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RESEARCH ARTICLE

Temporal life history plasticity of the Southern Ocean squid *Todarodes filippovae* from waters off Tasmania, Australia

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Abstract Population dynamics and maturity parameters were analysed for seasonal samples of the oceanic ommastrephid squid *Todarodes filippovae* from off the coast of Tasmania Australia from 2002 to 2004. Based on assumed daily periodicity in statolith increments, *T. filippovae* had a life cycle of about a year with the sexually dimorphic females reaching their larger size by predominantly growing faster than males. Due to the small sample size of males, analysis was undertaken on female individuals only. Growth in all samples was best described by a power curve and varied annually, with significantly faster growth in 2001 compared to the subsequent 2 years. Seasonal growth rates also varied with autumn- and winter-hatched squid significantly faster than summer-hatched squid. Spring growth rates were intermediate but not significantly different to the other three seasons. Peak hatching periods occurred in late autumn and early winter. ANOVA revealed a season × year interaction for mantle length and total body weight. Pairwise comparisons showed that the annual differences were likely driven by smaller squid in autumn 2002 compared to autumn samples in the other 2 years. Pairwise comparisons also revealed seasonal differences with winter-caught squid smaller than those from the majority of other samples. There were no seasonal effects on mature female gonad weights but females caught in 2002 had significantly lighter gonad weights than females from the following 2 years. There were no consistent trends among seasons or years in the age structure of mature females. This study revealed the plasticity and flexibility in growth and maturity parameters in this species, with a preference for faster growth during cooler periods.

Introduction

Squid are likely to play an increasingly important role in marine ecosystems. This could be due to their potentially greater abundance compared to past decades, resulting from the marked removal of many of their teleost predators (Meyers and Worm 2003). Pelagic squid stocks will potentially come under increasing pressure as global fisheries look to new populations to exploit (Caddy and Rodhouse 1998; Rodhouse et al. 2001). Furthermore, due to their short life cycles and fast growth rates, squid respond quickly to environmental change. It may also be feasible to use aspects of squid recruitment, abundance or growth parameters as a proxy for understanding ecosystem fluctuations (e.g. Waluda et al. 2004).

Squid populations can undergo dramatic fluctuations in abundance due to changes in oceanographic conditions (e.g. O'Dor and Dawe 1998; Dawe et al. 2000; Jackson and Domeier 2003). Such fluctuations can have consequences for squid predators as well as squid prey within their ecosystems. In the Southern Ocean food chain, squid are an important link between lower trophic levels and higher vertebrate predators (e.g. Rodhouse and White 1995).

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The life history and ecology of Southern Ocean squid within the Pacific and Indian Ocean sectors is an area currently needing further research. Many aspects of squid ecology and their role in the ecosystem still need considerable research for most species, particularly offshore and oceanic species. Such data are imperative for future issues of ecosystem modelling and management. Furthermore, large ommastrephid squid are important components of many of these oceanic regions.

In the northern and southern hemispheres, the ommastrephid genus *Todarodes* forms an important species complex. There are large stocks and targeted fisheries for both *Todarodes pacificus* (Rodhouse et al. 2001) and *Todarodes sagittatus* (Borges and Wallace 1993) in the Northern Hemisphere, while the Southern Hemisphere species of *Todarodes filippovae*, *Todarodes angolensis* and *T. pacificus pulsillus* (Dunning and Wormuth 1998) are relatively poorly studied. Within the waters off Tasmania, Australia, both *T. filippovae* and *T. angolensis* co-occur. However, *T. filippovae* is the more common species encountered in deepwater fishery bycatch. Earlier work considered that there was only a single Southern Ocean species referred to as *T. angolensis*. However, the taxonomic status of both *T. filippovae* and *T. angolensis* has now been established (Dunning 1998) with both species being easily separated by the size and number of teeth in the largest median manus suckers (Roeleveld 1989; Dunning and Wormuth 1998).

Data on collection localities suggests that *T. filippovae* has a circum-polar distribution, particularly in association with high velocity current systems. While currently identified as one species, there is the possibility that *T. filippovae* may represent a species complex (Rodhouse 1998). More detailed genetic work throughout the range would help resolve the genetic status of *T. filippovae* across its distribution. In the region of the Tasman Sea, *T. filippovae* is the most abundant ommastrephid in the subtropical convergence zone and in slope waters off southeastern Australia (Dunning 1993). *T. filippovae* is a large and muscular pelagic ommastrephid (> 500 mm mantle length and weight > 4 kg) and is likely to be an important part of this ecosystem. A number of Southern Ocean vertebrates prey on *T. filippovae* including sperm whales *Physeter macrocephalus* (Evans and Hindell 2004), New Zealand fur seals *Arctocephalus forsteri* (Page et al. 2005), southern elephant seals *Mirounga leonina* (Burton and van den Hoff 2002) as well as three species of albatross; black-browed *Diomedea* (*Thalassarche*) *melanophris*, yellow-nosed *Diomedea* (*Thalassarche*) *chlororynchos* and grey-headed *Diomedea* (*Thalassarche*) *chrysostoma* (Cherel and Klages 1997).

This study was aimed at obtaining key parameters of the age, growth and maturity of *T. filippovae* off the coast of Tasmania. Because data were collected over a number of years it was possible to consider the trends in maturity and growth rates over an extended time period.

Methods

Squid were obtained over 3 years between summer 2001/2002 and winter 2004. Squid were collected as a bycatch of the deepwater trawler Adriatic Pearl. The gear used was a cut-away wing demersal trawl with a headline height of 6 m. Typical trawling depth was between 700 and 1,200 m. During each year squids were sampled during summer, autumn and winter (except for winter 2003 where only a few individuals were obtained). The summer and autumn samples each year were obtained off the coast of southern Tasmania, in the regions of Maatsuyker Island, Pedra Branca and the Cascade Plateau (145–152°E, 44–46°S). The winter 2002 sample consisted of squid from off the east coast of Tasmania (~149°E, 41°S), while the winter 2004 sample included squid pooled from both the south and east coast of Tasmania.

Specimens were either frozen on board ship or immediately upon arrival at port, and were later defrosted and dissected. Parameters taken for each squid included sex, maturity stage (after Lipinski 1979), total weight (W) to the nearest gram, and mantle length (ML) to the nearest millimetre. Weights of ovary and oviducts were also taken to the nearest 0.1 g.

Statoliths were removed, rinsed in water and stored dry prior to ageing. Statolith preparation included mounting statoliths in crystal bond and grinding and polishing with lapping film after Jackson et al. (2003). However, for many of the specimens, especially larger ones, grinding and polishing was required on a third plane. This necessitated tilting the statolith with the dorsal dome slightly inclined and a further grinding plane was taken from the nuclear area to the outer edge of the dorsal dome. This produced a thinning of the statolith structure in the dorsal dome, which helped to reveal the increment structure in this region. This technique was similar to the technique needed for statoliths from large females of *Moroteuthis ingens* (Jackson 1997). Increment counts were taken using either a Nikon Eclipse E400 high power microscope directly or an Olympus CH 30 microscope counted via a digital camera and PC with a Sony Trinitron monitor. All counts were taken at 400×.

No validation work has been carried out for *T. filippovae*, thus the age estimates in this study are putative. However, there is validation of daily statolith increment periodicity for other closely related ommastrephids including *T. pacificus* in Japan (see Jackson 1994; Jackson and O'Dor 2001). Therefore, we are assuming that statolith increment counts represent a valid means of ageing this species.

Statistical analysis

Growth analyses were only undertaken on females ($n = 401$) due to the low sample size for males ($n = 61$). For growth analysis, individuals (all sized and aged females) were grouped according to hatch season in each year from 2001 to 2003. All summer samples for each year included January and February of that year along with the December sample of the previous year. Separate power law growth models were fitted to the weight-at-age data. We fitted a separate lines model to logged weight-at-age data to compare growth rates (slopes) by season and year. ANOVA was used to assess annual and seasonal trends in mean log-transformed W, ML, gonad weight (ovary + oviducts) and age of mature females. Mature females were grouped according to year and season of capture. These included summer, autumn and winter for the 3 years from 2002 to 2004. Where the presence of higher order interactions was indicated, pairwise multiple comparisons between groups were computed using the logical constraints method of Westfall et al. (1999). Significance in all analyses was taken at the 0.05 level.

Results

This species is sexually dimorphic with females reaching a much greater ML and weight than males. The range in mantle length and weight for females was 211–540 mm and 155–4,704 g, while males were 170–316 mm ML and 90–1,961 g (Fig. 1). It is not clear why females were more common in catches than males although it is likely that males are better at avoiding the trawl net compared to females. Interestingly, the majority of males captured showed considerable skin damage with much of the skin worn off whereas females (even of comparable sizes) were generally much less damaged. This may indicate a more vigorous effort by males to avoid net capture.

Pairwise comparisons across all seasons and years revealed that mature females were significantly heavier and had greater mantle lengths for each season with a mean weight that was 1,656 g (95% CI 1,472–1,840 g, $P < 0.0001$) and a mean ML that was 115 mm (95% CI 104–126 mm, $P < 0.001$) greater than mature males. Similarly, pairwise comparisons revealed that the mean age of mature females was significantly greater than mature males ($P < 0.0001$). The mean age of mature females (294 days) was 34 days greater than mature males (260 days, 95% CI 31–48, $P < 0.0001$).

The hatch-date distribution of *T. filippovae* over the 3 years of collections revealed year-round hatching with three prominent peaks (Fig. 2). In 2001 there was a peak in late April, whereas 2002 and 2003 had similar hatch peaks in early June. Thus the majority of specimens in this study were hatched in late autumn or early winter. To a large extent this pattern is governed by the

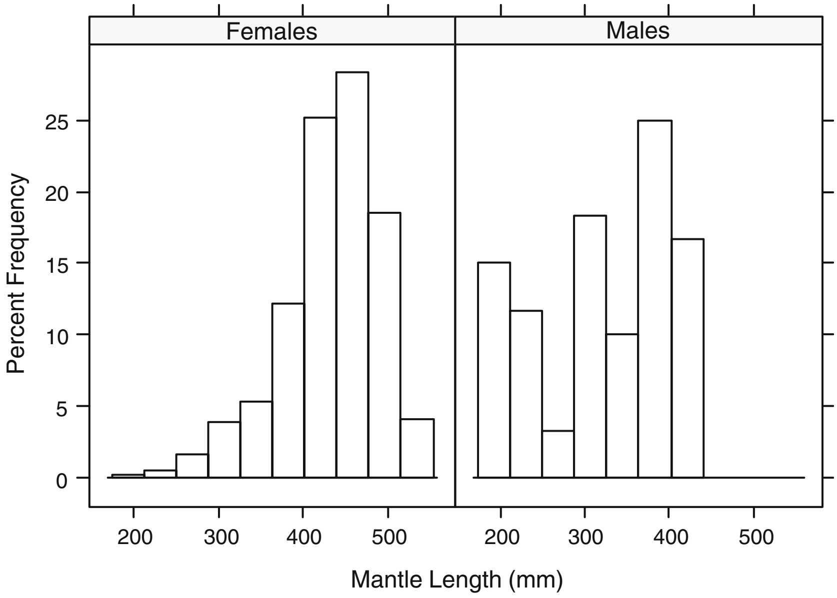
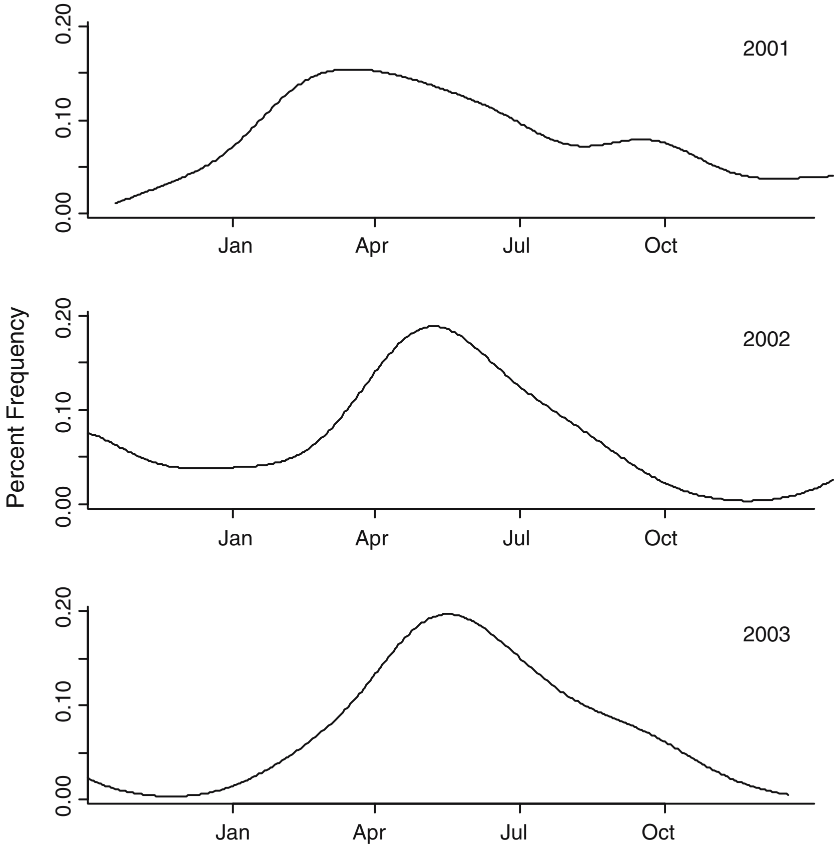


Fig. 1 The length–frequency distribution of all male and female individuals of *Todarodes filippovae* from Tasmanian waters in this study

Fig. 2 The hatch-date distribution of all aged individuals of *Todarodes filippovae*. The *lines* represent the trend in the monthly percent frequency

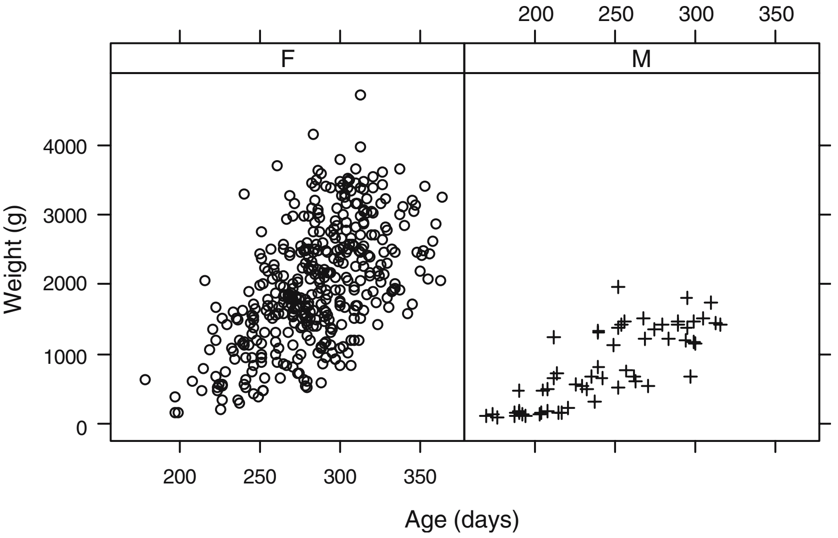


periods of time that squid were available from the fishery, with most squids collected during summer and autumn. However, it does reveal that hatching tended to occur during restricted periods.

Based on statolith ageing, *T. filippovae* appears to have a life cycle of around a year with females achieving a slightly greater age (> 360 days) than males (< 350 days and most < 325 days) (Fig. 3). Due to the greater size of females (which reached weights > 3 kg) they generally had faster growth rates than males that were all < 2 kg. Thus a much greater body size was reached for females for a comparable time period. Mature (stages 4, 5) females ranged in age from 239 to 364 days while males matured younger ranging from 190 to 310 days.

Individuals were grouped according to hatch season, and growth was described by the power model (Fig. 4). Due to the lack of age data for the smaller and younger squid, the form of growth in this study could only be

Fig. 3 The relationship between age and weight for female (F) and male (M) individuals of *Todarodes filippovae*



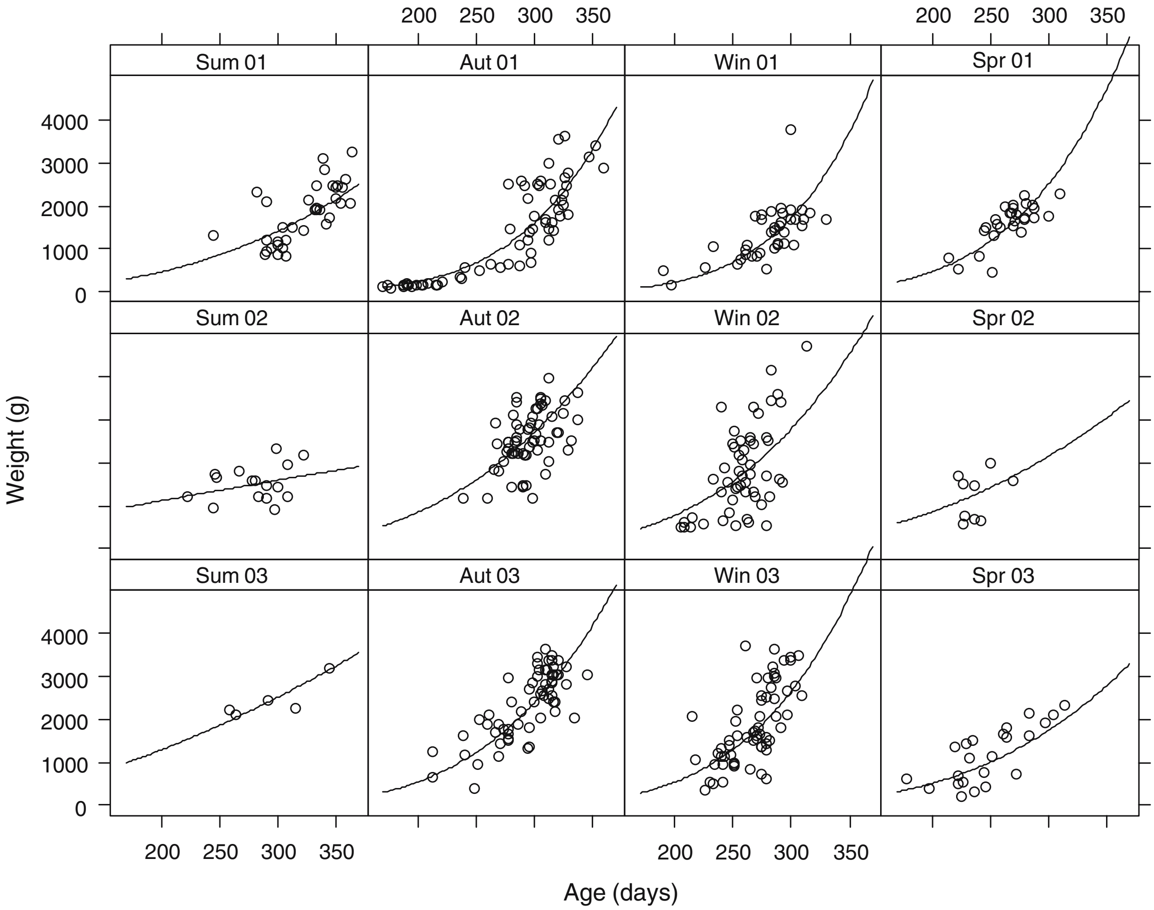


Fig. 4 The relationship between age and weight for all female individuals of *Todarodes filippovae* grouped according to hatch season for 2001–2003. The *fitted curves* represent power curve fits

described for the second half of the life span. Separate lines regression was undertaken for the female size-at-age data. Seasonal growth patterns of females showed no evidence of a season × year × log age interaction. Pairwise comparisons of years adjusting for seasonal differences revealed that squid hatched in 2001 had significantly faster growth rates than squid hatched in 2002 or 2003 (Fig. 5a). Furthermore, pairwise comparisons of seasons, adjusting for yearly differences revealed that autumn- and winter-hatched squid had the fastest growth rates which were both significantly higher than squid hatched in summer. Squid that hatched in spring showed intermediate growth rates, however, they were not significantly different from the other three seasons (Fig. 5b).

Females showed a greater spread of maturity stages throughout all capture seasons sampled (Fig. 6a) with the greatest predominance of mature females during the winter of 2002. In contrast, except for the summer sample of 2002, all males were mature (Fig. 6b).

Analysis of variance was undertaken according to season of capture for weight, ML, gonad weight and age of all mature females excluding the winter 2003 sample because of only one observation. There was a strong season × year interaction ($F_W = 3.47$, $df = 4{,}157$, $P < 0.01$) in the mean weight of mature females. Pairwise multiple comparisons revealed that the autumn sample in 2002 was significantly lighter ($P < 0.001$) than the 2003 and 2004 autumn samples, which were not significantly different from each other. The weight of individuals from winter 2002 and 2004 samples were not significantly different from each other, but were lighter than the majority of all other samples. The weight of mature winter-caught females (2002, 2004) were the same as autumn 2002, however, winter 2004 was also the same as summer 2002 (Fig. 7a). Similarly, ANOVA revealed a moderate season × year interaction in ML of mature females ($F_{ML} = 2.53$, $df = 4{,}158$, $P < 0.05$). The autumn 2002 individuals were shorter in ML than autumn 2004 individuals ($P < 0.01$) but not autumn 2003. Also mantle lengths of 2002 and 2004 winter squid were similar but significantly shorter in ML than all other samples ($P < 0.05$) with the exception of winter 2004 that was similar in ML to autumn 2002 (Fig. 7b).

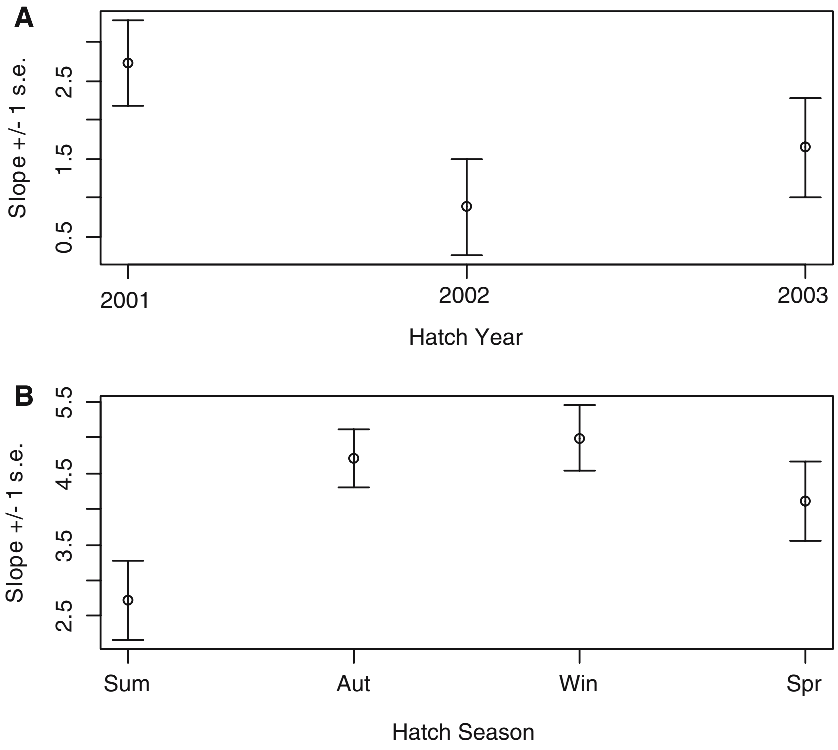


Fig. 5 The mean slope of the power law model fitted to the log-transformed weight-at-age data for female individuals of *Todarodes filippovae* grouped according to **a** hatch year and **b** hatch season

Analysis of variance of mature female gonad weights (i.e. ovary + oviduct weight) among all seasons did not reveal any evidence of a season × year interaction. However, when the interaction term was dropped from the analysis there was strong evidence of a year effect ($F_{\text{gonad weight}} = 6.24$, $df = 2{,}158$, $P < 0.01$) but no evidence of a season effect. Mean gonad weights of mature females sampled in 2002 were significantly lighter than for mature females caught in 2003 ($P < 0.01$) and 2004 ($P < 0.01$), which were similar to each other (Fig. 7c). Standard residual diagnostics revealed outliers, but deleting these did not alter the conclusions. Analysis of ovary weight alone revealed a similar pattern to that observed for ovary and oviduct weight combined.

There was a strong season × year interaction ($F_{\text{age}} = 6.47$, $df = 4{,}153$, $P < 0.001$) in the mean age of mature females for all seasons and years. Pairwise multiple comparisons failed to highlight any consistent trends. However, the summer 2002 females were significantly older compared to all other samples except summer 2004. There were no other consistent trends in age across seasons and years (Fig. 7d).

Discussion

As is typical of squid, *T. filippovae* displays rapid growth, short life spans and early maturity coupled with intra- and inter-annual plasticity in size and growth parameters. The life span does not appear to be longer than a year. These data agree with the growing body of literature on other cool water ommastrephid squid in which the majority appear to have a life cycle that is annual or slightly more than a year (e.g. Jackson 1994; Jackson and O'Dor 2001; Arguelles et al. 2001; Chen and Chiu 2003). Growth parameters of *T. filippovae* in this study agree with a similar study on *T. angolensis*, off Namibia (Villanueva 1992), although in much lower latitudes between 23 and 30°S. *T. angolensis* showed similar growth parameters to *T. filippovae* off Tasmania with a life cycle of around a year. Furthermore, both *Todarodes* species appear to grow faster in cooler oceanic conditions. This was indicated by the higher growth rates in *T. filippovae* in the winter and autumn as well as higher growth rates for *T. angolensis* during 1987 in the Benguela system. During 1987 the Benguela system had lower than normal temperatures with an intrusion of subantarctic water during that year and also the highest catches for this species compared to the previous decade.

Todarodes thus appears to be a species that favours cooler oceanic conditions. This contrasts with the other common ommastrephid in southern Australian waters *Nototodarus gouldi* that had faster growth rates during warmer water conditions (Jackson et al. 2003, 2005). However, these squid do live in different environments with *N. gouldi* being more inshore over the continental

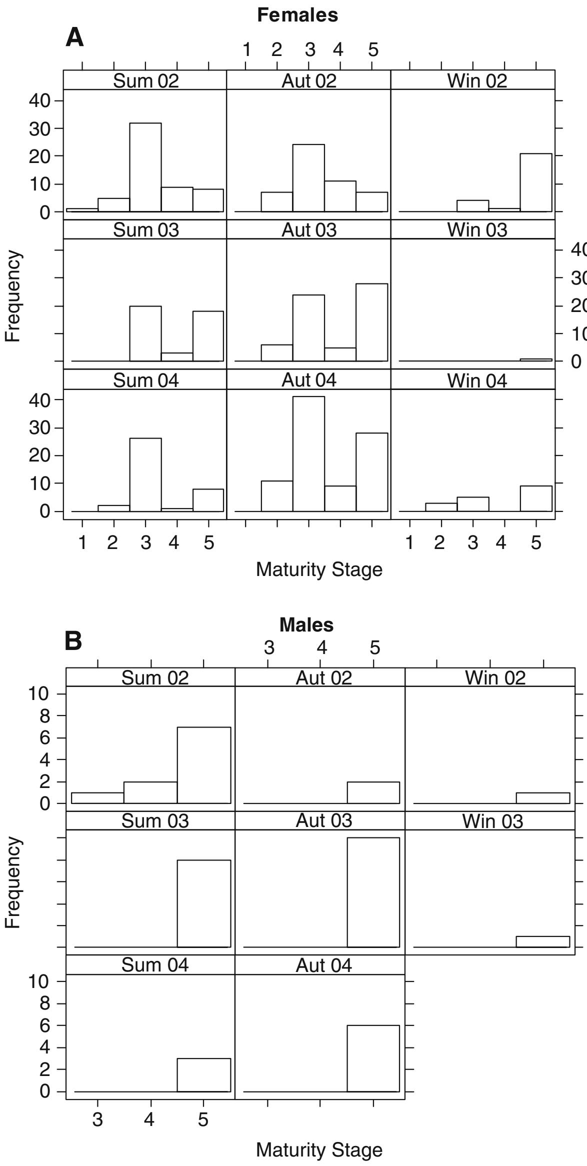


Fig. 6 The frequency distribution in maturity stages for *Todarodes filippovae* **a** females and **b** males for each capture season for the 3 years (2002–2004) of the study period

shelf compared to *T. filippovae* which inhabits deeper offshore continental slope waters and seamounts. The more usual strategy for squid is that warmer conditions produce faster growth rates (e.g. Hatfield 2000; Jackson et al. 1997; Forsythe 1993, 2004). However, the work on both these *Todarodes* species indicates that sometimes species prefer cooler conditions for optimum growth. This has been found with the small tropical loliginid squid *Loliolus noctiluca* (Jackson and Moltschaniwskyj 2001) as well as with the California market squid *Loligo opalescens* (Jackson and Domeier 2003) which favours cooler water periods with higher productivity. Similarly, Ichii et al. (2004) also found that the cooler autumn cohort of *Ommastrephes bartramii* grew faster than the warmer winter–spring cohort in the North Pacific. This was also attributed to the greater influence of food supply over temperature. Forsythe (2004) highlighted that such studies show that food can be an overriding factor influencing growth if food is limited. This is displayed by the results of Jackson and Domeier (2003) that revealed high growth of *L. opalescens* in cooler productive periods despite this species showing the typical marked increase in growth in warmer conditions in captivity (Vidal et al. 2002). Thus specific squid species will likely be responding to environmental conditions differently depending on habit and physiological constraints. An understanding of how a species responds to particular environmental conditions may help forecast how certain species will respond to environmental variability (Rodhouse 2001; Agnew et al. 2002). This therefore necessitates a sound understanding of their plasticity and how a specific squid species responds to changing oceanographic processes (Anderson and Rodhouse 2001).

The inter-annual variability in growth rates with substantially faster growth in squid hatched in 2001 compared to the following 2 years was also found to be the case in the spatial and temporal growth study of *N. gouldi* in Australia (Jackson et al. 2003) where the 2000/2001 hatched squid revealed faster growth rates across southern Australia compared to the previous year 1999/2000. These trends might represent differences in productivity and food availability in relation to oceanographic conditions. Considerable trends in body size and growth rate were also found in the inshore temperate loliginids *Sepioteuthis australis* over 5 years (Pecl et al. 2004) and particularly in *L. opalescens* tracked through El Niño and La Niña events (Jackson and Domeier 2003). Thus, interannual plasticity in the growth dynamics of squid, driven by environmental variability, appears to be a common phenomenon as we begin to collect longer time series of squid growth.

The factors responsible for the faster growth in the 2001 cohort in this study are currently unknown. However, these squid did hatch earlier (late April) compared to the following 2 years where hatching peaked in early June. Squid caught during this year also had significantly poorer somatic condition, gonad investment and lower gonad weights compared to the other 2 years (Jackson 2005). It is intriguing that even though the squid were growing faster in this year, there was a cost in reproductive and somatic condition. This suggests that there was a trade-off between growth and condition. The reasons for this trade-off are unclear but are likely to be complex and due to inter-relationships between temperature and food supply. It raises the

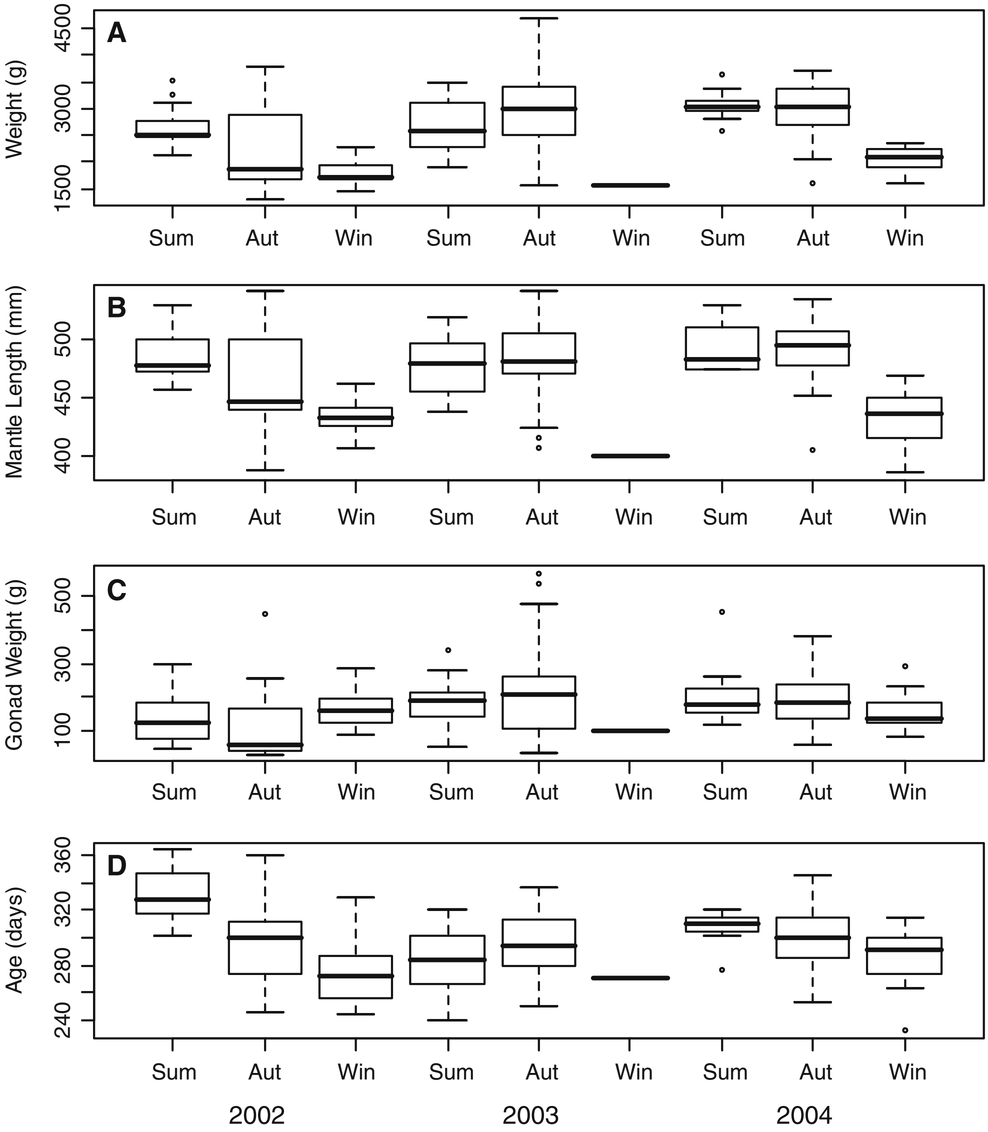


Fig. 7 The distribution of **a** weights, **b** mantle lengths, **c** gonad weights (ovary + oviduct) and **d** ages for mature female individuals of *Todarodes filippovae* for each season of capture for the study period 2002–2004. The *dark horizontal line* represents the median while the *upper* and *lower boxes* display the 75th and 25th percentiles, respectively. The *dashed lines* represent the range without outliers, while the *dots* indicate outliers

question as to whether growing fast is necessarily a good thing? Accelerated growth rates may be a strategy to speed individuals through unfavourable conditions, whereas when conditions are good it might be advantageous to grow slower, increase body condition and invest in greater reproductive output.

The life cycle of *T. filippovae* appears to favour timing of spawning to produce hatchlings during late autumn and early winter. However, due to sampling constraints (i.e., few squid obtained between August and September), these peaks may be biased due to the restricted periods when adult squid were available as bycatch from the deepwater fishery. The consistent presence of mature males compared to females suggests that spawning probably occurs year-round in Tasmanian waters. Villanueva (1992) also found year-round spawning for *T. angolensis* off Namibia. However, his data also suggested peak spawning times in late autumn and early winter in some years. Winter samples of *T. filippovae* from the east coast of Tasmania were always mature suggesting that this may be a spawning region for this species in the winter (Jackson 2005). Dunning (1993) suggested a summer spawning period for *T. filippovae*, with a possible spawning ground near the northern boundary of its distribution. It is likely that spawning takes place across a broad geographic region. Currently we still have little knowledge as to whether *T. filippovae* undertakes any extensive migrations and we don't understand the genetics of their population structure. Recent work by Dillane et al. (2005) found considerable population separation in *Todaropsis eblanae* in the East Atlantic and Mediterranean. It would be useful to obtain information on the genetic structure of east Australian populations, which would provide some information of movement in the Tasman Sea region. It would also be of interest to investigate further the winter spawning populations off the east coast of Tasmania. These squid had consistently smaller body size although not significantly smaller gonad weights. Thus, it is of interest as to whether these winter squid are smaller morphs (e.g. Jackson et al. 2003) associated with a different water mass (i.e. the East Australian Current) or whether there is no genetic separation and these specimens are simply controlled by phenotypic environmental constraints on body size. Future study incorporating greater sampling of *T. filippovae* as well as genetic analyses would help in answering these population ecology questions.

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References

Agnew DJ, Beddington JR, Hill SL (2002) The potential use of environmental information to manage squid stocks. Can J Fish Aquat Sci 59:1851–1857

Anderson CIH, Rodhouse PG (2001) Life cycles, oceanography and variability: ommastrephid squid in variable oceanographic environments. Fish Res 54:133–143

Arguelles J, Rodhouse PG, Villegas P, Castillo G (2001) Age, growth and population structure of the jumbo flying squid *Dosidicus gigas* in Peruvian waters. Fish Res 54:51–61

Borges TC, Wallace JC (1993) Some aspects of the fishery biology of the ommastrephid squid *Todarodes sagittatus* (Lamarck, 1798) from the northeast Atlantic. In: Okutani T, O'Dor RK, Kubodera T (eds) Recent advances in cephalopod fisheries biology. Tokai University Press, Tokyo pp 25–36

Burton H, van den Hoff J (2002) Humans and the southern elephant seal *Mirounga leonina*. Aust Mammal 24:127–139

Caddy JF, Rodhouse PG (1998) Cephalopod and groundfish landings: evidence for ecological change in global fisheries? Rev Fish Biol Fish 8:431–444

Chen C-S, Chiu T-S (2003) Variations of life history parameters in two geographical groups of the neon flying squid, *Ommastrephes bartramii*, from the North Pacific. Fish Res 63:349–366

Cherel Y, Klages N (1997) A review of the food of albatrosses. In: Robertson G, Gales R (eds) Albatross biology and conservation. Surrey Beatty & Sons, Chipping Norton pp 113–136

Dawe EG, Colbourne EB, Drinkwater KF (2000) Environmental effects on recruitment of short-finned squid (*Illex illecebrosus*). ICES J Mar Sci 57:1002–1013

Dillane E, Galvin P, Coughlan J, Lipinski M, Cross TF (2005) Genetic variation in the lesser flying squid *Todaropsis eblanae* (Cephalopoda, Ommastephidae) in east Atlantic and Mediterranean waters. Mar Ecol Prog Ser 292:225–232

Dunning MC (1993) Summer populations of *Ommastrephes bartramii* (Lesuer, 1821) and *Todarodes filippovae* Adam, 1975 (Cephalopoda: Ommastrephidae) from the Tasman Sea. In: Okutani T, O'Dor RK, Kubodera T (eds) Recent advances in cephalopod fisheries biology. Tokai University Press, Tokyo pp 97–118

Dunning MC (1998) Zoogeography of Arrow Squids (Cephalopoda: Ommastrephidae) in the Coral and Tasman Seas, Southwest Pacific. Smith Contrib Zool 586:435–454

Dunning MC, Wormuth JH (1998) The ommastrephid squid genus *Todarodes*: a review of systematics, distribution, and biology (Cephalopoda: Teuthoidea). Smith Contrib Zool 586:385–391

Evans K, Hindell MA (2004) The diet of sperm whales (*Physeter macrocephalus*) in southern Australian waters. ICES J Mar Sci 61:1313–1329

Forsythe JW (1993) A working hypothesis of how seasonal temperature change may impact the field growth of young cephalopods. In: Okutani T, O'Dor RK, Kubodera T (eds) Recent advances in cephalopod fisheries biology. Tokai University Press, Tokyo pp. 133–143

Forsythe JW (2004) Accounting for the effect of temperature on squid growth in nature: from hypothesis to practice. Mar Freshw Res 55:331–339

Hatfield EMC (2000) Do some like it hot? Temperature as a possible determinant of variability in the growth of the Patagonian squid (Cephalopoda: Loliginidae). Fish Res 47:27–40

Hatfield EMC, Hanlon RT, Forsythe JW, Grist EPM (2001) Laboratory testing of a growth hypothesis for juvenile squid *Loligo pealeii* (Cephalopoda: Loliginidae). Can J Fish Aquat Sci 58:845–857

Ichii T, Mahapatra K, Sakai M, Inagake D, Okada Y (2004) Differing body size between the autumn and winter-spring cohorts of neon flying squid (*Ommastrephes bartramii*) related to the oceanographic regime in the North Pacific: a hypothesis. Fish Oceanogr 13:295–309

Jackson GD (1994) Application and future potential of statolith increment analysis in squids and sepioids. Can J Fish Aquat Sci 51:2612–2625

Jackson GD (1997) Age, growth and maturation of the deepwater squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) in New Zealand waters. Polar Biol 17:268–274

Jackson CH (2005) Plasticity in the reproductive strategies of the Southern Ocean ommastrephid squid *Todarodes filippovae*—a morphometric, lipid and fatty acid approach. Master's Thesis, University of Tasmania, 94 pp

Jackson GD, Domeier ML (2003) The effects of an extraordinary El niño/La niña event on the size and growth of the squid *Loligo opalescens* off Southern California. Mar Biol 142:925–935

Jackson GD, Moltschaniwskyj NA (2001) Temporal variation in growth rates and reproductive parameters in the small near-shore tropical squid, *Loliolus noctiluca;* is cooler better? Mar Ecol Prog Ser 218:167–177

Jackson GD, O'Dor RK (2001) Time, space and the ecophysiology of squid growth, life in the fast lane. Vie Milieu 51:205–215

Jackson GD, Forsythe JW, Hixon RF, Hanlon RT (1997) Age, growth and maturation of *Lolliguncula brevis* (Cephalopoda:

Loliginidae) in the Northwestern Gulf of Mexico with a comparison of length-frequency vs. statolith age analysis. Can J Fish Aquat Sci 54:2920–2929

Jackson GD, McGrath-Steer BL, Wotherspoon S, Hobday AJ (2003) Variation in age, growth and maturity in the Australian arrow squid *Nototodarus gouldi* over time and space—what is the pattern? Mar Ecol Prog Ser 264:57–71

Jackson GD, Wotherspoon S, McGrath-Steer BL (2005) Temporal population dynamics in arrow squid *Nototodarus gouldi* in southern Australian waters. Mar Biol 146:975–983

Lipinski MR (1979) Universal maturity scale for the commercially-important squids (Cephalopoda: Teuthoidea). The results of maturity classification of the *Illex illecebrosus* (LeSueur, 1821) populations for the years 1973–1977. Int Comm Northwest Atl Fish Res Doc 79/II/38, Dartmouth, Canada

Meyers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. Nature 423:280–283

O'Dor RK, Dawe EG (1998) *Illex illecebrosus*. In: Rodhouse PG, Dawe EG, O'Dor RK (eds) Squid recruitment dynamics. FAO, Rome, pp 77–104

Page B, McKenzie J, Goldsworthy SD (2005) Dietary resource partitioning among sympatric New Zealand and Australian fur seals. Mar Ecol Prog Ser 293:283–302

Pecl GT, Moltschaniwskyj NA, Tracey SR, Jordan AR (2004) Inter-annual plasticity of squid life history and population structure: ecological and management implications. Oecologia 139:515–524

Rodhouse PG (1998) Todarodes filippovae in the Southern Ocean: an appraisal for exploitation and management. In: Okutani T (eds) Large pelagic squids. Japan Marine Fishery Resources Research Center, Tokyo, pp 207–215

Rodhouse PG (2001) Managing and forecasting squid fisheries in variable environments. Fish Res 54:3–8

Rodhouse PG, White MG (1995) Cephalopods occupy the ecological niche of epipelagic fish in the Antarctic Polar Frontal Zone. Biol Bull 189:77–80

Rodhouse PG, Elvidge CD, Trathan PN (2001) Remote sensing of the global light-fishing fleet: an analysis of interactions with oceanography, other fisheries and predators. Adv Mar Biol 39:261–303

Roeleveld MA (1989) The occurrence of two species of squid *Todarodes* in the Benguela system. South Afr J Sci 85:659–663

Vidal EAG, DiMarco FP, Wormuth JH, Lee PG (2002) Influence of temperature and food availability on survival, growth and yolk utilization in hatchling squid. Bull Mar Sci 71:915–931

Villanueva R (1992) Interannual growth differences in the oceanic squid *Todarodes angolensis* Adam in the northern Benguela upwelling system, based on statolith growth increment analysis. J Exp Mar Biol Ecol 159:157–177

Waluda CM, Trathan PN, Rodhouse PG (2004) Synchronicity in southern hemisphere squid stocks and the influence of the Southern Oscillation and Trans Polar Index. Fish Oceanogr 13:255–266

Westfall PH, Tobias RD, Rom D, Wolfinger RD, Hochberg Y (1999) Multiple comparisons and multiple tests using the SAS system. SAS Institute Inc, Cary