Seasonal influences on statolith growth in the tropical nearshore loliginid squid *Loligo chinensis* (Cephalopoda: Loliginidae) off Townsville, North Queensland, Australia

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Information is currently accumulating on age, growth, and maturity rates of squids, with a number of studies focusing on tropical and warm water species (eg. Jackson, 1990, a and b; Arkhipkin and Mikheev, 1992; Bigelow, 1992; Jackson and Choat, 1992; Arkhipkin and Nekludova, 1993; Jackson, 1993; Laptikhovsky et al., 1993; Young and Mangold, 1994; see also Jackson, 1994, for review). The interpretation of growth phenomena in squids is complicated owing to the high degree of temperature dependency in growth (O'Dor and Wells, 1987; Forsythe and Hanlon, 1989). Moreover, growth is highly variable even within particular temperature regimes (Lipinski, 1986; Natsukari et al., 1988). The use of validated daily increments in statoliths is a convincing tool for determining both the rate of growth and its variance. However, there is also the potential that temperature-induced variation in growth rates might be reflected in statolith growth rates.

Recent work on the uncoupling between otolith size and fish size (see Campana and Jones, 1992) has indicated that individual variation in growth rates can have profound effects on soma-otolith relationships. While such features make analysis such as back calculation of individual size less than straightforward (Campana, 1990), they do provide a mechanism for detecting past growth histories (or perhaps even past environmental histories) to which a fish has been exposed. For example, if two similar-sized fish of the same species show considerable disparity in otolith size, it suggests that the individual with the larger otolith has grown slower (e.g. Reznick et al., 1989; Wright et al., 1990). Lipinski et al. (1993) have also documented substantial uncoupling in squid statolith growth and in growth of the mantle in *Todaropsis eblanae* and *Todarodes angolensis* off southern Africa.

Statolith increments are produced daily in *Loligo chinensis* (Jackson, 1990b) as well as in other loliginid squids such as *Alloteuthis subulata* (Lipinski, 1986), *Loligo opalescens* (Yang et al., 1986), *Loliolus noctiluca* (Jackson, 1990b), and *Sepioteuthis lessoniana* (Jackson, 1990a; Jackson et al., 1993). However, compared with fish otolith analysis in which there is a substantial number of ageing and increment validation studies (e.g. Campana and Neilson, 1985; Stevenson and Campana, 1992), much of the work with statolith ageing and validation is still preliminary in nature. However, evidence does support daily periodicity in statolith increment production in many species (Jackson, 1994) although there is an ongoing need for further validation and ageing studies. Because age and population information is already available for *Loligo chinensis*[1] (Jackson, 1990b, 1993; Jackson and Choat, 1992), this study was undertaken to see if seasonal differences in growth rate are reflected in statolith-size:body-size relationships in this tropical nearshore squid.

Materials and methods

Individuals of *Loligo chinensis* were captured by using paired otter trawls (each net consisted of an 11-m gape and 3.8-cm mesh). Trawls were towed for approximately 20 minutes at a speed of 2–2.5 knots. Samples were taken in Cleveland Bay (19°15'S,146°50'E) in water <20 m deep off Townsville, North Queensland. Statoliths were obtained from squid caught during two seasonal periods, 12 January 1989 (austral summer, n=35) and 13 July 1989 (austral winter, n=33). Squid were preserved in 10% buff-

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[1] It is now known that the species *Loligo chinensis* which is found in shallow tropical waters off North Queensland is a distinct species from *L. chinensis* which is found elsewhere in the tropical Indo-Pacific. J. Yeatman. 1993. James Cook Univ. of North Queensland. Personal commun. Furthermore, all *Loligo* species in Australian waters will probably be referred to as *Photololigo* in the future. Until this is resolved, I have referred to the species of this study as *Loligo chinensis* which is the same species referred to as *Photololigo* cf. *chinensis* (east coast form) in Dunning et al. (1994) and *Photololigo* sp. 3 in Yeatman and Benzie (1994).

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ered seawater formalin and subsequently transferred to 70% ethanol. Mantle length (ML) measurements (nearest mm) were taken on the preserved individuals. Statoliths were removed shortly after preservation and mounted in Crystal Bond thermoplastic cement.

Total increment number was determined (with a camera lucida attached to an Olympus BH compound microscope) as the mean of three consecutive counts that differed less than 10% from the mean (see also Jackson and Choat, 1992; Jackson, 1993). Statolith length (to the nearest 10 μm) was measured with an eyepiece micrometer (with an Olympus BH compound microscope) along the longest axis from the dorsal dome to the tip of the rostrum.

Results

For the summer population, the relationship between statolith length and mantle length as well as statolith length and age was curvilinear. However, both relationships were linear for the winter population (Fig. 1; Table 1). Because all relationships were not linear, an analysis of covariance could not be applied to these data sets. However, a paired *t*-test was used to compare statolith lengths of similar-sized males and females (mantle lengths between 90 and 110 mm, $n=24$) from both January (summer) and July (winter). Squid statoliths from the July sample were significantly longer than statoliths from the January sample ($P<0.05$).

The relationship between statolith length and mantle length (Fig. 1A) suggested that somatic growth was greater than statolith growth as size increases (i.e. in larger squids the mantle was increasing in length faster than was the statolith). Moreover, in general, for any given length, a winter squid had larger statoliths than its summer counterpart.

There were also considerable seasonal differences in the growth of the statolith with age (Fig. 1B). There was a rapid increase in statolith length in summer over a relatively short period from 60 to 100 days. In contrast, statolith growth was much slower in the winter; the statolith gradually increased in length from 80 to 170 days. However, statoliths eventually reached a greater length in the older, winter-population squids. This feature was a factor of age because winter squids were not longer than summer squids. In comparing similar-aged squids between seasons, for any given age, a summer squid generally had a larger statolith than its winter counterpart.

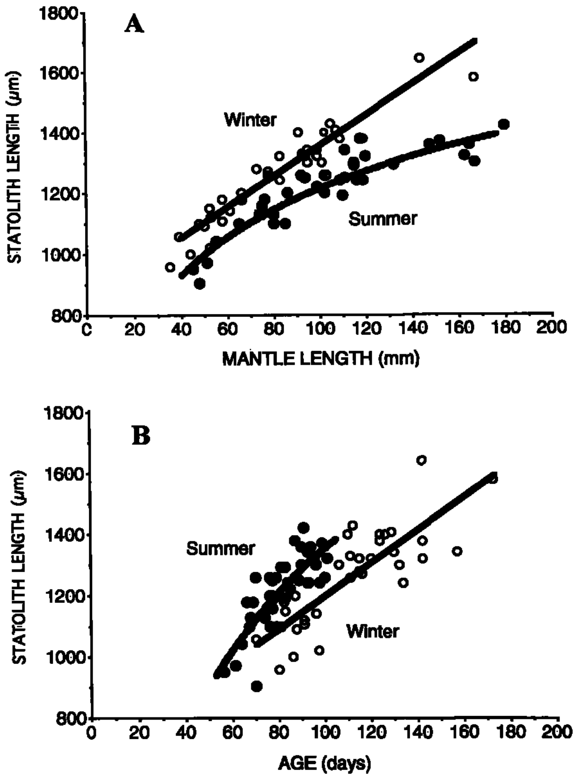

Figure 1

The relationship between (A) statolith length and mantle length and (B) statolith length and age for summer (January) and winter (July) samples of *Loligo chinensis*.

Discussion

Current research on fish somatic-otolith growth relationships provides a background for the possible mechanisms underlying somatic-statolith growth relationships for *L. chinensis*. The relationship between both statolith length and mantle length and statolith length and age shows striking similarities to otolith length versus fish length and age studies. Mosegaard et al. (1988), Secor and Dean (1989), Reznick et al. (1989), Wright et al.(1990), and Mugiya and Tanaka (1992) have shown that slower-growing fish have larger otoliths than similar-sized, faster-growing fish. Furthermore, for striped bass, *Morone saxatilis*, and Atlantic salmon, *Salmo salar*, slower-growing fish have larger otoliths at any given size, although faster-growing fish have larger otoliths at any given age (Secor and Dean, 1989; Wright et al., 1990). A similar relationship is evident between statolith length and both mantle length and age for *L. chinensis*.

These teleost studies provide insights into the growth dynamics of squid. The slower growing individuals of *L. chinensis* (winter population) had larger

Table 1

Regression equations for the relationship between mantle length and statolith length and for age and statolith length for individuals of *Loligo chinensis* collected in both summer and winter. ML = mantle length. All regressions were highly significant ($P \leq 0.001$).

Season	Relationship	n	Equation	r^2
Summer	ML vs. statolith length	38	$y = -238.4 + 731.2 \log x$	0.84
Summer	Age vs. statolith length	38	$y = -1585.8 + 1470.6 \log x$	0.63
Winter	ML vs. statolith length	33	$y = 849.4 + 5.03x$	0.91
Winter	Age vs. statolith length	33	$y = 672.7 + 5.3x$	0.67

statoliths because they were in reality much older than similar-sized, faster-growing squids (summer population). Alternatively, when statolith length and individual age were compared, faster-growing squids had larger statoliths than slower-growing squids for a given age because the individual itself was considerably larger (e.g. in the summer, squids were reaching adult sizes at around 80 days whereas in the winter, 80-day squid were still juveniles).

Morris and Aldrich (1985) have suggested that statolith length may be a better indicator of squid age than increment number because they observed less variation in the mantle length:statolith length relationship than in the mantle length:age relationship in *Illex illecebrosus*. However, the seasonal difference in the relationship between the statolith and the soma of *L. chinensis* suggests that this technique should be used cautiously until further research into temperature effects is conducted (see also Campana, 1990; Lipinski et al., 1993). On the basis of laboratory observations, Forsythe and Hanlon (1989) and Forsythe (1993) have suggested that even fairly small variations in ambient temperature can have a marked effect on somatic growth rates. Temperature has also been shown to be an important influence on growth rates of *Sepia australis* in the field (Roeleveld et al., 1993). This preliminary study with *L. chinensis* suggests that temperature variation will not only greatly influence somatic growth but statolith growth as well. The uncoupling of statolith growth and somatic growth in squid is certainly an area that deserves further research (see Lipinski et al., 1993).

Statoliths are structures which have accentuated both the differences and similarities between cephalopods and fish. The increment structure and the growth of the statolith in relation to the squid soma are remarkably similar to that of the otolith in fish. In contrast, the enumeration of growth increments in both otoliths and statoliths have accentuated very different growth strategies and life histories (e.g. Jackson and Choat, 1992; Alford and Jackson, 1993) of two organisms that are biologically very different but nevertheless show many similarities.

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Literature cited

Alford, R. A., and G. D. Jackson.
1993. Do cephalopods and larvae of other taxa grow asymptotically? Am. Nat. 141:717–728.

Arkhipkin, A., and A. Mikheev.
1992. Age and growth of the squid *Sthenoteuthis pteropus* (Oegopsida: Ommastrephidae) from the Central-East Atlantic. J. Exp. Mar. Biol. Ecol. 163:261–276.

Arkhipkin, A., and N. Nekludova.
1993. Age, growth and maturation of the loliginid squids *Alloteuthis africana* and *A. subulata* on the West African Shelf. J. Mar. Biol. Assoc. U.K. 1993. 73:949–961.

Bigelow, K. A.
1992. Age and growth in paralarvae of the mesopelagic squid *Abralia trigonura* based on daily growth increment in statoliths. Mar. Ecol. Prog. Ser. 82:31–40

Campana, S. E.
1990. How reliable are growth back-calculations based on otoliths? Can. J. Fish. Aquat. Sci. 47:2219–2227.

Campana, S. E., and J. D. Neilson.
1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42:1014–1032.

Campana, S. E., and C. M. Jones.
1992. Analysis of otolith microstructure data. *In* D. K. Stevenson and S. E. Campana (eds.), Otolith microstructure examination and analysis, p. 73–100. Can. Spec. Publ. Fish. Aquat. Sci. 117.

Dunning, M., S. McKinnon, C. C. Lu, J. Yeatman, and D. Cameron.
1994. Demersal cephalopods of the Gulf of Carpentaria, Australia. Aust. J. Mar. Freshwater Res. 45:351–374.

Forsythe, J. W.
1993. A working hypothesis on 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.

Jackson, G. D.
1990a. Age and growth of the tropical nearshore loliginid

squid *Sepioteuthis lessoniana* determined from statolith growth-ring analysis. Fish. Bull. 88:113–118.

1990b. The use of tetracycline staining techniques to determine statolith growth ring periodicity in the tropical loliginid squids *Loliolus noctiluca* and *Loligo chinensis*. Veliger 33:395–399.

1993. Seasonal variation in reproductive investment in the tropical loliginid squid *Loligo chinensis* and the small tropical sepioid *Idiosepius pygmaeus*. Fish. Bull. 91:260–270.

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

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.

Jackson, G. D., A. I. Arkhipkin, V. A. Bizikov, and R. T. Hanlon.
1993. Laboratory and field corroboration of age and growth from statoliths and gladii of the loliginid squid *Sepioteuthis lessoniana* (Mollusca: Cephalopoda). *In* T. Okutani, R. K. O'Dor, and T. Kubodera (eds.), Recent advances in cephalopod fisheries biology, p. 189–199. Tokai Univ. Press, Tokyo.

Laptikhovsky, V. V., A. I. Arkhipkin, and A. A. Golub.
1993. Larval age, growth and mortality in the oceanic squid *Sthenoteuthis pteropus* (Cephalopoda, Ommastrephidae) from the eastern tropical Atlantic. J. Plankton Res. 15:375–384.

Lipinski, M. R.
1986. Methods for the validation of squid age from statoliths. J. Mar. Biol. Assoc. U.K. 66:505–524.

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, p. 263–273. Tokai Univ. Press, Tokyo.

Morris, C. C., and F. A. Aldrich.
1985. Statolith length and increment number for age determination of *Illex illecebrosus* (Lesueur, 1821) (Cephalopoda, Ommastrephidae). NAFO Sci. Counc. Stud. 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. Nakanose, and K. Oda.
1988. Age and growth of loliginid squid *Photololigo edulis* (Hoyle, 1885). J. Exp. Mar. Biol. Ecol. 116:177–190.

O'Dor, R. K., and M. J. Wells.
1987. Energy and nutrient flow. *In* P. R. Boyle (ed.), Cephalopod life cycles, Vol. II, p. 109–133. Academic Press, London.

Reznick, D., E. Lindbeck, and H. Bryga.
1989. Slower growth results in larger otoliths: an experimental test with guppies (*Poecilia reticulata*). Can. J. Fish. Aquat. Sci. 46:108–112.

Roeleveld, M. A. C, M. R. Lipinski, and M. G. van der Merwe.
1993. Biological and ecological aspects of the distribution of *Sepia australis* (Cephalopoda: Sepiidae) off the south coast of southern Africa. S. Afr. J. Zool. 28:99–106.

Secor, D. H., and J. M. Dean.
1989. Somatic growth effects on the otolith-fish size relationship in young pond-reared striped bass, *Morone saxatillis*. Can. J. Fish. Aquat. Sci. 46:113–121.

Stevenson, D. K., and S. E. Campana (ed.).
1992. Otolith microstructure examination and analysis. Can. Spec. Publ. Fish. Aquat. Sci. 117, 126 p.

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.

Yang, W. T., R. F. Hixon, P. E. Turk, M. E. Krejci, W. H. Hulet, and R. T. Hanlon.
1986. Growth, behaviour, and sexual maturation of the market squid, *Loligo opalescens*, cultured through the life cycle. Fish. Bull. 84:771–798.

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

Young, R. E., and K. M. Mangold.
1994. Growth and reproduction in the mesopelagic-boundary squid *Abralia trigonura*. Mar. Biol. (Berl.) 119: 413–421.