

Abstract.—Sagittal otoliths of the Antarctic fish *Nototheniops nudifrons* (Family Nototheniidae) contain internal microincrements which are visible by scanning electron microscopy. Microincrements were deposited on a daily basis, as validated through tetracycline and acetazolamide marking experiments. This was the first validation of daily microincrement deposition for any Antarctic fish. Daily formation of microincrements continued throughout the year, including during the winter when daylight periods were short. Counts of daily microincrements in the otoliths of 32 juveniles and adults allowed the determination of age and growth rates. From this sample, a multivariate regression model relating fish age to otolith morphometrics and fish size demonstrated that age could be estimated reliably from sagittal otolith weight and length. Age was estimated for a large sample of *N. nudifrons*, which allowed the determination of growth and natural mortality. Fish grew slowly (15 mm per year), reaching sexual maturity at an age of 4–5 years, with the largest fish attaining ages of more than 8 years. Growth and survivorship were similar for males and females.

Age and Growth of the Antarctic Fish *Nototheniops nudifrons**

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The Antarctic fishes are characterized by a high degree of endemism and extensive adaptations to their unique environment (DeWitt 1971). Although commercial exploitation of several species has begun, much of their basic biology is still poorly understood (Kock et al. 1985). Of special importance to ecological and fisheries research is determination of the age of fish captured in the field. Growth, mortality, and fecundity can be derived from age data. Ageing studies can also provide basic life-history information, such as population structure, and changes in population growth due to environmental perturbations. These age-related data increase our understanding of fish biology and form the basis of population dynamics models.

Antarctic fishes appear to be slow growing and long lived (Shust and Pinskaya 1978, Freytag 1980a, Kock et al. 1985, Radtke et al. 1989). Although age and growth of Antarctic fishes have primarily been determined by counting scale annuli (Olsen 1954, 1955; Wohlschlag 1961, 1962; Everson 1970, 1980; Shust and Pinskaya 1978; and others), the results from this technique are often difficult to interpret and especially unreliable for older fishes, as scales may be regenerated or resorbed (Mugiya and

Watabe 1977; Freytag 1980a, 1980b). Therefore, an alternative ageing method, such as otolith increment analysis, is desirable. In contrast to scales, otoliths are neither regenerated nor resorbed, and are the most precise structure for ageing of fishes (Six and Horton 1977, Campana and Neilson 1985).

Otoliths are calcium carbonate structures deposited in the membranous labyrinth of the inner ear of fish. The otoliths of many fishes grow by daily accretion of layered increments (Pannella 1971). These increments are visible in sectioned otoliths as concentric rings, which can be enumerated to provide estimates of the age of temperate and tropical fishes (Pannella 1971, 1974; Campana and Neilson 1985; Jones 1986). Otoliths of temperate fishes may also form annual increments or annuli.

Several studies have utilized otoliths to age Antarctic fishes. Olsen (1955) found that the otoliths of icefishes were small and difficult to analyze by light microscopy. Rings in the otoliths of the icefishes *Chaenocephalus aceratus* and *Champsocephalus gunnari* were interpreted to be annuli (Olsen 1955). Subsequently, other researchers used rhythmic patterns in Antarctic fish otoliths for age determinations (Hureau 1966, Everson 1980, Freytag 1980b, North et al. 1980, Mucha 1980, Chojnacki and Palczewski 1981, Kock 1981,

Sosinski 1981, Kochkin 1982, Burchett et al. 1984). These patterns were interpreted to be annuli; however, no validation data were available for the deposition rates of these increments. These presumed annuli, which are often difficult to discern and interpret, may not represent yearly growth increments (Scherbich 1975, Freytag 1980b, Radtke and Targett 1984).

Townsend (1980) described the presence of microstructural growth increments in Antarctic fish otoliths. These increments appeared to be analogous to the daily increments found in a host of fish species (see review by Campana and Neilson 1985). Such microincrements were used by Radtke and Targett (1984) to age *Notothenia larseni*, and are the foundation for the present research. However, the daily or annual nature of rhythmic patterns in otoliths has not been experimentally validated for any Antarctic fish species. Microincrements may generally form in response to changes in daily periods of light and dark (Radtke 1984), suggesting that special problems may exist in the formation of daily increments during times of short daylight in the winter months.

Management programs for Antarctic fisheries require knowledge of population parameters of both commercial and sympatric, non-commercial, species. *Nototheniops nudifrons* (= *Notothenia nudifrons*) is among the most abundant demersal fishes in many habitats of the Antarctic Peninsula (DeWitt 1971). As such, this species may play a major role in the trophic structure of the Antarctic marine community, both as competitor with and prey for commercial species.

We recently reported on the reproductive biology of *N. nudifrons* (Hourigan and Radtke 1989). In the present study, the age and growth of *N. nudifrons* were determined by the examination of microincrements in sagittal otoliths. Microincrement deposition rates during different seasons were tested under experimental conditions. Correlations of age to otolith morphometrics allowed ageing of a large sample of fish and an estimation of their natural mortality rates.

Methods

Collection of fish and Initial measurements

A total of 32 *Nototheniops nudifrons* were collected on 28 March and 17 April 1985 by otter trawl in 54–110 m depths off Low Island (63°24'S to 63°27'S; 62°07'W to 62°17'W). An additional 30 fish were collected in the same area in February 1984, and used for preliminary otolith validation studies. All individuals were transported live to Palmer Station and placed in tanks with flow-through seawater. In addition to these fish, scuba divers collected three small juveniles near Palmer

Station in Arthur Harbor (64°46'S; 64°04'W) in May and July 1985.

The fish from the 1985 trawls were analyzed for length-weight relationships and growth. Standard length (SL) and total length (TL) were measured to the nearest millimeter. Whole body weights were measured to the nearest 0.001 g. Otoliths were removed from all fish, cleaned, dried at 60°C, and stored in a desiccator. The gonads were examined to determine sex and reproductive condition (Hourigan and Radtke 1989).

The remaining fish were injected intramuscularly with acetazolamide (samples from 1985 only) or tetracycline (samples from 1984 and 1985) and kept in 500-L tanks with flow-through seawater, at ambient temperatures and natural photoperiods. Ten fish were kept in each tank, along with 10 *Notothenia gibberifrons*. Rocks were added to the tanks to provide shelter and nesting sites. Fish in tanks were fed *ad libitum* with krill every 2 days.

Fish were kept alive for a maximum of 158 days after injection, from April to October, at which time they were sacrificed, weighed, and measured. Otoliths of these fish were removed, cleaned, and stored dry in vials.

Otolith structure and age determination from otolith microincrements

To determine the relationship of age to otolith size and shape, the length, width, and weight of sagittal otoliths were measured. Otoliths were segregated according to their lateral position in the cranium. Left and right sagittae from all fish were scanned using a computer-aided video digitizer, which produced a measure of maximum length (from the rostrum to antirostrum; nomenclature of Hecht 1978) and width (the widest distance in the dorsal-ventral plane). Otoliths were weighed on a microbalance to the nearest 0.01 mg.

A sample of 32 fish (from fish collected in 1985) was chosen for age determinations. This sample was composed of males and females of a representative size distribution. Left sagittae from these fish were attached to scanning electron microscope (SEM) viewing stubs with epoxy, carefully ground down to the central area by hand using a fine sharpening stone, and then polished with 0.3-micron alumina paste. The polished surfaces were etched for 1–20 minutes with 6% ethylene diamine tetraacetate (EDTA) with pH adjusted to 8 with NaOH. After etching, the sections were gently washed with water, dried, coated with gold, and viewed by SEM at various magnifications (50–10 000×).

Otoliths were examined for microincrements. A microincrement was defined as an unbroken incremental zone with discontinuous zones as boundaries (Radtke and Dean 1982). Sequential etching made it

feasible to enumerate all increments. Individual sections were etched for different lengths of time, with 15–20 minute etching times showing the inner increments most clearly, and shorter etching periods revealing the outer increments. Landmark scratches were placed on each section with an insect needle to follow increments uncovered by different etching times. The otolith was etched in steps of 1 minute and viewed with the SEM after each etching to follow the progression of the smallest increments found. Examination of the three-dimensional microstructure of the left sagitta demonstrated that the midtransverse plane was the best plane for routine sectioning.

Validation of otolith ageing technique

Microincrements are generally assumed to be deposited daily (Pannella 1971, 1974; Radtke and Dean 1982; Radtke and Targett 1984). To test this, individual fish were given a single intramuscular injection of either tetracycline hydrochloride or acetazolamide at 0.025 mg/g body weight. Tetracycline is incorporated into the otolith and, viewed under a compound microscope with filtered reflected wavelengths of 700–800 nanometers, appears as a fluorescent band inside the otolith. Tetracycline marks are not visible by SEM. Acetazolamide is a carbonic anhydrase inhibitor which temporarily inhibits the calcification processes in the otolith resulting in a disruption band which can serve as a reference location for SEM study (Mugiya and Muramatsu 1982, Radtke unpubl. data).

Left sagittae from the fish injected with tetracycline were embedded in epoxy-casing resin and serially sectioned using a low-speed saw. The sections were polished as above, placed in nonfluorescent immersion oil, and examined under reflected ultraviolet light through a compound microscope. Otoliths with acetazolamide marks were prepared for SEM analysis as described above. The number of microincrements from the reference mark to the margin of the otolith was compared with the number of days between injection and the day that the fish was sacrificed.

Relationship of otolith dimensions and fish age

In an effort to determine other predictors of age in *N. nudifrons*, the data generated from otolith and fish measurements were applied to the multiple regression model:

$$\text{Age} = a + b_1x_1 + b_2x_2 + b_3x_3 + b_ix_i$$

In this model, age in years was determined by counting microincrements, a = intercept, b = regression coefficients, x = variables. The data were checked for

Table 1

Variance component due to within-fish variance in ages of *Nototheniops nudifrons* predicted from left and right otolith measurements, compared with variance among fish.

Variance source	df squares	Sums of squares	Mean component	Variance	Percent
Between fish	200	341.24	1.71	0.96	95.87
Within fish	200	6.08	0.04	0.04	4.13
Total	400	347.32	1.00	1.00	100.00

normality, and the multiple regressions were determined in a stepwise fashion with the inclusion level for variables set at $p = 0.05$. As a measure of the variance associated with the otolith morphometric procedure, the percent of the total variance component due to variance between age estimates from the left and right sagittae of the same fish was calculated. Less than 5% of the total variance was due to variance between sagittae of the same fish (Table 1).

Results

A total of 216 *Nototheniops nudifrons* were collected in trawls off Low Island. Five were caught during six deep trawls in 100–110 m depth, with the remaining fish caught in four shallow trawls at depths of 54–80 m. Fish captured in trawls ranged in size from 70 to 149 mm SL. More females ($N = 127$) were collected than males ($N = 74$), and the modal size of females (100 mm SL) was slightly larger than that of males (90 mm SL; Fig. 1). Three smaller juveniles (each 45 mm SL) were collected by hand in 10 m depth at Arthur Harbor.

Length-weight relationships

Length-weight relationships of males and females are shown in Figure 2. Separate regression equations were calculated for males and females using a gonad-free body weight. Weight was approximately a cubic function of length, indicating nearly isometric growth. The length-weight relationship of the fish conformed to the power curve model $\text{Weight} = a(\text{SL})^b$. An analysis of covariance indicated that the slopes of the length-weight relationships for the sexes were not significantly different ($df = 1, 203; F = 2.30, 0.05 < p < 0.25$). The conversion of standard length (SL in mm) to total length (TL in mm) was:

$$\text{TL} = 1.136(\text{SL}) + 1.529; (N = 216; R^2 = 0.99).$$

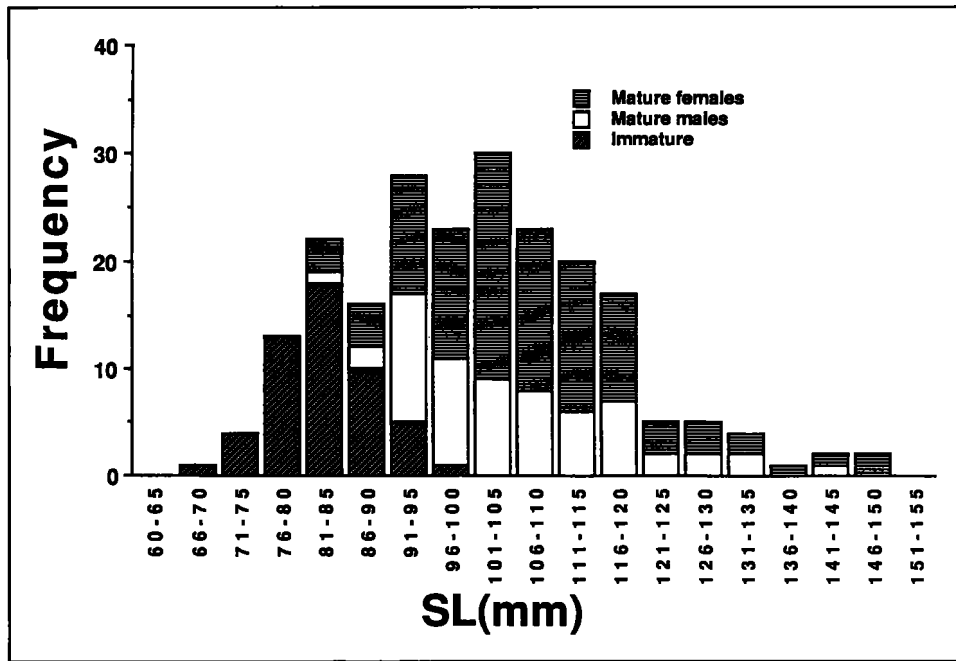


Figure 1
Length-frequency distribution of immature and sexually mature male and female *Notototheniops nudifrons* captured by trawls near Low Island in 1985.

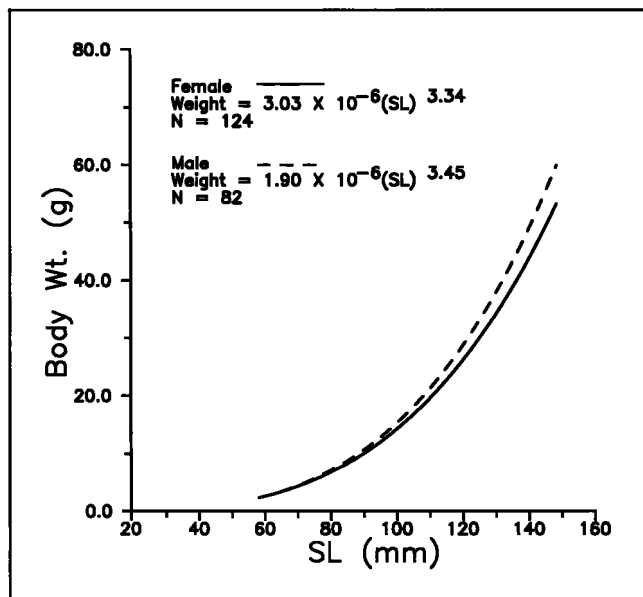


Figure 2
Length-weight relationship of male and female *Notototheniops nudifrons*. Wet body weight (with gonads removed) increased approximately as the cube of fish standard length (SL).

Description of otoliths

The sagittae of *N. nudifrons* were large and oval in shape (Fig. 3) with a well-defined rostrum. The size of the rostrum was directly proportional to fish size. The external surface was smooth and gently rounded. Sagitta length was related linearly to fish length (SL)

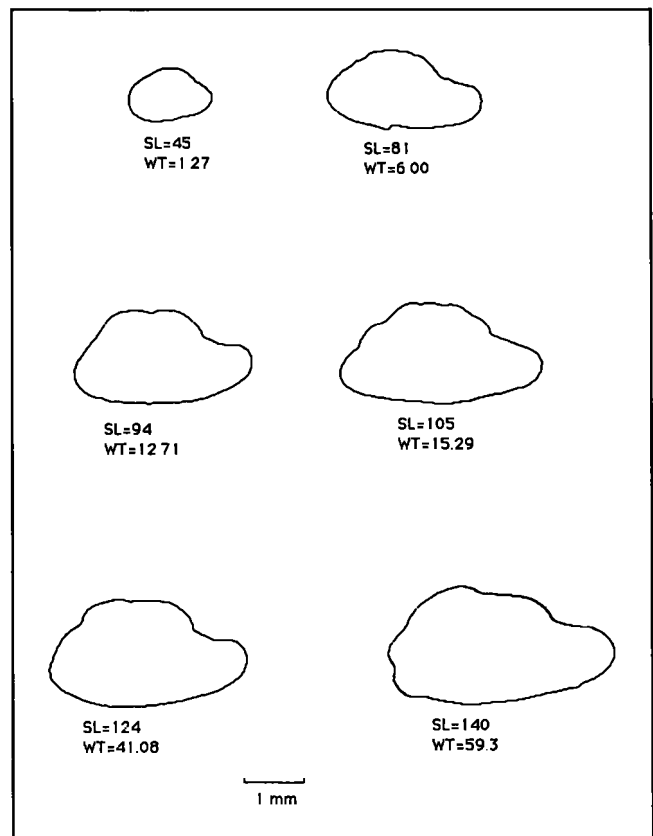


Figure 3
Change in size and shape of sagittal otoliths of *Notototheniops nudifrons* with increasing fish size. SL = standard length; WT = wet weight of fish.

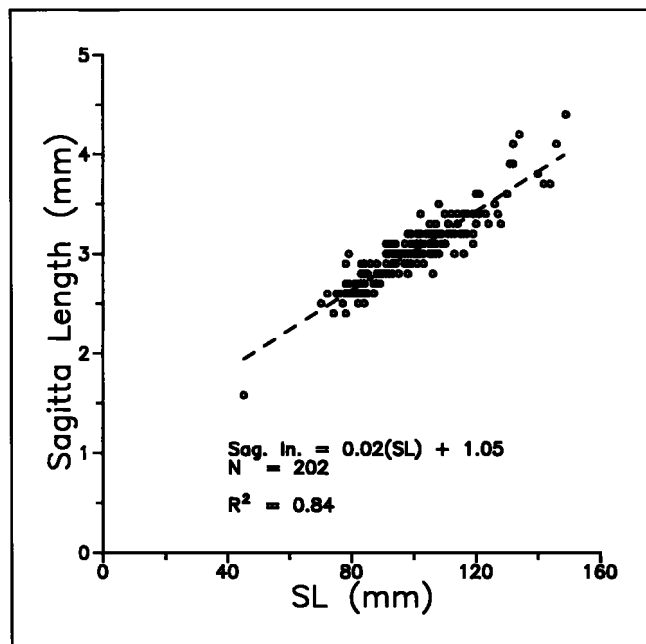


Figure 4

Relationship of sagittal otolith length to fish standard length (SL) for *Nototheniops nudifrons*.

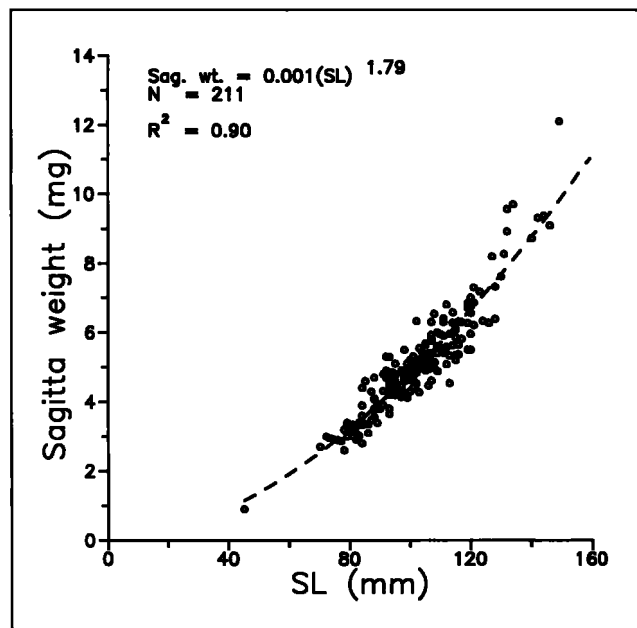


Figure 5

Relationship of sagittal otolith weight to fish standard length (SL) for *Nototheniops nudifrons*.

(Fig. 4), and sagitta weight was related exponentially to fish length (SL) (Fig. 5). Ground, polished, and decalcified sagittae were examined by SEM. A low magnification view of a sagittal otolith (Fig. 6) shows increments occurring concentrically from the center to the edge. Larger incremental patterns, or bands, were observed, but they could not be attributed to any specific environmental cues. Counts of microincrements within these bands showed that they were not true annuli. Sagittae exhibited a well-defined central core region or nucleus (Fig. 7a). Within the core region were concentric microincrements separated from the surrounding otolith by a distinct transition zone (Fig. 7b). Surrounding the core area were mineral crystals in a protein matrix which formed microincrements (Fig. 8a and 8b). Counts of microincrements were made beginning at the core transition zone and ending at the outer edge of the otolith. These microincrements varied in width from about $2\ \mu\text{m}$ (Fig. 8a) to less than $1\ \mu\text{m}$ (Fig. 8b). Differences in increment width may reflect periods of differential growth.

Validation of the daily nature of microincrements

The periodicity of growth increment formation was examined using tetracycline- and acetazolamide-marked specimens which were held in tanks at ambient light and temperature regimes after injection. After injec-

tion of tetracycline or acetazolamide, *N. nudifrons* displayed some evidence of short-term stress, including cessation of feeding for 2 or 3 days, but only one mortality occurred. Subsequently, the fish survived well in captivity, with 80% of all fish surviving the whole winter. Sagittae of 29 fish injected with tetracycline in February and March 1984 and held 4–34 days under natural daylight photoperiods were examined for post-treatment increments. A discrete fluorescent band was discernible in all specimens, and increments between the band and the margin of the otolith were counted (Table 2). The number of increments averaged 2.5 increments less than the number of days after injection. This difference corresponded well to the initial period of stress, and did not change with length of the experiment (Median test, $0.2 > p > 0.1$; Siegel 1956). Linear regression analysis (Model I, Sokal and Rohlf 1969) indicated that the slope ($b = 1.076$, 95% CI of 0.756–1.396) was not significantly different from 1 (Table 2). The y -intercept equaled -3.27 (95% CI of -7.73 – -1.19).

Sagittae from five fish injected with acetazolamide in April 1985 were examined by SEM. A discrete disruption of increments caused by the interruption of calcium deposition was discernible (Fig. 9). The number of increments from this disruption mark to the otolith margin averaged 9.2 increments less than the number of days after injection (Table 2). Acetazolamide disrupts metabolic processes and its effects can be expected to last longer than the tetracycline's, since the latter does

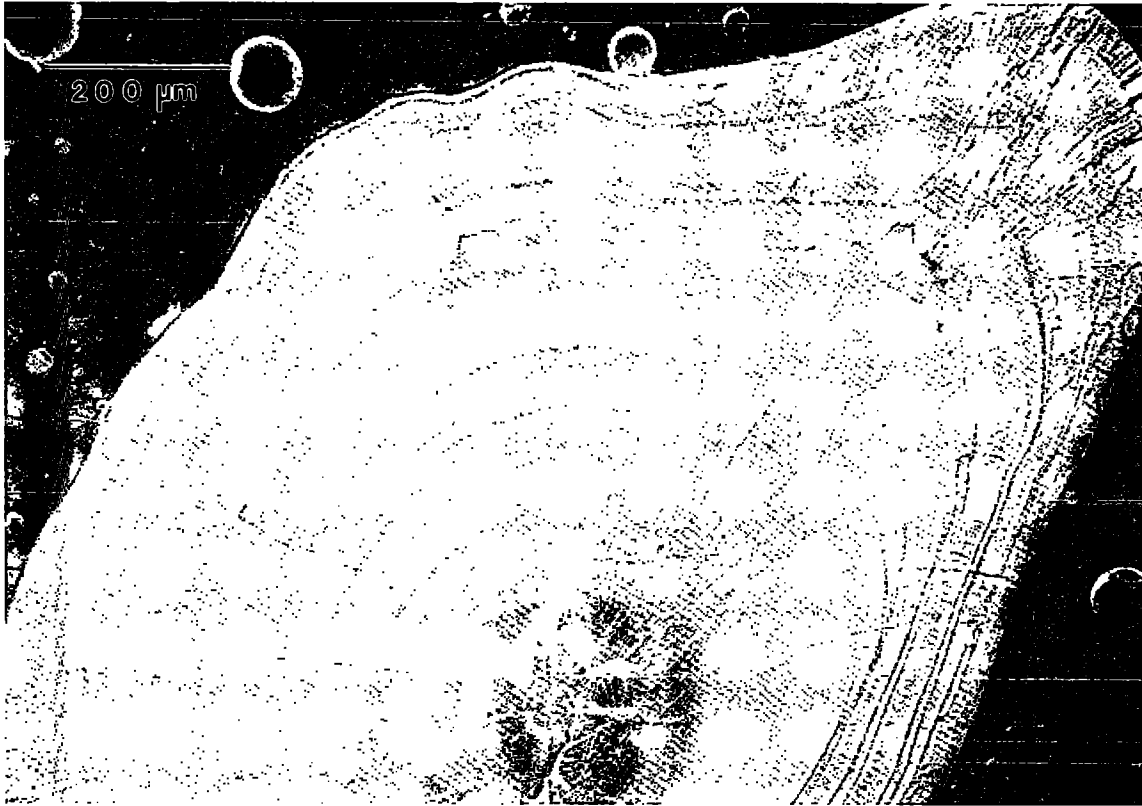


Figure 6

Low-magnification scanning electron micrograph of a sagittal otolith of *Nototheniops nudifrons*, showing concentric incremental patterns. The sagitta is from a 100-mmSL specimen.

not appear to affect the fish's metabolism. Linear regression results indicated a slope of 0.962 (95% CI of 0.983–0.941) and a y -intercept of -5.40 (95% CI of -2.80 to -8.01). The significance of this analysis is suspect because of the small sample size ($N = 5$). The discrepancy between postinjection days and microincrements counted increased from 5 to 12 with length of incubation period. However, this apparent increase in the discrepancy represents an actual percentage decrease in error from 50% to less than 10%. The longest incubation period in the acetazolamide experiment was 158 days, which was three times longer than the longest tetracycline incubation. This may explain why in the tetracycline experiment we did not observe an increase in the discrepancy between number of increments and days after injection.

During the experiment, the photoperiod varied from 9:15 hours Light:Dark, to a minimum of 5:19 L:D in June, to 15:9 L:D in October. The microincrements formed during incubation were uniform. Despite considerable variation in photoperiod, we found no indication that microincrements cease to form on a daily basis.

Age and growth

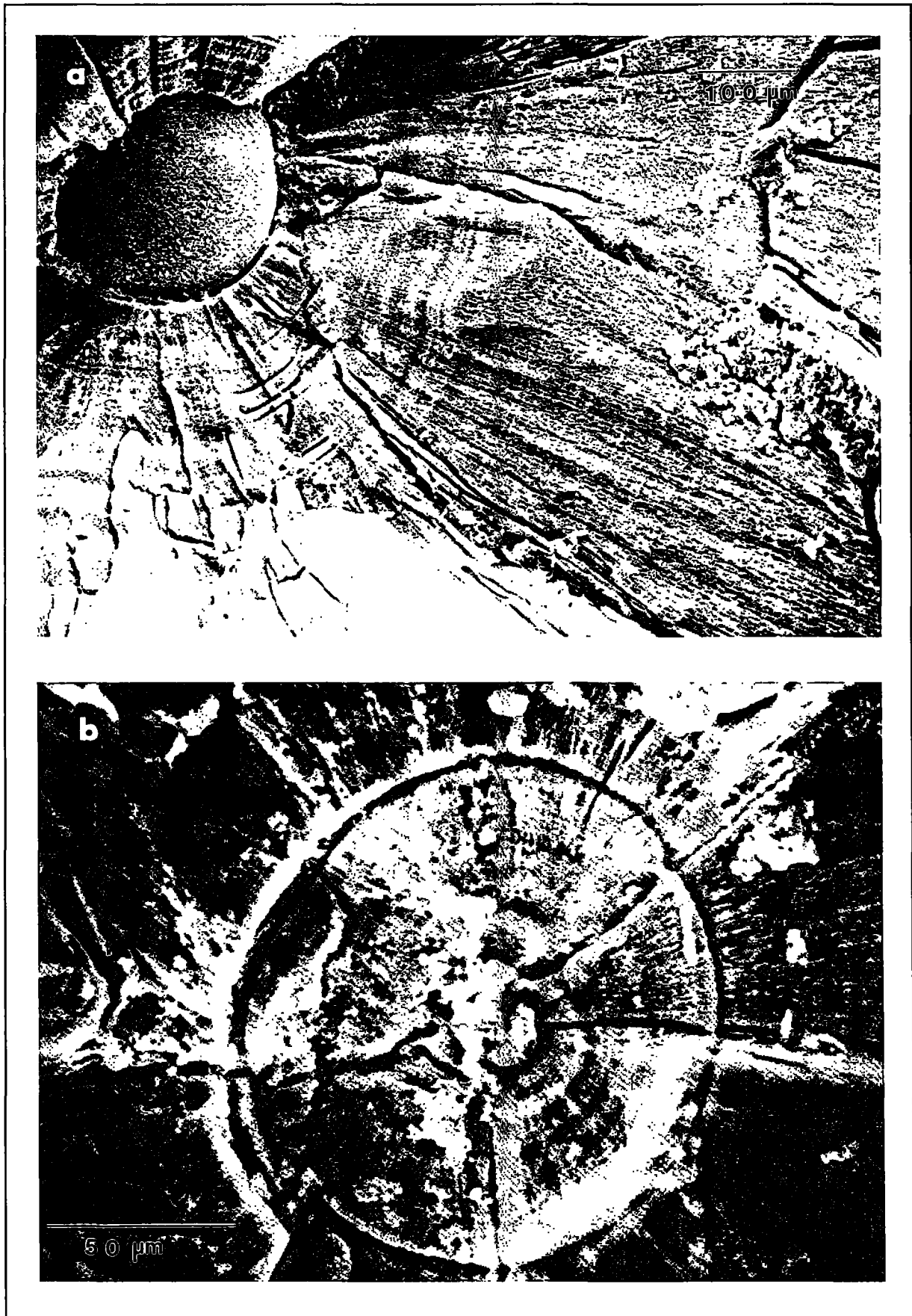
Microincrements were counted in the sagittal otoliths of 32 fishes. Ages ranged from 1.3 years for the small juveniles collected by hand, to 8.5 years for the largest individual collected. Fish length was related to the number of microincrements in the sagitta (Fig. 10). Length (mm) increased linearly with age (years), and was best described by the equation:

$$SL = 14.87(\text{Age}) + 23.56; (R^2 = 0.93, p < 0.0001)$$

No difference in growth was observed between the sexes in our sample (Fig. 10). When separate regressions were calculated for males ($N = 11$) and females

Figure 7

(a) Scanning electron micrograph of a sagittal otolith of a 130-mmSL *Nototheniops nudifrons*, showing the characteristic central core area, or nucleus, separated by a well-defined transitional zone from the outer zone with microincrements radiating outward. (b) Microincrements from a 100-mmSL fish found within the core area of the otolith.



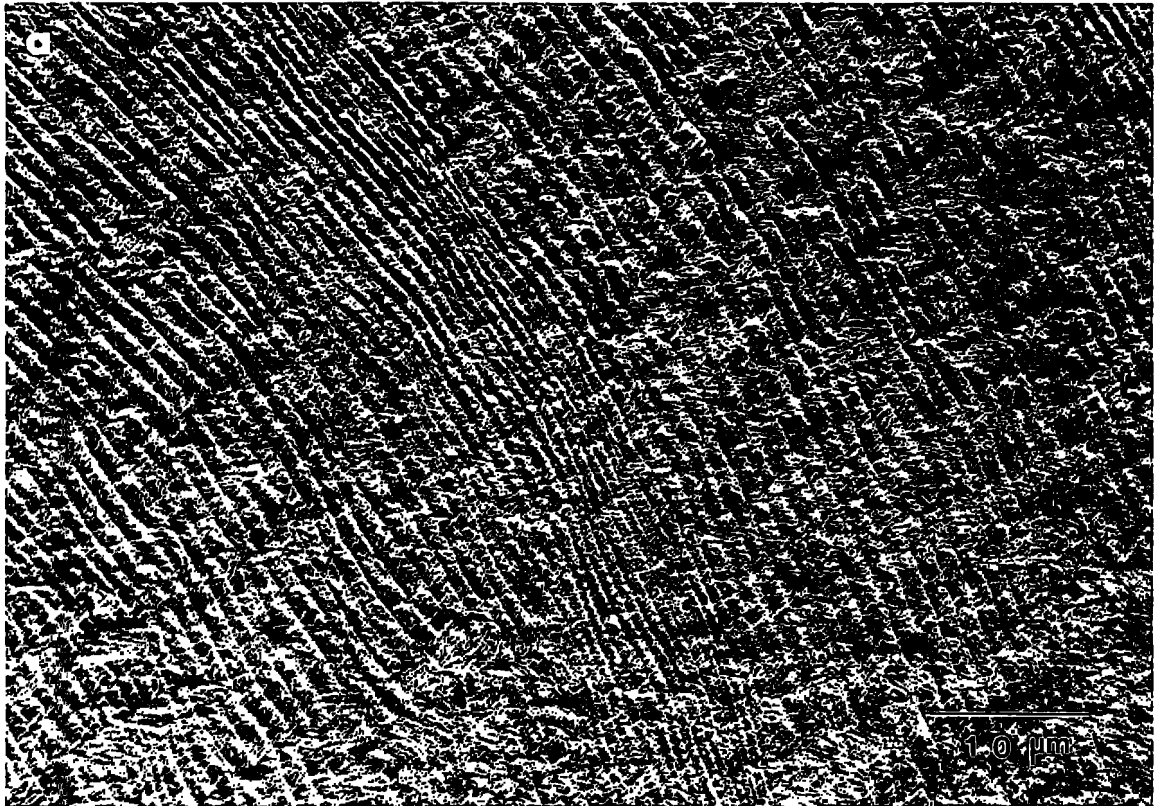


Figure 8

Scanning electron micrographs of microincrements of sagittal otoliths of *Nototheniops nudifrons*, as utilized for daily increment enumeration. (a) Wide and narrow patterns of microincrements from a 144-mmSL fish. (b) Narrow microincrements from a 70-mmSL fish.

($N = 18$), analysis of covariance indicated that the slopes of the two lines did not differ between the sexes ($df = 1, 26; F = 0.82, p > 0.37$).

Relationship of fish size and otolith dimensions to fish age

Stepwise multiple regression analysis relating fish size (mm), weight (mg), and otolith morphometrics (sagitta length in mm and weight in μg) to age (years), resulted in the acceptance of the following model:

$$\begin{aligned} \text{Age (Yrs)} = & 3.892 + 0.856(\text{sagitta wt}) \\ & - 2.206(\text{sagitta length}) + 0.041(\text{SL}) \\ & - 0.025(\text{fish wt}) \end{aligned}$$

Addition of the remaining variable (sagitta width) did not improve the regression ($N = 32, R^2 = 0.967, p < 0.05$; Table 3). The residuals were randomly distributed, which demonstrated that this multiple regression best explained the variability in age. Over 94% of the variance was explained by the regression of the two otolith measurements (weight and length). The variables in the model, such as otolith length, width, and weight, are not strictly independent variables, nor are length and body weight. This deviation from the assumptions of the model may result in an artificially inflated R^2 value; however, this should not decrease their practical value as predictors. Sagitta weight alone accounted for 92% of the variance in the regression, supporting the usefulness of otoliths as age-related structures.

The relationship between age and otolith morphometrics allowed the estimation of age for all the fish in the sample (Fig. 11). The growth curve derived from the multivariate model (Fig. 11) was comparable to that derived from microincrement counts (Fig. 10), and both were linear in form. Individuals in this population of *N. nudifrons* grow at approximately 15 mm per year, which is a slow growth rate. Analysis of covariance of

Table 2

Validation of the daily nature of otolith microincrement deposition in *Nototheniops nudifrons*. Otoliths of fish injected with tetracycline were examined by light microscope, while those injected with acetazolamide were examined by scanning electron microscope.

Injection	Number of replicates	Days after injection	Number of post-treatment microincrements counted		
Tetracycline	1	4	1		
Tetracycline	5	5	2, 3, 3, 3, 3		
Tetracycline	2	6	3, 3		
Tetracycline	3	7	4, 4, 4		
Tetracycline	2	9	5, 7		
Acetazolamide	1	9	4		
Tetracycline	5	10	7, 7, 7, 8, 10		
Tetracycline	1	11	6		
Tetracycline	2	14	10, 11		
Tetracycline	2	15	12, 12		
Tetracycline	3	16	14, 15, 16		
Acetazolamide	1	21	14		
Tetracycline	1	24	23		
Tetracycline	2	34	33, 34		
Acetazolamide	3	158	144, 147, 149		

Regression analysis					
	Regression coefficient	SE	t_s	df	p
Tetracycline	$b = 1.076$ $y\text{-intercept} = -3.268$	0.074 1.036	1.027	27	$0.4 > p > 0.2$
Acetazolamide	$b = 0.962$ $y\text{-intercept} = -5.402$	0.0049 0.606	7.755	3	$p < 0.01$

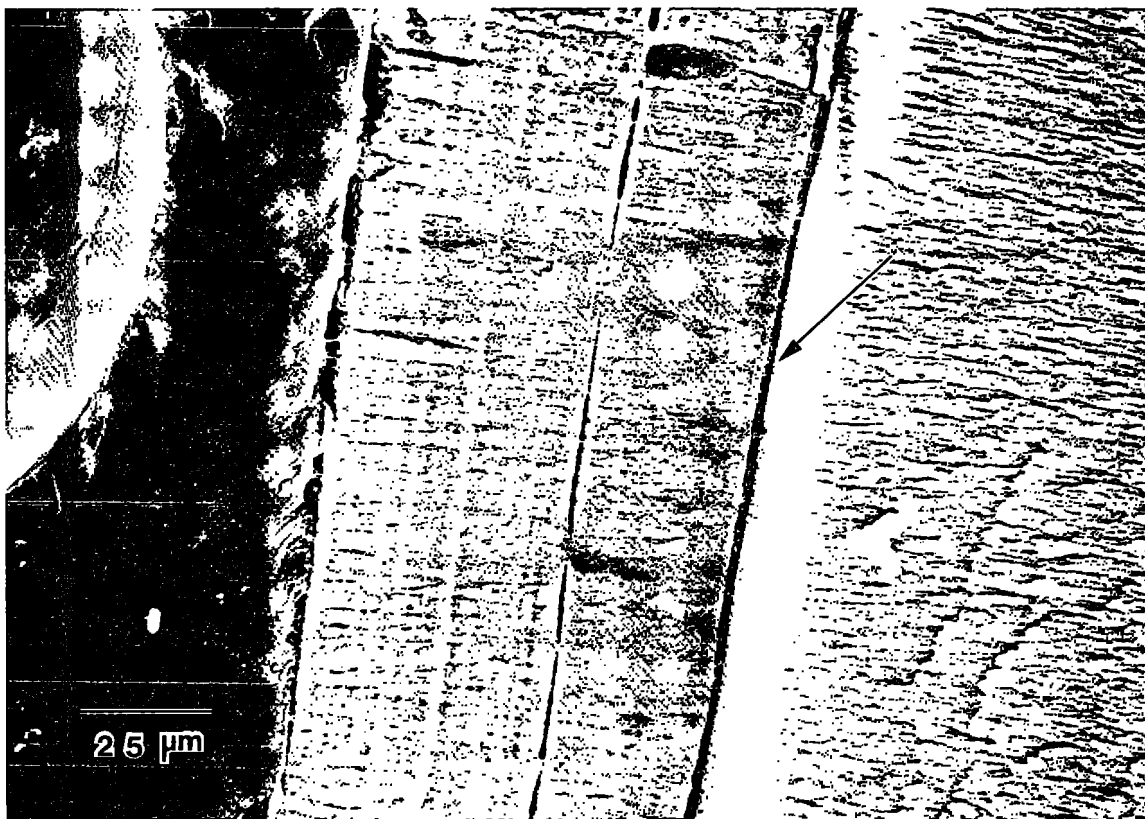


Figure 9

Scanning electron micrograph of a sagitta from a 100-mm SL *Nototheniops nudifrons* marked with acetazolamide. The acetazolamide mark (arrow) is visible as a disruption in the growth increments.

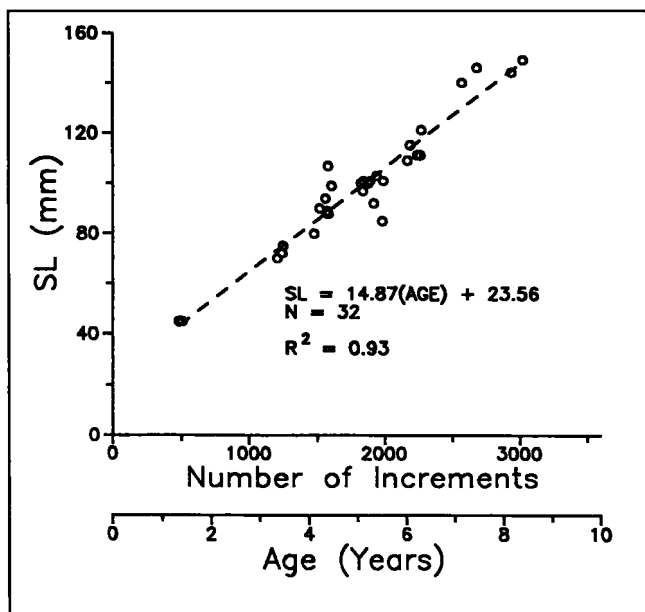


Figure 10

Regression of fish standard length (SL) on age as determined from the number of sagittal otolith microincrements for *Nototheniops nudifrons*.

Table 3

Associated statistics of one-way regression and stepwise multiple-regression model of fish age in years vs. size and weight variables for *Nototheniops nudifrons*. $N = 32$.

One-way regression					
Variable	F	$P > F$	Model R^2		
1 Sagitta weight	314.64	0.0001	0.921		
2 Fish length (SL)	213.31	0.0001	0.888		
3 Fish weight	134.64	0.0001	0.832		
4 Sagitta length	103.35	0.0001	0.793		
5 Sagitta width	92.43	0.0001	0.774		
Multiple regression					
Step	Variable entered	F	$P > F$	Partial R^2	Model R^2
1	Sagitta weight	53.68	0.0001	0.921	0.921
2	Sagitta length	23.16	0.0001	0.021	0.942
3	Fish length (SL)	17.43	0.0003	0.019	0.961
4	Fish weight	4.53	0.0437	0.006	0.967

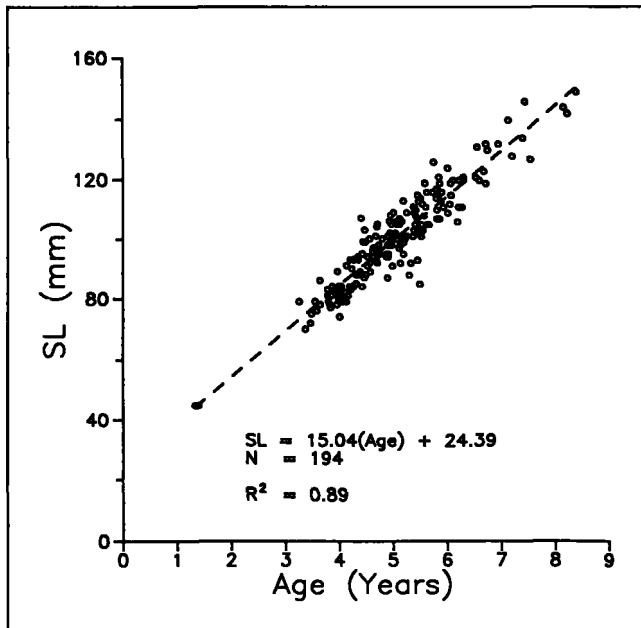


Figure 11

Regression of fish standard length (SL) on estimated age for *Nototheniops nudifrons*. Age was estimated by a multivariate mathematical model based on fish standard length, fish weight, otolith length, and otolith weight.

separate growth curves calculated for males and females showed no significant difference ($df = 1,177$; $F = 0.87$; $p > 0.36$), indicating that males and females grow at the same rate.

Discussion

Otolith microincrement deposition and age determination

The accuracy of age and growth estimates depends on the assumption that the microincrements viewed were deposited on a daily basis. Daily increments have been found in otoliths from many temperate and tropical fish species (see review by Campana and Neilson 1985). The daily nature of microincrement deposition in *Nototheniops nudifrons* was validated through the tetracycline and acetazolamide marking experiments. Daily increment deposition occurred even during the shortest days of the Antarctic winter. The formation of microincrements may become less regular in some fishes after sexual maturity (Pannella 1980), but our validation study included both immature subadults and mature males and females, which all deposited daily microincrements. Hourigan and Radtke (1989) found that daily microincrement deposition also occurs in larval *N. nudifrons*, beginning at or around the date of hatching.

Together, these studies provide the first validation of daily otolith microincrements for any Antarctic fish.

In addition to the microincrements, the otoliths of *N. nudifrons* contained larger banding patterns. In temperate regions, environmental factors such as temperature and food availability show regular and marked seasonal changes, giving rise to clearly identifiable growth periods in fish otoliths. The regular annual formation of these seasonal rings in the otoliths of temperate fishes provides a successful and widely used ageing technique. Growth increments laid down in the otoliths of some Antarctic fishes may be annuli (e.g., *Harpagifer bispinis antarcticus*; Daniels 1983); however, those observed in this study, as well as those in the otoliths of *Nototheniops larseni* (Radtke and Targett 1984), are not. Nevertheless, such increments have been used, perhaps erroneously, for ageing purposes. Compared with temperate zones, Antarctic habitats undergo smaller fluctuations in temperature, which may result in a lack of distinct annual growth increments.

Daily microincrements allow the ageing of Antarctic species without otolith annuli. Microincrements are the result of a discontinuous zone which is generally formed under changing light conditions, probably at daybreak (Tanaka et al. 1981). The near-constant light and constant dark conditions experienced by Antarctic fishes during the summer and winter, respectively, could potentially interfere with daily deposition patterns. However, in the present study, daily increment formation continued despite great variation in photoperiod. Although areas in otoliths were detected in which increment width decreased (Fig. 8), none of these appeared to indicate a cessation of increment formation. Slight changes in light intensity, which occur in both Antarctic summer and winter, or endogenous rhythms may be responsible for the daily pattern of otolith deposition. This problem is currently being investigated using Antarctic fishes kept in constant dark or constant light, and under different light intensities (Radtke and Hourigan unpubl. data).

Use of a multivariate mathematical model relating age to otolith length and weight and fish size is a simpler method of age determination. The preparation and counting of microincrements in fish over 1 year of age is time-consuming and impractical. However, the multiple regression equation calculated from the 32 individuals analyzed with SEM provided an alternative ageing method. Otolith weight (with its consistent relationship to body length) was the best predictor of age, demonstrating the usefulness of otoliths in such a regression. This method should be applicable to other fish species, serving as a quick means to provide growth information. The dimensions of otoliths have been used to estimate the age of temperate fishes (Templeman

and Squires 1956, Boehlert 1985, Radtke et al. 1985). Otolith-age equations are species-specific and possibly population-specific. Using otolith morphometrics for ageing will, therefore, require developing the equations for individual species. Nevertheless, in conjunction with ageing techniques using microincrement counts, otolith morphometrics offer a simpler method of ageing a large sample of individuals than is possible using more laborious techniques.

The external features of *N. nudifrons* otoliths were distinctive compared with those from eight other Antarctic fishes examined (*Chaenocephalus aceratus*, *Champscephalus gunnari*, *Harpagifer bispinis antarcticus*, *Notothenia angustifrons*, *N. gibberifrons*, *N. larseni*, *N. corriceps*, and *Trematomus newnesi*; Radtke, pers. observ.). Species-specific otolith features of Antarctic fishes have been described by Hecht (1987) and these may be useful in identifying Antarctic fishes from cetacean, pinniped, bird, or fish stomachs (Hecht 1987, North et al. 1984). Otolith morphological characteristics may also provide information on taxonomic relationships among Antarctic fishes (Hecht 1987), as they have for other fish groups (Hecht 1978, Hecht and Hecht 1978, Morrow 1979).

Life history of *Nototheniops nudifrons*

Nototheniops nudifrons is a slow-growing, relatively long-lived fish. Subadults and adults of both sexes were found in shallow-water (<100 m) benthic habitats along the Antarctic Peninsula, as reported by other researchers (Targett 1981, Daniels and Lipps 1978, Kellermann 1986). The absence of individuals smaller than 75 mm SL from trawls probably represented selection by the fishing gear for larger individuals. The growth curves determined by body length vs. microincrement count, as well as by body length vs. age calculated from the multivariate relations of otolith length and weight, were similar and linear in shape between 45 and 149 mm SL. Linear growth was observed even though the data included a large size-range of fish, with individuals near the largest sizes reported for this species. This type of linear growth, with no marked slowing toward an upper asymptote, has not been reported for other Antarctic fishes, although the growth curve of *Harpagifer bispinis antarcticus*, another small Antarctic fish, is nearly linear (Daniels 1983).

Males and females had similar growth rates. This was surprising, since mature males and females follow different strategies. Males and females reach sexual maturity at the same age (4–5 years); however, thereafter females invest much more energy into gonadal growth than do males (Hourigan and Radtke 1989). All parental care is provided by the males, which may spend at least 4 months in nest defense of a single

clutch of eggs (Hourigan and Radtke 1989). This probably requires increased energy costs, and may limit food intake by constraining the male to foraging near the nest. These two strategies may entail similar energy expenditures, resulting in similar somatic growth rates.

Estimation of mortality rates is central to the determination of demographic parameters (Gulland 1955). It is possible to estimate natural mortality (Z) from the data on trawl catches and age for this population of *N. nudifrons*. The most widely used method to estimate mortality is the Beverton and Holt mortality estimator which uses the von Bertalanffy growth curve (Beverton and Holt 1956). The age-length data for the 32 fish were fitted to the von Bertalanffy growth curve, and the parameters and their confidence limits are given in Table 4. These values are primarily useful for comparative purposes, since the actual shape of the growth curve approximated a linear relationship. Natural mortality, calculated from the von Bertalanffy parameters and derived from the sample of 32 fish of known ages, yielded a value of $Z = 0.68$ (Table 4). When Z was calculated using the von Bertalanffy growth parameters for the larger sample of 212 fish with predicted ages, $Z = 0.66$. These estimates assume that the fish grow according to a deterministic von Bertalanffy growth curve. Since the present sample was more accurately represented by a linear growth curve, this assumption was violated. An independent mortality rate was calculated using the actual age estimates from the otolith morphometrics. In this estimate, the mortality rate is the slope of the log-survivorship curve (Ricker 1975) and was calculated to be 0.89.

Kock et al. (1985) provide a summary of mortality estimates for larger Antarctic fishes of commercial interest. Both estimates of instantaneous mortality of *N. nudifrons* were higher than these estimates, which ranged from 0.20 to 0.35. Predation rates may be higher on *N. nudifrons* than on larger species. However, Daniels (1983) estimated the mortality of the still smaller *Harpagifer bispinis antarcticus* to be 0.22 and 0.25 for males and females, respectively (a recalculation of his data for both sexes combined, using the same methods as for *N. nudifrons*, resulted in a value of 0.223).

Although the high mortality rates for *N. nudifrons* accurately describe our sample, they may be subject to sampling errors. Our estimates were based on a single sample captured on two occasions 1 month apart. Both mortality calculations assume that the sampled population is age-stationary (i.e., the age distribution remains the same from year to year), an assumption which is frequently not met. Mortality estimates will also be biased if certain age classes larger than L_C (length at first capture) are less subject to capture. Our

Table 4

Parameter estimates derived from the Von Bertalanffy growth equation (L_{∞} constrained to 160 mm SL), natural mortality rates, and associated parameters for *Nototheniops nudifrons* collected from the Antarctic Peninsula.

Parameter	SL vs. age in days		SL vs. age in years	
	Estimate	Confidence limits	Estimate	Confidence limits
From otoliths (N = 32)				
K	0.0005	0.00049–0.00061	0.200	0.000–0.223
t_0	2.20	–158.10–162.50	0.006	–0.434–0.445
From predicted ages (N = 194)				
K	0.00048	0.00047–0.00050	0.175	0.172–0.183
t_0	–40.848	–94.681–12.986	0.112	–0.259–0.086
Mortality estimates (Beverton and Holt 1956)				
	All	Male	Female	
L_C	101	91	101	
L_{Mean}	113.1	106.6	112.5	
k	0.175	0.175	0.175	
Z	0.678	0.599	0.73	
From estimated ages where the mortality rate Z is the slope of the log-survivorship curve (Ricker 1975)				
Z	0.894	0.807	1.26	

sampling caught significantly more females than males (χ^2 , $p < 0.05$), and the modal size of males was smaller. This might mean that there are fewer large males in this population. Alternatively, larger males may be less subject to capture in spring, perhaps because of different habitat preferences of nesting males. This would skew mortality estimates upwards.

The life history of *N. nudifrons* is characterized by slow growth and a relatively long life for a small fish. Age at sexual maturity is late (4–5 years), and fecundity is low (Hourigan and Radtke 1989). Eggs take several months to hatch, followed by a pelagic larval stage of several months duration (Kellermann 1986, Hourigan and Radtke 1989). It has become clear that these life-history traits are the norm for Antarctic fishes (Daniels 1983, Kock et al. 1985). They combine to produce species that are vulnerable to overfishing and that recover slowly when stocks are depleted. Indeed, catches of both *Notothenia rossii* and *N. gibberifrons* on the shelves of certain islands of the Scotia Sea decreased drastically after several years of fishing (Kock et al. 1985). The methods used in the present study may provide more accurate estimates of the ages of Antarctic fishes, and facilitate management of Antarctic fisheries.

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