

NUMERICAL INTEGRATION OF DAILY GROWTH INCREMENTS: AN EFFICIENT MEANS OF AGEING TROPICAL FISHES FOR STOCK ASSESSMENT

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ABSTRACT

For an objective, cost-effective ageing methodology applicable to tropical species, a new approach to estimating parameters of the von Bertalanffy growth equation through the study of otolith microstructure was developed and applied to *Pristipomoides zonatus*, a deepwater snapper widely distributed throughout the Indo-Pacific region. The average width of sagittal daily growth increments was used to measure otolith growth rate, which was then related to the size of the otolith. The data were numerically integrated, providing estimates of age (in years) at regular 500 μm increments to otolith length, which was then used to predict fork length (FL mm) at age with regression analysis. The data were fitted to the von Bertalanffy growth model, resulting in $FL = 442 (1 - \exp(-0.234 (\text{Age} + 0.892)))$.

The method was critically examined and validated through the study of 1) annual hyaline and opaque markings that appear in the otoliths, 2) Monte Carlo simulation, 3) length-frequency analysis, 4) examination of spawning seasonality relative to back-calculated birth date taken from the time of first annulus formation, and 5) empirical comparisons with the literature concerning snapper growth.

Developing stock-assessment models tailored to the characteristics and needs of tropical fisheries is an area of active and productive research. In particular, significant progress has been made over the last several years in the area of length-based methods (Schnute and Fournier 1980; Jones 1981; Pauly 1982, 1987b; Fournier and Breen 1983; Fournier and Doonan 1987; Schnute 1987). With these advances, a powerful array of biologically realistic models is now available for analyzing length-frequency data.

Although tremendous strides have been made in developing these new length-based methods, the importance of acquiring other information besides length-frequency data and total catch statistics is all the more evident. Ancillary information usually helps to stabilize and improve the estimation of model parameters (Schnute and Fournier 1980; Fournier and Doonan 1987). Foremost is developing an independent knowledge of growth dynamics (Gulland 1987; Morgan 1987). It is now generally accepted that the analysis of length-frequency data,

in conjunction with age estimates derived from the study of hard parts, represents the most promising avenue for future assessment work on exploited tropical species (Pauly 1987a).

Nonetheless, estimating growth rates of tropical species by using otoliths has been a difficult and persistent problem. Investigators have often failed in their efforts, either because of an absence of conventional hyaline and opaque markings, as is true of most tropical species, or because of an aversion to direct enumeration of daily otolith increments. The latter can be an extremely difficult, time consuming, and tedious process.

Since Pannella (1971) first discovered the existence of daily otolith increments, a large body of work has developed on the subject. While many investigators have touted the potential benefits of ageing tropical species by using otolith microstructure, few have attempted to develop growth curves with assessment goals specifically in mind. Instead, most work to date has dealt with ageing larval forms (Jones 1986) and elucidating endogenous and environmental effects on increment formation (Campana and Neilson 1985). Although much useful information has been gained, daily increments have yet to fulfill their promise with respect to applications in the area of juvenile and adult population dynamics.

The purpose of this study was to develop a general method of ageing tropical fishes by using daily

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growth increments, specifically with stock-assessment applications in mind. In this regard, the von Bertalanffy growth equation (Ricker 1979) is of fundamental importance. Due to its widespread use in assessment models (e.g., the Beverton and Holt [1957] yield formulation), parameter estimates for this equation provide an ideal complement to many of the length-based methods that are currently in use (e.g., Morgan 1987). The ultimate goal of this study was, therefore, to develop a methodology to estimate the von Bertalanffy growth parameters K and L_{∞} from the study of daily increments. Ideally, the approach developed should be general in its application, easy to implement, simple in its technical requirements, and cost effective. Were such a uniform framework to the study of age and growth of exploited tropical species developed, it would assist routine assessment work greatly.

MATERIALS AND METHODS

As part of a larger program to assess stocks of deep slope fishes in the Mariana Archipelago (Polovina 1985; Polovina and Ralston 1986; Ralston in press b), a study of the age and growth of gindai, *Pristipomoides zonatus*, was initiated. This commercially important eteline snapper (Lutjanidae) is widely distributed in the Indo-Pacific region (Allen 1985) and is the most commonly caught species in Guam's deepwater hook-and-line fishery (Polovina 1986).

Field sampling for gindai specimens was conducted from the NOAA ship *Townsend Cromwell* during the 2 yr period spanning April 1982 to May 1984. During this time, six 40 d cruises were completed, such that samples of gindai were obtained during all months of the year except March, September, and October.

All gindai were caught during daylight hours by using hydraulic fishing reels equipped with circle fish hooks. When landed, fish were measured to the nearest millimeter fork length (FL) with a measuring board and weighed to the nearest 0.01 kg on a beam balance.

Specimens were sexed at the time of capture by gross examination of the gonads. In addition, a representative selection of the gonads was frozen for more detailed examination in the laboratory. There, they were preserved in a solution of 10% buffered formalin and weighed to the nearest 0.1 mg. Ovaries were staged with the classification of Everson (1984), developed for *Etelis carbunculus*, a related deepwater eteline lutjanid. His classification recognizes seven stages based on egg size, shape, and yolk content, i.e., (I) primordial, (II) early developing, (III)

developing, (IV) advanced developing, (V) early ripe, (VI) ripe, and (VII) residual. Gonadosomatic indexes (gonad weight expressed as a percentage of body weight) also were calculated where possible.

Otoliths

At the time of capture, sagittal otoliths were collected, by frontal section through the cranium, from certain individuals sampled uniformly from the full size range of gindai captured. The otoliths were rinsed in fresh water to remove adhering membranes and endolymph and were stored dry in glass vials. Later in the laboratory, they were examined with a dissecting microscope for the presence of hyaline (i.e., translucent) and opaque markings while illuminated with reflected light against a dark background. When markings were present, the distance from the focus to the beginning of each opaque zone was measured along the postrostral growth axis by using a calibrated ocular micrometer. Total otolith length (focus to postrostrum) also was recorded.

A random subsample of gindai otoliths was taken, and their microstructure examined for the presence of daily increments (Campana and Neilson 1985). To prepare the otoliths, they were first embedded in casting resin, which was allowed to harden completely. Cast otoliths were sectioned on a Buehler² ISOMET low speed jewelry saw. Thin (0.70 mm) sections were made through the focus along a frontal plane to the most distal portion of the postrostrum. Sections were polished sequentially on a Buehler ECOMET polisher/grinder with 180 and 600 grit abrasive disks. Samples were then briefly etched for 5–30 seconds in a dilute solution of 1% HCl, washed in water, and dried. Prepared sections were mounted on glass slides with Euparal or Flotexx and cover slips and allowed to clear and harden completely prior to viewing (approximately 2 weeks).

Mounted otolith sections were examined with a compound binocular microscope by using transmitted light at a magnification of 200 or 400 \times . Total lengths of the otoliths (i.e., the distance in micrometers between the focus and the postrostral margin) were measured ($N = 94$) and individual readings were made at selected points along the postrostral growth axis, wherever it was possible to distinguish the characteristic bipartite structure of daily increments. At each site sampled the average width of presumptive daily growth increments was determined by counting a small number (me-

²Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

dian = 14, range = 5–22) of increments and measuring the axial length of the short segment in which they occurred. In addition, the curvilinear distance between the midpoint of each segment and the otolith focus was measured along the focus to postrostral growth axis. Up to 12 readings were made from each preparation. The focus was defined to be the most posterior of what typically were several primordia (e.g., Radtke 1987).

The data were summarized by computing the ratio of segment length in micrometers to the included number of increments at each specific site examined, providing an estimate of the average increment width at some measured distance from the otolith focus. Under the assumption that one increment forms each day, these data can be used to estimate the instantaneous growth rate of the otolith (Ralston and Miyamoto 1981, 1983; Ralston 1985).

To estimate age, a simple form of numerical integration was employed. Starting at the focus, the data were subdivided into 500 μm intervals of otolith length. For each interval, the arithmetic mean growth rate of the otolith was calculated based upon the number of readings falling therein. This average growth rate was then divided into 500 μm to estimate the number of days needed to complete growth through the intervals, which were sequentially accumulated away from the focus, and finally divided by 365.25 to convert age estimates to years. The size of the otolith upon completion of growth through each interval was used to predict the corresponding FL of the fish after the natural logarithm of FL was regressed on the logarithm of total otolith length. These data (age [in years] and FL [mm]) were then fitted to the von Bertalanffy growth equation (Ricker 1979) by using a nonlinear regression routine (SAS Institute Inc. 1979, NLIN procedure).

Monte Carlo simulation techniques (Naylor et al. 1966) were applied to this analytical procedure to evaluate the accuracy (i.e., bias) of the estimator and to study the precision of parameter estimates. The structure of the simulation model was such that von Bertalanffy growth was assumed by stipulating a decreasing linear relationship between somatic growth rate and length, i.e., $d(\text{FL})/dt = K(L_\infty - \text{FL})$. Likewise, the relationship between otolith length (OL) and FL was assumed to be governed by the power function, so that $\text{FL} = \alpha \text{OL}^\beta$. Otolith growth rate, $d(\text{OL})/dt$, was then obtained by forming the ratio of $d(\text{FL})/dt$ and $d(\text{FL})/d(\text{OL})$. All parameters in the model were otherwise set equal to the estimates obtained from the otolith study, and the specific probability distributions invoked

were similar to those encountered with the actual data.

Length-Frequency Analysis

As an independent means of verifying results obtained through the study of otoliths, the regression method of Wetherall et al. (1987) was used to estimate specific growth and mortality parameters characterizing the study population. The analysis was based on the combined length-frequency distribution (FL rounded to the nearest 10 mm) of all gin-dai sampled (see Ralston [in press a] for a discussion of the effects of pooling length data taken at different times throughout the year).

Initially, this method requires determination of the least FL at which fish are fully represented in the catch ($\ell_{c,\text{min}}$). For this purpose, the first size class larger than the mode was assumed to be the smallest length category fully sampled (see, for example, Ricker 1975). Moreover, for this and any larger cut-off value ($\ell_{c,i}$), we were able to compute the mean size of fully vulnerable fish in the catch ($\bar{\ell}_i$), i.e., those fish greater than $\ell_{c,i}$. As $\ell_{c,i}$ was successively advanced through the fully vulnerable size range, the mean and variance in size of larger fish were recalculated at each step, and a series of ordered pairs was developed. The actual estimation procedure involved regressing values of $\bar{\ell}_i$ against successive values of $\ell_{c,i}$. The inverse of the standard error of $\bar{\ell}_i$ was used as a statistical weight for each point, leading to the best linear unbiased estimates of the slope (δ) and intercept (ζ). With the resulting regression statistics, the formulae provided in Wetherall et al. (1987) were used to obtain point estimates of the ratio of total instantaneous mortality rate to the von Bertalanffy growth coefficient (Z/K) and the von Bertalanffy asymptotic size parameter (L_∞). In particular, they showed that $Z/K = \delta/(1 - \delta)$ and $L_\infty = \zeta/(1 - \delta)$. Likewise, error estimates for these statistics were calculated as well.

RESULTS

Age Estimation from Increment Microstructure

In all, 440 otoliths were extracted, and of these, 94 were sectioned and examined for daily increments. As expected, there is a clear statistical basis for predicting FL from OL (Fig. 1). The regression equation relating these variables is highly significant ($P < 0.0001$) and is given by

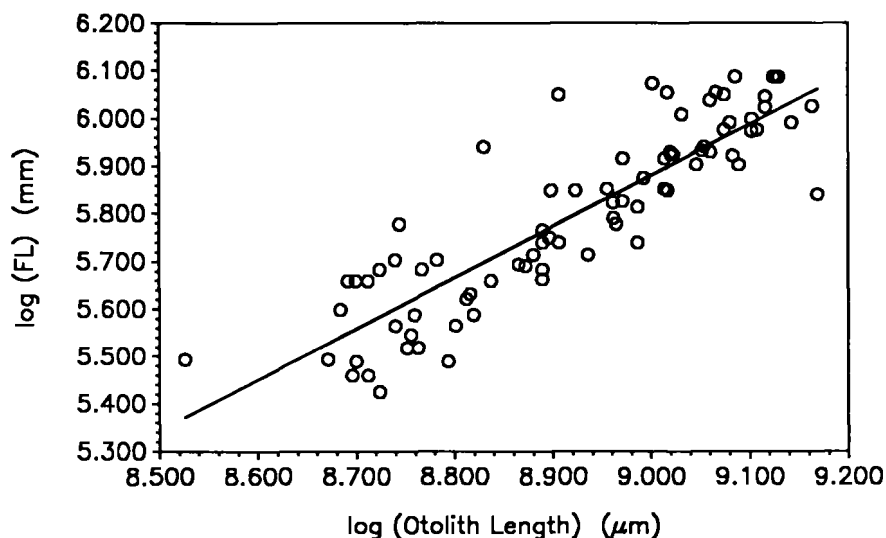


FIGURE 1.—Regression of the natural logarithm of FL on the log of otolith length (OL) (focus to distal margin of postrostrum).

$$\log(\text{FL}) = -3.783 + 1.074 \log(\text{OL}),$$

with $r^2 = 0.76$ and standard errors for the slope and intercept equal to 0.0634 and 0.5665, respectively.

The sagittae of gindai display microstructure (Fig.

2) typical of daily increments observed in other studies (Dunkelberger et al. 1980; Tanaka et al. 1981; Watabe et al. 1982). Light incremental zones and dark discontinuous zones are clearly visible in the photomicrograph. One daily growth increment is composed of the bipartite combination of a single

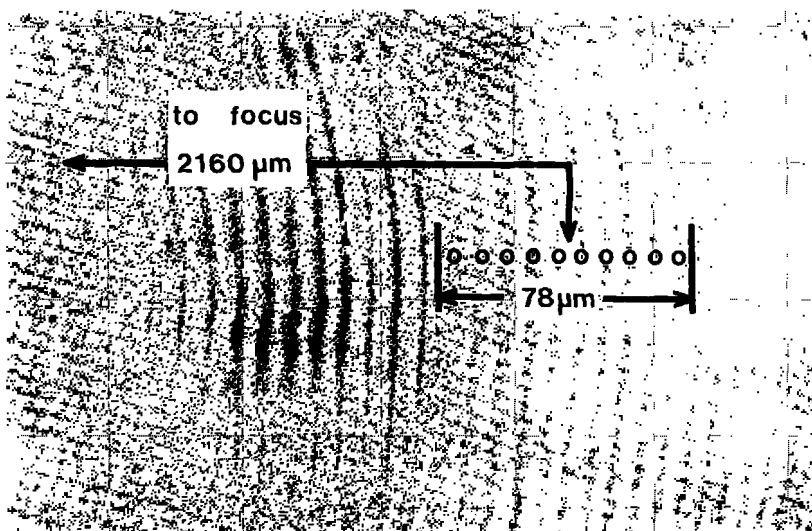


FIGURE 2.—Photomicrograph of a sectioned gindai otolith showing increment microstructure. The 10 daily increments in a short 78 μm segment are enumerated and increment width, i.e., otolith growth rate, is calculated (7.80 $\mu\text{m}/\text{d}$). The distance to the focus is also shown (2,160 μm).

incremental zone with its adjacent discontinuous zone. When counting daily increments, we enumerated the dark discontinuous zones.

From the 94 sectioned otoliths examined for the presence of growth increments (Fig. 2), a total of 852 determinations of otolith growth rate (i.e., increment width) were completed. Note that no increment width data were collected at otolith lengths in excess of 7,500 μm , although otoliths as long as 9,594 μm were measured and used in the regression analysis of $\log(\text{FL})$ on $\log(\text{OL})$ (see Figure 1). Beyond 7,500 μm (corresponding to 329 mm FL), the pattern of otolith growth became increasingly irregular,

and clearly distinguishable daily increments, composed of well-defined incremental and discontinuous zones, were difficult to resolve.

The data show that as otolith length increased the growth rate of the otolith declined (Fig. 3). No detectable difference in the relationship between otolith growth rate and otolith length could be attributed to sex. A partitioned analysis of covariance of the log-transformed data (Table 1) failed to reveal differences in either the slopes or adjusted means of males and females. Thus, data for the two sexes were combined.

The mean growth rate of the otolith $d(\text{OL})/dt$;

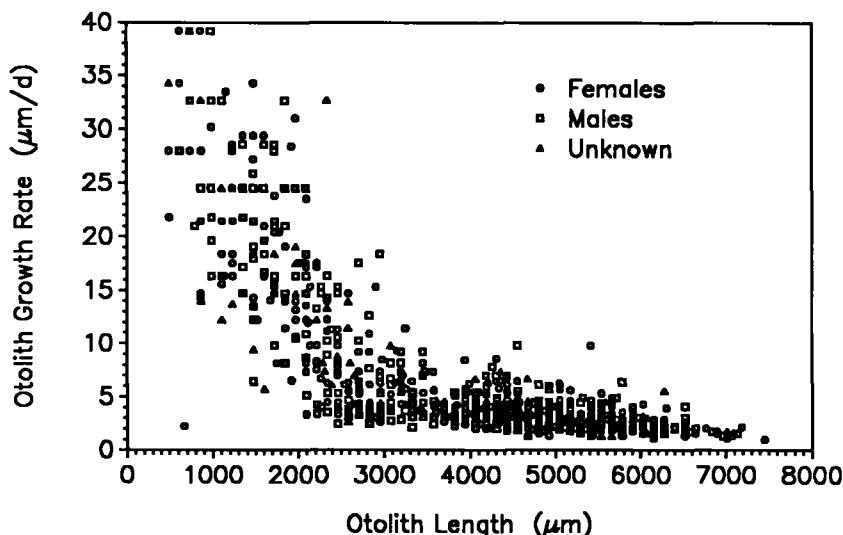


FIGURE 3.—The relationship between otolith growth rate and otolith length plotted for males, females, and specimens of unknown sex.

TABLE 1.—Partitioned analysis of covariance of log-transformed otolith growth rate $d(\text{OL})/dt$. Otolith length (OL) was used as the covariate and sex was the treatment variable. The data were divided into two separate linear partitions: data for which $\text{OL} \leq 3,700 \mu\text{m}$ and $\text{OL} > 3,700 \mu\text{m}$.

Source	df	Sum of squares	Mean square	F	P
OL $\leq 3,700 \mu\text{m}$					
Equality adjusted means	1	0.0015	0.0015	0.01	0.935
Zero slope	1	121.9917	121.9917	551.78	0.001
Error	316	69.8635	0.2219		
Equality slopes	1	0.7158	0.7158	3.26	0.072
Error	315	69.1477	0.2195		
OL $> 3,700 \mu\text{m}$					
Equality adjusted means	1	0.1334	0.1334	1.14	0.286
Zero slope	1	15.9656	15.9656	136.72	0.001
Error	389	45.4273	0.1168		
Equality slopes	1	0.2202	0.2202	1.89	0.170
Error	388	45.2071	0.1165		

and the variance in growth rate σ_i^2 within each of the $i = 1, 15$ intervals of otolith length (Table 2) show that as otolith length increased both $d(OL)/dt$ and σ^2 declined. The estimated age (in years) at the point of transition between each of the 15 otolith length intervals (i.e., upon completion of growth through interval k) was

$$\text{Age}_k = \frac{1}{365} \sum_{i=1}^k \frac{\Delta(OL)}{d(OL)/dt_i},$$

where $\Delta(OL)$ is 500 μm in the application presented here.

Otolith length upon completion of growth through interval k was converted to the equivalent FL (see Figure 1), and the data fitted to the von Bertalanffy growth equation. Because this model poorly represents growth during the early life history, only data representing otolith length intervals in excess of 3,000 μm (i.e., ages >0.8 year) were used in the regression analysis (see Discussion). Table 2 also provides a statistical weight for each of the age estimates. Weighting was desirable because 1) the sample size of each mean varied, 2) the σ_i^2 were heterogeneous (proportional to the square of the mean), and 3) compounding of error occurred because of the additive property of the estimator. Weights were calculated as the reciprocal of the sum of standard errors of the means through interval k . The weighted least squares fit to the von Bertalanffy equation (Fig. 4) was

$$\text{FL} = 442 (1 - \exp(-0.234 (\text{Age} + 0.892))),$$

with 99.99% of the total variation in FL explained by the model, and with asymptotic standard errors

for L_∞ , K , and t_0 equal to 14.85 mm, 0.0180 yr^{-1} , and 0.078 year, respectively.

The results of the Monte Carlo simulation indicate that the estimation procedure was unbiased. Following 50 computer replications of the same sampling procedures outlined above, there was no detectable bias in the estimation of either K or L_∞ , even though the coefficients of variation for the standard errors of these statistics were both small (0.64 and 0.34%, respectively). Moreover, variance estimates derived from the approximately normal simulation sampling distributions of K and L_∞ provided a basis for placing confidence intervals on the point estimates as follows: $P(0.213 < K < 0.255) = 0.95$ and $P(421 < L_\infty < 463) = 0.95$.

Annual Marks on the Otoliths

On occasion, hyaline and opaque zones were evident in the sagittae of gindai (Fig. 5). These were most easily viewed with light reflected off otoliths immersed lateral side up in water. Typically, however, the zonations were poorly developed or absent entirely. Nonetheless, of the 440 otoliths examined, some banding was evident in 171 (39%), and it was possible to classify the margins of these as either hyaline or opaque. The seasonal expression of hyaline or opaque zones on the margins of these otoliths shows what appears to be an annual periodicity; otoliths sampled during the November–December bimonthly period were characterized almost exclusively by the presence of hyaline margins (94%). Just 2 months later (January–February), only 13% of the otolith samples were similarly classified (Fig. 6). Thereafter, the percentage of otoliths with hyaline margins was never elevated, at least through the

TABLE 2.—Summary statistics of otolith growth by 500 μm intervals in otolith length.

Otolith length interval	Lower bound	Upper bound	<i>N</i>	Mean growth rate ($\mu\text{m}/\text{d}$)	Variance growth rate	Interval duration (d)	Age (yr)	Statistical weight
1	1	500	3	28.03	39.20	17.84	0.0	0.0696
2	501	1,000	30	27.89	90.28	17.93	0.1	0.0164
3	1,001	1,500	55	21.53	42.81	23.22	0.2	0.0132
4	1,501	2,000	60	18.43	41.68	27.14	0.2	0.0118
5	2,001	2,500	83	10.94	32.57	45.70	0.4	0.0115
6	2,501	3,000	71	5.97	12.76	83.68	0.6	0.0115
7	3,001	3,500	54	5.52	4.41	90.55	0.8	0.0114
8	3,501	4,000	49	3.99	1.61	125.25	1.2	0.0113
9	4,001	4,500	110	3.98	2.18	125.54	1.5	0.0113
10	4,501	5,000	99	3.36	1.72	149.02	1.9	0.0113
11	5,001	5,500	95	3.01	1.55	165.98	2.4	0.0112
12	5,501	6,000	78	2.87	1.03	174.03	2.9	0.0112
13	6,001	6,500	39	2.29	0.74	217.91	3.5	0.0112
14	6,501	7,000	18	2.03	0.45	246.60	4.1	0.0112
15	7,001	7,500	7	1.51	0.16	330.97	5.0	0.0111

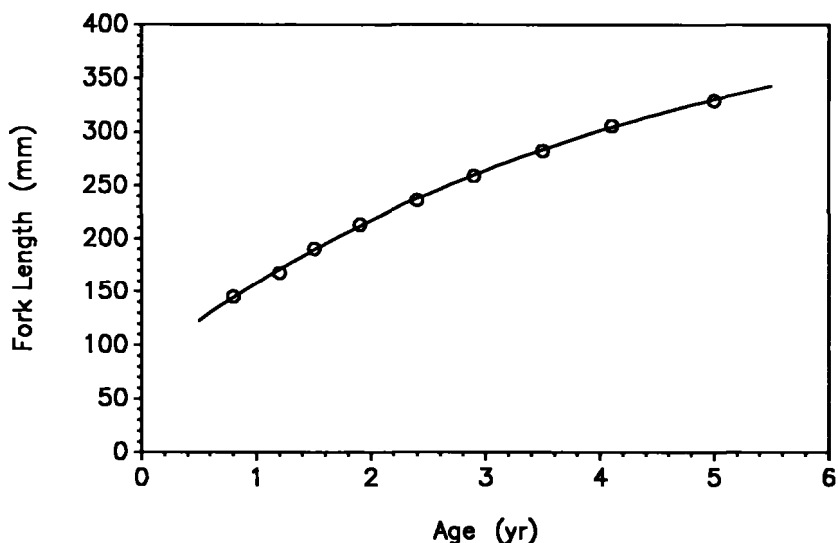


FIGURE 4.—Von Bertalanffy growth curve for gindai developed from the study of daily growth increments.

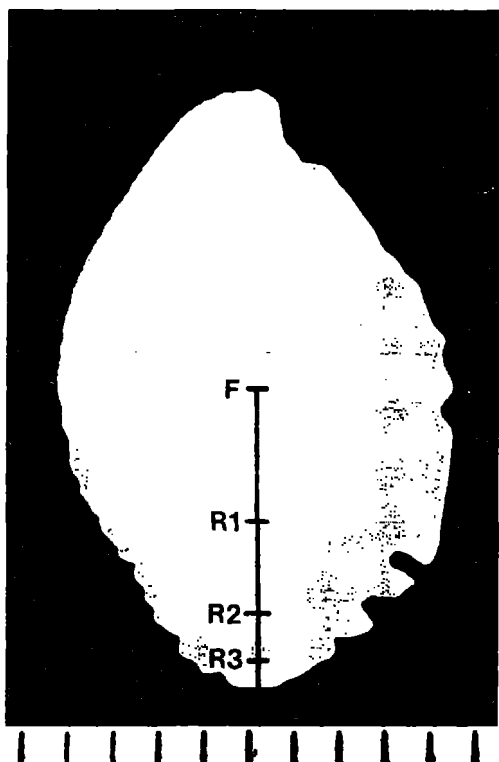


FIGURE 5.—Photomicrograph of a whole gindai sagitta showing the development of hyaline and opaque zones and distance measurements from the focus (F) to the otolith margin and each ring group.

end of August. No data were available for the months of September and October. These results indicate that the markings observed were annular and that the opaque zone first began to form during January–February.

Given the apparent annual periodicity of the markings, growth was estimated by examining their spatial pattern within the otolith. Table 3 presents mean otolith radii measured to the start of each new opaque zone, summarized by sampled age groups, for the 29 specimens that showed well-developed markings throughout their sagittae (e.g., Fig. 5). The table also presents the weighted mean radii converted to estimated FL's by using the regression developed earlier (Fig. 1).

The assembled data were then used to estimate

TABLE 3.—Back-calculated lengths based on annual markings in gindai otoliths. All measurements were taken along the focus to postrostrum growth axis.

Age group	N	Mean otolith radius (μm) at annulus				
		I	II	III	IV	V
I	0	—				
II	0	—	—			
III	6	3,233	4,700	5,600		
IV	13	3,054	4,400	5,408	6,315	
V	10	3,130	4,440	5,610	6,530	7,260
Weighted mean (μm)		3,117	4,476	5,517	6,409	7,260
Standard deviation		222	349	427	468	443
Fork length (mm)		128	189	237	278	318

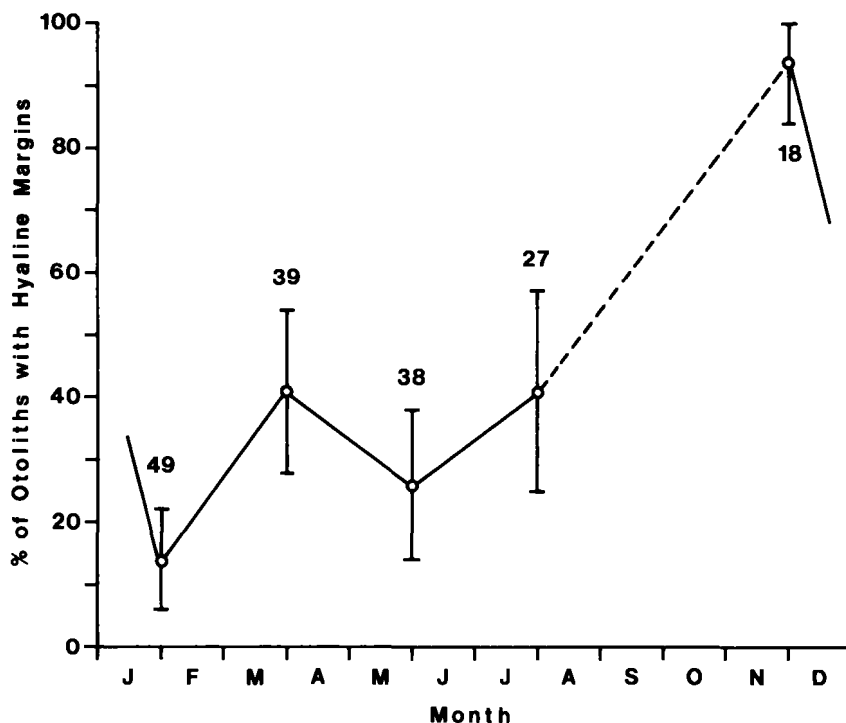


FIGURE 6.—The seasonal occurrence of hyaline and opaque markings on the margins of gindai otoliths.

parameters of the von Bertalanffy growth equation by means of a Walford plot (Ricker 1975), wherein results from a regression of FL at time $t + 1$ against FL at time t provide the basis for estimates of $K = 0.156 \text{ yr}^{-1}$ and $L_{\infty} = 537 \text{ mm FL}$.

Length-Frequency Analysis

The combined length-frequency distribution for all gindai sampled (Fig. 7) shows that the mean size was 368 mm FL (standard deviation = 43.1 mm). Fish ranged in size from 190 to 490 mm FL and the modal size was 380 mm FL. Thus, $\ell_{c,\min}$ was estimated to be 385 mm FL. There is evidence to show that, above this size, fish were equally vulnerable to the gear (Ralston 1982, unpubl. data), although smaller individuals were almost certainly underrepresented in the catch because of the selective sampling action of the fish hooks. As $\ell_{c,i}$ increased from 385 to 485 mm FL, the corresponding value of $\bar{\ell}_i$ increased (Table 4). Due to a sample size of one, estimates of the variance and standard error of the mean could not be calculated when $\ell_{c,i} = 485 \text{ mm}$. Without a statistical weight, the point was excluded from the analysis.

The regression of $\bar{\ell}_i$ on $\ell_{c,i}$ (Fig. 8) was highly significant ($P \ll 0.0001$), although there was an increasing lack of fit as $\ell_{c,i}$ increased, especially beyond 435 mm FL. This result was due to the diminished statistical weights accorded these points (Table 4). Estimates of the slope and intercept of the regression were $\delta = 0.7051$ and $\xi = 137.31$, with standard errors of 0.0200 and 8.138, respectively. Thus, the mortality to growth ratio (Z/K) is esti-

TABLE 4.—Length-frequency data fitted to the Wetherall et al. (1987) regression model for estimating Z/K and L_{∞} (fork length in mm).

Class fork length	N	$\ell_{c,i}$	$\bar{\ell}_i$	Variance	Standard error	Relative statistical weight
390	362	385	409.5	284.4	0.438	22.82
400	314	395	415.9	212.1	0.435	22.94
410	301	405	422.1	157.3	0.441	22.65
420	214	415	429.3	110.7	0.469	21.32
430	165	425	436.3	79.4	0.523	19.10
440	83	435	444.6	62.1	0.705	14.18
450	30	445	453.8	58.3	1.178	8.49
460	10	455	463.3	78.7	2.562	3.90
470	1	465	480.0	200.0	10.000	1.00
490	1	485	490.0	—	—	—

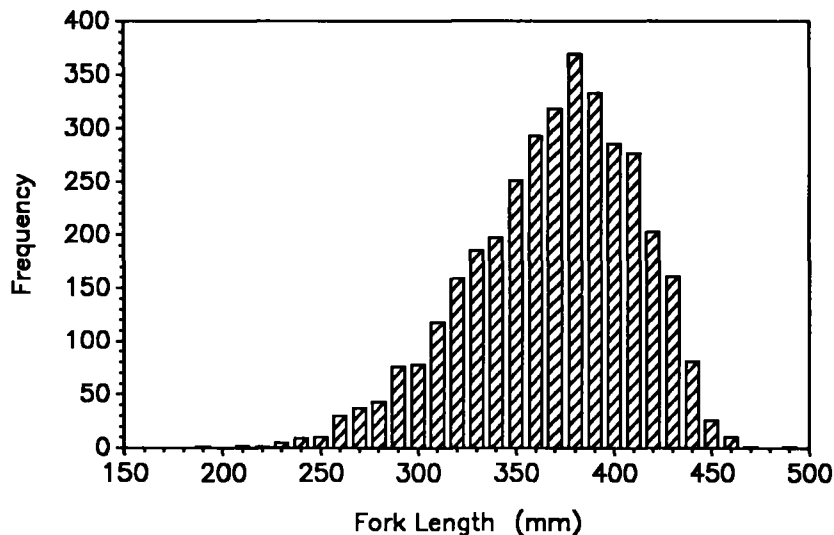


FIGURE 7.—Combined length-frequency distribution for all gindai sampled.

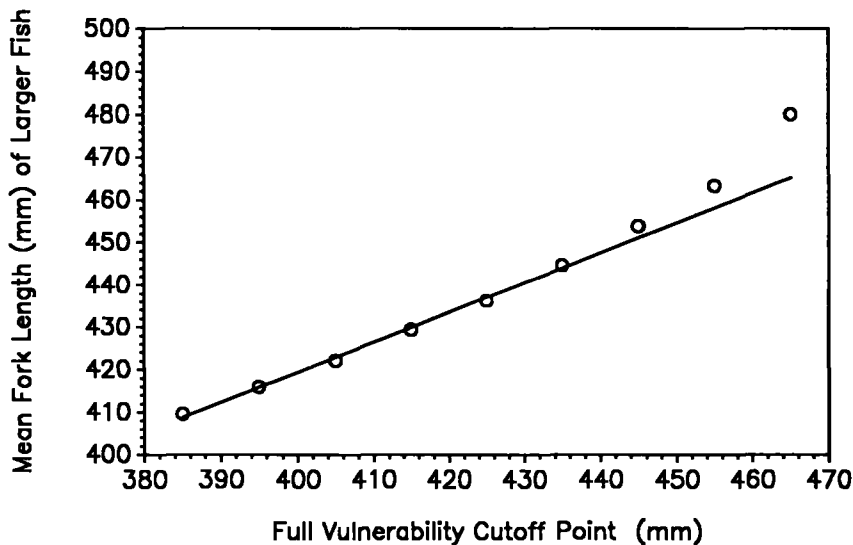


FIGURE 8.—Wetherall et al. (1987) regression of $\bar{\ell}_i$ on $\ell_{c,i}$ (see text for further discussion).

mated to be 2.39 and $L_\infty = 466$ mm FL. Confidence intervals for these estimates are $P(1.94 < Z/K < 2.62) = 0.95$ and $P(458 < L_\infty < 474) = 0.95$.

With the results presented earlier, it is possible to decompose the Z/K ratio and estimate total mortality rate (Z). For $K = 0.234 \text{ yr}^{-1}$ (increment microstructure), $Z = 0.56 \text{ yr}^{-1}$, and for $K = 0.156 \text{ yr}^{-1}$ (annual marks), $Z = 0.37 \text{ yr}^{-1}$.

Spawning Season

Gonadosomatic indexes for male and female gindai are summarized by month of capture in Figure 9. The relative size of gindai ovaries was considerably greater than the testes. More importantly, there was a distinct seasonal trend in the monthly mean gonadosomatic indexes of females, which

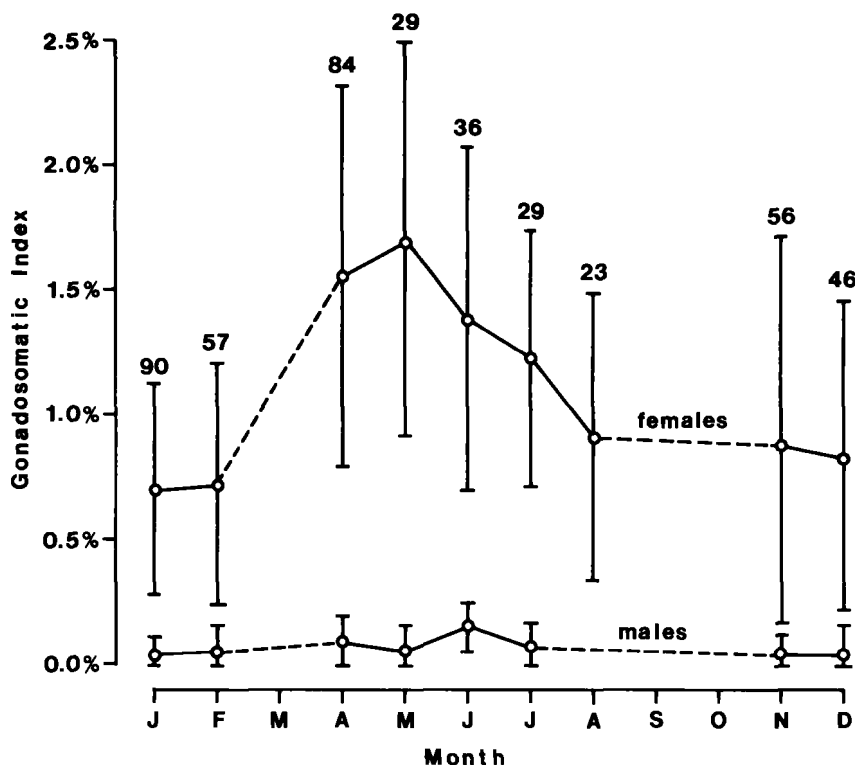


FIGURE 9.—The seasonal pattern of variation in mean gonadosomatic indexes of male and female gindai in the Mariana Archipelago. Note that mean index values are bracketed by sample standard deviations with the sample sizes given above.

reached a peak in May and diminished as the summer progressed.

The same pattern was mirrored in the percentage of ovaries classified to stages IV–VI (i.e., advanced developing to ripe). During the January–March quarter, only 1.4% of the ovaries sampled were so classified. This statistic rose to 48.3% during the April–June period, but then dropped to 19.2% in the July–September quarter and to 16.7% over the last quarter of the year (October–December). The similarity of these two patterns reinforces the interpretation of reproductive seasonality based on gonadosomatic indexes alone (but see deVlaming et al. 1982), and when taken together, these data indicate that peak spawning of gindai in the Mariana Archipelago occurs in late May and early June.

DISCUSSION

Other researchers also have measured the width of daily increments to study fish growth. Methot (1981) used the widths of the outermost three incre-

ments in the otoliths of *Engraulis mordax* and *Stenobranchius leucopsarus* as a measure of recent somatic growth rate. Brothers and McFarland (1981) measured the thickness of daily increments in newly recruited *Haemulon flavolineatum* to discriminate life history transitions, as did Gutiérrez and Morales-Nin (1986) in their study of *Dicentrarchus labrax*. Moreover, integration of increment width data to estimate age has been reported, both analytically for *Pristipomoides filamentosus* (Ralston and Miyamoto 1981, 1983) and numerically for *Merluccius angustimanus*, *Merluccius* sp., *Engraulis mordax*, and *Pristipomoides auricilla* (Brothers et al. 1976; Methot 1983; Ralston 1985).

Experimental work has revealed some of the factors that affect the width of daily growth increments. For example, decreased somatic growth in *Oncorhynchus tshawytscha* due to reduced temperature also results in reduced increment thickness (Neilson and Geen 1985). There is conflicting evidence, however, regarding the effect of food ration on daily increment width. Volk et al. (1984) experi-

mentally altered somatic growth rates of *O. keta* juveniles with different experimental feeding regimes and showed a direct linear effect on the mean width of daily increments. Similarly, Marshall and Parker (1982) presented data showing an increase in the relative size of otoliths of starved *O. keta* compared with that of fed controls, even though starvation had no effect on the number of increments. In contrast, Neilson and Geen (1985) found no effect due to ration alone on the thickness of increments in fry of *O. tshawytscha*, although an interactive effect due to ration level and water temperature was shown. These authors also found that increased feeding frequency significantly reduced mean increment width. Lastly, Campana (1984) found that increments of larval (<10 days old) *Porichthys notatus* were more irregularly spaced than in juveniles, as were the increments of fish exposed to a constant photoperiod environment. From these results, it is apparent that the effect of food ration on the width of daily increments is complex and is at present not well understood.

There is still some question concerning how close the coupling is between somatic and otolith growth rates (Brothers 1981; Bradford and Geen 1987). Over the entire lifespan, otolith length and FL typically are highly correlated (Templeman and Squires 1956; Blacker 1974). This situation could not arise were not the growth rates correlated over a similar scale. Still, in the most rigorous examination of the extent of rate coupling to date, Bradford and Geen (1987) found no correlation between the observed growth rates of individual *O. tshawytscha* fry and otolith increment widths over relatively short-term (7–15 d) intervals, although a good correlation over a 51 d interval was observed. These authors point to the relatively conservative character of otolith growth (Casselmann 1983; Gutiérrez and Morales-Nin 1986) as the reason for short-term uncouplings between somatic and otolith growth rates.

In our study, otolith microstructure typical of daily increments was observed in the sagittae of gindai (Fig. 2). Daily growth increments were previously described and illustrated for congeneric species by Ralston and Miyamoto (1981, 1983), Brouard et al. (1984), and Radtke (1987). Likewise, we observed annual hyaline and opaque zonations, which have been reported in the hard parts (otoliths and vertebrae) of other lutjanids (Loubens 1978; Chen et al. 1984; Edwards 1985; Manooch 1987; Samuel et al. 1987). Still, of the 11 deep slope species (*Pristipomoides zonatus*, *P. auricilla*, *P. filamentosus*, *P. sieboldii*, *P. flavipinnis*, *Aphareus rutilans*, *Etelis*

coruscans, *E. carbunculus*, *Lutjanus kasmira*, *Caranx lugubris*, and *Selar crumenophthalmus*) caught during the Marianas survey and whose otoliths were examined in some detail (Ralston and Williams 1988), only gindai displayed hyaline and opaque zonations, even though all species exhibited microstructure typical of daily growth increments. The absence of annuli in the otoliths of these other species is difficult to explain because many are congeners, most are confamilials, and all but one (*S. crumenophthalmus*) occupy the same general deep-water habitat where gindai are found. As a group, these fishes are exposed to virtually identical environmental conditions. Neither is the diet of gindai in the Marianas particularly distinctive (Parrish 1987).

In contrast to the situation in the Marianas, studies by Loubens (1978) in New Caledonia and Samuel et al. (1987) in the Persian Gulf document distinctive hyaline and opaque annuli in a wide variety of the taxa indigenous to these areas. Although the occurrence of annuli in the otoliths of a variety of tropical and subtropical species is now well documented (Manooch 1987), our understanding of when and how they form is quite limited (see below).

Von Bertalanffy growth curves were developed for gindai by using both increment microstructure (Fig. 4) and annual marks. Likewise, the L_{∞} parameter of the von Bertalanffy growth equation was estimated by using the regression method of Wetherall et al. (1987). Moreover, the analysis based on annual markings was tentatively validated with an abbreviated form of marginal increment analysis, wherein the seasonal presence or absence of opaque margins was established for the various pooled ring groups. A preferred approach is to measure the marginal increment for each ring group separately (e.g., Chen et al. 1984; Matheson et al. 1986). Although the importance of this type of validation has been overlooked (e.g., Beamish and McFarlane 1983), it is a very useful technique, especially in situations where capture is fatal.

A comparison of von Bertalanffy parameter estimates obtained by the three wholly independent approaches (increment microstructure, annuli, and length-frequency analysis) shows reasonable correspondence. The two estimates of growth coefficient (K) differed somewhat (0.234 versus 0.156 yr^{-1}), although estimates of L_{∞} were substantially closer (442, 537, and 466 mm FL, respectively). Given that the annual marks were only weakly expressed, these findings support the conclusion that the microstructure observed in gindai otoliths (Fig. 2) results from the daily accretion of increments and, to the extent

that annuli have been validated (Fig. 6), verifies the method of increment widths employed here. Likewise, the Monte Carlo simulation demonstrated that from an analytical point of view the method is free of significant bias.

The results obtained here were also compared to what we know of lutjanid growth by using the growth performance index developed by Munro and Pauly (1983) (see also Pauly and Munro 1983). For a specifically delimited taxon, this index empirically quantifies the well-known inverse correlation between K and L_{∞} (Beverton and Holt 1959; Cushing 1968) and provides a simple basis for predicting K with an estimate of L_{∞} . Specifically, Manooch (1987) tabulated the results of growth studies covering 46 snapper and 31 grouper (Epinephelinae) stocks and calculated the combined growth performance regression for these taxa ($r^2 = 0.57$). With his equation, we predicted K by using each of our three estimates of L_{∞} (see above). These calculations resulted in $K = 0.228, 0.200,$ and 0.220 yr^{-1} for maximum sizes derived from daily increment microstructure, annuli, and length-frequency analysis, respectively. The estimates compare favorably with the value obtained solely from the study of otolith microstructure ($K = 0.234 \text{ yr}^{-1}$), indicating that our results are in close agreement with existing information concerning lutjanid growth.

Calculating the age at first annulus formation provides additional evidence that the approach presented here is valid. The data presented in Table 3 indicate that the first annulus occurs at an otolith length of $3,117 \mu\text{m}$. An estimate of age at this otolith length can be obtained from Table 2 by linear interpolation of the data falling in otolith length intervals 6 and 7; i.e., the otolith is $3,000 \mu\text{m}$ at age 0.6 and is $3,500 \mu\text{m}$ at age 0.8. This calculation indicates that the first annulus forms at an age of 0.65 year. Given that the opaque zone forms in January–February (Fig. 6), the predicted birth date by back-calculation is early June, in close agreement with observed spawning activity (Fig. 9). Moreover, the mean monthly sea surface temperature at Tanguisson Point, Guam, reaches its annual minimum during January–March (data for the period 1963–72 from Eldredge (1983)), suggesting that temperature fluctuation may be responsible for the formation of the annuli, although this species is found below the thermocline throughout the year (Eldredge 1983) and other closely related sympatric species lack zonations.

Some consideration of the underlying assumptions, advantages, and disadvantages of the method presented here is required. Without doubt, the most

important assumption of the approach is that increments are deposited daily throughout the size range where increment width data are gathered. There is a substantial body of literature to show that interruptions to the daily increment record can occur (e.g., Geffen 1982, 1986; McGurk 1984; Jones 1986), especially in larger and older individuals (e.g., Pannella 1971; Ralston and Miyamoto 1983). Likewise, we know that with light microscopy the resolution of increments much less than $1.0 \mu\text{m}$ in width is physically impossible (Campana and Neilson 1985). This problem therefore becomes increasingly acute among the largest fish (see Table 2 and Figure 3). Together these findings have led to the view that daily growth increments are of little use in ageing large, old fish (Beamish and McFarlane 1987).

In this study, the deposition of daily increments became irregular at otolith lengths in excess of $7,500 \mu\text{m}$. Beyond this length, the increments were also difficult to resolve microscopically due to small size. Consequently, no increment width data were collected at otolith lengths $>7,500 \mu\text{m}$. This corresponds to a FL of 329 mm (Fig. 1), which, although of a size that is reproductively competent (S. Ralston, unpubl. data), is smaller than most of the gindai caught during the field surveys (Fig. 7). Thus, the estimated von Bertalanffy curve presented here is largely based on back-calculated data obtained from the younger stages of growth. Nonetheless, we believe that daily increments can be useful in developing growth curves for use in stock assessments, even if data representing the older stages are not included in the analysis. This is especially true if the L_{∞} parameter is estimated from length-frequency data (Fig. 8, Wetherall et al. 1987), avoiding the extrapolation problem described by Hirschhorn (1974). Still, validation of the increment periodicity assumption remains an essential component for future applications of the method.

Another assumption implicitly made is that no systematic bias was introduced into the estimation procedure by the manner in which sampling locations were chosen for measuring increment widths. For example, readings were made at specific points along the postrostral growth axis, i.e., where it was possible to distinguish the characteristic bipartite structure of daily increments. However, we also observed broad transition areas lacking in visually conspicuous microstructural features. If these ill-defined regions were elicited by periods of either fast or slow growth, then our estimates of mean otolith growth rate would be biased. To counter this we tried to representatively sample all daily increments (large and small) and we avoided measure-

ments beyond 7,500 μm (see above). Still, we must assume that otolith growth rates calculated from regions where daily increments are visible are otherwise no different from regions where they are not.

Numerical integration of otolith growth rates provided a series of ordered pairs of age and otolith length. Otolith lengths were then converted to FL through regression analysis. The only FL data included in the nonlinear von Bertalanffy regression (Fig. 4), however, were based on otolith lengths in excess of 3,000 μm . Note that the excluded data (intervals 1-6) represent the first year's growth, i.e., the early life history. Although the von Bertalanffy growth equation has historically been the model of choice in stock-assessment applications, including especially the Beverton and Holt (1957) dynamic pool model, it provides a poor description of growth during the early life history. Inflected growth typically characterizes this stage, which is better fit with a Gompertz-type curve (Zweifel and Lasker 1976). By excluding ages <0.8 years from the von Bertalanffy regression analysis, we constrain the data used to estimate the model to the domain over which meaningful predictions are made. Moreover, predictions of FL based on otolith length are also obtained from regression analysis (Fig. 1). Because the smallest otolith used in developing the regression equation was 5,043 μm (see Figure 1), application of the equation to predict the FL of a fish whose otolith is less than this size represents an unnecessary extrapolation of the fitted model.

One of the side effects of deleting points from the early life history is to diminish the importance of weighting. Note that the statistical weights of the data used in the regression (Table 2) are very similar (coefficient of variation = 0.78%). Thus, although it may be desirable from a theoretical perspective, weighting had a negligible effect on the parameter estimates.

One of the principal advantages recommending this approach is an increase in efficiency and objectivity relative to studies that obtain complete counts of daily growth increments (Uchiyama and Struhaker 1981; Brouard et al. 1984; Radtke 1987). Because all increments need not be visually conspicuous for a particular preparation to provide useful information, as is true of studies relying on whole counts, the observer can utilize only those portions of the otolith where the microstructure is clearly expressed. Enumeration of ill-defined increments in poorly developed regions of the otolith is avoided. This feature also makes it possible to automate the procedure (Casselman 1983; McGowen et al. 1987) and ultimately to realize the goal of standardizing

age determinations (Boehlert and Yoklavich 1984; Boehlert 1985).

Powerful statistical tests of growth heterogeneity also are possible with the acquisition of increment width data (Table 1, Fig. 3). Evaluation of statistical differences in populations with respect to the parameters of the von Bertalanffy growth equation is cumbersome at best (Gallucci and Quinn 1979; Bernard 1981; Kappenman 1981). Analysis of covariance of increment width data provides a convenient and widely available means of testing for growth heterogeneity among any statistical populations of interest.

One of the principal disadvantages of the method outlined here is that growth variation among individuals within the sampled population is lost through averaging of the data. The final growth curve given in Figure 4 describes the mean growth of the sampled population of gindai. Of course, length variation at age is extremely important, and its description is required for application of the more powerful and realistic stock-assessment models, especially in cohort or virtual population analysis (Ricker 1975). Nonetheless, given the difficult conditions surrounding assessment work in tropical environments (Gulland 1982), the application of yield/recruit models is a significant step forward (Munro 1982; Pauly 1982). In conjunction with the analysis of length-frequency distributions, the method proposed here is well suited to help meet that need.

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