

**Abstract.**—This study examined the relation between statolith and somatic growth in the tropical squid *Sepioteuthis lessoniana*. Five separate linear dimensions were measured on the statoliths of 103 individuals (17–245 mm mantle length). In addition the statoliths of 80 adults (82–245 mm mantle length) were weighed. Statolith increment analysis provided age estimates for 78 individuals. Statolith total length was correlated with age for squid less than ~60 days of age, although neither statolith total length nor weight was a useful predictor of age in older squid. Combining the five statolith dimensions to produce a description of statolith shape provided only slightly better estimates of age than statolith total length or weight alone. Statolith shape changed during ontogeny, developing from relatively elongate juvenile statoliths into the adult form with more robust dorsal and lateral domes. This development was reflected in wider spacing and superior optical definition of daily growth increments in the dorsal and lateral domes of adult statoliths, in relation to the slower growing rostrum. Growth of *S. lessoniana* statoliths does not appear to be strongly linked to mantle growth; both statolith total length and weight increase more slowly than mantle length.

## Ontogenetic changes in size and shape of statoliths: implications for age and growth of the short-lived tropical squid *Sepioteuthis lessoniana* (Cephalopoda: Loliginidae)

Ross Thomas

Natalie A. Moltshaniwskyj

School of Marine Biology and Aquaculture  
James Cook University

Townsville, Queensland 4811, Australia.

Present address (for N. A. Moltshaniwskyj, contact author): School of Aquaculture  
University of Tasmania  
PO Box 1214  
Launceston, Tasmania 7250, Australia.

E-mail (for N. A. Moltshaniwskyj, contact author): natalie.moltshaniwskyj@utas.edu.au

Knowledge of the age structure and growth rates in naturally occurring populations is fundamental to estimating demographic parameters and evaluating ecological processes. Periodic growth increments in squid statoliths are a reliable and accurate tool for determining the age structure of squid populations (Villanueva, 1992; Arkhipkin, 1993; Bigelow, 1994; Jackson, 1994). Growth-rate calculations based on statolith age estimates indicate that tropical squid are short-lived and grow continuously throughout their lifespan (Jackson, 1990; Jackson and Choat, 1992). Growth rates of tropical squid can be strongly influenced by changes in their environment, including temperature fluctuations (Forsythe and Hanlon, 1989), and availability of food (Forsythe, 1993). Consequently, growth rates, final size, and response to changing conditions of tropical squid may vary greatly within or between species (Jackson, 1990; Jackson and Choat, 1992). Apart from obtaining size-at-age information from statoliths, there is also the potential to obtain ecological information on past growth histories of some squid species (Jack-

son, 1994). Any attempts made at constructing growth histories of squid based on statolith microstructure will benefit greatly from a thorough understanding of growth and development of the statolith and how this relates to growth of somatic tissue.

Daily growth increments in fish otoliths, which are analogous to those in squid statoliths (Radtke, 1983), provide valuable data on the age structure and growth rates of exploited fish species (Campana and Neilson, 1985; Jones, 1986; Stevenson and Campana, 1992). Recent studies of fish somatic-otolith growth relationships may contribute to investigations of somatic-otolith growth relationships in squid. Evidence exists supporting the direct relationship between age and otolith weight for several fish species (Boehlert, 1985; Fletcher, 1991), although further validation is required before otolith weight can be used reliably to estimate age. Several authors have also demonstrated that slower-growing fish have larger otoliths than similar sized, faster-growing individuals (Mosegaard et al., 1988; Secor and Dean, 1989; Wright et al., 1990;

Mugiya and Tanaka, 1992), indicating a possible disassociation between otolith and somatic growth. Similarly, disassociation between statolith and somatic tissue growth has been demonstrated in the tropical loliginid squid *Loligo chinensis* (Jackson, 1995), and also in two ommastrephid squids, *Todarodes angolensis* and *Todaropsis eblanae* (Lipinski et al., 1993).

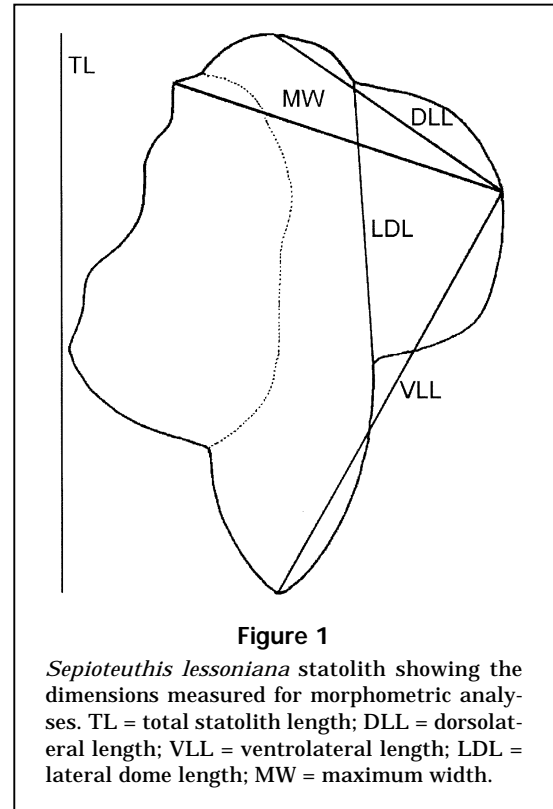
The periodic growth increments in squid statoliths are bipartite structures consisting of a discontinuous zone and an incremental zone comprising aragonite ( $\text{CaCO}_3$ ) crystals (Lipinski, 1986). Specific morphological differences in the aragonite crystal structure have been illustrated between statolith regions within several squid species (Lipinski, 1993). Crystals of the lateral dome region often display greater variation in shape, size, and orientation than the more homogenous wing crystals (Lipinski, 1993). These variations in crystal structure suggest that accretion is not uniform and that different regions of the statolith may grow at different rates.

The present study provides an assessment of the growth and shape of *Sepioteuthis lessoniana* statoliths based on the linear measurement of statolith dimensions. The potential for using statolith shape descriptions as a proxy for age estimations and the relation between statolith and somatic tissue growth in these squid are examined. Overall descriptions of individual statolith shape covered a broad length and weight range of squid, providing a basis for comparison with age estimates determined by using traditional analysis techniques. With the increased use of statoliths in squid age and growth studies, it is important to understand how statoliths grow and how this growth relates to growth of somatic tissue.

## Materials and methods

### Study species and collection methods

A total of 103 *Sepioteuthis lessoniana* individuals were captured from waters around the Townsville region of north Queensland, Australia, between January and August 1995. Twenty-three juvenile squid (16–43 mm mantle length [ML]) were captured by using purse seines and dip nets. Juveniles often shelter in surface waters among floating debris or artificially constructed shade devices and are easily netted. Eighty adult squid (82–245 mm ML) were captured from coastal waters at night with squid jigs and by means of light attraction. Individuals were separated into two age groups for these descriptions: juvenile ( $\leq 60$  days) and adult ( $> 60$  days). This separation was based on the techniques used to capture



**Figure 1**

*Sepioteuthis lessoniana* statolith showing the dimensions measured for morphometric analyses. TL = total statolith length; DLL = dorsolateral length; VLL = ventrolateral length; LDL = lateral dome length; MW = maximum width.

the individuals, which may be related to differences in life style and ecology.

### Size measurements

Mantle length was measured from all *Sepioteuthis lessoniana* specimens upon capture. Wet weight was not obtained for the majority of individuals because of the inability to weigh animals accurately on a boat. Statoliths were removed and stored in 70% alcohol, and adult statoliths were later weighed to the nearest 0.01 mg. Weights of juvenile statoliths were not recorded because they were too small to obtain accurate measurements. Five dimensions were measured from each statolith following the descriptions of statolith shape by Clarke (1978): total length, dorsolateral length, ventrolateral length, lateral dome length, and maximum width (Fig. 1). Dimensions were measured from whole statoliths viewed with the anterior (concave) side positioned upward by using an Ikegami-290 high-resolution black and white video camera mounted on a compound microscope. Squid ages were estimated by using statolith increment analysis on ground and polished statoliths (Jackson, 1990). All increment counts were made in the dorsal-dome region of statoliths because increment definition was consistently clearest in this area. Age estimates for 62

adult and 16 juvenile squid were calculated from a mean of three separate counts made by one reader.

### Statistical analyses

Paired-sample *t*-tests indicated no significant difference between left and right statolith total length measures ( $t=0.67$ ,  $df=101$ ,  $P=0.50$ ,  $n=102$ ), or adult statolith weight measures ( $t=0.47$ ,  $df=79$ ,  $P=0.64$ ,  $n=80$ ), but wherever possible, the left statolith was used for analyses. For the purpose of this study, statolith "size" refers to the length of each statolith dimension, whereas "shape" indicates that all statolith dimensions have been combined to describe overall statolith structure.

Rates of growth calculated from size-at-age data were not significantly different between adult males and females (Table 1). A size comparison of males and females, adjusted for age, found no significant difference in size between the sexes (Table 2). Individuals were therefore classified as either juveniles or adults, with no distinction made between adult sexes. This classification avoided over-complicating analyses and also provided a larger adult sample size.

Principal components analysis (PCA) was performed on statolith dimensions with the covariance matrix of transformed ( $\log_{10}$ ) data, allowing complete descriptions of statolith shape for all dimensions simultaneously. The magnitude of coefficients in the

first eigenvector varies because of changing statolith proportions and relative growth patterns. These coefficients indicate the nature of allometric growth for each variable (dimension) (Jolicoeur, 1963). The coefficients for each variable in the first eigenvector describe the relative growth rates of all the components simultaneously (Shea, 1985). Variables with coefficient scores on the first principal component vector equal to the mean coefficient ( $(1/p)^{0.5}$ , where  $p$  is the number of variables in the analysis) are isometric. Positive and negative allometry is indicated by values greater than and less than the mean coefficient, respectively (Jolicoeur, 1963).

The resampling technique jack-knifing provided means and standard errors (SE) of each coefficient (Marcus, 1990). The probability that the mean coefficient was significantly different from the hypothesized value (Marcus, 1990) is

$$P\left(\frac{|mean\ coefficient - hypothesized\ coefficient|}{> T \times SE \times mean\ coefficient}\right) < 1/T^2 \quad (1)$$

where  $T$  = the number of standard errors for which the probability statement is made.

In this case  $T = 4.47$  provides a probability of 0.05. Simply, the difference between the mean coefficient and the hypothesized coefficient is greater than a critical difference ( $T \times SE \times$  calculated coefficient) with a probability  $< 1/T^2$ .

Table 1

Linear regression equations for the size-at-age data of male and female *Sepioteuthis lessoniana*.  $SE_b$  = standard error of the slope.  $ML$  = mantle length (mm).  $H_0$  for *t*-test:  $b = 0$ .

Sex	<i>n</i>	Equation	$SE_b$	$r^2$	<i>t</i>	<i>P</i>
Male	32	$age = 0.08ML + 5.02$	0.02	0.44	4.84	0.0001
Female	31	$age = 0.08ML + 5.44$	0.02	0.43	4.64	0.0001

## Results

### Statolith size relationships

The smallest statolith total length (648  $\mu$ m) was observed in the youngest specimen (17 days old). The largest adult statolith total length (2167  $\mu$ m) was observed in a 162-day-old mature female, although

Table 2

Analysis of covariance table, comparing mantle length (ML) of male and female *Sepioteuthis lessoniana*, using age as a covariate.

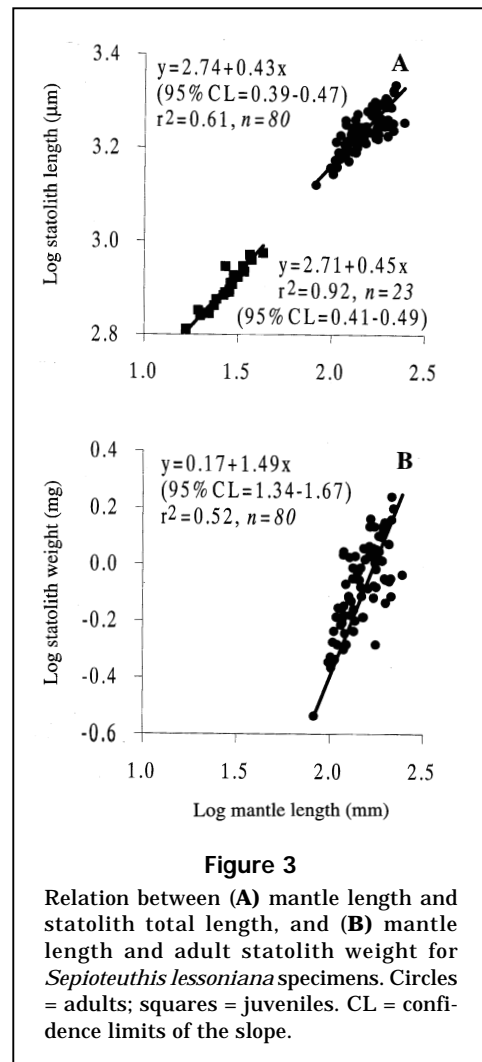
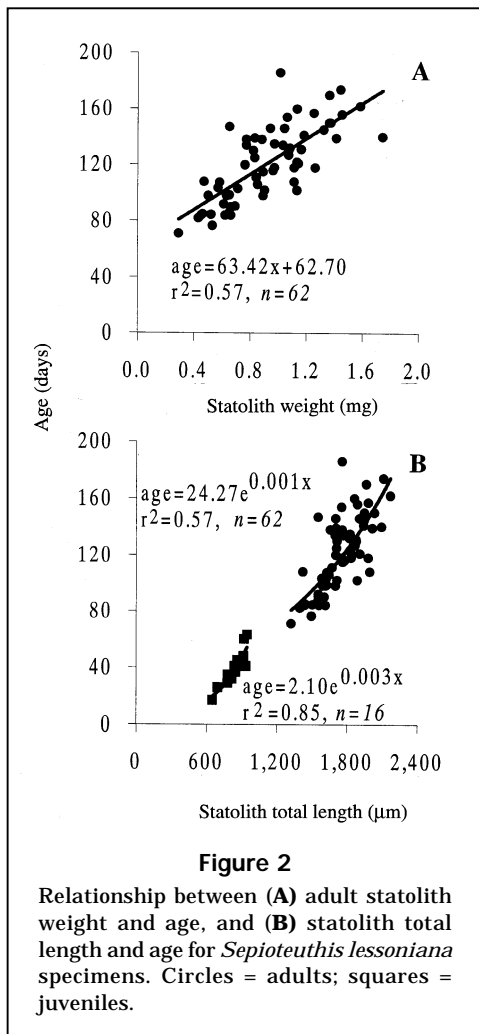
Source	df	Sum of squares	Mean square	<i>F</i> -value	<i>P</i> > <i>F</i>
Test for equal slopes					
Sex	1	1.46	1.46	0.32	0.5764
Age (covariate)	1	329.60	329.60	71.21	0.0001
Sex $\times$ age (equal slopes)	1	1.20	1.20	0.26	0.6128
Test for differences in ML					
Sex	1	0.40	0.40	0.09	0.7681
Age (covariate)	1	333.23	333.23	73.01	0.0001

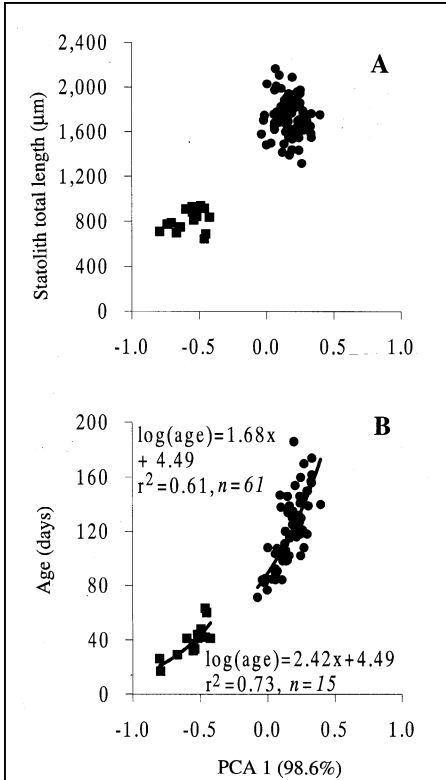
the oldest individual was a 186-day-old mature female. Adult statolith weights ranged from 0.29 mg in a 72-day-old immature male to 1.74 mg in a 144-day-old mature female.

Adult statolith weight was not a reliable predictor of squid age, with only 57% ( $n=62$ ) of the variation in adult ages attributable to weight of the statoliths (Fig. 2A). The strength of the relation between age and statolith total length differed between juvenile and adult squid (Fig. 2B). For juvenile squid, 85% ( $n=16$ ) of the variation in age was attributable to differences in statolith total length, indicating statolith total length maintains a close correlation with age during the first 60 days of squid growth. In adult squid, the ability to predict age based on statolith total length is poor, and only 57% ( $n=62$ ) of the variation in squid ages can be explained by statolith length. Statolith total length grew relatively slower than ML for both adult and juvenile squid (Fig. 3A). Adult statolith weight displayed positive allometric growth with ML (Fig. 3B).

### Changes in statolith shape

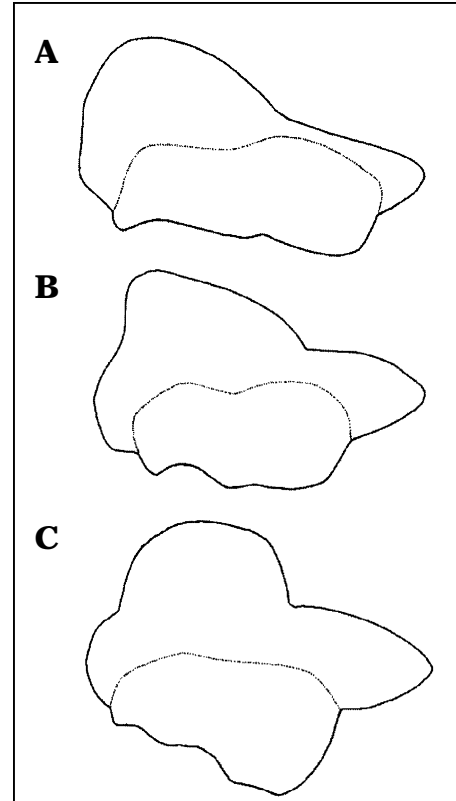
The first PCA axis described 98.6% of the variation among individuals, which is due to statolith shape or the size of all statolith dimensions combined. If we use the PCA score on the first axis as a descriptor of statolith shape, we can account for only 9% and 7% of the variation in statolith total length of juvenile ( $n=16$ ) and adult ( $n=78$ ) squid, respectively (Fig. 4B). This result confirms that the first PCA axis contains statolith shape information and not predominantly size information. Growth of the statolith along the total length, ventrolateral and lateral dome axes and in total length was relatively slow, as evidenced by negative allometric growth (Table 3). In contrast, growth of the statolith along the dorsolateral axis and in total width grew relatively faster, as evidenced by the positive allometric growth (Table 3). This finding indicates that the statoliths of juvenile squid are relatively thin and elongate, becoming comparatively





**Figure 4**

Relative growth of the length of statolith dimensions. The relation between the principal component score on the first axis for each statolith against (A) statolith total length, and (B) age. The percentages indicate the variation in the data set that has been described by each principal component axis. Circles = adults; squares = juveniles.



**Figure 5**

Statoliths of *Sepioteuthis lessoniana*, demonstrating the change in shape from juvenile to adult squid. Mantle lengths and total statolith lengths were (A) 16 mm, 648 µm; (B) 119 mm, 1525 µm; (C) 190 mm, 1875 µm, respectively. Statoliths are shown in anterior view at different scales to facilitate shape comparison.

**Table 3**

Relative growth of statolith dimensions. Coefficient = coefficient of the first eigenvector. Isometric growth occurs when the coefficient equals  $(1/p)^{0.5} = 0.447$ . The difference equals the coefficient minus 0.447, which must be greater than the critical difference if allometric growth has occurred; data are  $\log_{10}$ -transformed; SE = standard errors.

Variable	Coefficient		Critical difference	Difference	Allometric growth
	Mean	SE			
Total length	0.435	0.004	± 0.008	-0.012	negative
Dorsolateral	0.503	0.010	± 0.022	0.056	positive
Ventrolateral	0.387	0.006	± 0.010	-0.060	negative
Lateral dome	0.349	0.005	± 0.008	-0.098	negative
Total width	0.535	0.007	± 0.017	0.088	positive

fatter and bulkier during growth (Fig. 5). Statoliths of the adults continued to grow (Fig. 3); however, there is no relation between the PCA score on the

first axis and statolith size for the adults (Fig. 4A), suggesting that the overall shape of individual adult statoliths showed no further change.

**Table 4**

Relative growth of statolith dimensions. The coefficients for the first three principal component axes (PCA) of the analysis on length variables; data are  $\log_{10}$ -transformed and the covariance matrix was used.

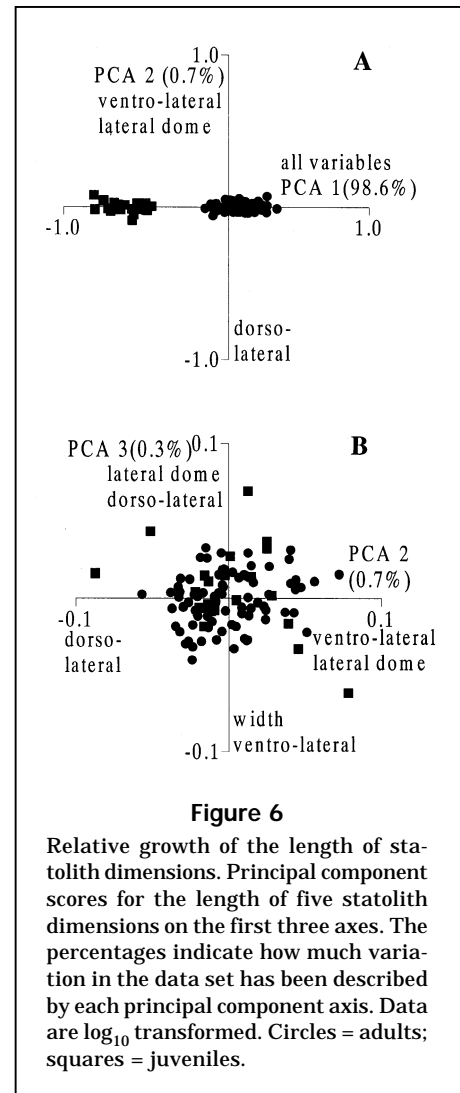
Variable	Eigenvector		
	PCA 1	PCA 2	PCA 3
Total length	0.435	0.308	0.154
Dorsolateral	0.503	-0.695	0.321
Ventrolateral	0.387	0.592	-0.108
Lateral dome	0.349	0.210	0.579
Total width	0.535	-0.163	-0.726

Additional variation in statolith shape described on the second and third PCA axes was attributable to differences among juvenile, rather than adult squid (Fig. 6, A and B; Table 4). Growth of the statolith along the ventrolateral and lateral dome axes and in total length were all important as statoliths approached their final size and shape. The ventrolateral and total lengths were proportionally larger in juveniles, whereas the dorsolateral length and total width were proportionally smaller immediately before individual statoliths attained their final adult shape.

If the PCA score of each individual statolith on the first axis, as a descriptor of shape, is used to estimate age of the squid, then an improved correlation between age and statolith shape is seen when compared to the correlation between age and statolith total length alone (juveniles  $n=15$ ,  $r^2=0.73$ ; adults  $n=61$ ,  $r^2=0.61$ ) (Fig. 4B). There is an exponential relationship for both juvenile and adult squid but changes in statolith shape slow in older individuals. Analysis of adult and juvenile statoliths as separate groups to eliminate gross statolith size differences that were identified in the PCA only highlighted the overall variability in statolith shape within the two age groups, particularly among adult squid.

## Discussion

Results from this study suggest that neither statolith total length nor weight measurements can be reliably used to predict the age of a *Sepioteuthis lessoniana* individual. Statolith total length is a reasonable predictor of age for juvenile squid (less than 60 days old) but cannot be used to predict age in older individuals of this species. This conclusion is in contrast with that of González et al. (1996) who observed that statolith length in *Illex coindetti* shows signifi-



cant dependence on age (males  $n=170$ ,  $r^2=0.71$ ; females  $n=171$ ,  $r^2=0.74$ ). However, they also suggested that the use of statolith length for age estimations would require verification over several years to confirm this relationship. Statolith length has also been shown to reflect age in *Illex illecebrosus* females ( $n=31$ ,  $r^2=0.96$ ) (Morris and Aldrich, 1985), whereas statolith weight provided a better reflection of age ( $n=112$ ,  $r^2=0.88$ ) than statolith total length in *Todarodes angolensis* (Villanueva, 1992). Even combining all five statolith dimensions to produce a description of statolith shape in this study provided only marginally better age estimates for *S. lessoniana* individuals than statolith total length or weight measurements alone.

Variation was evident in size between adult statoliths in this study because the heaviest statoliths did not necessarily possess the longest total lengths. Additionally, as much as half of the variation in statolith total lengths was not attributable to age of the

individuals. This indicates a disassociation between statolith and somatic (mantle length) growth in *S. lessoniana*. The disassociation of otolith and somatic growth has been demonstrated in several fish species (e.g. Mosegaard et al., 1988; Secor and Dean, 1989; Francis et al., 1993). In squids, *Loligo chinensis* (Jackson, 1995), and *Todaropsis eblanae* and *Todarodes angolensis* (Lipinski et al., 1993) also display disassociation between statolith and somatic tissue growth. Comparison of statolith size and shape between *Todarodes angolensis* and *Todaropsis eblanae* also has revealed distinct species differences (Lipinski et al., 1993). Jackson (1995) suggested that the use of the relation of statolith length to mantle length as a predictor of squid ages should proceed with caution until temperature-related effects on squid growth (e.g. seasonal effects), as well as the relation between statolith and somatic growth are better understood.

The disassociation between statolith and somatic growth rates is possibly a function of differences between the mechanisms responsible for these two processes. A process related to metabolic rate, rather than somatic growth, seems to govern the rate of otolith accretion in fish (Wright, 1991). Although a close correlation often exists between fish somatic growth and metabolic rate in early life-history stages, intrinsic or extrinsic constraints on somatic growth may affect this relationship and result in a disassociation between otolith and somatic growth (Wright, 1991). Recently, Lombarte and Leonart (1993) proposed that otolith growth in fish may occur under dual regulation: overall shape is genetically determined whereas otolith size is governed by environmental factors. Several workers have also suggested that temperature plays a particularly important role in determining otolith growth, primarily through the effect of temperature on metabolic rate (Wright, 1991; Bradford and Geen, 1992). In order to demonstrate a link between otolith and somatic growth rates the age-independent variability in the relationship needs to be assessed (Hare and Cowen, 1995). The mechanisms governing statolith growth in *S. lessoniana* remain to be determined but may possibly be related to the high plasticity of somatic growth and a fixed growth trajectory of the statolith. Ontogenetic behavioral adaptations may also play a key role. Nonetheless, there are important considerations for age and growth studies based on the morphological features of statoliths; whereas many squid are known to grow continuously throughout their life (Jackson and Choat, 1992; Jackson, 1994), growth of statoliths in our study appears to approach a final asymptotic size and shape. Statoliths grow with the age of the squid, but statolith accretion may respond differently to environmental factors than to growth of somatic tissue.

The breakdown in the relation between statolith total length and age in older *S. lessoniana* individuals may be attributed to variable accretion rates in the statoliths of adult squid, possibly in relation to environmental conditions. Varying aragonite accretion within statoliths could bring about fluctuations in daily increment widths that ultimately lead to differences in overall length and weight of similar aged statoliths. These differences are likely to be more detectable in the older, larger statoliths of adult squid. Alterations in otolith increment widths leading to different sized otoliths of the same age have been shown for several fish species in response to both biotic and abiotic factors (e.g. Eckmann and Rey, 1987; Sogard, 1991; Burke et al., 1993). Further work on other fish species has shown that changes in increment width may lag or be unrelated to changes in somatic growth (Molony and Choat, 1990; Milicich and Choat, 1992). Variable statolith increment widths, that may be attributable to environmental conditions, have been shown in at least one squid species (*Abralia trigonura*, Bigelow, 1992), and one cuttlefish (*Sepia hierredda*, Raya et al. 1994).

Modifications of otolith shape and daily increment structure in fish have been attributed to environmental changes or fluctuations in individual fish physiology (Morales-Nin, 1987; Nishimura, 1993; Wright, 1993; Tzeng and Tsai, 1994). As some fish migrate, modifications are often necessary in order to meet unique requirements for balance, orientation, and navigation (Blaxter, 1988). A transformation of otolith shape may occur, resulting in discontinuities and secondary growth structures (Sogard, 1991; Hare and Cowen, 1994). Statoliths are the major sensory structure responsible for balance and orientation of squid (Budelmann, 1990). The shape and structure of the statocyst chamber itself are important to the swimming performance and sensory perception capabilities of cephalopods (Williamson, 1991). Statolith shape and structure is, therefore, also likely to affect the response of this unique and complex sensory organ. Although *S. lessoniana* does not display distinct life-style changes or habitat shifts, a transition from the observed juvenile habitat, where it commonly shelters among floating surface debris, to an adult lifestyle that is typically more reef-associated, may involve behavioral adaptations that lead to differential growth of statoliths. Knowledge of the mechanism by which this growth occurs and how it can be modified during ontogeny will be critical to understanding how statoliths grow.

Most growth of adult statoliths in this study occurred in the dorsal and lateral dome regions, producing a more rounded and bulkier form than that of the juveniles. The negative allometric growth in

total length and along the lateral dome and ventro-lateral length axes suggests that relative growth of these regions is slow and that statoliths retain the elongate region of the rostrum as they grow. This was reflected in the superior definition and clarity of daily increment structures in the lateral dome region of adult statoliths when viewed under a light microscope. This may also explain why optical acuity of daily increment structures in the rostrum region of adult statoliths was poor. Slower growth of statoliths in the rostrum indicates deposition of less aragonite material compared with other faster growing regions of the statolith and in turn suggests that daily increment widths in the rostrum will be narrower and therefore harder to discern with light microscopy. In contrast, daily growth increments have been reported as displaying optimal definition in the rostrum of two other squid species (*Photololigo edulis*, Natsukari et al., 1988; *Beryteuthis magister*, Natsukari et al., 1993). Therefore, it is likely that differences occur in statolith accretion between species, possibly related to behavior. Optical definition of daily increments in statoliths has important consequences when ageing and growth studies are based on counts and distances between increments. Age and growth calculations based on narrower less distinct increments may not reveal true patterns otherwise evident in optically more distinct incrementation.

Results from this study suggest that prediction of age of *S. lessoniana* individuals from the size and shape of their statoliths remains doubtful on account of the disassociation between statolith and somatic tissue growth. Changes in statolith shape during growth may also be important if statoliths are to be employed as a tool for constructing growth histories of *S. lessoniana*. Variable levels of statolith accretion ultimately leading to slight modifications in shape may not necessarily be indicative of changes in somatic growth. Ageing studies based on analyses of statolith size from other squid species need to be aware of the possible disassociation between statolith and somatic tissue growth. The changes in size and shape of *Sepioteuthis lessoniana* statoliths described in this study are likely due to differing aragonite accretion levels, possibly on a daily basis, in response to physiological and behavioral adaptations during ontogeny.

## Acknowledgments

We thank G. Jackson for providing constructive reviews of early manuscripts. We also acknowledge J. Semmens, G. Pecl, and P. Martinez for their assistance in the field and laboratory. This research was completed in partial fulfillment of an Honours de-

gree by RT and was supported by a Merit Research Grant from James Cook University awarded to NAM.

## Literature cited

- Arkhipkin, A.**  
1993. Statolith microstructure and maximum age of *Loligo gahi* (Myopsida: Loliginidae) on the Patagonian Shelf. *J. Mar. Biol. Assoc. U.K.* 73:979–982.
- Bigelow, K. A.**  
1992. Age and growth in paralarvae of the mesopelagic squid *Abralia trigonura* based on daily growth increments in statoliths. *Mar. Ecol. Prog. Ser.* 82:31–40.  
1994. Age and growth of the oceanic squid *Onychoteuthis borealijaponica* in the North Pacific. *Fish. Bull.* 92:13–25.
- Blaxter, J. H. S.**  
1988. Sensory performance, behaviour and ecology of fish. *In* J. Atema, R. R. Fay, A. N. Popper, and W. N. Tavolga (eds.), *Sensory biology of aquatic animals*. Springer-Verlag, New York, NY, p. 203–232.
- Boehlert, G. W.**  
1985. Using objective criteria and multiple regression models for age determination in fish. *Fish. Bull.* 83:103–117.
- Bradford, M. J., and G. H. Geen.**  
1992. Growth estimates from otolith increment widths of juvenile chinook salmon (*Oncorhynchus tshawytscha*) reared in changing environments. *J. Fish Biol.* 41:825–832.
- Budelmann, B. U.**  
1990. The statocysts of squid. *In* D. L. Gilbert, W. J. Adelman Jr., and J. M. Arnold (eds.), *Squid as experimental animals*, p. 421–436. Plenum Press, London.
- Burke, J. S., D. S. Peters, and P. J. Hanson.**  
1993. Morphological indices and otolith microstructure of Atlantic croaker, *Micropogonias undulatus*, as indicators of habitat quality along an estuarine pollution gradient. *Environ. Biol. Fishes* 36:25–33.
- Campana, S. E., and J. D. Neilson.**  
1985. Microstructure of fish otoliths. *Can. J. Fish. Aquat. Sci.* 42:1014–1032.
- Clarke, M. R.**  
1978. The cephalopod statolith—an introduction to its form. *J. Mar. Biol. Assoc. U.K.* 58:701–712.
- Eckmann, R., and P. Rey.**  
1987. Daily increments on the otoliths of larval and juvenile *Coregonus* spp., and their modification by environmental factors. *Hydrobiologia* 148:137–143.
- Fletcher, W. J.**  
1991. A test of the relationship between otolith weight and age for the pilchard *Sardinops neopilchardus*. *Can. J. Fish. Aquat. Sci.* 48:35–38.
- Forsythe, J. W.**  
1993. A working hypothesis of how seasonal temperature change may impact the field growth of young cephalopods. *In* T. Okutani, R. K. O'Dor, and T. Kubodera (eds.), *Recent advances in cephalopod fisheries biology*, p. 133–143. Tokai Univ. Press, Tokyo.
- Forsythe, J. W., and R. T. Hanlon.**  
1989. Growth of the eastern Atlantic squid, *Loligo forbesi* Steenstrup (Mollusca: Cephalopoda). *Aquacult. Fish. Manage.* 20:1–14.
- Francis, M. P., M. W. Williams, A. C. Pryce, S. Pollard, and S. G. Scott.**  
1993. Uncoupling of otolith and somatic growth in *Pagrus auratus* (Sparidae). *Fish. Bull.* 91:159–164.



**González, A. F., B. G. Castro, and A. Guerra.**

1996. Age and growth of the short-finned squid *Illex coindetii* in Galician waters (NW Spain) based on statolith analysis. *ICES J. Mar. Sci.* 53:802–810.

**Hare, J. A., and R. K. Cowen.**

1994. Ontogeny and otolith microstructure of bluefish *Pomatomus saltatrix* (Pisces: Pomatomidae). *Mar. Biol.* 118:541–550.

1995. Effect of age, growth rate, and ontogeny on the otolith size–fish size relationship in bluefish, *Pomatomus saltatrix*, and the implications for back-calculation of size in fish early life history stages. *Can. J. Fish. Aquat. Sci.* 52:1909–1922.

**Jackson, G.D.**

1990. Age and growth of the tropical near shore loliginid squid *Sepioteuthis lessoniana* determined from statolith growth ring analysis. *Fish. Bull.* 88:113–118.

1994. Application and future potential of statolith increment analysis in squids and sepioids. *Can. J. Fish. Aquat. Sci.* 51(11):2602–2626.

1995. Seasonal influences on statolith growth in the tropical nearshore loliginid squid *Loligo chinensis* (Cephalopoda: Loliginidae) off Townsville, North Queensland, Australia. *Fish. Bull.* 93:749–752.

**Jackson, G. D., and J. H. Choat.**

1992. Growth in tropical cephalopods: an analysis based on statolith microstructure. *Can. J. Fish. Aquat. Sci.* 49:218–228.

**Jolicoeur, P.**

1963. The multivariate generalisation of the allometry equation. *Biometrics* 19:497–499.

**Jones, C.**

1986. Determining age of larval fish with the otolith increment technique. *Fish. Bull.* 84:91–103.

**Lipinski, M. R.**

1986. Methods for the validation of squid age from statoliths. *J. Mar. Biol. Assoc. U.K.* 66:505–526.

**Lipinski, M. R.**

1993. The deposition of statolith—a working hypothesis. *In* T. Okutani, R. K. O'Dor, and T. Kubodera (eds.), Recent advances in cephalopod fisheries biology, p. 241–262. Tokai Univ. Press, Tokyo.

**Lipinski, M. R., M. A. Compagno Roeleveld, and L. G. Underhill.**

1993. Comparison of the statoliths of *Todaropsis eblanae* and *Todarodes angolensis* (Cephalopoda: Ommastrephidae) in South African waters. *In* T. Okutani, R. K. O'Dor, and T. Kubodera (eds.), Recent advances in cephalopod fisheries biology. Tokai Univ. Press, Tokyo, p. 263–273.

**Lombarte, A., and J. Leonart.**

1993. Otolith size changes related with body growth, habitat depth and temperature. *Environ. Biol. Fishes* 37:297–306.

**Marcus, L.**

1990. Traditional morphometrics. *In* F. J. Rohlf and F. L. Bookstein (eds.), Proceedings of the Michigan morphometrics workshop, p. 77–122. Univ. Michigan Museum of Zoology, Special Publication 2

**Milicich, M. J., and J. H. Choat.**

1992. Do otoliths record changes in somatic growth rate? Conflicting evidence from a laboratory and field study of a temperate reef fish, *Parika scaber*. *Aust. J. Mar. Freshwater Res.* 43:1203–1214.

**Molony, B. W., and J. H. Choat.**

1990. Otolith increment widths and somatic growth rate: the presence of a time-lag. *J. Fish Biol.* 37:541–551.

**Morales-Nin, B. Y. O.**

1987. The influence of environmental factors on microstruc-

ture of otoliths of three demersal fish species caught off Namibia. *S. Afr. J. Mar. Sci.* 5:255–262.

**Morris, C. C., and F. A. Aldrich.**

1985. Statolith length and increment number for age determination of *Illex illecebrosus* (LeSueur, 1821) (Cephalopoda: Ommastrephidae). *NAFO Scientific Council Studies* 9:101–106.

**Mosegaard, H., H. Svedang, and K. Taberman.**

1988. Uncoupling of somatic and otolith growth rates in Arctic char (*Salvelinus alpinus*) as an effect of differences in temperature response. *Can. J. Fish. Aquat. Sci.* 45:1514–1524.

**Mugiya, Y., and S. Tanaka.**

1992. Otolith development, increment formation, and an uncoupling of otolith to somatic growth rates in larval and juvenile goldfish. *Nippon Suisan Gakkaishi.* 58:845–851.

**Natsukari, Y. T., T. Nakanose, and K. Oda.**

1988. Age and growth of loliginid squid *Photololigo edulis* (Hoyle, 1855). *J. Exp. Mar. Biol. Ecol.* 116:177–190.

**Natsukari, Y., H. Mukai, S. Nakahama, and T. Kubodera.**

1993. Age and growth estimation of a gonatid squid, *Berryteuthis magister*, based on statolith microstructure (Cephalopoda: Gonatidae). *In* T. Okutani, R. K. O'Dor, and T. Kubodera (eds.), Recent advances in cephalopod fisheries biology, p. 351–364. Tokai Univ. Press, Tokyo.

**Nishimura, A.**

1993. Occurrence of a check in otoliths of reared and sea-caught larval walleye pollock *Theragra chalcogramma* (Pallas) and its relationship to events in early-life history. *J. Exp. Mar. Biol. Ecol.* 166:175–183.

**Radtke, R. L.**

1983. Chemical and structural characteristics of statoliths from the short-finned squid *Illex illecebrosus*. *Mar. Biol.* 76:47–54.

**Raya, C. P., M. M. Fernandez-Nunez, E. Balguerias, and C. L. Hernandez-Gonzalez.**

1994. Progress towards ageing cuttlefish (*Sepia hierredda*, Rang 1837) from North West African coast using statoliths. *Mar. Ecol. Prog. Ser.* 114:139–147.

**Secor, D. H., and J. M. Dean.**

1989. Somatic growth effects on the otolith-fish size relationship in young pond-reared striped bass, *Morone saxatilis*. *Can. J. Fish. Aquat. Sci.* 46:113–121.

**Shea, B. T.**

1985. Bivariate and multivariate growth allometry: statistical and biological considerations. *J. Zool. Lond.* 206:367–390.

**Sogard, S. M.**

1991. Interpretation of otolith microstructure in juvenile winter flounder (*Pseudopleuronectes americanus*): ontogenetic development, daily increment validation, and somatic growth relationships. *Can. J. Fish. Aquat. Sci.* 48:1862–1871.

**Stevenson, D. K., and S. E. Campana (eds.).**

1992. Otolith microstructure examination and analysis. *Can. Spec. Publ. Fish. Aquat. Sci.* 117, 126 p.

**Tzeng, W. N., and Y. C. Tsai.**

1994. Changes in otolith microchemistry of the Japanese eel, *Anguilla japonica*, during its migration from the ocean to the rivers of Taiwan. *J. Fish Biol.* 45:671–683.

**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.

**Williamson, R.**

1991. Factors affecting the sensory response characteris-

tics of the cephalopod statocyst and their relevance in predicting swimming performance. Biol. Bull. 180:221–227.

**Wright, P. J.**

**1991.** The influence of metabolic rate on otolith increment width in Atlantic salmon parr, *Salmo salar* L. J. Fish Biol. 38:929–933.

**1993.** Otolith microstructure of the lesser sandeel, *Ammodytes marinus*. J. Mar. Biol. Assoc. U.K. 73:245–248.

**Wright, P. J., N. B. Metcalfe, and J. E. Thorpe.**

**1990.** Otolith and somatic growth rates in Atlantic salmon parr, *Salmo salar* L: evidence against coupling. J. Fish. Biol. 36:241–249.