et al. 1996). Krill (*Nyctiphanes australis*) in particular, form dense aggregations in Storm Bay during the summer (Ritz & Hosie 1982), when jig fisheries target *N. gouldi*. Ontogenetic changes in depth distribution may also be an adaptive strategy to reduce cannibalism, with large *N. gouldi* consuming significant quantities of smaller conspecifics (O'Sullivan & Cullen 1983). For some species sampled over a wide depth range however, the change in size structure appears to be driven primarily by the distribution of large, mature individuals (e.g. Quetglas et al. 1998), with juveniles distributed more widely over the slope and shelf (although their depth in the water column may be of a more limited range). Mature squid may be restricted to deeper offshore waters for successful spawning (Bakun & Csirke 1998), while juvenile squid may disperse more widely, with their distribution dependent on the availability of prey.

This depth structuring complicates regional scale predictions of abundance based on fishery catch and effort data (e.g. Chapter 3), as no fishery that harvests *N. gouldi* operates over its entire depth range. It is impossible to separate the variability in fishery derived abundance estimates that is due to annual recruitment levels, from that driven by shifts in distribution (i.e. availability). If, for example, inshore feeding conditions are particularly good one year, then a significant proportion of the juvenile *N. gouldi* in the population may be available on the jig fishing grounds, while in other years it may be in offshore slope waters. This type of behaviour may account for the negative correlation between jig and trawl derived indices of abundance on the Bonney coast (Chapter 3). Although the relative depth distribution of *N. gouldi* in any year and region is likely to be driven by the *local* environmental conditions, the different oceanographic systems may be linked by large scale climatic

processes. Indeed, in years of extremely high summer abundance on the southeast Tasmanian jig grounds (as in 1999/00 and again recently in 2006/07; Chapter 4, J. Lyle *pers comm.*), the jig fishery off western Victoria in autumn has been relatively poor (Chapter 3, AFMA unpublished data), and this warrants further investigation. Without a better understanding of the dynamics between the inshore and offshore fishing grounds, abundance indices derived from the different fisheries may only have limited utility in trying to understand the ecology of *N. gouldi* when considered in isolation.

Implications for fisheries assessment and management

There is currently no formal assessment of the *N. gouldi* stock in Australian waters, although there has been recent interest in applying a Leslie-DeLury depletion method of assessment (e.g. Basson et al. 1996, Agnew et al. 1998, Morales-Bojorquez et al. 2001, Royer et al. 2002, Ichii et al. 2006) to the SSJF. This study however, has highlighted some aspects of *N. gouldi* ecology which need careful consideration in any such assessment.

The genetic structure of *N. gouldi* in Australian waters is uncertain, and thus the appropriate spatial boundaries for any such assessment unknown. The seasonality of *N. gouldi* biomass production varies at regional scales (Chapter 2), however it is not known if this reflects any genetic differentiation (e.g. Shaw et al. 1999) or if the year-round hatching of *N. gouldi* (Jackson et al. 2005) and seasonal nature of any potential oceanographic barriers (e.g. upwelling) allow sufficient gene flow (e.g. Shaw et al. 2004). Although there is no evidence of cryptic speciation in *N. gouldi*, the Australian meta-population does not appear to be panmictic, with some population structuring suggested, at least on the east coast of Australia (Triantafillos et al. 2004). Further studies of the stock structure of *N. gouldi* using more powerful genetic markers and larger sample sizes are needed to resolve this issue.

Leslie-DeLury methods assume that the fishery catch and effort data are from a closed population, with negligible emigration or immigration. However, this study has shown that the available population on the jig fishing grounds is quite dynamic, with recruitment and emigration occurring throughout the jig season (Chapters 4 & 5). The negative correlation between jig and trawl abundance on the Bonney coast (Chapter 3) also suggests that there is considerable year to year variability in the proportion of the stock that is inshore, while the study of population structure and movement in southeastern Tasmania (Chapters 4 & 5) suggest that residency times on the inshore jig grounds may also differ between years, and between the sexes. The dynamic nature of the distribution and movement of *N. gouldi* between the jig and trawl fishing grounds underscores the need for the inclusion of trawl catches in any assessment of *N. gouldi*. The challenge is how to incorporate information from both these fisheries into a single assessment model. Although different model structures (under different ecological assumptions) could be compared to determine the most precautionary approach (e.g. Basson et al. 1996), a better knowledge of the ecology of *N. gouldi*, specifically the inshore-offshore dynamics would greatly assist model development. It is also worth noting that incorporating trawl fishery data into the assessment process, although necessary from a stock dynamics viewpoint, may also have significant management repercussions, as the two fisheries are managed separately under different management plans.

Pre-season estimates of recruitment strength may greatly enhance the assessment of squid stocks (Agnew et al. 2002), and allow management strategies that provide a better balance between maintaining a sustainable stock and maximising the economic efficiency of the fishery. However, as discussed previously, predictive models using time lagged environmental variables (e.g. Chapter 3) can only be useful while the relationship remains valid (Agnew et al. 2002), and there is considerable risk in assuming this when there is no understanding of the mechanisms driving these relationships (Dawe et al. 2007). Determining the direct mechanisms underlying such relationships is difficult, as environmental parameters are often strongly linked through larger-scale atmospheric and oceanographic processes, and different variables may be important at different stages of the life cycle or indeed in different oceanographic environments. However, without an understanding of the causal link, there is no way of predicting if or when the relationship might change or break down completely (Rodhouse 2001, Agnew et al. 2002, Dawe et al. 2007). This is of particular concern under scenarios of climate or other environmental change, as the environmental variables being used for prediction may move beyond the range of values previously observed, and the response of squid may not be a simple linear extrapolation of the models previously developed. Thus once relationships are identified through correlative studies (e.g. Chapter 3), further investigations are needed to test hypotheses regarding the mechanisms that may be driving these relationships. Testing for consistency in results for squid of similar habits and in similar ecosystems (e.g. Waluda et al. 2004), and closer examination of years where patterns of squid distribution and abundance are unusual (e.g. Dawe et al. 2007), may help fine-tune hypotheses regarding causative mechanisms (Myers 1998).

Future research directions

Although this study has made considerable progress to the knowledge of *N. gouldi* ecology in southern Australia, further research is needed. In particular, investigation into the linkages between populations on jig and trawl fishery grounds and the relationship between ontogeny and depth distribution appear to be critical for understanding patterns of distribution and abundance, and for the development of appropriate fishery assessment models.

The abundance of *N. gouldi* on inshore jig grounds is highly variable, and this may be driven to some extent by variability in individual residency times (Chapter 4). While movement off the jig grounds appears to be related to growth and maturation (Chapter 4), it is not clear if the triggers for such movement are indeed internal (i.e. reaching some age, size or reproductive development threshold), or also related to some environmental (e.g. photoperiod, temperature, prey availability) threshold. Further investigation of inter-annual variability in the timing of movement away from the inshore jig grounds in relation to population biology and environmental variables over a longer time series could provide useful insight into the proximate cues to movement (e.g. Comeau et al. 2002a), and thus those variables controlling the accumulation of biomass on the jig grounds. Extending acoustic tracking work (Chapter 5) over several seasons, with greater numbers of tagged animals and additional receivers along the shelf edge (e.g. Comeau et al. 2002b) could also provide insight into the timing of movements, especially in those areas where there is insufficient fishery data to infer timing of migration (e.g. on the southeast Tasmanian

jig grounds where effort is extremely low in most years). An added benefit of acoustic tracking is that it can provide individual-level information on residency times, and these can be examined in relation to biological characteristics (e.g. sex, length, weight) measured at the time of tagging.

A negative correlation between *N. gouldi* annual abundance on jig and trawl grounds of the Bonney coast (Chapter 3) prompts the question: what *proportion* of the population is available on the jig versus trawl grounds, and how does this vary between years? Ideally these questions should be investigated by conducting fishery independent, depth-stratified surveys in a variety of regions and seasons, using a consistent sampling technique. A simpler comparison of the population structure of jig versus trawl caught samples from a similar region could provide at least some insight into depth distribution and ontogeny (although differences in the size selectivity and the water column depth sampled by the different fishing gears will need to be accounted for). However, such a study could not provide information on the relative proportion of the population in different depths unless catchability for the different fishing gears in the different areas can be determined.

Statolith microchemistry analysis may also provide a useful tool for studying the timing and dynamics of *N. gouldi* movements between jig and trawl grounds. Squid statoliths contain a unique record of both the growth chronology and the environmental history the animal has been exposed to, and are therefore potentially useful tools for reconstructing migratory pathways and investigating connectivity between different habitats (see Campana 1999 for a detailed review in relation to fish otoliths, Semmens et al. 2007 for cephalopod applications). Repeated sampling along the axis of statolith growth with a laser coupled to a high resolution inductively coupled plasma mass spectrometer allows an investigation of the changes in an individuals' chemical environment between discrete periods of time, over the entire life history of the individual. This chemical information can then be coupled to growth increments to determine the ecological history of an individual.

Relationships between water temperature and levels of barium and/or strontium concentrations have been used to infer movement patterns for *T. pacificus* (Ikeda et al. 1998), *Loligo gahi* (Arkhipkin et al. 2004b) and *Gonatus fabricii* (Zumholz et al. 2007). However in other studies such relationships have been found to be highly variable (Ikeda et al. 2002a, 2002b, Ikeda et al. 2003, Rodhouse et al. 2004) and the technique may have only limited application. Considerable experimental work would need to be conducted before such relationships could be considered robust predictors of location. Multi-element analyses may instead prove more useful for approaching questions of movement between different water masses (e.g. shelf versus offshore water masses; Elsdon & Gillanders 2003). The multivariate signatures should reflect the combined effects of temperature, salinity and water chemistry, and if consistent differences between inshore and offshore areas can be demonstrated over time and for different ontogenetic stages, the timing of movements of *N. gouldi* may be reconstructed using the chemical signatures and growth increments in the statolith. The proportion of the population that spends some time inshore, and estimates of the length of that time could also be examined. However, the differences between inshore and offshore waters would need to override any regional differences in chemical signatures, otherwise the indicators of cross-shelf movement may be confused with along-shelf movement between regions. A better understanding of the

stock structure of *N. gouldi* would be needed so that the appropriate spatial scale of such a study could be determined.

Nototodarus gouldi stock structure has been examined using allozyme electrophoresis, and although constrained by low numbers of genetic markers and alleles per marker, there was some suggestion of population sub-structuring on the east coast of Australia (Triantafillos et al. 2004). Possible size ‘morphs’ of *N. gouldi* on the east coast have also been suggested by Jackson et al. (2003), and anecdotal information from commercial fishers suggests that body morphometrics of *N. gouldi* caught on the Tasmanian jig grounds may be quite different to those caught off western Victoria. This study also found that biomass cycles varied on a regional scale, apparently in response to local oceanographic features. Some of these oceanographic features may also act as barriers to gene dispersal (e.g. Shaw et al. 1999). Thus further investigation of the stock structure of *N. gouldi* is needed, particularly for determining the appropriate spatial structuring in assessment models and management procedures. There are a wide variety of methods that could be used, and a study that compares several methods would be most informative, e.g. genetic analyses using microsatellite analysis and/or mitochondrial DNA sequence data (Kassahn et al. 2003, Shaw et al. 2004, Buresch et al. 2006), studies on body and/or statolith morphometrics (e.g. Pierce et al. 1994, Kassahn et al. 2003, Lombarte et al. 2006), examination of parasites (e.g. Bower & Margolis 1991, Shukhgalter & Nigmatullin 2001), tag-recapture studies (Sauer et al. 2000), and whole statolith microchemistry analyses (e.g. Arkhipkin et al. 2004b).

Conclusions

This study has made considerable advancements to the knowledge of *N. gouldi* ecology in southern Australia by addressing how abundance varies in space and time, and what factors may be driving these patterns. The ecology of *Nototodarus gouldi*, like many other commercially exploited ommastrephid squid, appears to be closely linked to patterns of hydrography and ocean productivity. They are in greatest abundance where the shelf break is strongly defined or where other mesoscale oceanographic activity is present (e.g. upwelling), and variability in biomass cycles also appears to be related to the seasonality and nature of local mesoscale oceanography. Ontogenetic structuring in relation to bathymetry and movements between inshore and offshore waters however complicate regional scale predictions of abundance, with environmental conditions influencing both annual recruitment level and the bathymetric distribution of squid. Further investigations are needed to elucidate the finer-scale variability and detail of the mechanisms driving these patterns. In particular, investigation into the linkages between populations on jig and trawl fishery grounds and the relationship between ontogeny and depth distribution appear to be critical for understanding patterns of distribution and abundance, and for the development of appropriate fishery assessment models.

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Appendix A.1

This appendix provides additional results for Chapter 2; the CE-GAM and CE-GLM results using identified *N. gouldi* catch data only (i.e. excluding unspecified squid records). PA models were not fitted as unbiased determination of the presence or absence of *N. gouldi* was not possible.

In 50% of the 0.5° spatial blocks in which squid catches occurred, the inclusion of unspecified squid catch changed the mean catch rate by less than 1.5 kg.hr⁻¹ (Figure A.1.1). In 90% of spatial blocks the difference was 10 kg.hr⁻¹ or less.

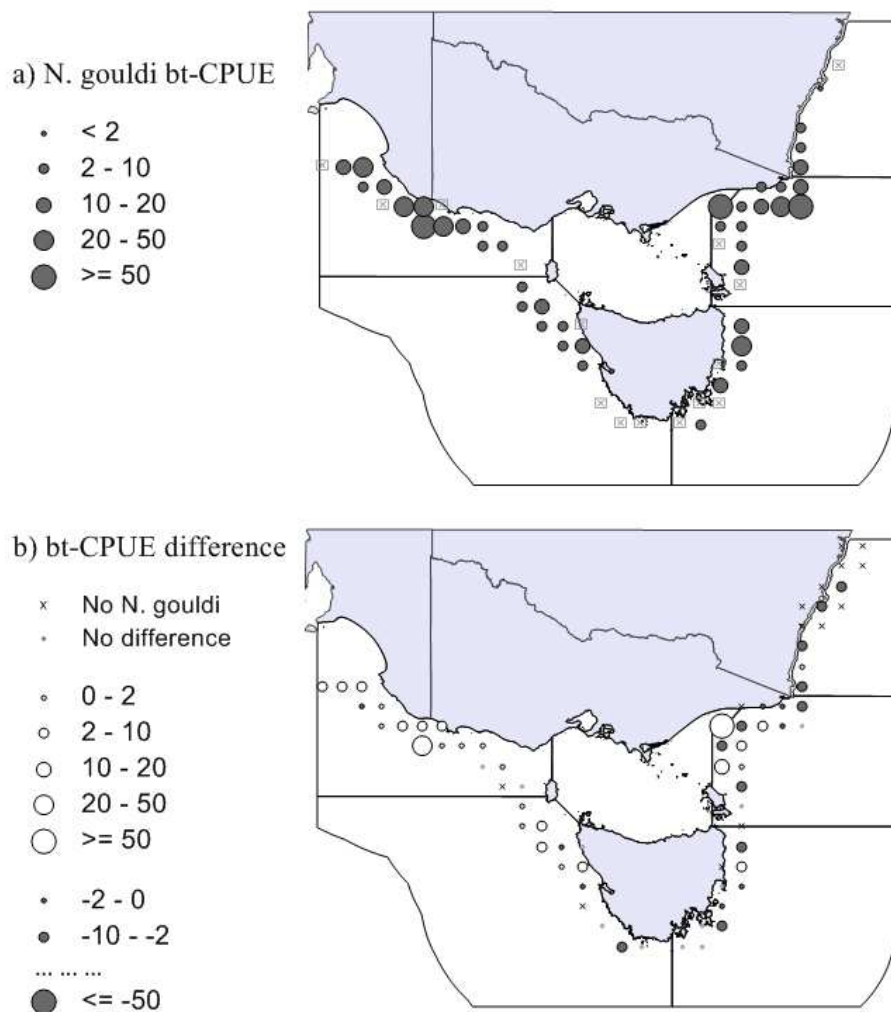


Figure A.1.1 Map of a) average *N. gouldi* CPUE where present (back-transformed; kg.hr⁻¹), by 0.5° spatial block; ☒ denotes data that cannot be shown due to confidentiality agreement, and b) difference in bt-cpue by 0.5° spatial block between analyses using general squid catch and *N. gouldi* catch (Chapter 2, Figure 2.2), and those using only *N. gouldi* catch. Positive differences (i.e. greater bt-CPUE for combined catch) are dark grey circles, and negative differences (i.e. greater bt-CPUE for *N. gouldi* catch) are white circles.

The CE-GAM plots using *N. gouldi* data only (Figures A.1.2 & A.1.3) were very similar for all spatio-temporal covariates to those using the combined squid data (Chapter 2), suggesting that the inclusion of unidentified squid catch had little influence on the overall catch rates.

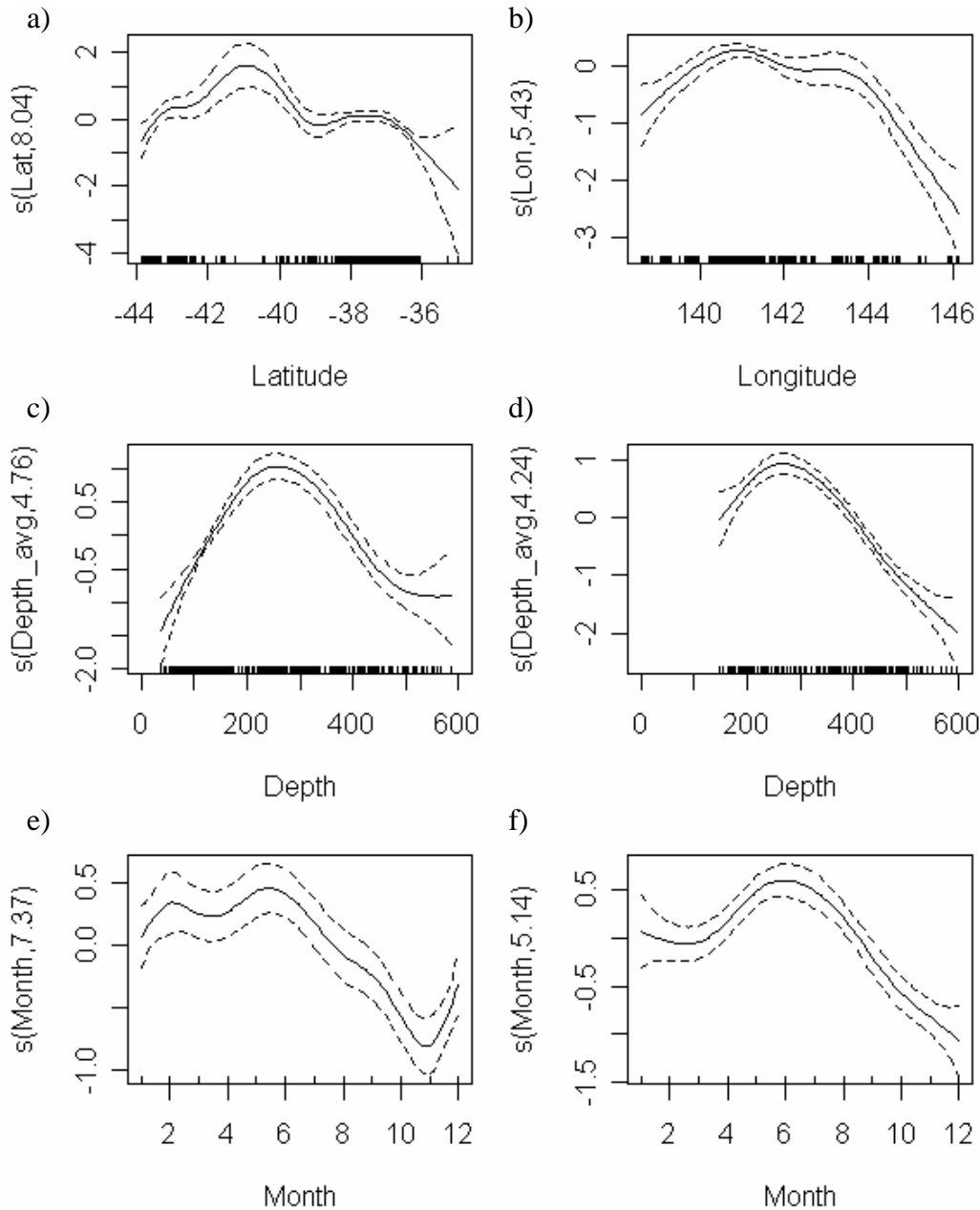


Figure A.1.2 East (a, c & e) and west (b, d & f) region spatio-temporal CE-GAM plots based on identified *N. gouldi* data only. Dashed lines are 95% pointwise confidence intervals. Y-axis label includes the approximate degrees of freedom for each covariate. Small markers along the x-axis indicate where observations occurred. Note the different y-axis scales.

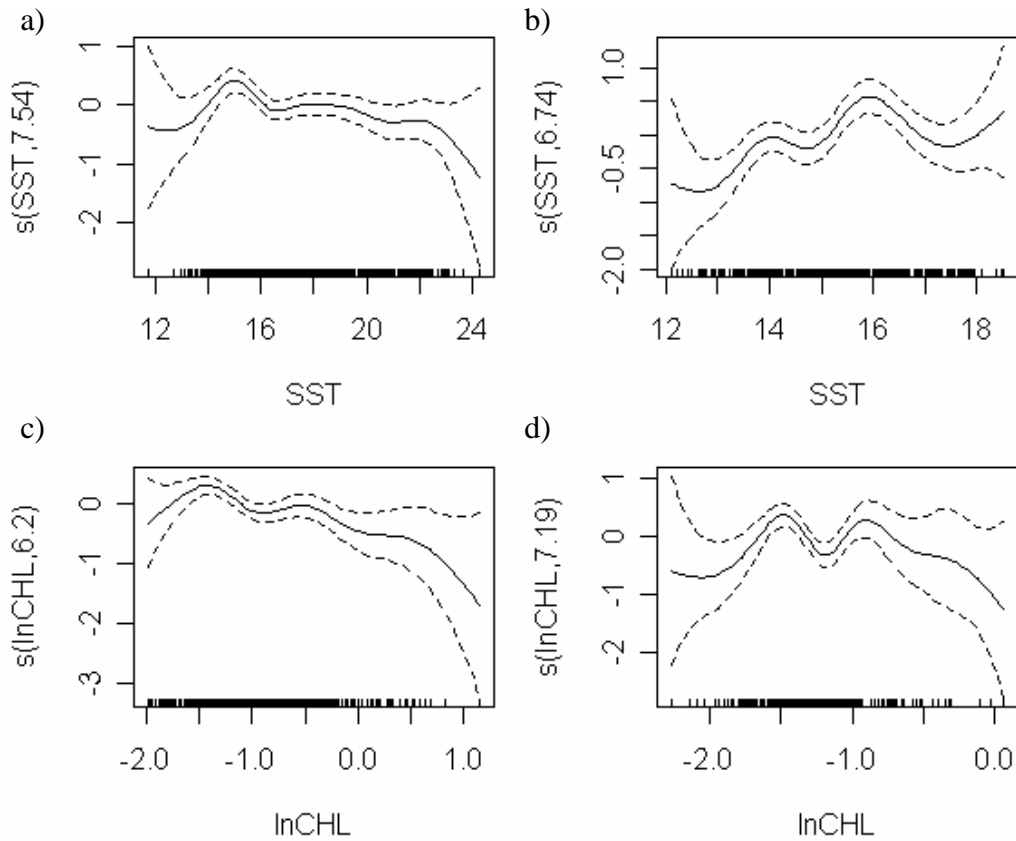


Figure A.1.3 East (a & c) and west (b & d) region environmental CE-GAM plots based on identified *N. gouldi* data only. Dashed lines are 95% pointwise confidence intervals. Y-axis label includes the approximate degrees of freedom for each covariate. Small markers along the x-axis indicate where observations occurred. Note the different y-axis scales.

The exclusion of unspecified squid catches from the data increased the percentage of deviance explained in the spatio-temporal CE-GLMs by 8% in the east region, but only 0.25% in the west region (Table A.1.1a & b, Chapter 2). In the environmental GLMs, the deviance explained was increased by 0.7% in the east region, but reduced the deviance explained by 2.4% in the west region (Table A.1.1c & d, Chapter 2).

Table A.1.1 CE-GLM results for a) & c) east region, b) & c) west region, based on identified *N. gouldi* data only. For spatio-temporal models (a & b) depth and latitude/longitude were entered as 2nd order polynomials; Month and year were categorical variables. For environmental models (c & d), 2nd order polynomials are indicated by *p* subscript; year was a categorical variable. Predictors are shown in the order that they were added to the model. See text for explanation of variable selection process.

	Region	Model	Predictor	Df	Deviance	% Deviance Explained		Region	Model	Predictor	Df	Deviance	% Deviance Explained
a)	East	CE- <i>N. gouldi</i>	<i>Null Model</i>	1363	3525.5		b)	West	CE- <i>N. gouldi</i>	<i>Null Model</i>	657	1485.5	
			Depth	2	440.0	12.5				Depth	2	483.3	32.5
			Latitude	2	88.7	2.5				Longitude	2	48.5	3.3
			Month	11	211.9	6.0				Month	11	172.7	11.6
			Year	6	37.1	1.1				Year	6	100.6	6.8
			Month: Year	62	400.5	11.4				Depth: Month	22	113.6	7.7
			Depth: Year	12	131.4	3.7				Longitude: Month	22	65.6	4.4
			Depth: Latitude	4	82.5	2.3				Month: Year	49	93.3	6.3
			Depth: Month	22	139.6	4.0				Longitude: Year	12	24.2	1.6
			Latitude: Month	22	97.0	2.8				Depth: Year	12	19.8	1.3
			Latitude: Year	12	37.4	1.1				<i>Full Model</i>	519	363.8	75.5
			<i>Full Model</i>	1208	1859.5	47.3							
c)	East	CE- <i>N.gouldi</i>	<i>Null Model</i>	1363	3525.5		d)	West	CE- <i>N.gouldi</i>	<i>Null Model</i>	657	1485.5	
			SST _{<i>p</i>}	2	13.8	0.4				SST _{<i>p</i>}	2	28.4	1.9
			logCHL	1	38.4	1.1				logCHL _{<i>p</i>}	2	10.2	0.7
			Year	6	85.4	2.4				Year	6	48.2	3.2
			<i>Full Model</i>	1354	3387.9	3.9				SST _{<i>p</i>} :logCHL _{<i>p</i>}	4	53.0	3.6
										<i>Full Model</i>	643	1345.7	9.4

Appendix A.2

This appendix provides additional results for Chapter 2; the GAM and GLM results for (combined) squid data between 600 and 1000m depth only.

Depth response functions were much more complex in shape when deepwater trawl were included, although confidence intervals around the encounter and catch rates in waters greater than 600m depth were large (Figures A.2.1 - A.2.4).

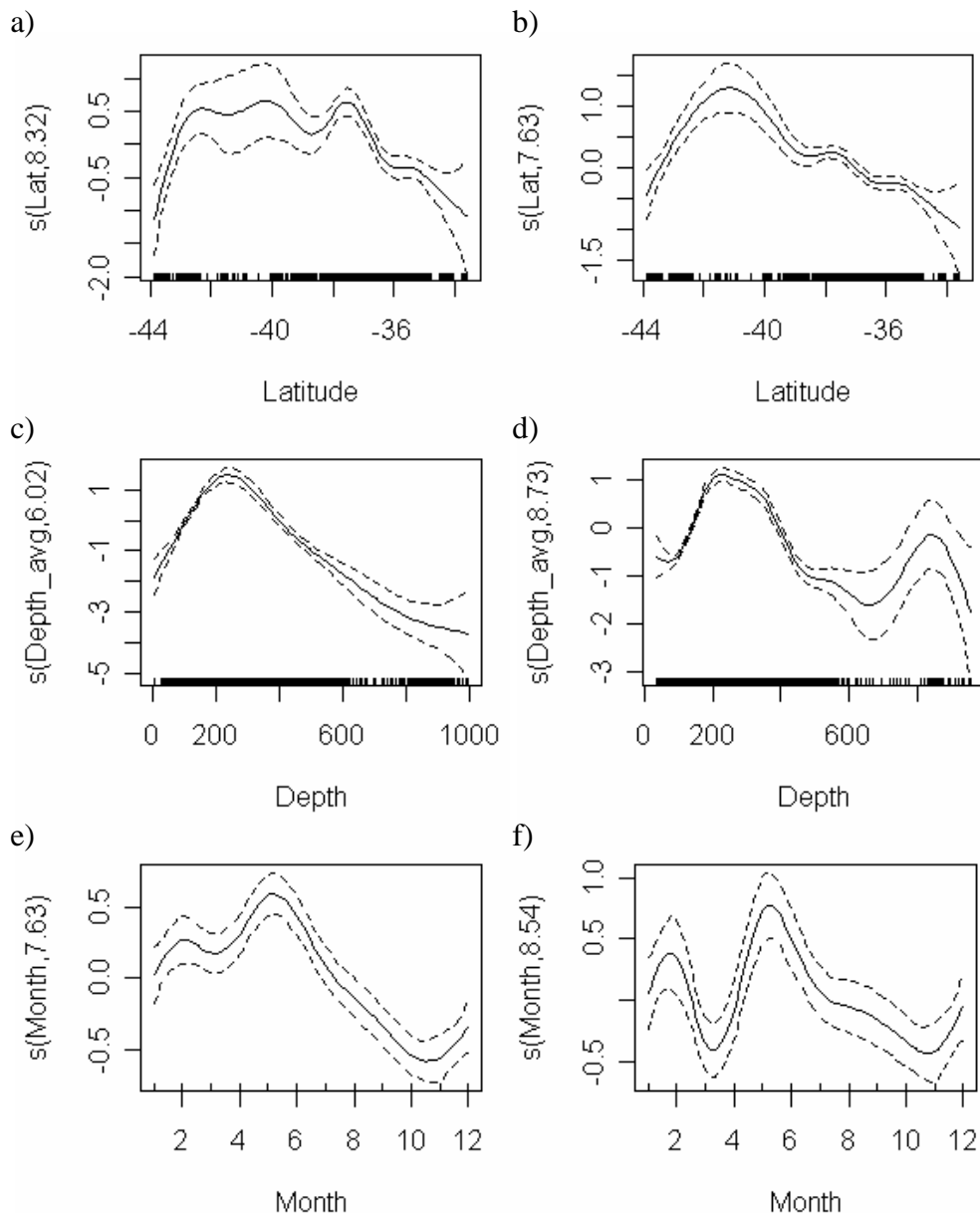


Figure A.2.1 East region PA (a, c & e) and CE (b, d & f) spatio-temporal GAM plots. Dashed lines are 95% pointwise confidence intervals. Y-axis label includes the approximate degrees of freedom for each covariate. Small markers along the x-axis indicate where observations occurred. Note the different y-axis scales.

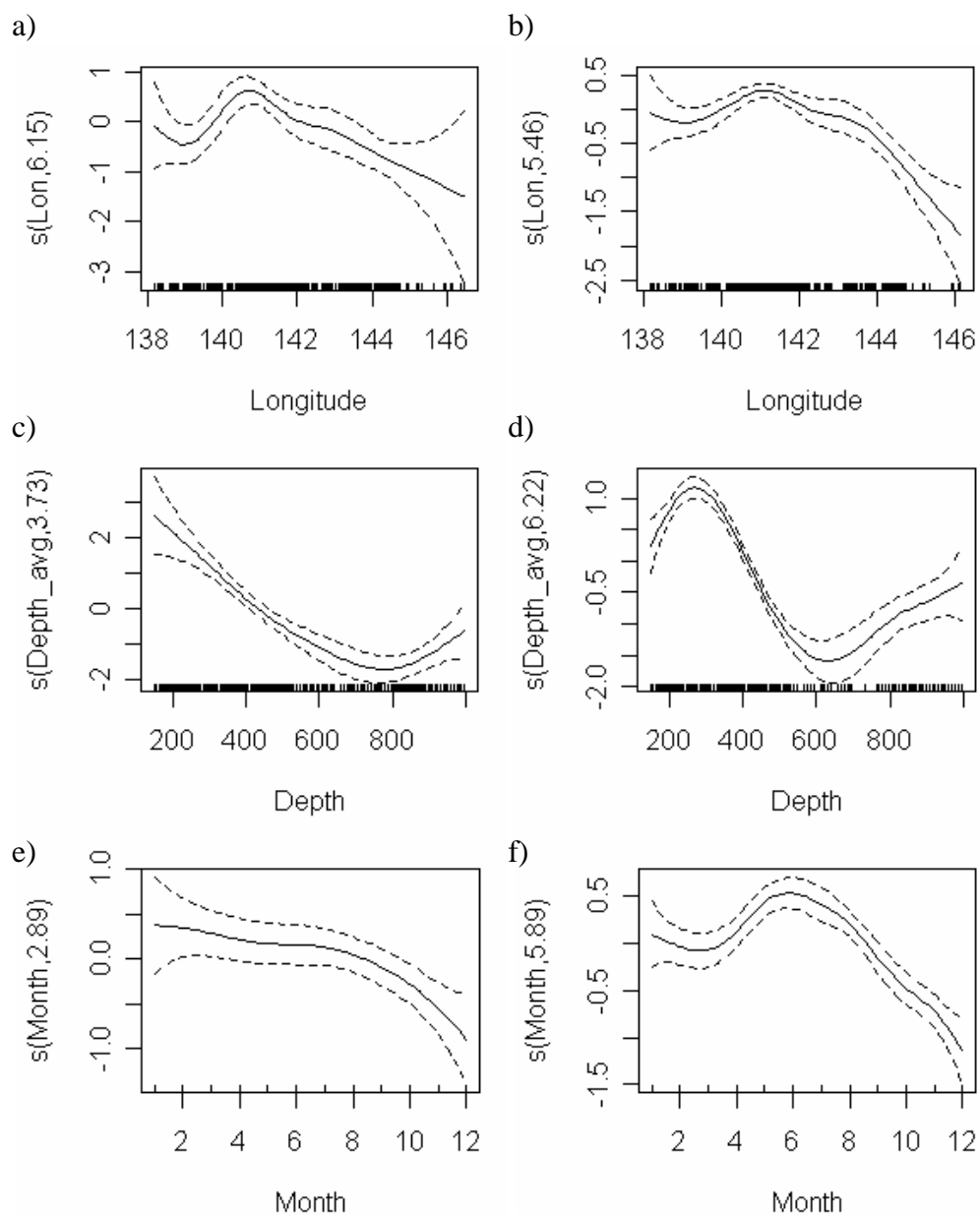


Figure A.2.2 West region PA (a, c & e) and CE (b, d & f) spatio-temporal GAM plots. Dashed lines are 95% pointwise confidence intervals. Y-axis label includes the approximate degrees of freedom for each covariate. Small markers along the x-axis indicate where observations occurred. Note the different y-axis scales.

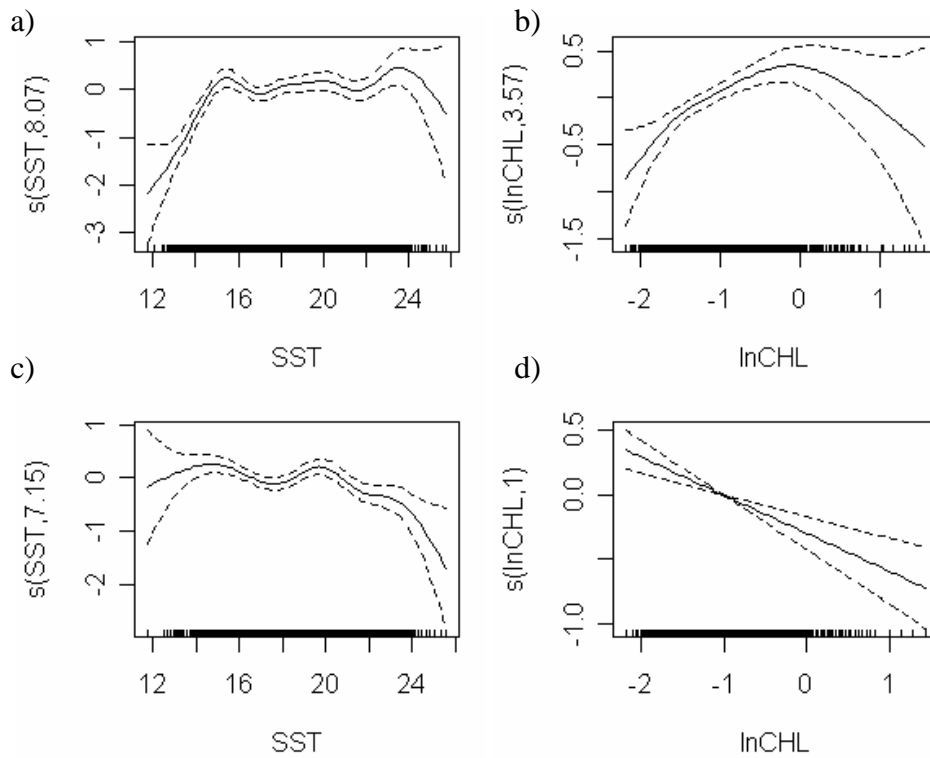


Figure A.2.3 East region PA (a & c) and CE (b & d) environmental GAM plots. Dashed lines are 95% pointwise confidence intervals. Y-axis label includes the approximate degrees of freedom for each covariate. Small markers along the x-axis (rug plot) indicate where observations occurred. Note the different y-axis scales.

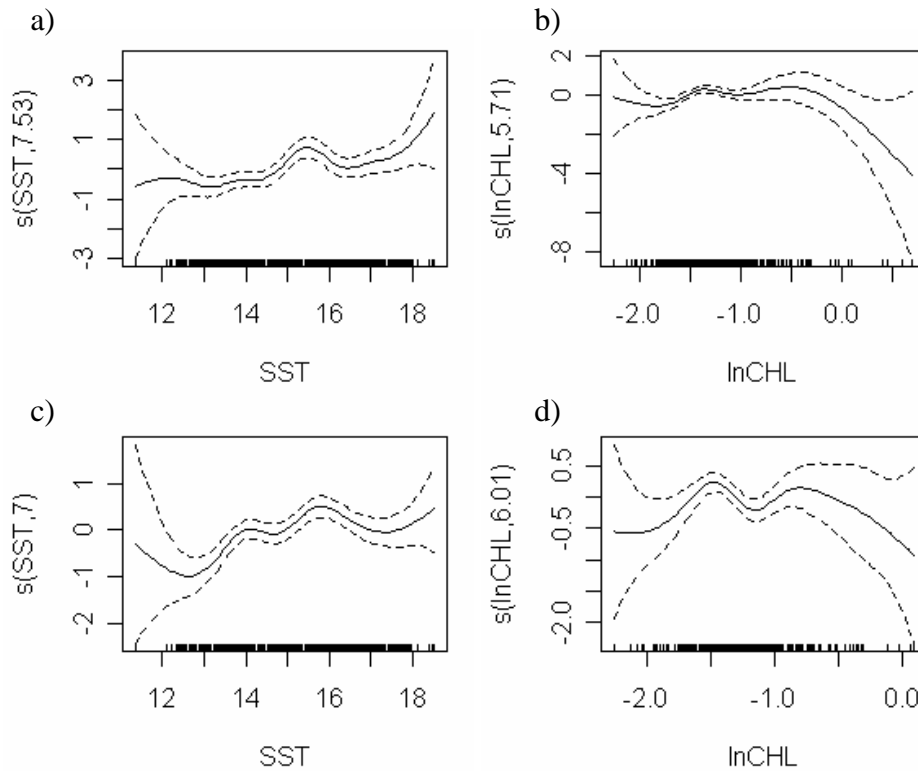


Figure A.1.4. West region PA (a & c) and CE (b & d) environmental GAM plots. Dashed lines are 95% pointwise confidence intervals. Y-axis label includes the approximate degrees of freedom for each covariate. Small markers along the x-axis (rug plot) indicate where observations occurred. Note the different y-axis scales.