CSIRO PUBLISHING

www.publish.csiro.au/journals/mfr *Marine and Freshwater Research*, 2004, **55**, 439–446

Effects of genetic and environmental factors on growth of southern calamary, *Sepioteuthis australis*, from southern Australia and northern New Zealand

Lianos Triantafillos

South Australian Research and Development Institute, Aquatic Sciences, PO Box 120, Henley Beach, SA 5022, Australia. Present address: 39 Danby Street, Torrensville, SA 5031, Australia.
Email: calamary@iprimus.com.au

Abstract. Extreme plasticity in growth is consistently found by ageing studies on squid. This study examined the contribution that genetic and environmental factors had on growth of the southern calamary, *Sepioteuthis australis*, from sites in southern Western Australia, South Australia and New Zealand. A total of 147 adults, comprising three sympatric genetic types (two parental taxa and one hybrid), were aged by counting microincrements in statoliths. Estimates of age ranged from 121 to 268 days and varied with mantle length, sex, genetic type and region. Males grew much faster and attained a larger size than females. Significant differences were also detected between genetic types, with the hybrids always growing faster (at least 60% larger at 150 days old) than the two parental taxa, a phenomenon commonly referred to as hybrid vigour. Spatial differences in growth were also detected, with individuals from Western Australia usually growing faster than those from South Australia and New Zealand. Possible explanations for these growth patterns are discussed.

Extra keywords: growth plasticity, intraspecific, life history, statolith age.

Introduction

For exploited species, knowledge of life history is imperative for the proper assessment and the subsequent development of management strategies that will ensure the sustainable utilisation of that fishery (Beamish and McFarlane 1983). Such knowledge is particularly important for highly exploited but poorly understood species like squid.

A consistent finding of most squid life-history studies is extreme plasticity in growth (Villanueva 1992; Jackson *et al*. 1997; Hatfield 2000). A good example of such plasticity is the length-at-age data of the ommastrephid *Sthenoteuthis pteropus* (Arkhipkin and Mikheev 1992). Despite being caught at the same time and locality, the size of an 8-month-old male ranged from 180 to 420 mm mantle length (ML). Numerous factors have been proposed for this growth variability in squid. One of the most commonly cited factors is water temperature (Forsythe 1993; Jackson *et al*. 1997; Hatfield 2000; Forsythe 2004), but there are numerous others, including food availability (Brodziak and Macy 1996), population density (Dawe 1988), and sexual maturation (Moltschaniwskyj 1995). Up till now, intraspecific genetic variation has received little attention as a source of this variability. This is surprising given the high incidence of cryptic speciation in squid (Brierley *et al*. 1993; Yeatman and Benzie 1994; Triantafillos and Adams 2001) and the growth variability in other molluscan species with heterogeneous genetic forms (see review by Zouros and Pogson 1994).

The southern calamary, *Sepioteuthis australis* Quoy and Gaimard, is a large loliginid, endemic to southern Australian and northern New Zealand waters (Winstanley *et al*. 1983). Throughout these waters, this species is heavily targeted by both commercial and recreational fishers and is an important component of coastal ecosystems, not only as a primary consumer of crustaceans and fishes, but also as a food source for numerous marine species (Gales *et al*. 1993). Previous ageing studies on this species have revealed considerable variability in growth for juveniles, females and males over small spatial and temporal scales (Triantafillos 2002; Pecl 2004).

The southern calamary is ideal for examining the relative contribution genetic and environmental factors have on squid growth for two reasons. First, the number of microincrements found in the statoliths of juvenile southern calamary, of known-age, corresponds closely with their age (Pecl 2004). This suggests that these microincrements are formed on a daily basis, thereby making it possible to accurately age this species. Second, the unique population structure of this species permits the potential separation of genetic and environmental influences on growth. Southern calamary consist of three genetic types that occasionally occur in sympatry. One type (‘peripherals’) is mainly found near the western

 10.1071/MF03157 1323-1650/04/040439

and eastern limits of the geographic range of this species, whereas another ('centrals') is found typically in the intervening region (Fig. 1). Where these two parental types overlap, a third hybrid-type ('hybrids') is found (Triantafillos and Adams 2001). Since large distances separate the regions where all three genetic types occur in sympatry, it is possible to measure growth of these different types of southern calamary at several discrete regions. Moreover, there is evidence that suggests that each genetic type has a unique reproductive strategy. First, individuals from Newcastle in New South Wales spawned less frequently than those from Coles Bay in Tasmania (Pecl 2001), and according to the allozyme study of Triantafillos and Adams (2001), 98% of southern calamary from Newcastle were peripherals, whereas those from Tasmania were almost all centrals. Second, the hybrids are thought to have dysfunctional gonads (Triantafillos and Adams 2001). Given these differences in reproductive strategy, southern calamary are also ideal for assessing the relationship between reproductive investment and growth.

The objectives of this study were twofold: (*i*) to quantify the effects of genetic and environmental factors on the growth of southern calamary; (*ii*) to investigate how varying reproductive strategies affect the growth of this species.

Materials and methods

Sample collection

Southern calamary were collected from four sites across southern Australia by hand jigging and from one site in northern New Zealand by trawling (Fig. 1). In addition, a temporal replicate was collected at Albany 16 months after the original collection date by hand jigging. After a small piece of tentacular tissue was removed for electrophoresis and placed in liquid nitrogen, each individual was examined for three parameters: ML (measured to the nearest millimetre), sex and maturity status. Maturity status was assigned according to the maturation scale described by Lipinski (1979), with stages V and VI considered

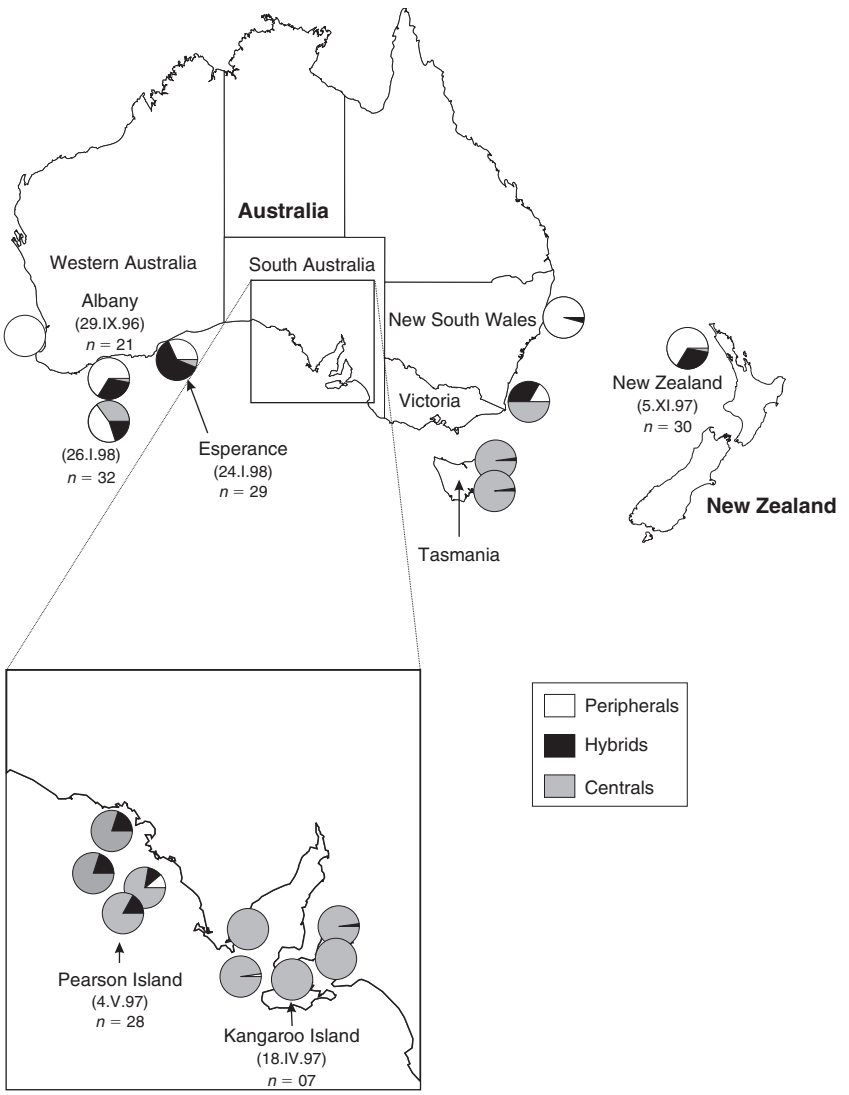

Fig. 1. Map of Australia and New Zealand showing distributions of the three different genetic types of *Sepioteuthis australis* (after Triantafillos and Adams 2001), as well as sampling locations, dates of sampling and the number of individuals aged in this study.

sexually mature. Once these three parameters were determined, the calamary were frozen at −30°C in individually labelled plastic bags, whereas tissue samples were stored at −80°C, pending genetic analysis. Allozyme electrophoresis sorted all individuals into one of the three genetic types (peripherals, centrals and hybrids). Details of the methods used and the results obtained for this allozyme analysis are presented in Triantafillos and Adams (2001). Mean size at first maturity (L_{m50}) for each genetic type was determined from the relationship: $P_L = 1/1 + e^{-(a+bL)}$ where P_L = proportion mature at length L, a and b are constants and $L_{m50} = -a/b$ = length at which 50% of animals are mature. This relationship was fitted with a logistic function by non-linear least-squares regression (Marquardt method) using the SPSS statistical software package (SPSS Inc, Chicago, IL, USA).

Statolith preparation and ageing

Terminology for analysis of statolith microstructure follows Jackson (1994). Statoliths were extracted within 1 week of capture and stored dry in plastic 96-well immunoassay microplates, awaiting preparation. The method used to prepare the statoliths was modified from that of Lipinski and Durholtz (1994). After cleaning in alcohol, each statolith was embedded in thermoplastic cement (Crystal Bond®, Aremco Products, Valley Cottage, NY, USA) with the ventral side projecting over the edge of a glass slide. The statolith was then ground, parallel to the plane that passed through the nucleus and dorsal dome (in a transverse plane), until the centre of the primordium was reached. The extent and intensity of grinding was monitored continuously under a binocular light microscope (×40 magnification). This grinding removed the wing and rostrum of the statoliths. The statolith was then polished with 1200-grit carborundum wet paper and two grades of imperial-lapping film (9 μ and 3 μ). The polished surface was then fixed onto a glass slide with Crystal Bond® and ground down to obtain a section thin enough for examination. A drop of immersion oil was smeared over the surface to clear scratch marks. Sections were viewed under a Zeiss compound microscope at ×400 magnification (Zeiss, Oberkochen, Germany). Microincrements were counted from the nucleus (natal ring) to the margin of the dorsal dome using a hand counter. A minimum of three counts was made for each statolith. Counts were rarely accomplished in a straight line and it was usually necessary to transverse the statolith in either a dorsal or ventral direction to complete a count because the microincrements in some areas were obscure. When the three counts differed by less than 5%, their mean was used as an estimate of the number of microincrements. If the difference was greater, further counts were made until a satisfactory estimate of the number of microincrements was obtained, or the statolith was rejected. Microincrements in the outermost portion of the dorsal dome could not be counted in 9% of the prepared statoliths. Consequently, the number in this margin was estimated by extrapolation, using the technique of Jackson and Choat (1992). In all cases, the extrapolated counts constituted less than 3% of the total count.

Growth rates

Instantaneous growth rate (G) was calculated for each individual using the equation of Forsythe and van Heukelem (1987):

$$G = (\ln W_2 - \ln W_1)/(t_2 - t_1) \times 100$$

where W_2 is ML at capture at time t_2, and W_1 is the ML at hatching at time t_1. Individual growth calculations assume a ML of 4.8 mm, based on values measured from 60 hatchlings (Triantafillos 2002). The slopes of the length-at-age regressions were used to derive estimates of 'average growth rates'. Several functions were fitted to the length and age data, including power, exponential and linear. The von Bertalanffy and Gompertz models were not used because there was no evidence of asymptotic growth. The curve of best fit was determined by the highest r^2 and the lowest coefficients of variance of estimated parameters, as well as an examination of residuals for any systematic pattern. A Student's t-test was used to test the significance of the differences between pairs of curves while an analysis of covariance was used when more than two curves were compared (Zar 1984).

Results

Analysis of estimates of age

The statoliths of 147 southern calamary were examined for growth microincrements. Estimates of age ranged from 121 to 268 days, depending on ML, sex, region and genetic type (Fig. 2). The curve of best fit for the length-at-age relationships varied among sex, region and genetic types. Of the curves tested, and over the size range examined, the linear curve gave the best fit for nearly all (81%) datasets and did not differ significantly from the other curves in the remainder. For this reason, growth was modelled using linear curves.

Comparisons between genetic types, regions and sexes

Since the slopes and intercepts of the length-at-age data for the two Albany samples and the other Western Australian site (Esperance) were alike, these data were subsequently pooled

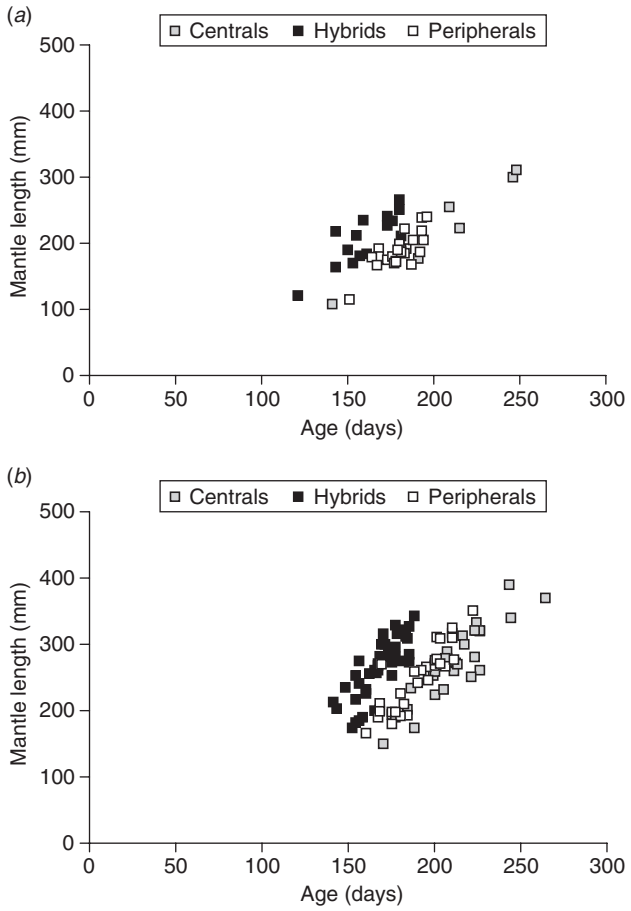

Fig. 2. Age–length relationships for (*a*) females and (*b*) males of the three genetic types of *Sepioteuthis australis*.

Table 1. Linear relationships for the length-at-age data of three genetic types of *Sepioteuthis australis*, for both sexes, from three regions
The growth rate (bold) in this table is an average rate, derived from the slope of the respective length-at-age relationships

Type of calamary	Regions		
	Western Australia	South Australia	New Zealand
Hybrid males	$y = \mathbf{2.85}x - 203.5$ (0.61), $n = 33$	$y = \mathbf{2.70}x - 184.7$ (0.37), $n = 4$	$y = \mathbf{2.59}x - 195$ (0.99), $n = 5$
Peripheral males	$y = \mathbf{2.72}x - 268.5$ (0.75), $n = 26$		$y = \mathbf{2.17}x - 178$ (0.81), $n = 5$
Central males	$y = \mathbf{2.70}x - 276.6$ (0.94), $n = 5$	$y = \mathbf{2.64}x - 271.0$ (0.88), $n = 22$	
Hybrid females	$y = \mathbf{1.90}x - 80.4$ (0.71), $n = 6$	$y = \mathbf{2.14}x - 138.2$ (0.99), $n = 3$	$y = \mathbf{1.40}x - 34.0$ (0.64), $n = 6$
Peripheral females	$y = \mathbf{1.87}x - 139.1$ (0.73), $n = 12$		$y = \mathbf{1.19}x - 31.4$ (0.73), $n = 13$
Central females		$y = \mathbf{1.90}x - 166.8$ (0.95), $n = 6$	

and treated as a single region. For the same reason, the length-at-age data for the two sites in South Australia (Pearson Island and Kangaroo Island) were also pooled and treated as a single region. Slopes, intercepts and correlation coefficients of the linear regressions for length-at-age data in the three regions (Western Australia, South Australia and New Zealand) for the different types and sexes are shown in Table 1.

The linear relationship between length and age was developed independently for each genetic type in each region, for both sexes. Within each region, there were significant differences among these relationships. For instance, in the Western Australia samples there was a significant difference between the intercepts of the length-at-age relationship for males of the three genetic types ($F = 48.9$; d.f. = 2,69; $P < 0.001$). A comparison of the three curves indicated that at any given age, hybrids were significantly larger than either the peripherals or the centrals. There was, however, no difference in the slopes ($F = 0.6$; d.f. = 2,58; $P = 0.55$). As there were no central females from Western Australia, the comparison of the length-at-age relationship could only be done for hybrid and peripheral females. This comparison also revealed a significant difference between intercepts ($F = 34.4$; d.f. = 1,17; $P < 0.001$), but not among the slopes ($F = 0.07$; d.f. = 1,14; $P = 0.79$). Again, the hybrids were found to be larger at equivalent ages than the peripherals. In New Zealand, independent analyses were done for both sexes comparing only between hybrids and peripherals. A difference between the intercepts of the hybrid and peripheral males was the only significant difference found ($F = 0.36$; d.f. = 1,9; $P = 0.02$), and indicated that the hybrids were larger at a given age than the centrals. Due to a lack of peripherals in South Australia, the comparison of the length-at-age relationship for this region could only be done for hybrids and centrals. A significant difference was found between intercepts, for both males ($F = 52.9$; d.f. = 1,25; $P < 0.001$) and females ($F = 5.9$; d.f. = 1,8; $P < 0.001$). There was, however, no difference in the slopes for either of the sexes. Spatial differences in the length-at-age relationship were also detected for each genetic type. Hybrid males from Western Australia, South Australia and New Zealand had similar slopes ($F = 0.013$; d.f. = 2,37; $P = 0.99$), but significantly different intercepts ($F = 41.8$; d.f. = 2,41; $P < 0.001$). Significantly different intercepts were also found among peripheral males ($F = 20.4$; d.f. = 1,50; $P < 0.001$) and hybrid females ($F = 12.5$; d.f. = 1,11; $P < 0.01$) from Western Australia and New Zealand. In all the spatial comparisons mentioned above, individuals from Western Australia were larger at an equivalent age than those from South Australia or New Zealand. No spatial differences in slopes or intercepts were found in central males or peripheral females. Differences in the length-at-age relationship were also detected among sexes, with males and females having significantly different intercepts ($F = 55.5$; d.f. = 1,146; $P < 0.001$), but similar slopes ($F = 0.002$; d.f. = 1,143; $P = 0.97$). A comparison of curves revealed that females were significantly smaller at equivalent ages than males.

Table 2. Instantaneous growth rates ± standard error (% mm day^{-1}) for the three genetic types of *Sepioteuthis australis* from Western Australia, South Australia and New Zealand

Type of calamary	Regions		
	Western Australia	South Australia	New Zealand
Hybrid males	1.86 ± 0.14	1.76 ± 0.14	1.21 ± 0.02
Peripheral males	1.32 ± 0.12	–	1.15 ± 0.08
Central males	1.31 ± 0.13	1.30 ± 0.17	–
Hybrid females	1.40 ± 0.14	1.24 ± 0.21	1.19 ± 0.08
Peripheral females	1.07 ± 0.14	–	1.03 ± 0.05
Central females	–	1.07 ± 0.20	–

Growth rates

Despite being derived by different means, rates of instantaneous growth (Table 1) and average growth (Table 2) exhibited three notable patterns: (*i*) males grew faster than females, a pattern consistent among types and regions; (*ii*) in each region, hybrids always had the highest growth rate, whereas the centrals typically had the slowestgrowth rate; and (*iii*) all three types grew faster in Western Australia than they did in South Australia or New Zealand. Some of the differences in length-at-age between types were pronounced. For example, based on the equations in Table 1, a 150-day-old male hybrid from Western Australia was 60.6% and 74.5%

Table 3. Predicted mantle length (mm) at 150 days for three genetic types of *Sepioteuthis australis* from Western Australia, South Australia and New Zealand
These estimates are based on the equations in Table 1

Type of calamary	Regions		
	Western Australia	South Australia	New Zealand
Hybrid males	224.0	220.3	193.5
Peripheral males	139.5	–	147.5
Central males	128.4	125.0	–
Hybrid females	204.6	182.8	176.0
Peripheral females	132.8	–	147.1
Central females	–	118.2	–

Table 4. Size- and age-at-maturity of three genetic types of *Sepioteuthis australis* for both sexes

Type of calamary	*n*	Size (mm)	Age (days)
Hybrid males	42	319.4	159.3
Peripheral males	31	213.1	156.8
Central males	28	254.5	163.9
Hybrid females	15	237.9	159.7
Peripheral females	25	161.1	168.6
Central females	6	175.7	190.7

larger than a similar-aged peripheral and central male, respectively, from the same region (Table 3). The difference in size-at-age between hybrid and central males from South Australia at age 150 days was even greater (92.1%). Comparable differences in length-at-age between types were found in females. For instance, a 150-day-old female hybrid from Western Australia was 54.1% larger in ML than a peripheral female from this region. This difference was similar in magnitude to that found between female hybrids and centrals from South Australia. Differences in size-at-age between sexes of the same type were less pronounced, ranging from 1 to 20%, but typically between 5 and 10%. Despite the disparity in size between males and females, the lifespan of both sexes was similar among their respective types (Fig. 2).

Reproductive maturity

The youngest sexually mature male and female found in this study were both 143 days. Thereafter, the proportion of sexually mature calamary increased rapidly with age. Mean age at first maturity for males was consistent among types, ranging from 156.8 to 163.9 days. Similar values were found for female hybrids and peripherals, but compared to the other types of calamary, the mean age at first maturity for central females was much higher at 190.7 days. Although mean length at maturity was much more variable than mean age at maturity (Table 4), it exhibited two notable patterns. Mean length at maturity for males were much larger than females and hybrids were always significantly larger at the onset of sexual maturity than either the peripherals or centrals.

Discussion

Differences between genetic types, regions and sexes

Significant differences in southern calamary growth were observed between genetic types, sexes and regions. Of these factors, the former had by far the largest influence on length-at-age. Since both the direction and magnitude of the differences between types were consistent, with regard to both sex and region, it suggests that the plasticity seen in southern calamary growth was, for the most part, genetically derived and not, as commonly cited, attributable to environmental factors. Because there is thought to be a link between genetic type and reproductive strategy for southern calamary, such growth patterns may be a consequence of varying reproductive investment. Similar conclusions have been reached in other studies on molluscs (Arnold *et al*. 1991). If southern calamary growth is a function of reproductive strategy and the amount of energy available to any organism is limited due to trade-off that exists between reproduction and continued growth (Stearns 1992), then expectations are that the genetic type that invests the least amount of energy into reproduction should be the fastest growing. The preliminary data of this study support such a hypothesis. Many hybrids, particularly those from Australia, were immature, even though many were larger than 300-mm ML. At this size, all but one of the centrals and peripherals were sexually mature. Although an unequivocal comparison of gonads could not be undertaken because many were insufficiently preserved, a macroscopic examination revealed that the gonads of the hybrids were clearly much smaller and weighed less than the other two genetic types. This supports Triantafillos and Adams (2001), who suggested that the gonads of the hybrids were dysfunctional. While a few hybrids seemingly had fully formed reproductive organs, it did not mean they were able to produce reproductively competent offspring. Galbreath and Thorgaad (1995) found that seemingly mature hybrid salmon produced offspring that never progressed past 30 days. Similarly, male triploid plaice crossed with flounder produce hybrids that seem sexually mature, but they only produce sterile gametes (Lincoln 1981).

In this study, multiple-spawning central southern calamary were smaller at a given age than the peripheral southern calamary, which spawn only once or twice. One possibility for these size differences is that multiple-spawning cephalopods require more energy for reproduction, over a lifetime, than do those that spawn less frequently. These differences complement Rodhouse *et al*. (1988), who found that the reproductive investment of the semelparous squid *Alloteuthis subulata* was substantially less, on a proportional basis, than the lifetime investment of iteroparous molluscs.

Growth has been found to vary in other marine species with heterogeneous intraspecific genetic forms, including bivalves such as mussels (Gardner and Skibinski 1991) and scallops (Cruz *et al*. 1998), as well as carp (Bakos and Gorda 1995). Many of these studies ascertained that, like southern

calamary, the hybrids were generally faster growing than the putative parental forms, a phenomenon referred to as hybrid vigour or heterosis. While hybrid vigour is not uncommon, especially among molluscs, differences greater than 90%, as seen in this study, are rare. In most cases of hybrid vigour, hybrids usually only grow between 5 and 10% faster than parents (see reference cited above). Life-history traits, such as fast growth and possible sterility, make the hybrids ideal for aquaculture.

Significant differences were also found between growth rates of both sexes, with males growing faster and attaining a larger size than females at equivalent ages. This pattern was consistent among regions and genetic types. Differences between sexes were less pronounced than those between genetic types, ranging from 1 to 20.5%, but typically between 5 and 10%. A reproductive study of southern calamary in Gulf St Vincent, South Australia found that up to 23.7% of body-weight (gonad-free) of central females was invested into the formation of gonads compared with less than 5% for central males (Triantafillos 2002). Thus, it is speculated that females grow slower than males because females invest significantly more energy into reproduction than do the males. This premise is consistent with the findings of Forsythe and van Heukelem (1987), who suggested that male maturity in several species of cephalopods (e.g. *Octopus dofleini*, *Sepia pharaonis* and *Loligo vulgaris*) was achieved at little cost to somatic growth, and that, in most cases, males continue to grow after reaching maturity.

Compared to genetic types and sexual dimorphism, variability in growth attributed to spatial differences, although sometimes significant, was small. Indeed, the maximum spatial difference found for any type, male or female, was 16.3%. In this study, the fastest growing calamary came from Western Australia, while the slowest growing animals were from New Zealand. Spatial differences such as these may be related to sea-surface temperatures as the average yearly sea-surface temperature of coastal waters near Esperance and Albany are warmer than the waters in South Australia and New Zealand (see www.aodc.gov.au). The relationship between water temperature and growth is well documented for many marine species, including squid. Both Triantafillos (2002) and Pecl (2004) found an apparent effect of seasonal environmental variation on the growth rate of southern calamary from South Australian and Tasmanian waters respectively. Individuals that developed during periods of warming water temperatures grew faster than those that developed through periods of cool water temperatures. Despite this, differences in water temperature cannot wholly explain the variation in growth of southern calamary because sea temperatures in South Australia are, on average, a few degrees warmer than in Tasmania, yet southern calamary from this region grew more slowly than those in Tasmania (Pecl 2004).

Besides the disparity in growth between regions, plasticity in growth among individuals was widespread within each region, another well-documented phenomenon for squid (Villanueva 1992). The fact that this plasticity was found in all three genetic types examined is further evidence that growth variability is a consistent feature of squid growth. Plasticity levels found in this study were, however, somewhat less than those found for most other squid species. In this study, differences in length for male southern calamary from the same region of the same age and type were typically around 5–15%, with a maximum of 25%. This was an order of magnitude lower than that found in *Sthenoteuthis pteropus* (Arkhipkin and Mikheev 1992) and a quarter of that found in southern calamary from Tasmania (Pecl 2004).

Based on the results of this study, and the high incidence of cryptic speciation in squid, it is reasonable to suggest that genetic variability has contributed to some of the growth plasticity found in ageing studies on squid. Anecdotal evidence supports this suggestion. To date, the only other study to correct for genetic type before ageing aside from this one was Jackson and Yeatman (1995). Coincidentally, the amount of growth variability found in that study for *Photololigo* was similar to that seen in this study. There is some circumstantial evidence that genetic variability can also provide a powerful explanation for the large differences in life-history characteristics observed by Jackson and Moltschaniwskyj (2002) in *Sepioteuthis lessoniana* from Australia and Thailand. First, allozyme data indicate the presence of three species of *S. lessoniana* in Japanese waters (Izuka *et al*. 1996) and more than one in Australian waters (L. Triantafillos, unpublished data). Second, differences in age, growth and maturity for *S. lessoniana* mirror those found among the different types of *S. australis*, a closely related species.

Growth rates

The largest southern calamary sampled in this study was a male of 390-mm ML and only 264 days of age. Had this individual continued growing at a conservative rate of 1% ML day^{-1}, which is well below the mean growth rate of adults (Triantafillos 2002), it would easily reach the maximum-recorded size for this species of 550-mm ML (Wadley and Dunning 1998) within another 30–40 days. Given this, the lifespan of southern calamary is here proposed to be approximately 1 year, which is within the estimated age-range for southern calamary from Tasmania (Pecl 2004) and the majority of other large loliginids (reviewed by Jackson 1994, 2004). Although the central types had the slowest growth of the three types, they attained the largest size, primarily because they lived the longest. In marked contrast, the hybrids, which were the fastest growing calamary, had the shortest lifespan, existing for an average of 31 and 43 days less than the peripherals and centrals, respectively. It is not known why the hybrids have such a short lifespan, but one possibility for the conspicuous lack of hybrids greater than 190 days of age is that they have excess energy (due to minimal reproductive investment) and owing to genetic limits

cannot increase their length. The stored energy may lead to physiological and histological changes in older hybrids that cause death (Craig *et al*. 1995).

The results of this study clearly indicate that each genetic type of southern calamary needs to be treated as a separate stock. Since there are few regions in the distribution of this species where only one type is found, it greatly complicates the construction of stock assessment models. It also complicates the development of sustainable management strategies because where stocks differed in their relative strengths in space and time, none could be harvested at an optimal level, since either the weaker stocks would be over-exploited or the stronger ones would remain under-exploited (Ryman and Utter 1987). The present study also cast doubts over growth estimates obtained in other ageing studies on squid for which there is taxonomic uncertainty. For this reason, before undertaking any assessment of age the first step in any study on the biology of squid should be a molecular assessment of the target species. Furthermore, the molecular assessment should be examined on a regular basis because it can change over a relatively short period of time (Triantafillos and Adams 2001).

Acknowledgments

This project was partially funded by the South Australian Marine Scalefish Fishery, and was conducted as part of a PhD of the Northern Territory University. I am extremely grateful to Mark Adams of the Evolutionary Biology Unit (South Australian Museum) for statistical advice and for help during the development of allozyme markers. I am also grateful to Drs Tony Fowler, Tim Ward, Scoresby Shepherd and three anonymous referees for comments on the manuscript. Gretta Pecl kindly provided manuscripts before they had been published.

References

Arkhipkin, A. I., and Mikheev, A. (1992). Age and growth of the squid *Sthenoteuthis pteropus* (Oegopsida: Ommastrephidae) from Central-East Atlantic. *Journal of Experimental Marine Biology and Ecology* **163**, 261–276. doi:10.1016/0022-0981(92)90054-E

Arnold, W. S., Marelli, D. C., Bert, T. M., Jones, D. S., and Quitmyer, I. R. (1991). Habitat-specific growth of the hard clam *Mercenaria mercenaria* (L.) from the Indian River, Florida. *Journal of Experimental Marine Biology and Ecology* **147**, 245–265. doi:10.1016/0022-0981(91)90185-Y

Bakos, J., and Gorda, S. (1995). Genetic improvement of common carp strains using intraspecific hybridisation. *Aquaculture (Amsterdam, Netherlands)* **129**, 183–186. doi:10.1016/0044-8486(94)00245-J

Beamish, R. J., and McFarlane, G. A. (1983). The forgotten requirement for age validation in fisheries biology. *Transactions of the American Fisheries Society* **12**, 735–743.

Brierley, A. S., Rodhouse, P. G., Thorpe, J. P., and Clarke, M. R. (1993). Genetic evidence of population heterogeneity and cryptic speciation in the ommastrephid squid *Martiala hyadesi* from the Patagonian Shelf and Antarctic Polar Frontal Zone. *Marine Biology* **116**, 593–602.

Brodziak, J. K. T., and Macy, W. K. III (1996). Growth of long-finned squid, *Loligo pealeii*, in the northwest Atlantic. *Fishery Bulletin* **94**, 212–236.

Craig, J. F., Babaluk, S. G., Stevenson, S. G., and Williams, P. C. (1995). Variation in growth and reproduction of walleye (*Stizostedion vitruem*) in three Manitoba lakes. *Canadian Journal of Zoology* **73**, 367–372.

Cruz, P., Ramirez, J. L., Garcia, G. A., and Ibarra, A. M. (1998). Genetic differences between two populations of catarina scallop (*Argopecten ventricosus*) for adaptations for growth and survival in a stressful environment. *Aquaculture (Amsterdam, Netherlands)* **166**, 321–335. doi:10.1016/S0044-8486(98)00285-3

Dawe, E. G. (1988). Length–weight relationships for short-finned squid in Newfoundland and the effect of diet on condition and growth. *Transactions of the American Fisheries Society* **117**, 591–599.

Forsythe, J. W. (1993). A working hypothesis of how seasonal temperature change may impact the field growth of young cephalopods. In 'Recent Advances in Cephalopod Fisheries Biology'. (Eds T. Okutani, R. K. O'Dor and T. Kubodera.) pp. 133–143. (Tokai University Press: Tokyo, Japan.)

Forsythe, J. W. (2004). Accounting for the effect of temperature on squid growth in nature: from hypothesis to practice. *Marine and Freshwater Research* **55**, 331–339.

Forsythe, J. W., and van Heukelem, W. F. (1987). Growth. In 'Cephalopod Life Cycles. Vol. II'. (Ed. P. R. Boyle.) pp. 135–156. (Academic Press: London, UK.)

Galbreath, P. F., and Thorgaad, G. H. (1995). Sexual maturation and fertility of diploid and triploid Atlantic salmon × brown trout hybrids. *Aquaculture (Amsterdam, Netherlands)* **137**, 299–311. doi:10.1016/0044-8486(95)01115-3

Gales, R., Pemberton, D., Lu, C. C., and Clarke, M. R. (1993). Cephalopod diet of the Australian fur seal: variation due to location, season and sample type. *Australian Journal of Marine and Freshwater Research* **44**, 657–671.

Gardner, J. P. A., and Skibinski, D. F. (1991). Biological and physical factors influencing genotype-dependent mortality in hybrid mussel populations. *Marine Ecology Progress Series* **71**, 235–243.

Hatfield, E. M. C. (2000). Do some like it hot? Temperature as a possible determinant of variability in the growth of the Patagonian squid, *Loligo gahi* (Cephalopoda: Loliginidae). *Fisheries Research* **47**, 27–40. doi:10.1016/S0165-7836(99)00127-7

Izuka, T., Segawa, S., and Okutani, T. (1996). Biochemical study of the population heterogeneity and distribution of the oval squid *Sepioteuthis lessoniana* complex in southwestern Japan. *American Malacological Bulletin* **12**, 129–135.

Jackson, G. D. (1994). Application and future potential of statolith increment analysis in squids and sepioids. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 2612–2625.

Jackson, G. D. (2004). Advances in defining the life histories of myopsid squid. *Marine and Freshwater Research* **55**, 357–365.

Jackson, G. D., and Choat, J. H. (1992). Growth in tropical cephalopods: an analysis based on statolith microstructure. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 218–228.

Jackson, G. D., and Moltschaniwskyj, N. A. (2002). Spatial and temporal variation in growth rates and maturity in the Indo-Pacific squid *Sepioteuthis lessoniana* (Cephalopoda: Loliginidae). *Marine Biology* **140**, 747–754. doi:10.1007/S00227-001-0746-9

Jackson, G. D., and Yeatman, J. (1995). Variation in size and age at maturity in *Photololigo* (Mollusca: Cephalopoda) from the northwest shelf of Australia. *Fishery Bulletin* **94**, 59–65.

Jackson, G. D., Forsythe, J. W., Hixon, R. F., and Hanlon, R. T. (1997). Age, growth, and maturation of *Lolliguncula brevis* (Cephalopoda: Loliginidae) in the northwestern Gulf of Mexico with a comparison of length–frequency versus statolith age analysis.

Canadian Journal of Fisheries and Aquatic Sciences **54**, 2907–2919. doi:10.1139/CJFAS-54-12-2907

Lincoln, R. F. (1981). Sexual maturation in female triploid plaice, *Pleuronectes platessa*, and plaice × flounder, *Platichthys flesus*, hybrids. *Journal of Fish Biology* **19**, 499–507.

Lipinski, M. R. (1979). 'Universal Maturity Scale for the Commercially Important Squids (Cephalopoda: Teuthoidae). The Results of Maturity Classification of the *Illex illecebrosus* (LeSeur 1821) Populations for the Years 1973–77.' Research Document 79/II/38. (International Commission for Northwest Atlantic Fisheries: Novia Scotia, Canada.)

Lipinski, M. R., and Durholtz, M. D. (1994). Problems associated with ageing squid from their statoliths: towards a more structured approach. *Antarctic Science* **6**, 215–222.

Moltschaniwskyj, N. A. (1995). Multiple spawning in the tropical squid *Photololigo* sp.: what is the cost in somatic growth? *Marine Biology* **124**, 127–135.

Pecl, G. (2001). Flexible reproductive strategies in tropical and temperate *Sepioteuthis* squids. *Marine Biology* **138**, 93–101. doi:10.1007/S002270000452

Pecl, G. T. (2004). The *in situ* relationships between season of hatching, growth and condition in the southern calamary, *Sepioteuthis australis. Marine and Freshwater Research* **55**, 429–438.

Ryman, N., and Utter, F. (1987). 'Population Genetics and Fishery Management.' (University of Washington Press: Washington, DC, USA.)

Rodhouse, P. G., Swinfen, R. C., and Murray, A. W. A. (1988). Life cycle, demography and reproductive investment in the myopsid squid *Alloteuthis subulata. Marine Ecology Progress Series* **45**, 245–253.

Stearns, S. C. (1992). 'The Evolution of Life Histories.' (Oxford University Press: New York, USA.)

Triantafillos, L. (2002). 'Population Biology of Southern Calamary, *Sepioteuthis australis*, in Gulf St Vincent, South Australia.' PhD Thesis. (Northern Territory University: Darwin, Australia.)

Triantafillos, L., and Adams, M. (2001). Allozyme analysis reveals a complex population structure in the southern calamary *Sepioteuthis australis* from Australia and New Zealand. *Marine Ecology Progress Series* **212**, 193–209.

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. *Journal of Experimental Marine Biology and Ecology* **159**, 157–177. doi:10.1016/0022-0981(92)90034-8

Wadley, V. A., and Dunning, M. C. (1998). 'Cephalopods of Commercial Importance in Australian Fisheries.' (CSIRO Marine Research: Hobart, Australia.)

Winstanley, R. H., Potter, M. A., and Caton, A. E. (1983). Australian cephalopod resources. *Memoirs of the National Museum of Victoria* **44**, 243–253.

Yeatman, J., and Benzie, J. A. H. (1994). Genetic structure and distribution of *Photololigo* spp. in Australia. *Marine Biology* **118**, 79–87.

Zar, J. H. (1984). 'Biostatistical Analysis.' (Prentice-Hall: Englewood Cliffs, NJ, USA.)

Zouros, E., and Pogson, G. H. (1994). Heterozygosity, heterosis and adaptation. In 'Genetics and Evolution of Aquatic Organisms'. (Ed. A. R. Beaumont.) pp. 135–146. (Chapman and Hall: London, UK.)

Manuscript received 8 December 2003; revised 26 February 2004; and accepted 9 March 2004.