## RESEARCH ARTICLE

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# Temporal population dynamics in arrow squid *Nototodarus gouldi* in southern Australian waters

**Abstract** Nine monthly samples of arrow squid *Nototodarus gouldi* were obtained off Portland, Australia, during 2001. Statolith age analysis was used to determine growth rates and cohort structure during the study period. The results of statolith increment periodicity experiments were inconclusive due to difficulties in discerning increments in the cultured squids, although the region of the statolith in the maintained squids did increase over time. The maximum age obtained was 360 days, which is consistent with a 1-year life cycle in this species. Squid obtained were >150 days old and usually >200 mm mantle length. While there was often a mix of maturity stages for females, the majority of males were mature. Monthly length frequency distributions suggested that there was a complex mixture of cohorts in the samples obtained. Fitting a Normal mixture model to the age frequency distribution suggested that at least four cohorts were present during the period of the study. Growth was modelled with an exponential function with individuals grouped according to hatch season. The rate of growth for seasonal groups of squid was considerably different between males and females. There was no evidence of seasonal differences in growth rates of males. In contrast, the summer hatched females had significantly greater growth rates than winter and spring at $P = 0.05$, and the growth rates of autumn hatched females were found to be significantly different to the winter hatched females at the 0.1 level.

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## Introduction

Developing techniques for understanding the population dynamics of squids continues to pose challenges. Their short life spans, extended reproductive events, and growth rates that are rapid and closely tied to environmental features produce a complex population structure. Unlike their teleost competitors, squid live life fast, take advantage of patchy resources, but lack the capacity to store reserves to 'ride out' lean periods (O'Dor and Webber 1986, Jackson and O'Dor 2001). The ability to identify and track cohorts can greatly aid in modelling growth rates and understanding squid population dynamics. The complex sub-structuring of squid populations has been suggested to be driven by episodic spawning that produces 'micro-cohorts'. However, alternatively, it is possible that these 'microcohorts' may be more apparent than real and influenced by the sampling interval (Boyle and Boletzky 1996). Furthermore, the life styles of squid mean that their populations are often subject to extreme variations in abundance.

Cephalopod biomass worldwide has been estimated to be up to 500 Mt. However, due to the rapid recycling of populations, this high biomass may only occur for a restricted period of time. Biomass of a species may reach a peak as a cohort approaches maturity, but subsequently may drop to very low levels. Therefore, while the turnover in biomass of a species might be quite large, the biomass of a species for a large proportion of the year might in fact be relatively low (Rodhouse et al. 2001). Understanding the dynamics of squid populations, biomass levels and the rate of population turnover is of profound ecological importance. This is highlighted by the fact that in certain instances there has been a shift in some major fisheries from traditional groundfish to

cephalopods, probably as a result of both overfishing finfish along with predator removal (Caddy and Rodhouse 1998). However, it has been suggested that analysing fishing statistics alone may be inflating the degree of ecosystem change that has been hypothesised (Balguerias et al. 2000). Nonetheless, as fisheries around the world continue to be exploited, we are going to see increasing pressure on harvesting cephalopod populations and in some regions they may be the only component left to exploit. Thus, understanding the population dynamics and their role in the ecosystem will continue to be a high priority.

The Australian arrow squid *Nototodarus gouldi* is an abundant ommastrephid spread across southern Australian and northern New Zealand waters and is common in continental shelf regions and sometimes occurs in shallow and even estuarine waters (Winstanley et al. 1983; Dunning 1998). Recent research has focused on the reproduction and population dynamics of arrow squid in Australian waters. This species appears to be a multiple spawner with eggs being released over time in discrete batches. Reproduction in females occurs at no apparent cost to somatic tissues (McGrath and Jackson 2002). Analysis of the spatial and temporal population dynamics of *N. gouldi* from a number of locations across Southern Australia revealed a complex pattern of growth and reproduction with marked differences in growth rates, body size and maturation (Jackson et al. 2003). *N. gouldi* does not appear to show a large degree of genetic separation between populations across its range within Australian waters (Triantafillos et al. 2004). Thus, observed regional differences in growth appear to be largely due to responses to environmental differences rather than genetic segregation.

We were interested in obtaining a better understanding of the temporal population dynamics of this species at a single location to discern how growth, recruitment and maturity change over time. For this study, we chose continental shelf waters off Portland, Australia, to follow the trends in the population of *N. gouldi*. This location served our research purposes well as it is an established fishing port and squid can be obtained from commercial vessels throughout the year. It is also of oceanographic interest as this maritime region of Australia is subject to regular and predictable upwelling events (Bonney Upwelling Area) which greatly enhance the productivity of these waters (Butler et al. 2002).

## Materials and methods

Samples of *N. gouldi* (≥100) were obtained from commercial fishing vessels trawling in waters off the coast of Portland (Victoria), Australia. All samples were collected randomly and were not sorted by size. During 2001, monthly samples were obtained from February to September, and November. Squid were frozen within 12 h of capture and subsequently shipped to and dis-

sected at the Institute of Antarctic and Southern Ocean Studies laboratory. Data recorded for each specimen included sex, dorsal mantle length (ML, mm) and total body weight (TBW, g). Additionally, each squid was also assigned a maturity stage after Lipinski (1979). Statoliths were removed, rinsed with water and stored dry at room temperature.

A sub-sample of statoliths was chosen for age estimates representing the entire size range of individuals for each month. In preparation for ageing, statoliths were mounted in the thermoplastic cement Crystal Bond on a microscope slide. Statoliths were then ground dry on the anterior and posterior plane to create a thin section using 30-μm lapping film and polished using a 5.0-μm lapping film.

A Nikon Eclipse E400 high power microscope (400×) under polarised light was used in estimating the total number of increment counts. The mean of two counts that varied less than 10% of the mean, was taken as the age estimate in days. The majority of counts were very close to each other (within 5%).

An experiment for validating the periodicity of statolith increments was carried out during January 1991 using squid from Tasmanian waters. Squid were captured at night using a commercial jigging vessel and were maintained in holding tanks on board the vessel. They were then transferred to a large circular 20,000-l tank with flow-through seawater at the University of Tasmania, Tasmanian Aquaculture and Fisheries Institute. Squid were fed ad libitum with locally captured fish. Before release into the maintenance tank, squid were injected in the region of the base of arm I with a saturated solution of tetracycline-seawater. Statoliths were later examined under a fluorescent microscope and photographed. These photographs were then used as a guide for identifying the region of the tetracycline mark under light microscopy.

Statistical analysis

For growth analysis, individuals were grouped according to hatch season; winter 2000, spring 2000, summer 2000/2001 and autumn 2001. The winter 2000 sample also included 14 individuals that had hatched in the last 12 days of autumn. Growth (weight-at-age) was compared across sexes and hatch seasons using factorial ANOVA. In each case, season was treated as a fixed factor in the analysis. Pairwise comparisons among groups were computed using the logical constraints method of Westfall et al. (1999), except for the comparisons of age, where strong heterogeneity of variance was detected. In this case pairwise comparisons across months using Bonferroni adjusted $t$-tests assuming unequal variance were used.

Growth was analysed by fitting separate lines regression to log transformed weight-at-age data to determine the effects of season and sex on body weight. The model was fitted with both log age (i.e. assuming an

underlying power law growth model) and age (assuming an underlying exponential growth model) as covariate. As growth data are more closely influenced by conditions experienced post-hatching individuals were grouped according to season of hatch.

To model the cohort structure of the sample a finite Normal mixture model was fitted to the totality of hatch dates. That is, the hatch dates within each cohort were assumed to be Normally distributed, with density

$$f_i(x; \mu, \sigma) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{-(x-\mu)^2/(2\sigma^2)}$$

and mean $\mu$ and variance $\sigma^2$. The overall distribution of hatch dates is then a mixture of Normal components,

$$f(x) = \sum_{i=1}^{k} \lambda_i f_i(x; \mu_i, \sigma_i)$$

one component for each cohort, the multipliers $\lambda_i$ representing the proportion that each cohort makes up of the entire distribution.

The mixture model was fitted using the mclust library (Fraley and Raftery 2002) in Splus. This library fits Normal mixture models by the EM algorithm, using the Schwarz Bayesian information criterion (BIC) (Schwarz 1978) for model selection.

## Results

### Validation experiment

Eight specimens were successfully maintained in captivity for up to 10 days post capture. In all specimens, an obvious tetracycline mark was apparent under fluorescent microscopy. Increments could not be easily discerned in the region post staining.

Alternatively, the width of the statolith region that had grown post staining was measured for each individual. The total width in the post-staining region appeared to be linear with time, suggesting regular growth (Fig. 1). However, the spread of the data suggested that error variance increases with width. We therefore fitted a model in which error variance was proportional to the fitted values by generalised least squares. While there was no evidence of a nonlinear trend, there was insufficient data to rule this out entirely. The average daily increment width was 0.75 μm, with a 95% confidence interval of 0.60–0.90 μm. While we were not able to directly validate the increment periodicity in this study, we are assuming increments are produced daily. Thus 'days' in this study refer to the total number of statolith increments.

### Portland study

Overall we collected and processed 856 individuals (503 males and 353 females) with an average of 55 males and 40 females sampled per month. Of these, a total of 602
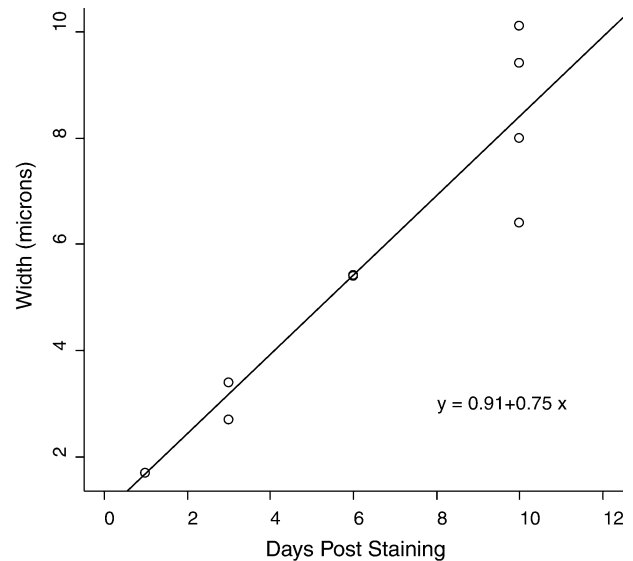


**Fig. 1** The relationship between the number of days post-staining and the width of the statolith of arrow squid *Nototodarus gouldi* during the period of maintenance

(70%) were aged (309 males and 209 females), with an average of 34 males and 33 females aged each month.

The size of squid captured were greater than 90 mm ML and the majority of squid caught were >200 mm ML. This would have been due to the selectivity of the net along with the fact that the fishers probably did not collect smaller squid. The length frequency distribution over the study period did not reveal any obvious progression in the modes (Fig. 2). This suggested that multiple cohorts were being sampled. However, during some consecutive months there was the suggestion that we may have sampled the same cohort (e.g., April–June, females; April–May, males; Fig. 2). Females had a greater mantle length range than males with individuals > 400 mm while males did not exceed 350 mm.

The majority of males captured in all months were mature (Fig. 3). This is especially apparent after June where there were very few immature males caught in the second half of the year. The highest number of immature males was caught during February where 23.9% were immature. Alternatively, females showed considerable variability in the proportion of individuals at each maturity stage (Fig. 3). Mature females were only in the majority in the months of May, August, September and November, with the greatest percentage in November (76.9%). In contrast, 95% of females were immature in April and there was a majority of immature females for February (70.3%), March (61.9%), June (60.5%) and July (67.5%).

The observed age range was 150–325 days for males, and 153–360 days for females. The mean age distribution for each sex across all months of capture did not show a great level of variability (Fig. 4). Our data showed a strong degree of heterogeneity of variance among months. We therefore compared individual months using Bonferroni adjusted pairwise *t*-tests assuming unequal variances. The

**Fig. 2** The length–frequency distribution of all males and females in this study captured off Portland, Victoria
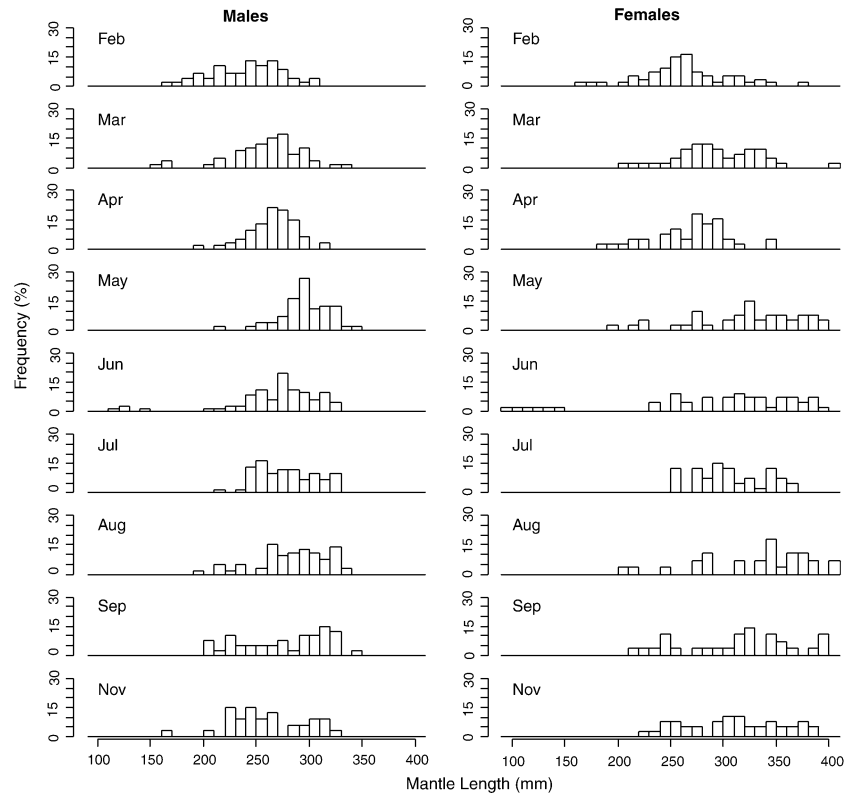


mean age for males in March was significantly less than all later months, but not significantly different to February. There was, however, no clear pattern in the distribution of mean ages of females. The high degree of variance in some months (e.g. June; Fig. 4) suggests that during some sampling months there were a mixture of cohorts.

In order to identify how many cohorts were present, we examined hatch date by capture month for both sexes

**Fig. 3** The distribution in maturity stages for *Nototodarus gouldi* males and females captured during each month of the study off Portland, Victoria
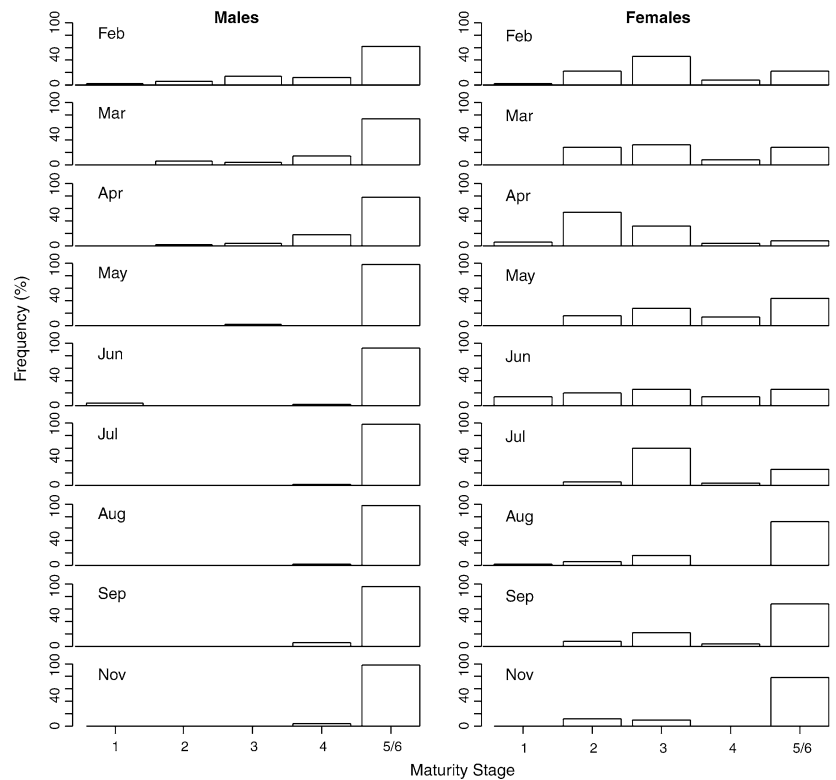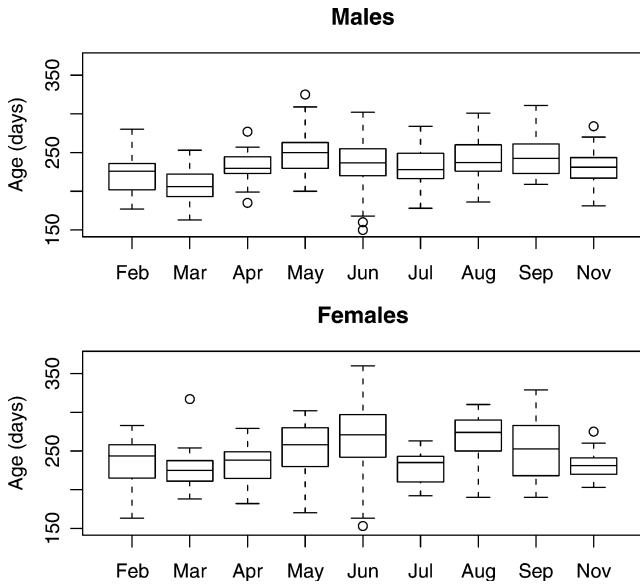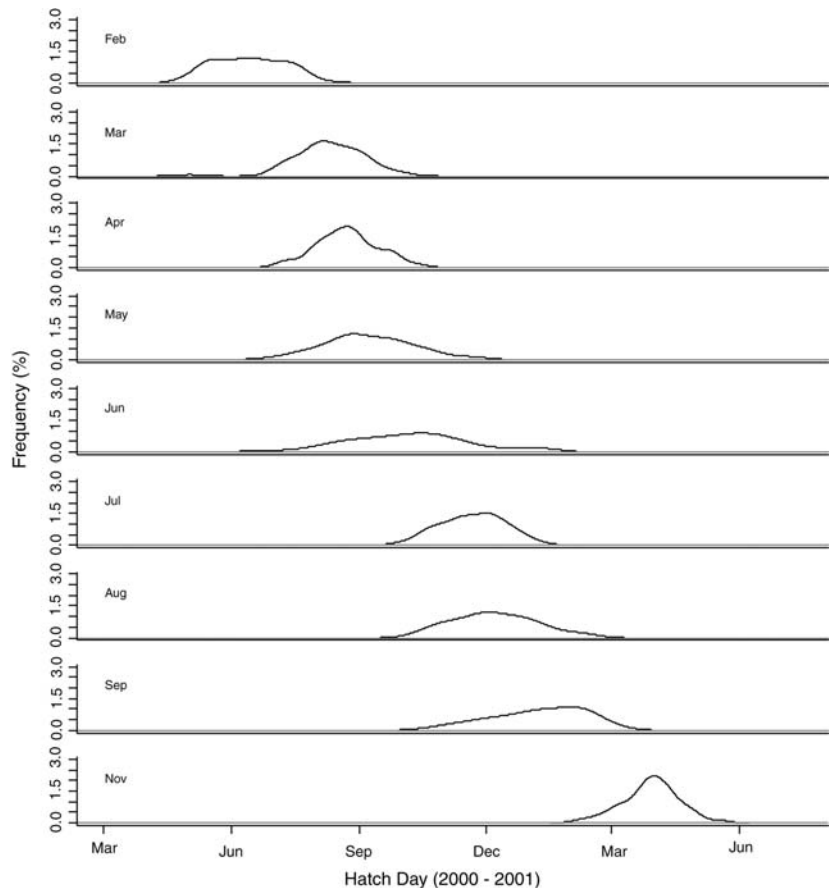
**Males**



**Females**



**Fig. 4** The distribution of ages of *Nototodarus gouldi*, for males (*top*) and females (*bottom*) for each month of capture

combined (Fig. 5). There appear to be at least four discernible cohorts, the first disappearing after February, the second lasting from March through June, the third from May through to at least September, and the final cohort appearing in September and clearly evident in November.

Proceeding on the assumption that there are a number of discrete cohorts, we fitted a finite Normal mixture to the totality of hatch dates to model the cohort structure. Based on BIC, the best fitting model had four components (Fig. 6), each with a common variance. This suggestion of multiple cohorts was also consistent with the complex monthly length frequencies (Fig. 2).

*Growth*

Tests based on grouping squid according to hatch month showed few significant differences, possibly due to the smaller number of observations per degree of freedom. Therefore, growth in weight was analysed according to season of hatch (Fig. 7). There was also little discernible difference in adequacy of fit for the power law and exponential models, as over the age range considered, log age is very nearly linear. The differences in these two models would be more apparent if we had a fuller compliment of younger individuals. As both models yield ostensibly the same conclusions, we present only the results of the exponential model to allow comparison with future work.

Separate lines regression models were fitted to age versus log weight (exponential growth model) allowing both slopes and intercepts to vary with hatch season and gender. The model showed strong evidence ($P=0.009$, $F=3.8$, $df=3,577$) of a sex × age × hatch season inter-

**Fig. 5** The age frequency of *Nototodarus gouldi* for each month of capture of the study period
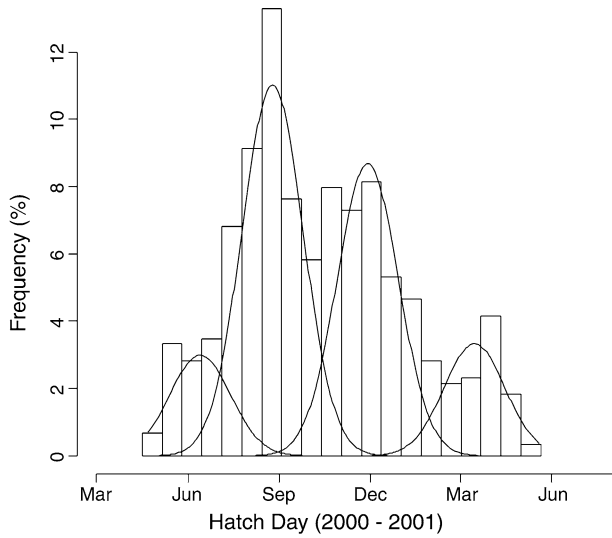
**Fig. 6** The Normal mixture model fitted to the totality of all hatch dates for *Nototodarus gouldi*. The x-axis is the number of days from 1 January 2000

action, and to simplify further analysis, the two sexes were considered separately.

Multiple comparisons of slopes for the males revealed no evidence of seasonal differences in growth rates (Fig. 8a). In contrast, multiple comparisons of slopes for the females revealed a different pattern, with strong evidence for a hatch season by age interaction ($P < 0.001$, $F = 9.80$, $df = 3,282$). At the 0.05 level of significance, the summer-hatched sample had a significantly faster growth rate compared to both winter and spring. The growth rate for the autumn sample appeared to be most similar to

that of the summer sample. However, presumably due to the lower sample size, the autumn sample could not be shown to be different to the winter and spring samples at the 0.05 level, but was found to be different to the winter sample at the 0.1 level (Fig. 8b).

## Discussion

A number of techniques were used to discern important temporal patterns in age, growth, maturity and cohort structure off Portland. The combination of sequential sampling along with statolith ageing has proven to be an effective means to obtain important parameters in the population dynamics of *N. gouldi*. While we know that this species has a short life span and rapid growth, this study extends the use of statolith-derived age data to identify temporal patterns in cohort structure. Such an analysis holds promise for similar studies on other key squid species. This study also complements earlier work that focused on broad-scale spatial and temporal dynamics of growth and reproduction in *N. gouldi* across a number of sites in southern Australia (Jackson et al. 2003). Ages of the Portland squid were somewhat higher than in the previous study. The maximum age of females (360 days) and males (325 days) contrasts with the previous study where maximum age obtained was 329 days. These data further suggest an annual life cycle for *N. gouldi*.

We continue to assume daily periodicity in increment formation in *N. gouldi*. While statolith-based ageing studies have been carried out on ommastrephids (review in Jackson and O'Dor 2001), there have been no validation studies on ommastrephids for over a decade (review in
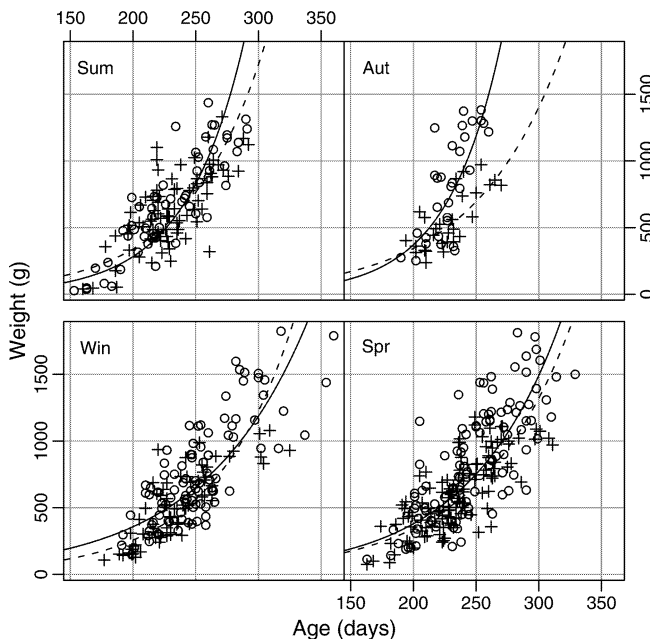


**Fig. 7** The relationship between age and total body weight for *Nototodarus gouldi* grouped according to hatch season shown with fitted exponential growth curves. Males shown as ( + ) and *dashed line*, females shown as (∘) and *solid line*
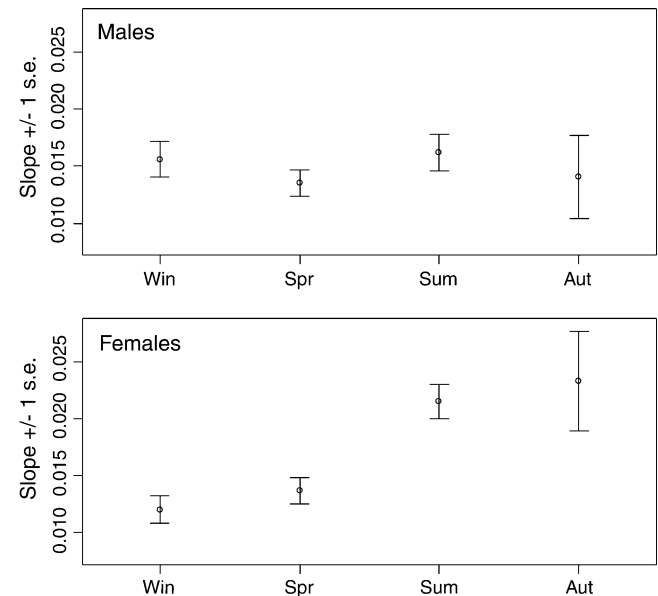


**Fig. 8** The mean slope of the separate lines regression model fitted to log transformed weight at age data for each seasonal hatch group of *Nototodarus gouldi*

Jackson 1994). However, earlier successful studies based on direct chemical marking and captive maintenance of *Illex illecebrosus* (Hurley et al. 1985) and *Todarodes pacificus* (Nakamura and Sakurai 1991), along with indirect field-based methods of *Illex illecebrosus* (Hurley et al. 1979), *I. argentinus* (Uozumi and Shiba 1993) and *Nototodarus sloanii* (Uozumi and Ohara 1993) give some confidence on the daily nature of statolith increments in ommastrephids. While our attempts at validation of *N. gouldi* were disappointing, the assumption of one increment per day is not unreasonable. Our experiments do highlight the difficulties with capturing and maintaining ommastrephid squid in good condition. The mean increment width of 0.75 μm per day seems to be narrow, based on work on other ommastrephids where increment widths range between 1.5–5 μm (e.g. Morris and Aldrich 1985; Hurley et al. 1985; Arkhipkin 1993; Uozumi and O'Hara 1993). This suggests that the individuals of *N. gouldi* were probably growing at a considerably slower rate due to the captive maintenance conditions. This would also be a factor in the poor increment resolution in the period of growth during maintenance.

Previous large-scale spatial and temporal analysis of size, age and maturity of *N. gouldi* also found a complexity in growth dynamics (Jackson et al. 2003). This species appears to show considerable flexibility in reproduction and growth dynamics. The differing patterns in seasonal growth rates between males and females suggests that males and females may be responding to the environment differently. It is interesting that we could not discern any seasonal changes in growth of the males compared to the females, which showed faster growth in the summer cohort. Jackson et al. (2003) found that sea surface colour (SSC), i.e. a proxy for productivity, helped explain differences in growth rates of females captured during winter but not summer. Similarly SSC failed to explain variability in male growth rates for any season. This suggests that females might be more sensitive to environmental change compared to the males.

A companion study to this research (McGrath Steer and Jackson 2004) also found sex differences in reproductive investment during the same sampling months off Portland. Both females and males showed lower gonad investment during winter and greater investment during summer, with males showing a drop in gonad investment several months prior to females. An increase in gonad investment in females resulted in a drop in somatic investment. This suggested that gonad investment in females occurred at the expense of somatic growth. However, males showed a different pattern. An increase in gonad investment in males in the warmer months was generally associated with a concomitant increase in somatic investment. Therefore, during some periods, males appear to be able to allocate energy to both gonads and somatic tissue.

Given the gender differences in both the relationship between growth rate and productivity (Jackson et al. 2003) and in gonad investment (McGrath Steer and

Jackson 2004) it is not surprising that we found differences between males and females in seasonal growth rates. However, the mechanisms driving these differences remain unclear. The lack of seasonal growth in males was unexpected, but could simply be due to low power due to insufficient sample size and deserves further research. The oceanography off Portland is complex and influenced by regular upwelling events that occur in this region between November/December and March/April as part of the Bonney Upwelling Area. This is the most prominent and regular upwelling region in southeast Australia and results in a highly productive marine environment. This is driven predominantly by alongshore winds that produce classical upwelling plumes (Butler et al. 2002). Currently, the timing of periods of high productivity during our study is unknown. Available data has not yet been analysed to assess periods of high productivity. This is the focus of future research on the relationship between both SSC and sea surface temperature on squid growth rate.

The high growth rates displayed by the summer-hatched females are consistent with our understanding on the influence of warm temperature accelerating squid growth (Forsythe 1993, 2004; Forsythe et al. 2001; Hatfield 2000; Jackson et al. 1997; Pecl 2004). However, the Portland situation is complicated by the lack of any variation in growth rates detected in males. *N. gouldi* is clearly capable of inhabiting a wide range of habitats (Dunning 1998; Jackson et al. 2003) with flexible growth patterns according to local conditions experienced. If we assume that food is not limited off Portland, then perhaps other factors are controlling the difference in growth responses observed between males and females. Jackson and Domeier (2003) also found gender differences with male individuals of *Loligo opalescens* off California tracking the environment more closely than females.

The sex differences in *N. gouldi* contrasts with work by Brodziak and Macy (1996) for *Loligo pealei* and Hatfield (2000) for *Loligo gahi*, in which both studies found seasonally induced differences in growth rates were reflected in both males and females. Oceanographic analysis in relation to squid growth may help to elucidate the role the environment is playing in influencing squid growth rate, especially for females.

Identifying squid cohorts within squid populations can be extremely difficult due to problems of uncoupling of squid size and age. This study identifies the usefulness of the combination of age data and sequential samples for identifying the numbers of cohorts present over time. Without age data it can be virtually impossible to identify cohorts. Arkhipkin (1993) employed statolith ageing techniques to identify 'waves' of individuals of *Illex argentinus* passing through fishing grounds in the South Atlantic. Thus, ageing identified that the fishery was not harvesting squid from a stationary population, but rather, the situation was much more dynamic with successive cohorts passing through the fishing region. Similarly, Jackson and Pecl (2003) also found marked dynamics in spawning groups of the near-shore Australian loliginid

*Sepioteuthis australis* in Tasmanian waters. Samples of this species taken approximately weekly found no difference in either the size or age structure of squid sampled sequentially. While discrete cohorts were not identified by Jackson and Pecl (2003), their work displayed that there was a continuation of new recruits moving through the spawning region at least on a weekly basis.

The mixture model we used assumes that we have fully sampled each cohort. This is unlikely for the first and last cohorts in our study off Portland. It seems more reasonable to assume that our sampling has missed the early-hatched squid in the first cohort, and the later-hatched squid in the last cohort. This will lead to bias in estimates of the cohort means. Most likely the first cohort occurs somewhat earlier than we have estimated, and the last cohort somewhat later. This problem could be better addressed by a longer time series of collections off Portland. Furthermore, a longer time series would also help to identify the number of cohorts that may move through an area that is subject to fishing pressure. We now know that the fishery is targeting a transient population off Portland with at least four cohorts occurring on nearly a seasonal basis. Although these cohorts appear to be distinct, this may be a by-product of our sampling scheme. It may be that there is a single extended cohort that appears as a sequence of distinct cohorts due to the nature of our sampling scheme, as has been alluded to by Boyle and Boletzky (1996).

There is a substantial proportion of the population that we do not sample. For example, very few immature males are captured. This can influence when we detect a new cohort. While we can detect a new cohort when the animals are large enough (usually older than 150 days) that cohort is likely to be present earlier although we will not detect it with our sampling regime. Continued work will help provide a clearer insight into the important dynamics of the stock structure in this region.

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