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Age and growth of the mesopelagic squid *Ancistrocheirus lesueurii* (Oegopsida: Ancistrocheiridae) from the central-east Atlantic based on statolith microstructure

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Abstract Statolith microstructure was studied in 56 Ancistrocheirus lesueurii (25 to 423 mm of mantle length, ML) caught in the central-east Atlantic. Statolith growth increments were grouped into three main growth zones, distinguished mainly by increment width. The second transition in the statolith microstructure (from Zone 2 to Zone 3) coincides with the life history shift from epipelagic and upper mesopelagic to a bathyal habitat. Second-order bands (mean 27.65 growth increments) and sub-bands (mean 13.6 growth increments) within statolith microstructure appeared to be related to the lunar cycle. Striking sexual dimorphism is reflected in the age and growth rates: males live ca. 1 yr, while females only start maturing at this age and obviously live >1.5 yr. A. lesueurii is a slow growing squid, attaining 25 to 30 mm ML at the age of 100 d. After ontogenetic migrations into bathypelagic waters at $ML > 30$ to 35 mm, growth rates gradually decrease to the minimum known values for squids. Based on backcalculated hatching dates, A. lesueurii hatches throughout the year with a peak between November and March.

Introduction

Ancistrocheirus lesueurii (d'Orbigny, 1842) is a common mesopelagic squid occurring worldwide in tropical and temperate open ocean waters (Roper et al. 1984). Planktonic juveniles of this species were previously thought to be *Thelidioteuthis alessandrinii* (Vérany, 1851). However it is now known that T. alessandrinii is a lesser synonym of A. lesueurii (Bello 1992). The planktonic juveniles are abundant in upper mesopelagic

A.I. Arkhipkin

waters (Clarke 1966; Nesis 1987). A. lesueurii adults attain a mantle length (ML) of 390 mm and are believed to migrate into deeper mesopelagic layers to spawn near the bottom (Nesis 1993). Although this species is not fished (Roper et al. 1984) mainly due to a high concentration of the ammonium in body tissues (Guerra 1992), it is an important component of the mesopelagic trophic web. A. lesueurii and other abundant large mesopelagic squids of the families Histioteuthidae, Architeuthidae, Lepidoteuthidae and Octopoteuthidae are important in the diet of large oceanic predators such as the sperm whale (Clarke 1966; Clarke and MacLeod 1974) and the pelagic sharks Sphyrna zygaena, S. lewini, Prionace glauca and Carcharhinus longimanus (Dunning et al. 1993).

Despite a good description of body morphology and change in form during early ontogenesis (Chun 1910; Pfeffer 1912), little is known about the ecology of An cistrocheirus lesueurii and nothing is known about its age, growth and maturation, except for a description of the reproductive system and oocyte morphology in one mature female (250 mm ML) from Japanese waters (Okutani 1976).

In contrast, growth and maturation of other mesopelagic/epipelagic squids of the related family Enoploteuthidae are well studied. It is notable that before an elevation of Ancistrocheirinae to the family rank by Clarke and Trueman (1988), this subfamily was included in the Enoploteuthidae (Nesis 1978, 1987). Statolith aging studies have showed that the small enoploteuthids Abraliopsis atlantica (Arkhipkin and Murzov 1990), Abralia trigonura (Young and Mangold 1994), Abraliopsis hoylei (Arkhipkin 1996) and the mediumsized Enoploteuthis leptura (Arkhipkin 1994) have a short, 6-mo life span, slow growth rates, and mature at 3 to 4 mo. Daily periodicity of growth increment deposition has been validated for hatchlings of A. trigonura (Bigelow 1992).

This study provides estimates of age, growth, duration of spawning period and age at maturation of Ancistrocheirus lesueurii. These estimations are made using

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statolith aging techniques, which are now the only practical tool in squid age and growth studies (Jereb et al. 1991).

Materials and methods

A total of 52 specimens of Ancistrocheirus lesueurii (25 to 290 mm ML) were caught during a biological survey on the orange-back squid Sthenoteuthis pteropus (Ommastrephidae) carried out in the central-east Atlantic between August and September 1988. The survey was conducted from the R.V. "Ocher" in the open waters of the western part of the Gulf of Guinea ($2^{\circ}15'$ N to $3^{\circ}30'$ S; $4^{\circ}05'$ to 15° W) off the Exclusive Economic Zones of African countries. Squids were captured at night at depths of 250 to 500 m using the Russian pelagic rope trawl RT/TM-33 (vertical opening 8 to 10 m) equipped with a 6 mm mesh liner. Four large mature females of A. lesueurii (222 to 423 mm ML) were taken near the bottom above the continental slope off the southern part of the west Sahara $(21°22' N; 17°33' W at 700 m depth)$ by R.V. "Bakhchisaraj" in August 1987.

Measurements on captured squid included dorsal mantle length (ML) measured to the nearest 1 mm and body wet weight (BW) to the nearest 0.1 g. Maturity stages were assigned after the scale developed for ommastrephid squids (Zuev et al. 1985).

Statoliths were extracted from squids aboard ship, placed in seawater to remove organic debris and stored in 96% ethanol for further analysis (after Arkhipkin 1991) in the Laboratory of Commercial Invertebrates of AtlantNIRO. Terminology used is after Clarke (1978) and Lipinski et al. (1991). Before grinding, the total statolith length (TSL) and rostrum length (RSL) were measured using an Olympus B071 zoom microscope $(32x)$. The length from the focus to the tip of the rostrum (focus-rostral length, FRL) was also measured in ground statoliths for further analysis of individual growth. The direction of growth of the rostrum changes during ontogenesis (i.e. the rostrum curves laterally), therefore the FRL was measured along the curved rostrum axis. During grinding, the rostrum was broken into nine statoliths, and FRL could not be measured.

Usually, one statolith from each pair was ground on both sides using wet waterproof sandpaper (600 grit) and polished with fine sandpaper (1000 grit). Ground statoliths were embedded in Canada balsam and placed in an oven (80 to 90°C) for 1 h to dry. Canada balsam substantially increased the resolution of growth increments. Growth increments were examined under a Nikon 104 microscope $(400\times)$ and counted by two observers using an eye-piece micrometer (Arkhipkin 1991) from the nucleus to the edge of the rostrum as previously described for loliginids (Natsukari et al. 1988) and for Abralia trigonura (Young and Mangold 1994). If the statolith was overground, the other statolith from the same specimen was examined. Growth increments were invisible near the rostrum edge in two squids, and these statoliths were not used in further analysis. The total number of growth increments for each statolith was taken as the mean of the two replicate counts if the deviation between the two counts was less than 5%.

Assuming growth increments to be daily, hatching dates were back calculated and growth curves were fitted to the increment number-at-length and increment number-at-weight data using the Fishparm software (Saila et al. 1988). The growth curves were constructed for estimation of daily growth rates and instantaneous rates of growth, with no biological significance given to their coefficients.

To estimate daily growth rates (DGR, mm or g d⁻¹) and instantaneous rate of growth (G), values of both ML and BW were

Fig. 1 Ancistrocheirus lesueurii. Light micrograph of the statolith from an immature female, age 201 d, mantle length 72 mm. A General view of the ground statolith (N nucleus; R rostrum; LD lateral dome; D dorsal dome; L lunar bands) **B** nucleus (N) ; C growth increments calculated for each 25-d interval using the formula of the best fitted curve. DGR and G were calculated after Ricker (1958) as:

$$
DGR = (W_2 - W_1)/T ,
$$

 $G = (\ln W_2 - \ln W_1)/T$,

where W_1 and W_2 are calculated ML or BW values at the beginning and end of the time interval $(T = 25$ d).

Results

Statolith microstructure

The initial point of increment formation (focus) is dark, irregularly shaped and situated within the oval nucleus (Fig. 1A, B). The maximum diameter of the nucleus varied between 18 and 28 μ m (mean 23.33 μ m, $SD = 2.77$, $N = 10$). In adult statoliths, the nucleus lies deeply under the spur, unlike statoliths of loliginids and ommastrephids where it is situated near the anterior surface of the statolith (Figs. 5 and 6 in Lipinski 1993a). The pointed tip of the rostrum first appears on the outline of the second or third growth increment. The wing does not touch the nucleus but attaches to the 10th to 15th growth increment (Fig. 1B). Statoliths of the two largest mature females and the two mature males were chosen to show the variation in increment widths along the rostrum (Fig. 2). In general, the first 50 to 60 growth increments were narrow (5 to 6 μ m), and then increased in width to $7-10$ µm. However, the presence of several narrow $(5 \text{ to } 6 \text{ \mu})$ increments within the wide increments (from Increment No. $50-60$ to No. $90-100$) resulted in a "saw-tooth" pattern in the increment widths (Fig. 2A). Increment width decreased gradually to $2 \mu m$ in mature males from Increment No. $100-120$ to No. $280-300$ (Fig. 2B). In a mature female of 327 mm ML, increment width remained approximately constant from Increment No. 120 to 350, then slightly decreased in width to Increment No. 500. In a female of 423 mm ML, after a sudden drop in the width in Increments No. 90 to 170 (3 to 4 μ m) another peak appeared in Increments No. 171 to 190 (6 to 7 μ m).

Thus, three growth zones could be distinguished by increment width, namely the zones of medium (Zone 1, Increment No. 1 to $50-60$), wide (Zone 2, Increment No. $50-60$ to $100-120$ and narrow (Zone 3, Increment No. $>100-120$) growth increments. However, there were no distinct boundaries between these zones, and increment width varied (sometimes considerably) between adjacent increments within each zone, i.e. in a female of 423 mm ML (Fig. 2A). The growth zones were not distinguished by colour, although the nucleus was opaque and the microstructure became more translucent towards the margin (Fig. 1A, D).

within the rostrum with additional center (AC) of increment formation; **D** terminal point of the rostrum; **E** lunar bands (L) in the lateral dome. Scale bars = 100 μ m (A) and 25 μ m (C). Magnification ratio of B , D and E is the same as in C

Fig. 2 Ancistrocheirus lesueurii. Statolith increment widths of A mature females and B males measured along the rostrum. Data smoothed by five-increment running average Fig. 3 Ancistrocheirus lesueurii. Allometric growth of A the statolith

Distinct second-order bands were revealed within all Ancistrocheirus lesueurii statoliths (Fig. 1E). The opaque colour of each band (towards the statolith margin) was weaker than that of the previous band. Growth increments were wider in the inner portion and narrower in the outer portion of each band. It is noteworthy that the bands within the dorsal and lateral dome were more prominent than within the rostrum (Fig. 1D, E). Growth increments were enumerated in 20 randomly chosen bands of various statoliths. The number of growth increments within each band varied from 24 to 32 (mean 27.65, $SD = 1.904$). It was also possible to distinguish two "sub-bands" within each band by the presence of a well-resolved check between them (Fig. 1E). The number of growth increments within the "sub-band" varied from 10 to 16 (mean 13.6, $SD = 1.463$).

Statolith growth

Statoliths of Ancistrocheirus lesueurii are relatively large with the TSL ranging from 0.79 mm (3.04% ML) in an immature male of 26 mm ML to 2.9 mm (0.69% ML) in a large mature female of 423 mm ML. The allometric relationship between TSL and ML was negative (Fig. 3; Table 1). Absolute statolith growth was best described by the power function (Fig. 3). There was no sexual dimorphism in either allometric or absolute growth of A. lesueurii statoliths.

length versus mantle length and B relationship between statolith length and age (number of growth increments)

Age and growth of squid

The smallest male (25 mm ML) had 92 increments, while the smallest female (38 mm ML) had 91 statolith increments. Maximum number of growth increments in males (mature male of 90 mm ML, 360 increments) was considerably lower than that in females (mature female of 423 mm ML, 609 increments). The increment number-at-length data were best fitted by a Gompertz growth curve in females and a von Bertalanffy growth curve in males. However, the increment number-atweight data were best described by other functions: a power curve in females and Gompertz curve in males, respectively (Fig. 4; Table 1). Sexual dimorphism in length (females became larger) was obvious in individuals having >200 to 250 growth increments (Fig. 4A), that in body weight later $(>250$ to 300 increments) (Fig. 4B). Assuming the "one day-one increment" hypothesis, the ML DGR in females increased constantly, achieving maximum values of 1.15 mm d^{-1} at an age of 600 d, whereas the ML DGR in males decreased to 0.1 mm d^{-1} at 320 d. The BW DGR had a similar trend with a maximum of 11.2 g d^{-1} at 600 d in females (Fig. 5). Instantaneous rates of growth in ML and BW decreased gradually in both sexes, although faster in males than in females (Fig. 6).

An attempt was made to construct individual growth curves for the two largest females and the three largest Table 1 Ancistrocherius lesueur $ii.$ Different relationships between total statolith length (TSL, mm) , mantle length $(ML,$ mm), body wet weight (BW, g) and age (d). Parameters of the power (allometric) function $Y = aX^b$, Gompertz growth function $W = W_0 \times$ $exp{G[1 - exp(-gt)]}$, and von Bertalanffy growth function $L(t) = L\{1 - \exp[-K(t - t_0)]\},\,$ their asymptotic standard errors and R^2

Fig. 4 Ancistrocheirus lesueurii. Relationships between A mantle length and age (number of growth increments) and B total body weight and age (f female; m male; imm immature; mat mature)

males to compare them with the group length-at-age growth curves. The individual growth curves were backcalculated using: (1) mantle length of a given squid at capture; (2) the widths of growth increments along the

Fig. 5 Ancistrocheirus lesueurii. Daily growth rates of A mantle length and B body weight

rostrum axis within the statolith (Fig. 3) and (3) the calculated relationship between mantle length and rostrum length (Fig. 7). The relationships between the ML and either RSL or FRL were best described by the power function (Fig. 7). However, the relationship between ML and FRL had a higher correlation coefficient

Fig. 6 Ancistrocheirus lesueurii. Instantaneous growth rates of A mantle length and B body weight

 $(R^2 = 0.853)$ than ML versus RSL $(R^2 = 0.773)$, and the former relationship was used for further calculations. Assuming

$$
ML = a \times (FRL)^b,
$$

the daily difference in FRL is

$$
FRL_2 - FRL_1 = (ML_2/a)^{1/b} - (ML_1/a)^{1/b} ,
$$

where $FRL₂$ and $FRL₁$ are the focus-rostral lengths and $ML₂$ and $ML₁$ are the mantle lengths on present (2) and previous (1) days. Hence,

$$
ML_1 = a \times [(ML_2/a)^{1/b} - FRL_2 + FRL_1]^b
$$
.

Starting from the known ML_2 (mantle length at capture) with known values of $FRL₂$ and $FRL₁$ and previously estimated values of a and b , the individual growth curve was back-calculated to Increment No. 90 (age 90 d). Further back-calculation (prior 90 increments) was not undertaken since the relationship between FRL and ML was estimated for the ML ranging from 25 mm (90 increments) to 423 mm (609 increments).

Calculated individual growth curves for both sexes were somewhat different in comparison with the group growth curves (Fig. 8). They were more linear and

Fig. 7 Ancistrocheirus lesueurii. Relationships between A mantle length and rostrum length of the statolith and B mantle length and focus-rostral length of the statolith

Fig. 8 Ancistrocheirus lesueurii. Calculated individual growth curves of mature A females and B males. Symbols as in Fig. 4

Fig. 9 Ancistrocheirus lesueurii. Back-calculated hatching frequencies by month for 1986

slightly curved (asymptotically?) during the last 50 to 60 d. Based on the individual growth curves, larger specimens had a greater length during the whole age range studied (Fig. 8).

Size and increment number at maturity and hatching dates

Both sizes and increment numbers at maturity differed in both sexes (Fig. 4). The minimum number of increments in mature males was 194 (102 mm ML), and the maximum number of increments in immature males was 244 (95 mm ML). Females became mature at larger sizes and had more growth increments than males. The minimum number of increments in mature females was 365 (196 mm ML), and the maximum number of increments in immature females was 326 (145 mm ML). Except for the two mature females (196 mm ML, 365 increments and 185 mm ML, 404 increments, respectively), all mature females had been copulated and had sperm reservoirs attached to the inner mantle wall. None of the immature females had copulated. Assuming the daily nature of statolith growth increments, the mature phase of growth in Ancistrocheirus lesueurii appeared to last for about 176 d in males (48.3% of the life) and 244 d in females (40.0% of the life). Based on backcalculated hatching dates, A. lesueurii hatches throughout the year with a peak between November and March (Fig. 9).

Discussion

Statolith growth increments of Ancistrocheirus lesueurii were well resolved, unambiguous and similar to the ammoniacal mesopelagic squid Histioteuthis miranda (Lipinski 1993a), the closely related Abralia trigonura (Bigelow 1992), and the ommastrephid squid Illex illecebrosus (Dawe et al. 1985). The validation of daily deposition of statolith growth increments has been confirmed for the postembryonic period in a number of squid species (reviews: Jackson and Choat 1992; Lipinski 1993a). Growth increments in A. lesueurii statoliths were therefore assumed to be formed daily in the present paper.

Growth increments within Ancistrocheirus lesueurii statoliths can be grouped into three growth zones based on increment width. This pattern is similar to the increment width sequence in the mesopelagic squid Abralia trigonura (Young and Mangold 1994). The growth increment widths in the statolith rostrum of both species were ca. 3 to 5 μ m in the first increments, increased sharply up to 8 -10 µm and then decreased steeply to 1.8 $2 \mu m$. The peak in increment width within the increment sequence in A. trigonura (Increment No. 38 to 45) occurred earlier than in A. lesueurii (Increment No. 50 to 120). Furthermore, the period of maximum statolith growth rates in A. trigonara (first 8 to 10 increments, Young and Mangold 1994) was much shorter than in A. lesueurii (first 50 to 70 increments). Comparing the width of growth increments in two directions (i.e. from the focus to rostrum, FRL; and from the focus to the dorsal dome, FDDL), it was possible to see that the first growth zone (with narrow growth increments) in the FRL could not be seen in the FDDL of A. lesueurii statoliths. The same results were obtained for the FDDL in A. trigonura, where the width of the initial 41 growth increments was the greatest (Bigelow 1992). Differences in increment width in the FRL and FDDL appeared to be due to different growth rates of the rostrum and dorsal dome of the statolith during the paralarval phase. During the first days of paralarval life, the statolith is tear-drop shaped with a small rostrum, i.e. the growth rates of the rostrum are slower than those of the dorsal dome (Bigelow 1992). However, at an age of 38 to 45 d in A. trigonura and at 50 to 120 d in A. lesueurii, the rostrum grows more quickly, and the statolith takes on the adult form. After the period of rapid rostral growth, the statolith increased in size proportionally (Bigelow 1992; present paper).

Bigelow (1992) proposed that the transition in the FDDL increment width of Abralia trigonura statoliths correlated with a life history transition from the paralarval to postparalarval phases. However, the increment width change is not as well defined in the FRL of A. trigonura (Young and Mangold 1994). Transition from the wide to narrow growth increments in the FRL in Ancistrocheirus lesueurii corresponded to 30-35 mm ML. These sizes are very close to the maximum ML (29 mm) of Thelidioteuthis alessandrinii (Clarke 1966), which is now considered to be a juvenile of A. lesueurii (Bello 1992). Typically, T. alessandrinii (= juveniles of A. lesueurii \leq 29 mm ML) are caught at depths \leq 1000 m; while A. lesueurii >30 mm ML are captured mainly near underwater mountains or oceanic islands, where there is strong upwelling of deep bathyal waters, or they are taken from the stomachs of nektonic predators hunting in deep water (Clarke 1966; Dunning et al. 1993; Nesis 1993). In the present study, A. lesueurii $>$ 30 mm ML were captured at depths of 250 to 500 m only in the region of the equatorial divergence, where there is upwelling of bathyal waters (together with bathyal fauna, Arkhipkin and Schetinnikov 1989). Thus, it appears that the second transition in the rostrum growth of the statolith (from the Zone 2 to Zone 3) coincides with the life history shift of A. lesueurii from epipelagic and upper mesopelagic to a bathyal habitat. Unfortunately, because of a lack of squid <26 mm ML in my material, it is not possible to relate the transition in rostrum growth (from the Zone 1 to Zone 2) to the paralarval/juvenile life history shift.

Periodic bands and sub-bands (i.e. second-order bands sensu Lipinski et al. 1991) in the microstructure of Ancistrocheirus lesueurii statoliths appeared to be related to the lunar cycle due to a mean number of growth increments within them. Formation intervals of 2 to 4 wk could be related to 2-wk periods in the tidal cycle. Similar bands have been observed in juveniles of many marine fishes (i.e. Campana 1984). The origin of such bands has been explained either by an endogenous lunar rhythm (Kavaliers 1982) or tidally induced ambient temperature fluctuations (Campana 1984). The same periodic lunar bands have been observed in the squids Loligo opalescens (Spratt 1978) and Gonatus fabricii (Kristensen 1980). However, the second-order bands form irregularly in some squids. No significant periodicity in the number of growth increments within the second-order bands has been found in the statoliths of Photololigo edulis (Natsukari et al. 1988), Loligo vulgaris (Natsukari and Komine 1992) or Berryteuthis magister (Natsukari et al. 1993).

The extreme sexual dimorphism in Ancistrocheirus lesueurii has not been documented previously due to the small number of adults examined in earlier studies (Clarke 1966). Females can reach 3 to 3.5 times the length and 10 times the weight of males. Sthenoteuthis pteropus (Zuev et al. 1985) is the only other squid to show such extreme sexual dimorphism. In other small and medium-sized enoploteuthids, males and females are either of the same size or females are slightly larger (Arkhipkin and Murzov 1990; Arkhipkin 1994; Young and Mangold 1994).

The striking sexual dimorphism is also reflected in the age and growth rates of Ancistrocheirus lesueurii. Males live ca. 1 yr, while females only start maturing at this age and obviously live >1.5 yr. Based on their possible spawning grounds in the bathyal, deep-water layers with low temperatures and corresponding prolonged embryogenesis (several months, see Fig. 1 in Boletzky 1994), the whole life span of females may last ca. 2 yr. It seems that the life span >1 yr is characteristic to mesobathypelagic squids which spend the major part of their life in cold deep water. Similar results have been obtained for the meso-bathypelagic Architeuthis sp. which is assumed to live at least ca. 3 yr based on statolith microstructure analysis (Lipinski 1993b). Different maximum ages have been previously observed in males and females of other oceanic squids, but not as great as in A. lesueurii. Females of Abraliopsis atlantica live only 1 to 1.5 mo longer than males (Arkhipkin and Murzov 1990), while females of Sthenoteuthis pteropus live 2 mo longer than males (Arkhipkin and Mikheev 1992). The biological reasons for such marked sexual dimorphism in the age of A. lesueurii are unclear.

Ancistrocheirus lesueurii is a slow-growing squid. It attains 25 to 30 mm ML at an age of 100 d, which is similar to the other small mesopelagic enoploteuthids Abraliopsis atlantica (Arkhipkin and Murzov 1990) and Abralia trigonura (Young and Mangold 1994). These sizes are much smaller than those of the same-aged, medium-sized enoploteuthid Enoploteuthis leptura (Arkhipkin 1994) and abundant epipelagic juveniles of the ommastrephid Sthenoteuthis pteropus (Arkhipkin and Mikheev 1992). After ontogenetic migrations into bathypelagic waters at the ML $>$ 30 to 35 mm and age >120 d, the instantaneous growth rates of A. lesueurii gradually decrease to the minimum known values for squids.

The year-round spawning of Ancistrocheirus lesueurii is similar to other oceanic and neritic squids (Arkhipkin and Murzov 1990; Arkhipkin and Mikheev 1992; Jackson and Choat 1992). Males probably mate at the end of their 1-yr life due to the minimum age (ca. 1 yr) of copulated females. However, it is possible that males copulate earlier with older females belonging to prior seasonal generations. After mating, females live at least 6 to 7 mo. Taking into account the sampling localities of large mature females which have copulated $(>200 \text{ mm})$ ML), they might spawn at great depths either near the continental slope (as proposed by Nesis 1993) or in the open ocean.

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