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## Age and growth of *Electrona antarctica* (Pisces: Myctophidae), the dominant mesopelagic fish of the Southern Ocean

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**Abstract** Numerically and in biomass, the lanternfish *Electrona antarctica* is the dominant fish in the vast pelagic region of the Southern Ocean bounded on the north by the Antarctic Convergence and in the south by the Antarctic continental shelf. It is an important krill predator, and in turn is important in the diets of flighted and swimming seabirds. Further, it is the southernmost and coldest-dwelling representative of the globally distributed fish family Myctophidae. The present study was undertaken to estimate the species' growth rate and average life span, to incorporate the information in a basic energy budget, and to compare the growth of *E. antarctica* with more northerly confamilials. Fishes were aged using primary growth increments that were resolved on sagittal otoliths using three sequential techniques: thin-section grinding and polishing, etching, and scanning electron microscopy (SEM). Based on increment width (0.8 to 1.2  $\mu\text{m}$ ), continuity, and previous studies on confamilials, the microincrements were assumed to be deposited on a daily basis. Montages of SEM photomicrographs were constructed for each sagitta to allow the daily rings to be counted over the entire life span of 31 individuals representing the entire size range of the species. Results suggest a larval stage of 30 to 47 d and a maximum life span of 3.5 yr, with females growing faster than males in the last 1.5 yr of life and reaching a larger maximum size. Construction of a

simple energy budget using the best information available suggests that a surplus of energy is available to support the observed growth rates (0.05 to 0.07 mm  $\text{d}^{-1}$ ). The results of the present study contrast markedly with previous estimates of an 8 to 11 yr maximum age for *E. antarctica*. These results provide important data addressing the ecology and population dynamics of the pelagic Antarctic ecosystem. *E. antarctica* is the end-member species in the continuum of vertically migrating myctophids that extend from the equator to the polar circle. Its growth rate is consonant with that of all other myctophid species examined using primary growth increments to determine age. The present study, in conjunction with earlier studies, suggests that growth rates of mesopelagic species are far higher than previously thought.

### Introduction

The fish fauna within the Southern Ocean is characterized by a low diversity of species and a high level of endemism. The most abundant oceanic fishes in Antarctic waters are the lanternfishes (family Myctophidae), deepsea smelts (family Bathylagidae), barracudinas (family Paralepididae), and bristlemouths (family Gonostomatidae; Andriashev 1965; Hempel 1985; Kock 1985). Taxa from these families account for >95% of the biomass of mesopelagic fishes in the upper 1000 m of the Weddell-Scotia sea region (Lancreft et al. 1989).

Three species of the genus *Electrona* are abundant in the Southern Ocean, *E. antarctica* (Günther, 1878), *E. carlsbergi* (Tåning, 1932), and *E. rissoi* (Cocco, 1829). Of these, *E. antarctica* is the numerical dominant in midwater trawl samples taken throughout the Southern Ocean (Rowedder 1979b; Hulley 1981; McGinnis 1982; Linkowski 1987; Lancreft et al. 1989). It is considered to be the only lanternfish endemic to Antarctic waters, as it is only found south of the Antarctic convergence (Hulley 1981; McGinnis 1982).

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*Electrona antarctica* is a strong diurnal vertical migrator, with peak abundance at 0 to 300 m at night and 650 to 920 m during the day. The diet of postmetamorphic *E. antarctica* (30 to 110 mm standard length, SL) consists primarily of copepods, ostracods, and euphausiids, including the krill, *Euphausia superba*; (Hopkins and Torres 1989; Lancaft et al. 1991). Thus, the lanternfish *Electrona antarctica* is significant to the pelagic ecosystem as a major component of the fish biomass and as a dominant krill predator (Williams 1985; Kock 1987; Lancaft et al. 1989). In turn, as an important prey item of seabirds in the open waters of the Antarctic region (Ainley et al. 1986), *E. antarctica* plays a pivotal role in the transfer of energy from the macrozooplankton (e.g. krill, *Euphausia superba*) to higher trophic levels (e.g. Antarctic seabirds and mammals).

There is a notable lack of information available on the growth rates and life spans of *Electrona antarctica* and for Antarctic mesopelagic fishes in general (Linkowski 1987), particularly compared to the information on tropical, temperate, and subarctic species. Accurate age determinations provide basic life-history information and are imperative for describing a species' population dynamics. Two age-related studies were attempted for *E. antarctica* (Rowedder 1979a; Linkowski 1987), but they yielded inconclusive results, further emphasizing the clear need for this fundamental information.

Most aging studies on high-latitude fish species are based on ages determined from annual rhythmic depositions (seasonal "rings") in otoliths as time marks (Blacker 1974; Williams and Bedford 1974). The otoliths of Antarctic fishes do not appear to contain interpretable annual deposition-patterns, perhaps because of the lack of strong periodicity in Antarctic hydrographic conditions (Radtke 1984), particularly in sea-surface temperature. Similar complications have been documented for tropical species, where seasonally induced marks are irregular, indistinct or absent. Otoliths from Antarctic fish are usually small and difficult to analyze using conventional methods.

Application of microstructural techniques to otoliths of Antarctic fishes has proven successful for the few species analyzed. The focus has been almost exclusively on the age and growth of the dominant, coastal-dwelling, demersal species of the suborder Notothenioidei (Wohlschlag 1961; North et al. 1980; Townsend 1980; Radtke and Targett 1984; Radtke 1987; Radtke and Hourigan 1990). These taxa are abundant shallow-water dwellers that can be maintained in captivity for validation experiments.

The focus of the present study was to resolve primary growth increments from sagittal otoliths in order to estimate the average life span and calculate growth rates for the numerically dominant Antarctic lanternfish *Electrona antarctica*. The data will allow better evaluation of the role of *E. antarctica* in the energetics of the Southern Ocean ecosystem. In addition, because *E. antarctica* is the only polar species in a pan-oceanic

family, the data will allow a better understanding of growth in mesopelagic species in general.

## Materials and methods

### Sampling

Sampling was conducted in the Southern Scotia Sea (60°S; 40°W) in the austral spring (1983) and in the northwest Weddell Sea (65°S; 46°W) during the austral fall (1986), as part of the Antarctic Marine Ecosystem Research at the Ice Edge Zone (AMERIEZ) project (Fig. 1). Pelagic fishes were sampled with an opening-closing Tucker trawl (9 m<sup>2</sup> mouth opening) at depths between 0 and 1000 m in the open water near the marginal ice zone. Details of the trawling procedures are given in Lancaft et al. (1989). Aboard ship, the myctophid *Electrona antarctica* was identified, and measured to the nearest millimeter standard length. The sex of individuals was recorded when possible. Sagittal otoliths were removed from each fish with forceps, and were stored dry on micropaleontological slides.

### Preparation of otoliths

Sagittal otoliths were prepared for analysis using three sequential microstructural techniques: grinding and polishing, thin-sectioning, and scanning electron microscopy (SEM). These techniques have proven useful in discerning microstructural growth increments in the sagittal otoliths of several species (see review by Campana and Neilson 1985). All three techniques were applied consecutively to the same otolith, from the grind- and-polish technique to the more elaborate SEM application.

Due to their small size (<2 mm) and the protocol to be followed (e.g. thin-sectioning), sagittae were embedded in a low-viscosity epoxy resin following the hard-formula recipe of Spurr (1969). After embedding, the whole sagittae were ground by hand to the mid-sagittal plane with water and wet/dry sandpaper (400, 600, 1500, and 2000 grit), and then polished using a polishing cloth and a 0.05  $\mu$  gamma alumina slurry. All samples were sonicated between successive grinding and polishing to avoid cross-contamination of grits and to reduce surface scratches. Abrading revealed three distinct regions within each sagitta. Using the terminology and definitions of Gartner (1991a), the regions were the premetamorphic or larval zone (LZ), perinuclear or postlarval zone (PLZ), and postmetamorphic zone (PMZ) (Fig. 2). These regions are described in "Results-Internal otolith morphology".

Initially, the external morphologies of sagittae were examined for analysis of whole-otolith growth ( $n = 117$ ). Two radius measurements were recorded using an ocular micrometer. The radius of the entire otolith (total radius; TR) was measured from the central core (nucleus, NU) to the outer edge along the posterior axis (40 $\times$  magnification) and the larval zone radius (LZR) from the central core (NU) to the last clear continuous increment (metamorphic check) in this region (250 $\times$  magnification). All micrometer measurements were converted to millimeter units. The radii of the sagittae were then regressed against standard length.

Sixty of the original 117 sagittae were further abraded until a plane through the core was visible. Primary growth increments within the larval zone could then be enumerated under oil using a compound microscope coupled to a high-resolution video camera and monitor system. All counts were initiated from a well-defined medial increment (i.e. hatch check, 630 $\times$  magnification) within the larval zone. This region was counted at least three times by 2 to 3 independent readers. Counts were accepted if readers agreed within a 3% range of error. If counts between readers differed by more than 3%, two readers repeated the count together. If repeated counts did not agree, then the sample was not included in the analysis.

Following enumeration of the larval zone with light microscopy, whole sagittae were sliced along a frontal plane using an Isomet

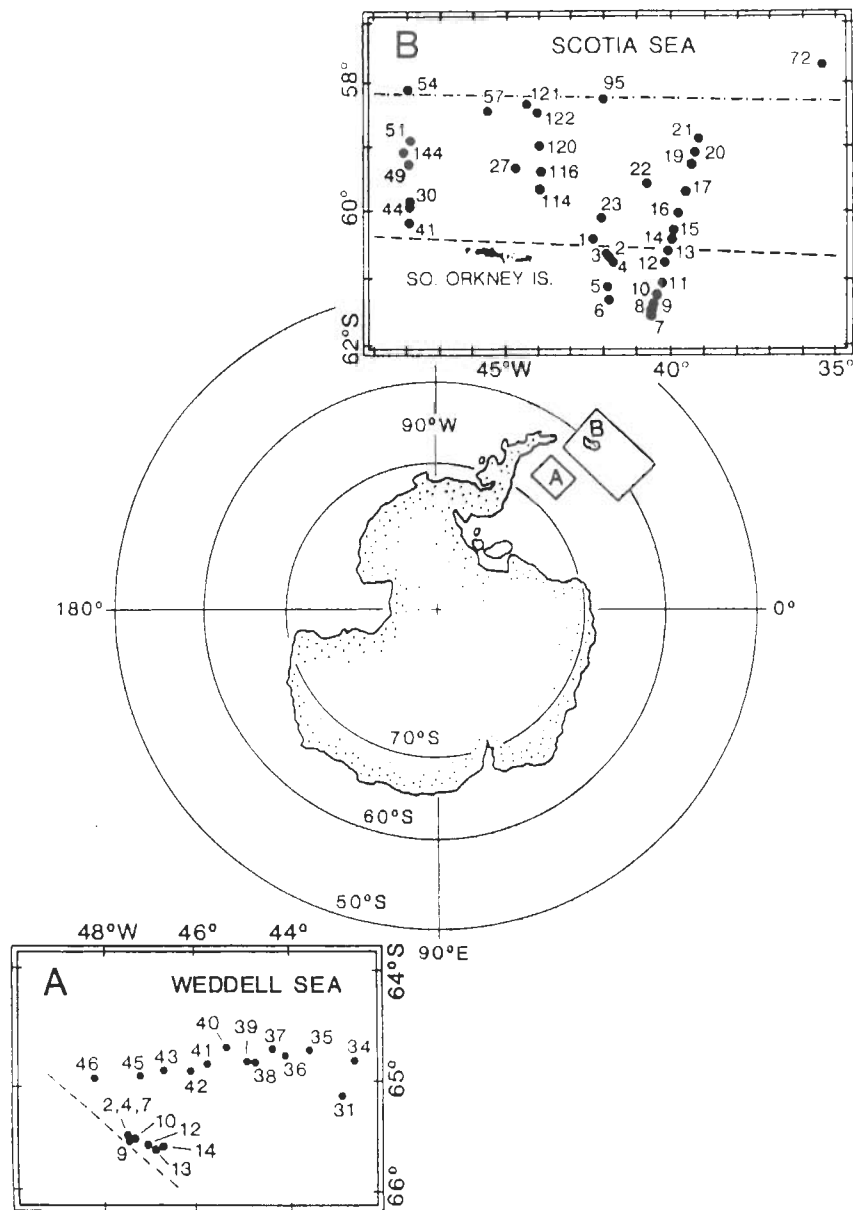


Fig. 1 Sampling areas in Weddell Sea (A) and Scotia Sea (B) (Dashed lines correspond to ice edge) Adapted from Lancraft et al. (1989)

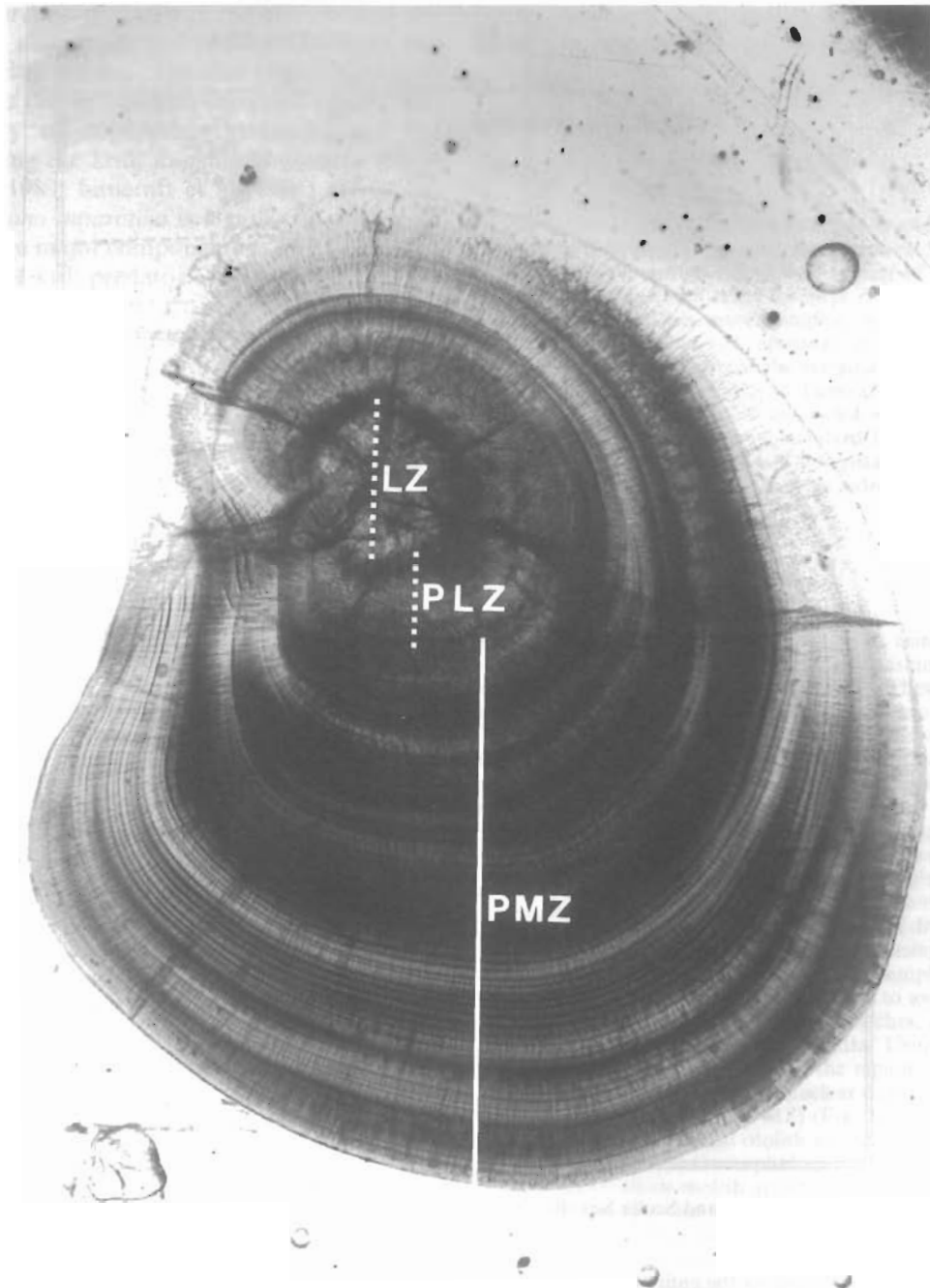
saw to obtain a flat section containing the entire core region. The frontal section was selected because of the anteroposterior growth of the sagitta. This axis also incorporated the entire growth history of the individual and contained the least compressed increments. Sections were rinsed, remounted on modified slides, and abraded until a plane through the core and peripheral regions was visible and primary growth increments could be discerned using light microscopy. Sections were polished smooth and then etched using solutions of 1% HCl (12*N* hydrochloric acid; pH 2.0 to 3.0). Etching is essential for SEM analysis, and produces a three-dimensional relief that provides consistent patterns throughout the sections.

After etching, sections were secured to metal stubs with double-sided sticky tape, coated with gold-palladium alloy in a sputter-coater, and examined with the scanning electron microscope (15 to 20-kV). Thirty-one of the remaining 60 sagittae survived the entire preparation for SEM analysis. A series of photomicrographs was taken of each sagitta to record the PMZ increments comprising the entire posterior growth axis. Montages of SEM photomicrographs

were constructed to reproduce the entire growth history of the individual. The PMZ primary growth increments were enumerated from each photomontage. All counts were made along the longest axis (posterior) between the last larval growth increment and the otolith periphery, exclusive of accessory primordia. The posterior axis was chosen for PMZ counts because primary growth-increment clarity and width along this growth axis allowed the most consistent and repeatable counts. Each pre- and postmetamorphic zone was counted in triplicate from the nucleus to the posterior edge. Primary growth increments were generally enumerated along the same radius. When this was not possible, counts were made along adjacent radii by following the clearest increments from the main primary radius to alternate radii.

#### Data analysis

Life spans were determined for each sex by adding the pre- and postmetamorphic zone increment-counts. Growth rates were de-



**Fig. 2** *Electrona antarctica*. Lateral view of internal morphology of sagitta of 82 mm (standard length) female, with three primary zones (LZ larval zone; PLZ postlarval zone; PMZ postmetamorphic zone). Transmitted light (magnification  $\times 100$ )

terminated by regressing standard length against age in days. All analyses and comparisons were considered statistically significant at the  $p < 0.05$  level. First-order decisions for determining the best fitting regressions were made using the coefficients of determination ( $r^2$ ). The models fitting the data were further compared using the mean-square errors of the residual sums of squares. Analysis of covariance (ANCOVA; SAS Institute) was used to analyze growth curves for significant differences between sexes. The mean-square errors of the residual sum of squares of the growth curves were compared using  $F$  values to determine the significance of regressions. If the  $F$  values were not significantly different, the intercept ( $a$ ) and slope ( $b$ ) for each growth curve were compared using chi-square or a Student's  $t$ -test.

## Results

The size distribution of postmetamorphic *Electrona antarctica* from which sagittae were extracted ranged from 23 to 103 mm SL. The maximum size of females (43 to 103 mm SL) exceeded that of males (37 to 83 mm SL) by 20 mm in both spring and fall collections. The results from the present study corroborate the size-related sexual dimorphism previously reported for *E. antarctica* (Rowedder 1979a). This trend is observed in

other myctophid species as well, e.g. *Ceratoscopelus warmingii* (Linkowski, et al. 1993; Gartner unpublished data).

Because of the intrinsic difficulties (e.g. small size, thickness, and increment width) in observing the primary growth increments within the sagittae of *Electrona antarctica*, a combination of all the techniques described above were necessary for consistent and repeatable resolution. To summarize, the larval zone (LZ) and accessory primordia (AP) were enumerated using oil-immersion under transmitted light, while counts of primary growth increments within the PLZ and PMZ zones were made from SEM photomontages. Two a priori assumptions regarding the present research were made: the first assumption was that one growth increment is deposited per day (cf. Linkowski, et al. 1993); the second that sagitta primary growth-increment size was a function of growth rate.

#### External otolith morphology

External morphology was analyzed in a total of 117 sagittae. Two measurements of radius taken along the anteroposterior axis were made: the total radius (TR) and larval zone radius (LZR). Pooled measurements of radii from males and females ranged from 0.425 to 1.9 mm for the TR and from 0.114 to 0.165 mm for the LZR. Morphometric measurements varied between males and females. Application of Tukey's multiple-range analysis of means (Manugistics Corp.) revealed significant differences in pairwise tests between mean standard length and total radius, while larval zone radius did not differ significantly as a function of sex.

Regression analysis of standard length on otolith radius showed a strong linear pattern. Results of significance testing (ANCOVAs) of all regressions revealed a significant difference in slope ( $p < 0.04$ ) and intercept ( $p < 0.02$ ) between males and females for standard length on total radius (SL:TR). Testing for standard length on larval zone radius (SL:LZR) revealed no significant difference in slopes ( $p < 0.56$ ), although the difference in intercepts ( $p < 0.0005$ ) was significant between sexes.

#### Internal otolith morphology

For the following descriptions of internal morphology, the terminologies for otolith microstructure defined by Campana and Neilson (1985) and Gartner (1991a) are used. For clarification, the term "primary growth increment", termed "ring" by Gartner (1991a), refers to a bipartite structure, composed of a calcified incremental zone and a proteinaceous discontinuous zone, formed over 24 h (Mugiya et al. 1981). One primary growth increment is assumed to represent one day of growth in the life of a fish, e.g. 100 growth increments represents a 100 d-old fish. Internally, three distinct regions were

apparent within each sagitta: the larval zone and accessory primordia, postlarval zone, and postmetamorphic zone. Examination of the internal morphology revealed inconsistencies in the clarity of primary growth increments. Of the initial 117 otoliths processed for this study, only a portion yielded the concordant and repeatable counts of primary growth increments that were used for final estimates of daily age and growth ( $n = 60$  otoliths for larval growth,  $n = 31$  otoliths for adult growth).

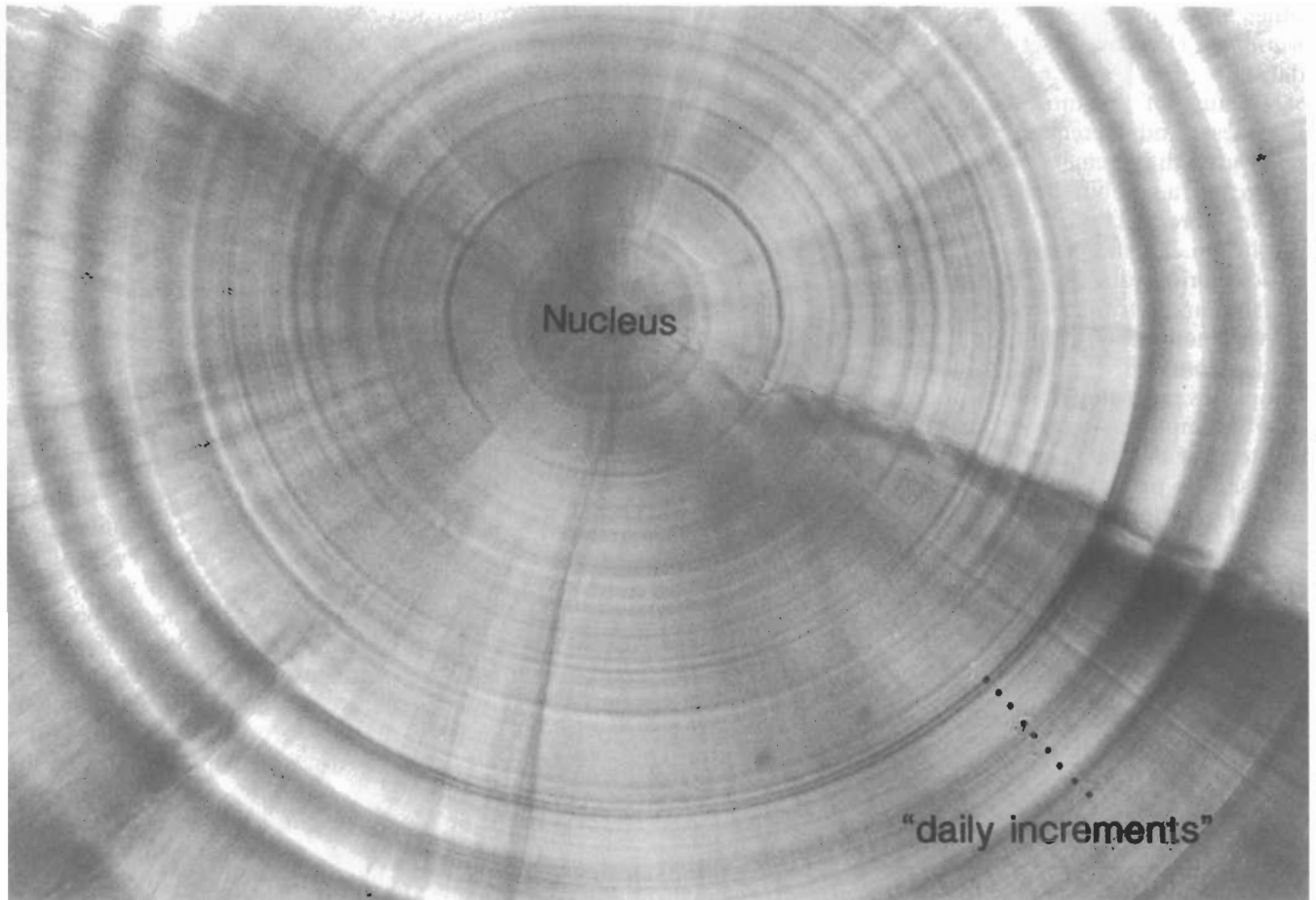
#### Larval zone, LZ

The larval zone included the core out to the metamorphic check usually located at the last continuous circular increment within the larval zone. Primary growth increments within the LZ were quite clear (Fig. 3), resulting in an 80% success rate for repeatable counts. Larval zone increments ranged in width from 2  $\mu\text{m}$  towards the center to 6  $\mu\text{m}$  near the periphery at the metamorphic check. Subdaily or nondaily increments (Geffen 1982) were also visible throughout the larval zone and generally ranged from 1 to 2 increments juxtaposed to form primary growth increments. Subdaily increments were not included in estimates of life spans.

Sixty of the initial 117 otoliths were successfully enumerated for estimates of larval stage-duration. Mean increment number varied, with counts ranging from 27 to 48 primary growth increments. Counts did not vary significantly by sex (Tukey's test,  $p < 0.05$ ). No correlation was apparent between the number of increments in the LZ and standard length of individuals.

#### Postlarval zone, PLZ

This portion of the sagitta was extremely dark, suggesting a high concentration of protein matrix and further suggesting a slower growth phase. The PLZ was nearly impermeable to transmitted light; only broad bands, ranging in number from 5 to 12, were visible. These broad bands may be analogous to the postlarval zone bands (PZB) described by Gartner (1991a). The width of the PLZ ranged from 1.38 to 1.55 mm, nearly the same as the LZ radius. The primary growth increments within this region were elucidated using SEM. However, the broad bands were no longer visible at high magnifications. Within this region, increments were often indistinct or incongruous. When the primary growth increments could not be successfully (5% repeatability) enumerated, an average increment count of 50 (range 38 to 60) calculated from readable sagittae was added to the total. The effects of estimating this portion of the growth axis accounted for < 5% of the total lifespan. Of the 60 otoliths evaluated for larval growth, a total of 31



**Fig. 3** *Electrona antarctica*. Daily growth-increments (●) within larval zone of sagitta of 60 mm (standard length) male. Transmitted light (magnification  $\times 630$ )

were successfully enumerated for estimates of the post-larval growth phase.

#### *Postmetamorphic zone, PMZ*

The postmetamorphic zone comprised the region from the terminal increment of the PLZ to the sagitta periphery (outermost edge). The PMZ was abruptly demarcated by a transition in elemental composition. Under transmitted light, the dark, nearly opaque, proteinaceous PLZ sharply contrasted with the contiguous, more translucent, predominantly aragonitic matrix of the PMZ. Within the PMZ, a regular pattern of alternating continuous and discontinuous zones defined the remainder of the growth axis. When observed with SEM, the incremental (accretion) zones were broader and only lightly etched, while the discontinuous areas were narrow and deeply-etched. PMZ increments were strikingly consistent; widths ranged from 0.8 to 1.4  $\mu\text{m}$  (Fig. 4). Increments observed in frontal sections began as narrow U-shaped structures, then became elongated and broadly U-shaped posteriorly toward the outer growth edge.

Of the 60 otoliths evaluated for larval growth, the same 31 used for analysis of the postlarval zone yielded reliable, repeatable counts of adult stage growth. Of those 31 sagittae, 20 were females and 11 were males.

#### Life spans and growth rates

Life spans were determined for each sex by addition of the LZ, PLZ and PMZ regions. The overall ages ranged from 403 to 1355 d for *Electrona antarctica* over the size range 40 to 103 mm SL. Males exhibited a slightly shorter life span than females. Life spans for males ranged from 403 to 1254 d. The largest female (103 mm SL) was also the oldest *E. antarctica*: (1355 d).

An initial growth curve for *Electrona antarctica* was estimated from pooled data (males and females combined; Table 1). The growth model selected was the linear equation: length =  $a + b$  (age), where length is standard length in mm,  $a$  is estimated intercept,  $b$  is estimated slope, and age (in days) is estimated from primary growth increments. The linear growth model described trends in the data well, best reflected the individual growth trajectories, accounted for the greatest

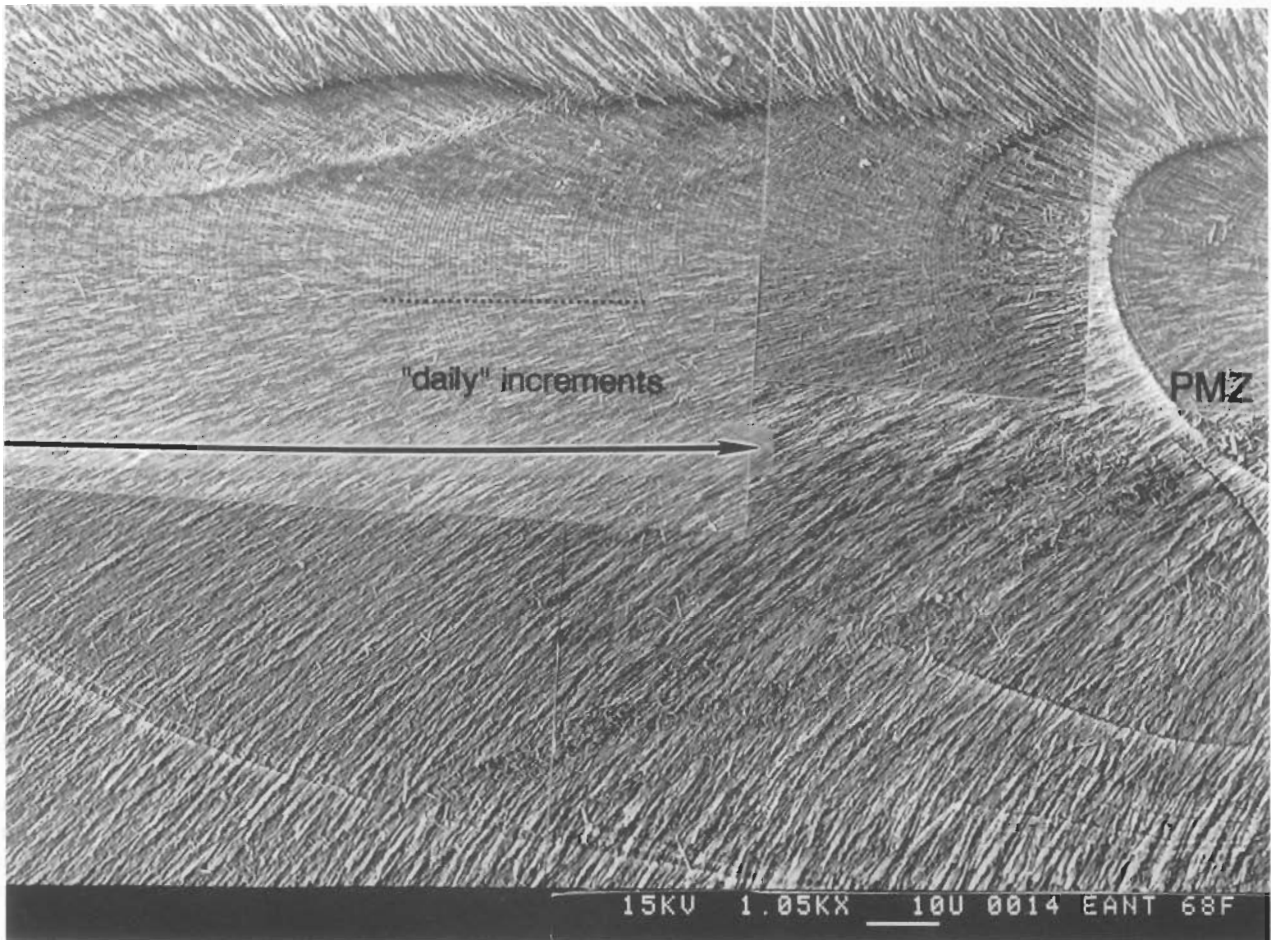


Fig. 4 *Electrona antarctica*. Photomontage of postmetamorphic zone (PMZ) of sagitta of 68 mm (standard length) female, showing daily growth increments (•). SEM (magnification  $\times 1005$ )

variability, and had the most realistic estimates of maximum length.

Separate growth curves were generated for each sex (Fig. 5). ANCOVA revealed a significant difference in growth rates for males and females (slopes =  $p < 0.007$  and intercepts  $p < 0.01$ ). Female growth continued along an established trajectory, while male growth rate showed a downward inflection from an earlier high growth rate consistent with that of females. Female growth was constant at  $0.07 \text{ mm d}^{-1}$ ; males showed a slower average growth of  $0.05 \text{ mm d}^{-1}$ .

Table 1 *Electrona antarctica*. Equations for overall growth curve (pooled data) and individual growth curves for males and females

Sex	Growth equation	(n)	$r^2$
Pooled (males and females)	$8.869 + 0.063 (\text{age})$	(31)	0.946
Males	$16.618 + 0.051 (\text{age})$	(11)	0.987
Females	$2.225 + 0.072 (\text{age})$	(20)	0.985

## Discussion

Depositional patterns in otoliths are indicative of an individual's growth and its environmental conditions. Major and minor events are reflected in the characteristic "banding" of the sagittae, including monthly signatures that reflect disruptions cued by lunar cycles, and transition zones representing hatching and metamorphosis. In the present study, primary growth increments within sagittae were assumed to represent the day-by-day developmental history of *Electrona antarctica*. Annual deposition patterns have not been detected within the otoliths of Antarctic fishes (Radtke and Targett 1984; Radtke et al. 1989; Radtke and Hourigan 1990), perhaps because of the lack of distinct annual periodicity in hydrographic conditions (Radtke 1987). There is a striking regularity of primary growth increments within the sagitta of *E. antarctica*; the lack of distinct annual rings leaves the investigator with daily rings as the best (and only) means of estimating individual age. This trend may apply to other mesopelagic fishes inhabiting the Southern Ocean (Linkowski 1987).

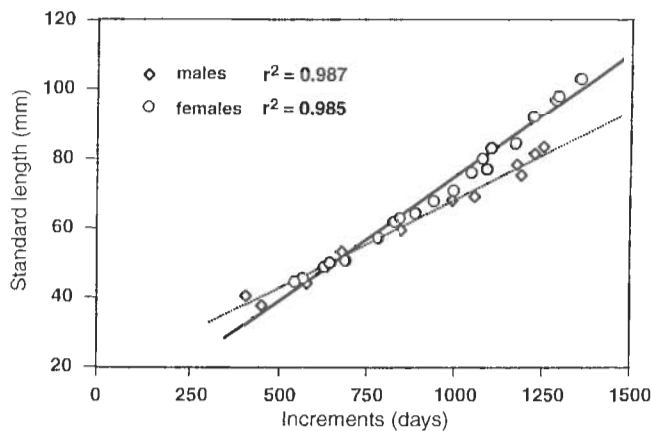


Fig. 5 *Electrona antarctica*. Growth rates estimated for males and females

There is general agreement that deposition of daily increments is governed by an endogenous rhythm, but that ring structure can be influenced by exogenous factors such as temperature, light, and pH (cf. Campana and Neilson 1985). Gartner (1991a) proposed that for myctophid species from the Gulf of Mexico, ring (primary growth increment) formation may be linked to activity levels and that light may be an indirect zeitgeber. Radtke et al. (1989), using the Antarctic nototheniid, *Trematomus newnesi*, demonstrated that daily increments were deposited even during the winter months, despite considerable variation in photoperiod during this season. The solar light-dark cycles at high latitudes ( $60^{\circ}$  to  $70^{\circ}$ ) are characterized by long periods of daylight (18 to 24 h) during summer followed by long periods of low light intensity (0 to 6 h) during winter. In an elegant study, Townsend and Shaw (1982) tested the importance of a diel light dark cycle in the deposition of daily increments by examining blue whiting, *Micromesistius putassou*, collected in summer above and below the Arctic circle. Results showed no modification of daily increment formation in fish exposed to 24 h continuous daylight above the Arctic circle. Thus, all high-latitude species that have been examined possess an endogenous rhythm of ring deposition that persists independent of an environmental light cue. This almost certainly explains the primary growth (daily) increment formation observed in *Electrona antarctica*.

#### Previous studies

Although the cosmopolitan importance of myctophids has been well documented, age and growth studies based on primary growth increments in otoliths have primarily focused on tropical and subtropical species (Gjøsaeter 1987; Young et al. 1988; Gartner 1991b; Giragosov and Ovcharov 1992; Linkowski, et al. 1993). Higher-latitude species, because of the presumed seasonal effects on growth, have been aged using annual growth increments

(Odate 1966; Halliday 1970; Smoker and Percy 1970; Gjøsaeter 1973, 1978; North et al. 1980; Burchett et al. 1984). Linkowski (1987) observed primary growth increments in the otoliths of two subantarctic species, *Electrona rissoi* and *E. (Metelectrona) ventralis*. Maximum ages in tropical-subtropical species ranged from 1.0 to 2.0 yr and in subantarctic species from 1.5 to 2.0 yr.

The first published age data for *Electrona antarctica* was contributed by Rowedder (1979a), who found it impossible to determine age by means of otoliths or operculae. Consequently, based on the trimodality of the length-frequency distribution ( $n = 1373$ ; 23 to 104 mm SL), he concluded that *E. antarctica* reached a maximum age of 3 yr, assuming that each mode represented a single year class. Miya et al. (1986) found similar modality in size-distribution data ( $n = 82$ ) for *E. antarctica* collected in the Southern Ocean south of Australia. Miya et al. proposed that *E. antarctica* matured in 2 yr at 70 to 85 mm SL and reached a maximum age of 3 yr. The estimates of age presented by Rowedder and by Miya agree with the results of the present study, although they are subject to the problems associated with length-frequency analysis for age and growth determinations; namely, as older fishes asymptotically approach a maximum size, an all-inclusive mode at the largest size class can mask the presence of several year classes.

Prior to the present work, no study has successfully used otolith microstructural techniques for age determinations of *Electrona antarctica*. Linkowski (1987) was unsuccessful in finding primary growth increments in the sagittae of *E. antarctica*. Therefore, he enumerated alternating opaque and hyaline zones, assuming that one opaque and one consecutive hyaline ring represented an annual time mark. His results using external features suggested that males attained 8 and females 11 yr of age, resulting in maximum ages nearly three times those estimated in the present study.

Our findings suggest that Linkowski's age estimates for *Electrona antarctica* are a consequence of using false annual time-marks, resulting in an overestimation of age. Other authors have noted that using presumed annual time-marks can result in an overestimation of age for mesopelagic species (Methot 1981; Lancraft et al. 1988; Young et al. 1988; Gartner 1991b). Examination of the internal morphology of *E. antarctica* sagittae revealed that no annual deposition patterns were visible, suggesting that externally visible features were the result of differences in compositional densities within the three-dimensional structure of the whole sagitta. Although numerous rhythmic discontinuities (possible monthly time-marks) were observed internally, they could not be correlated to external features.

Correlation of external and internal otolith features was further tested by measuring the distance between externally visible "annual" time-marks using reflective light microscopy, and comparing the same regions (equidistant) internally using SEM. Internally, several monthly or lunar checks (Fig. 6) were visible throughout the test regions. However, the number of monthly

checks never approached 12 (range 3 to 6), which would have supported the interpretation of externally viewed features as annual time-marks, nor did the number of primary growth increments within these regions approach 365 in number. We therefore suggest that the use of primary growth increments to estimate the age and growth rates of *Electrona antarctica* is more reliable than previously described "annual" time-marks (Linkowski 1987).

#### Validation

Daily growth studies for Antarctic fishes have focused almost exclusively on the dominant demersal coastal members of the suborder Notothenioidei (North et al. 1980; Townsend 1980; Radtke and Targett 1984; Radtke 1987; Radtke et al. 1989; Radtke and Hourigan 1990). Two studies confirmed that the microincrements found within the otoliths of Antarctic fishes were deposited daily (Radtke et al. 1989; Radtke and Hourigan 1990).

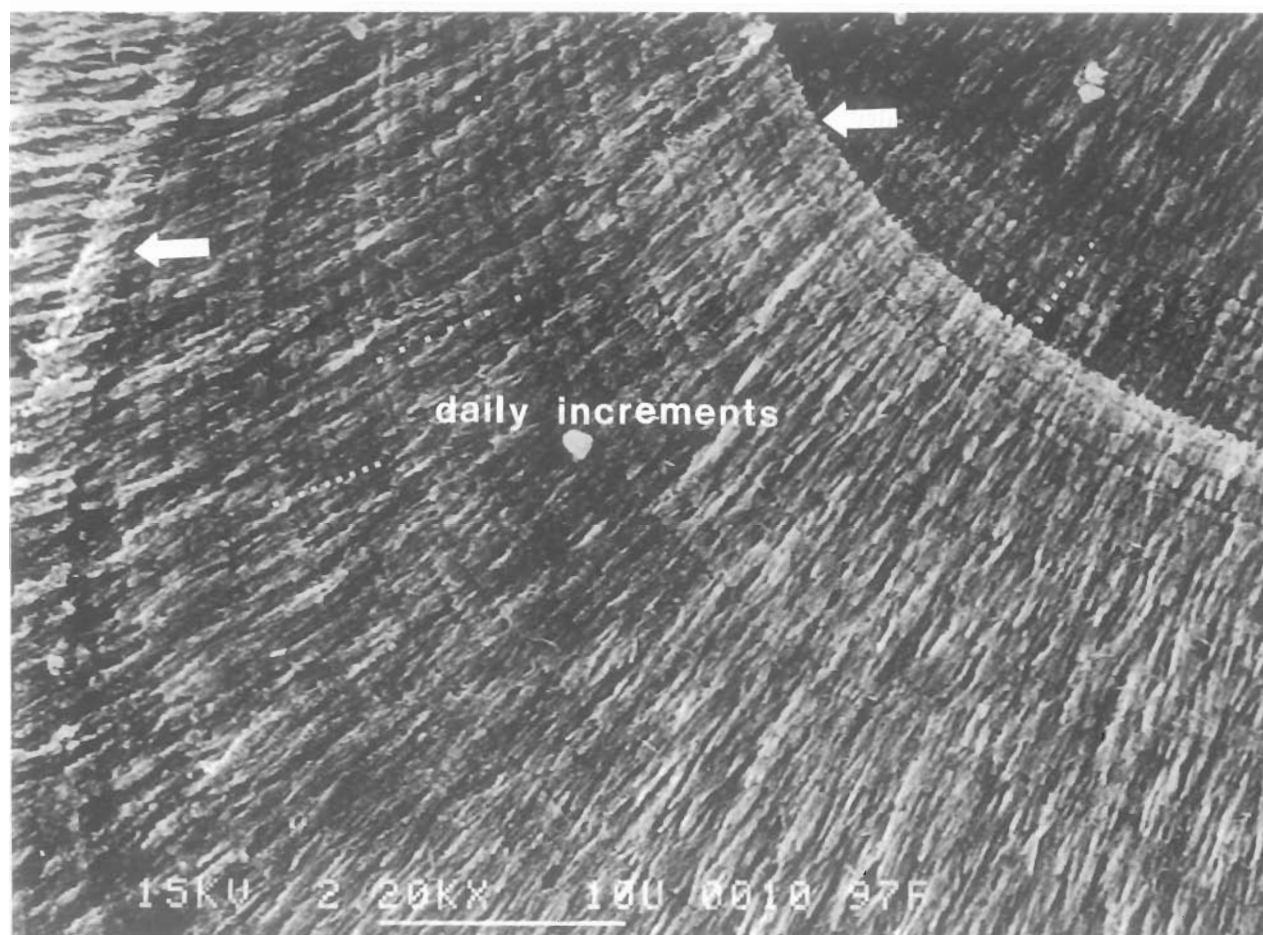
**Fig. 6** *Electrona antarctica*. Daily growth increments (white dots) within postmetamorphic zone of sagitta of 97 mm (standard length) female (arrows lunar or monthly time marks) SEM (magnification  $\times 2020$ )

Growth increments were validated by use of tetracycline incorporation into sagittae.

The only validation of daily increment formation in mesopelagic fishes was contributed by Gartner (1991a). Using marginal increment analysis, he verified daily increment formation for three myctophid species inhabiting the Gulf of Mexico. His work stands alone as the only study to validate daily growth increments in a midwater fish. Validation of daily increment deposition in the sagittae of *Electrona antarctica* may eventually be obtained by the marginal increment analysis described by Gartner, but was not attempted in the present study because of limitations in the sampling regime when specimens were collected. The rings observed in *E. antarctica* were identical to those validated as daily by Gartner (1991a) for low-latitude myctophids in all aspects but increment width. For further discussion, a brief treatment of validation and daily rings in lanternfishes may be found in Linkowski et al. (1993).

#### Physiological energetics

The rates of physiological processes (e.g. respiration) reported for *Electrona antarctica* are similar to those of non-polar myctophids (Torres and Somero 1988 a,b;



Donnelly et al. 1990). Characteristics unique to *E. antarctica* are its high lipid content, narrow diet, large size, and longevity. A simple energy budget can be calculated for *E. antarctica*'s third year of life using the growth data presented for the first time in this paper and a variety of data from published and unpublished sources that will be described in the following subsections. The basic form of the energy-budget equation will be that described in Brett and Groves (1979):

$$I = G + M + E,$$

where  $I$  = ingestion rate,  $G$  = growth rate,  $M$  = metabolic rate and  $E$  = excretion rate.

Since the calculations for energy utilization are strongly dependent on size, growth will be addressed first.

### Growth in mass and energy

Preliminary information on reproduction suggests that *Electrona antarctica* reproduces in its last year of life (Greely, Gartner and Torres unpublished data). A female between 2 and 3 yr of age was chosen as a model case for an energy budget. The choice was made partially to avoid the complications of reproduction, and partially because *E. antarctica* within this size range feed primarily on small *Euphausia superba*, having made the switch from a diet dominated by copepods (Rowedder 1979b; Hopkins and Torres 1989; Kozlov and Tarverdiyeva 1989).

Growth in mass was calculated by first using the equation for increase in length with age for females [(length in mm) = 0.072  $X$  (age in days) + 2.225] to generate a series of lengths, then the lengths were converted to masses using the relationship:

$$M(\text{wet mass in g}) = 3.99 \cdot 10^{-6} L^{3.27}(\text{length in mm}),$$

( $df = 105$ ,  $F = 2320.75$ ,  $P < 0.0001$ ,  $r^2 = 0.957$ , Donnelly and Torres unpublished data). The equation for length vs mass was generated using *Electrona antarctica* captured in the same area and at the same time as those used for the growth study described in the present paper.

The values for age vs mass were used to generate a new curve relating age and mass:

$$M(\text{wet mass in g}) = 8 \cdot 10^{-9} X^{2.93}(\text{age in days}).$$

The new age vs mass curve served two useful functions: (1) it allowed us to calculate the mass for fishes at 2 and 3 yr of age, yielding the total mass increase over the year by difference; (2) by integrating the function over the third year of life, we were able to calculate the average yearly mass. The average yearly mass was important in calculating the yearly values for metabolism and for ingestion.

Results yielded an average mass of 4.03 g for *Electrona antarctica* during its third year of life. The growth in mass during the year was 4.6 g (2.00 g at 730 d of life,

6.60 g at 1095 d). We used the mean energetic value of 1.62 kcal  $g^{-1}$  for *E. antarctica* reported in Donnelly et al. (1990) to calculate caloric growth for the year: 7.45 kcal (22.84 kJ).

### Metabolism

The energy required for metabolism during the third year of life was calculated using measurements of metabolic rate in *Electrona antarctica* from Torres and Somero (1988a) and a few assumptions on daily activity levels. Centers of day night distribution for *E. antarctica* are 650 m during the day and 100 m at night (Lancraft et al. 1989) for a vertical migration of ~550 m each way. The average size of *E. antarctica* during Year 3 is 68 mm. Optimum cruising speed for those fish that have been examined is one body length (BL) per second (Weihs 1973). Using a value of 1 BL  $s^{-1}$  results in a total travel time of 4.5 h for a 68 mm individual's diel round-trip. We assumed that during the vertical migration the metabolic rate was that reported by Torres and Somero (1988a) as "active", or 0.069 ml  $O_2 g^{-1} h^{-1}$ , and that the rest of the time the rate was "routine", or 0.042 ml  $O_2 g^{-1} h^{-1}$ . Using these assumptions, the yearly consumption of oxygen would be 412.45 ml  $g^{-1}$ . Multiplying by the average yearly mass and the oxycaloric equivalent of 4.63 cal  $ml^{-1}$  given in Brett and Groves (1979) yielded a value of 7.69 kcal (32.22 kJ) for the yearly energy expended in metabolism.

### Ingestion

We have no direct measurements of ingestion rate for *Electrona antarctica* (only analysis of gut contents), but estimates of daily ration reported (Hopkins 1985) for the larger sizes of another vertically migrating myctophid, *Lampanyctus alatus*, were 2.4% of body mass per day. A figure of 2.4% body mass  $d^{-1}$  as a ration agrees well with the literature available for myctophids (cf. Clarke 1978) and fishes in general (Brett and Groves 1979). If we use our previously determined value for average yearly mass (4.03 g) and a ration level of 2.4%, we obtain a value of 35.26 g for yearly ingestion. If we further assume that the ingested mass is entirely krill and that krill tissue has a caloric value of 0.939 kcal  $g^{-1}$  (Torres et al. 1994), we arrive at a total of 33.11 kcal (138.73 kJ) for the ingested energy during Year 3.

### Excretion and heat increment

Excretion has been estimated as 27% of the ingested energy for the average carnivorous fish (Brett and Groves 1979). This value includes energy lost both to feces and to nitrogen excretion. In the absence of direct measurements, energy lost to excretion was assumed to be 27% of the 33.11 kcal previously calculated for yearly ingestion, or 8.94 kcal (37.46 kJ). An additional loss

term for the energy-budget equation that is normally calculated is the heat increment (*HI*), or specific dynamic effect. This is the energy consumed during digestion and metabolic transformation of foodstuffs. A value of 14% of ingested energy is a reasonable approximation for the heat increment (Brett and Groves 1979), which yields a caloric value of 4.64 kcal (19.44 kJ). Heat increment is a metabolic cost outside that associated with routine and active metabolism.

#### Energy budget

Summing the elements of the energy budget affords us some interesting conclusions with regard to growth in *Electrona antarctica*.

$$I(33.11 \text{ kcal}) = G(7.44 \text{ kcal}) + M(7.69 \text{ kcal}) \\ + E(8.94 \text{ kcal}) + HI(4.64 \text{ kcal})$$

$$\text{Totals : } [I] = 33.11 \text{ kcal} [G + M + E + HI] = 28.71 \text{ kcal.}$$

Agreement between the two sides of the equation is quite reasonable; 87% of the estimated ingested energy is accounted for by metabolic costs. Most important is the conclusion that the growth rate reported in this paper is easily achievable using the best data available on metabolism and caloric content of *E. antarctica* in conjunction with conservative assumptions on elements missing from the equation. For example, our estimates of yearly ingested mass ( $35.26 \text{ g yr}^{-1}$ ) are less than half that of Rowedder (1979b), who estimated an annual ration of 21 times body mass (84.6 g using our average yearly mass) using individuals captured during summer.

#### Ecology

*Electrona antarctica* is the most abundant lanternfish endemic to the Antarctic region of the Southern Ocean, being geographically restricted to south of the Antarctic Convergence (McGinnis 1982). As is characteristic of many myctophid species, *E. antarctica* is a strong diurnal vertical migrator, with peak abundance between 0 and 300 m at night and 650 and 900 m during the day (Lancraft et al. 1989). Seasonal variations in vertical distribution are most pronounced during wintertime. Depths of maximum nighttime (100 to 400 m) and daytime (>1000 m) abundance are greater in winter than during the fall and spring (Lancraft et al. 1991). Although shifts in depth of occurrence are evident, these population shifts do not appear to affect the growth rates of *E. antarctica*, as evidenced by the continuity of inter-increment widths throughout the PMZ (i.e. there is no obvious decrease in calcium carbonate deposition nor a protein-rich overwintering band). Zooplankton population maxima also shift dramatically during the winter months (Hopkins et al. 1993) as the dominant copepods sink from the top 200 m of the water column to an overwintering depth of >400 m. There is little seasonal

difference in the biomass of prey, merely in its location (Lancraft et al. 1991). It would therefore appear that the coupling of abundant prey and high lipid reserves affords *E. antarctica* a continuous growth rate throughout the year. Concurrent with population shifts in prey items there is a decrease in the number of krill consumed in winter (Lancraft et al. 1991), which could easily be supplemented by use of lipid stores (Reinhardt and Van Vleet 1986). In conjunction with increased lipids in late autumn and early winter, energy levels increase by  $\approx 15\%$  from spring to fall and from fall to winter (Donnelly et al. 1990). The estimated energy budget predicts a surplus of available energy for growth and metabolism even using a conservative feeding rate.

Linkowski (1987) suggested that the growth parameters estimated for four Antarctic and subantarctic species of *Electrona* conformed well with their patterns of distribution. He proposed a slower growth rate for species occupying colder Antarctic waters throughout their life cycle (e.g. *E. antarctica*), while those that migrate to Antarctic waters as adults (*E. carlsbergi*, *E. rissoi* and *E. ventralis*) exhibit a decrease in growth rate only after reaching Antarctic waters. The present study partially supports this explanation in that *E. antarctica* does have a slower growth rate and greater longevity than its more northern congeners (*E. rissoi*, 1.5 yr; *E. ventralis*, 2 yr), but the magnitude is far less than predicted by Linkowski (8 to 11 yr; see present Fig. 7). An *E. antarctica* that lives for 8 to 11 yr would exhibit a growth pattern quite similar to that of other myctophid species which have been aged using concentric zones in otoliths assumed to correspond to annual growth (cf. Childress et al. 1980). Concurrent with this longevity is an extremely slow growth rate that is diffi-

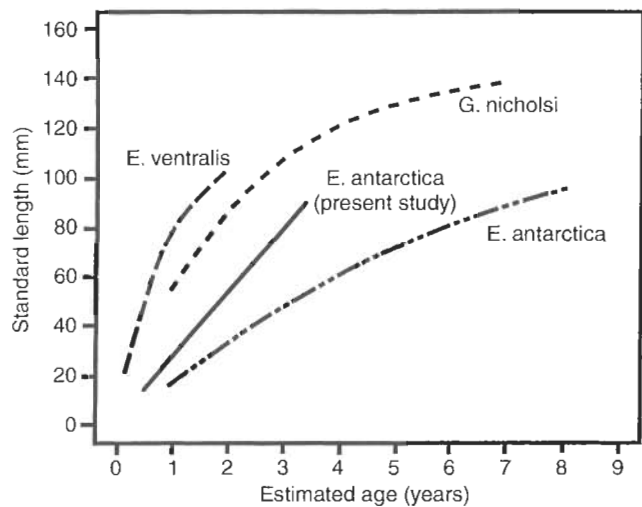


Fig. 7 Antarctic and subantarctic myctophids. Comparison of growth rates estimated from yearly and daily time marks. *Gymnoscopelus nicholsi* and *Electrona antarctica* determined from concentric zones in otoliths assumed to correspond to 1 yr growth (Linkowski 1985, 1987); *E. antarctica* (present study) and *E. ventralis* (Linkowski 1987) determined from daily growth increments

**Table 2** Maximum age estimates for six tropical-subtropical and two subantarctic myctophid species based on primary growth increments (SL standard length)

Species	Max. SL (mm)	Max. age (mo)	Source
<i>Benthoosema suborbitale</i>	33	10-11	Gartner (1991b)
<i>Diaphus dumerilli</i>	63	18-24	
<i>Lepidophanes guentheri</i>	65	12-15	
<i>Benthoosema fibulatum</i>	100	12	Gjosæter (1987)
<i>Benthoosema pterotum</i>	50	9-12	
<i>Lampanyctodes hectoris</i>	73	36	Young et al. (1988)
<i>Electrona risso</i>	72	18	Linkowski (1987)
<i>Electrona ventralis</i>	110	24	

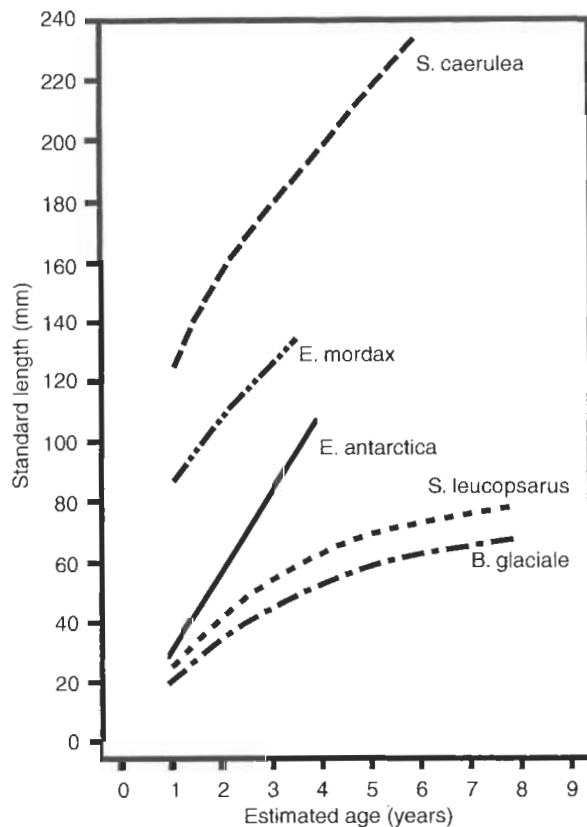
cult to explain ecologically as an adaptive advantage, especially in the predator-driven ecological niche occupied by lanternfishes (e.g. Frost 1988; Ainley et al. 1991).

*Electrona antarctica* is the end-member species in the continuum of vertically migrating myctophids that extends from the equator to the polar circle. Its growth rate is consonant with all other myctophid species that have been examined using microincrements to determine age (Table 2). The present data, in conjunction with that of previous studies (Lancraft et al. 1988; Gartner 1991b) suggest that growth rates of mesopelagic species are far

higher than has previously been thought (Childress et al. 1980). Relative to shallow-dwelling, temperate, coastal pelagics, *E. antarctica* exhibits an initially slower growth rate (0 to 2 yr). By Year 2, the absolute growth rate of  $0.07 \text{ mm d}^{-1}$  is equivalent to that of the Pacific sardine, a temperate coastal pelagic species (Fig. 8). This is most striking considering the  $10 \text{ C}^\circ$  temperature difference between the cold-temperate and polar environments.

Rather than being perceived as sluggish, slow-growing fishes that occupy a midwater niche, it would perhaps be more accurate to think of lanternfishes as the sardines and anchovies of the open sea. Like their shallower-dwelling counterparts, the engraulids and clupeids, the myctophids are slow-growing, short-lived fishes (Gartner 1991b). Their growth rate is neither much faster nor much slower than other small pelagic fishes with similar feeding habits living at similar temperatures. Vertical migration as a foraging strategy provides the myctophids a continual cloak of darkness to shield them from visual predation in the open ocean, while allowing them to maintain a zooplanktivorous feeding habit similar to that of the engraulids and clupeids.

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**Fig. 8** Cold-temperate and polar species. Comparison of growth rates estimated for two epipelagic species, *Sardinops caerulea* (Lasker 1970) and *Engraulis mordax* (Collins and Spratt 1969); two cold-temperate myctophids, *Stenobrachius leucopsarus* (Smoker and Pearcy 1970) and *Benthoosema glaciale* (Gjosæter 1978), and the polar myctophid *Electrona antarctica* (present study). *S. leucopsarus* and *B. glaciale* were aged using yearly time-marks. Note differences in maximum age and growth rate between *E. antarctica* and other two myctophid species

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