ANALYZING THE WIDTH OF DAILY OTOLITH INCREMENTS TO AGE THE HAWAIIAN SNAPPER, *PRISTIPOMOIDES FILAMENTOSUS*

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ABSTRACT

Studies of otolith microstructure in Hawaiian snapper, *Pristipomoides filamentosus*, indicate that growth increments are deposited daily in immature fish (<40 cm FL and <3 yr of age). Laboratory experiments with tetracycline-injected fish and analysis of modal progression in size-frequency distributions of field-sampled fish validate this conclusion. Given a 1:1 correspondence between increments and days, one can determine otolith growth rate by measuring increment width. Based on the relationship between otolith growth rate and otolith length, we conclude that increment deposition in mature *P. filamentosus* is episodic, i.e., interrupted.

Using regression analysis, a model is developed relating otolith growth rate to otolith length. It is shown that integration of the regression equation provides estimates of the age of individual fish. Assumptions involved in the model are discussed, and it is concluded that this method of aging adequately represents the growth of *P. filamentosus* when time is measured on a scale of years. Age estimates derived here are entirely consistent with those of related forms (Lutjanidae) reported in the literature.

Studies of fish otoliths have now revealed that these calcified structures often grow by daily accretion of increments, in a manner analogous to the annual rings of trees. Pannella (1971, 1974) was the first to demonstrate this, and now many other researchers have substantiated and extended his findings to a wide variety of temperate and tropical species in both marine and freshwater environments (Brothers et al. 1976; Struhsaker and Uchiyama 1976; Le Guen 1976; Ralston 1976; Timola 1977; Taubert and Coble 1977; Barkman 1978; Brothers 1978; Methot and Kramer 1979; Dunkelberger et al. 1980; Pannella 1980; Schmidt and Fabrizio 1980; Steffensen 1980; Wild and Foreman 1980; Wilson and Larkin 1980; Worthmann 1980; Brothers and McFarland 1981; Mugiya et al. 1981; Uchiyama and Struhsaker 1981; Tanaka et al. 1981; Ralston and Miyamoto 1981; Campana and Neilson 1982; Watabe et al. 1982; Radtke and Dean 1982; Radtke[3]). Daily growth structures from a wide variety of plant and animal tissues were known for some time prior to Pannella's discovery (Choe 1963; Neville 1967). In fact, several publications which predate his work presented photographs of otoliths in which typical daily increments are evident (Hickling 1931; Morris and Kit-

tleman 1967; Degens et al. 1969), yet their temporal significance was unappreciated at the time.

We are now developing a more sophisticated understanding of the processes which control the incremental growth of otoliths, with multiple factors influencing accretion, including photoperiod, food, and temperature (Hickling 1931; Irie 1960; Degens et al. 1969; Mugiya 1974, 1977; Taubert and Coble 1977; Brothers 1978; Dunkelberger et al. 1980; Pannella 1980; Mugiya et al. 1981; Tanaka et al. 1981; Watabe et al. 1982; but see Campana and Neilson 1982). Furthermore, some studies have revealed the existence of subdaily increments (Taubert and Coble 1977; Brothers 1978; Pannella 1980; Wilson and Larkin 1980; Campana and Neilson 1982) which complicates considerably the temporal interpretation of increment periodicities.

A powerful application of daily increment research has been the use of increment width as a measure of otolith and somatic growth rate. Pannella (1974) first presented this view when he stated, "Increment thickness is the spatial expression of time" and "... is the faithful expression of the conditions and rate of growth." In substantiating this claim, Struhsaker and Uchiyama (1976), Taubert and Coble (1977), and Barkman (1978) showed that otolith ring counts depend purely on specimen age and not otolith size. Slow-growing fish had small otoliths, while in comparably aged fast-growing fish the otoliths were larger but contained no more increments. Moreover, Wild and Foreman (1980) used the change in otolith dimension subsequent to mark-

ing to estimate change in fish length and, ultimately, somatic growth rate. Similarly, Brothers et al. (1976) and Methot and Kramer (1979) numerically integrated increment thickness data to estimate age. Although of some significance, no formal or detailed treatment of the subject was presented. More recently Methot (1981) has measured the widths of the outer three daily increments in the otoliths of larval fishes, using them as explicit measures of recent daily growth rate. Brothers (1981) discussed this kind of application and cautions against short-term uncouplings of otolith growth with changes in fish length.

In this paper, we intend to analytically formalize the concept that increment width can be used as a measure of otolith growth rate. This eliminates the constraint of having to count all increments in an otolith, providing a framework for studying age and growth in large, slow-growing species of fish in which increment microstructure frequently becomes ambiguous with age (Brothers 1979; Pannella 1980). Rather than attempting a numerical solution to this problem, we have analytically integrated increment growth–rate data obtained from the otoliths of Hawaiian snapper, or opakapaka, *Pristipomoides filamentosus* (Lutjanidae). This is a commercially important species of bottomfish harvested in the Hawaiian deep-sea handline fishery (Ralston 1981; Ralston and Polovina 1982). While admittedly sacrificing some of the extreme precision theoretically possible with daily increments, the intent here is to provide reasonably reliable age estimates, economically obtained, when age is measured on a scale of years. Preliminary results of this research have been reported elsewhere (Ralston and Miyamoto 1981).

METHODS

Marking Experiment

A marking experiment was done to validate the existence of daily growth increments in opakapaka. Otoliths are composed primarily of the aragonitic crystalline form of calcium carbonate in association with small amounts of otolin protein (Hickling 1931; Irie 1960; Degens et al. 1969). The presence of calcium carbonate allows otoliths to be successfully marked in vivo with the antibiotic tetracycline (Blacker 1974; Wild and Foreman 1980; Campana and Neilson 1982). A dated, visible time-mark in otoliths provides direct validation of the periodicity of presumed daily increments.

Six juvenile opakapaka (30-34 cm FL (fork length)), captured by hook and line, were acclimated to a 1,135 l flowthrough aquarium. The fish were exposed to a natural photoperiod through an overhead skylight and were fed to satiation twice daily (midmorning and late afternoon). All six fish were initially in good condition, and after 12 d they appeared well adjusted to the tank, having resumed what seemed to be normal feeding behavior.

Three 1 kg specimens were injected intraperitoneally with 30 mg of oxytetracycline (dosage from A. Wild[4]). Following injection, all six fish were exposed for 18 h to 125 ppm acetazolamide in seawater (dosage from J. Dean[5]). This compound has been shown to affect otolith calcification by inhibition of carbonic anhydrase (Mugiya 1977), providing a simple means of creating a checkmark on otoliths. The fish resumed feeding 2 d after treatment. One fish jumped out of the tank 27 d later, and the experiment ended prematurely when the remaining five specimens died unaccountably 38-39 d after treatment.

Preparation of Otoliths

All otoliths in this study were prepared for viewing as outlined in Ralston and Miyamoto (1981). Thin sections (0.5 mm) were made through the focus along a frontal plane to the most distal portion of the postrostrum (Figs. 1, 2). Preliminary observations showed that increment counts made in a transverse plane were less than those made from frontal sections, presumably due to pinching and coalescing of rings along the shorter transverse axis (Pannella 1974; Taubert and Coble 1977; Dunkelberger et al. 1980). Tetracycline marks were obliterated by the clearing agent (Euparal[6]) and were located prior to etching by viewing with an ultraviolet fluorescence microscope. In addition, several otoliths were prepared for scanning electron microscope (SEM) examination.

Otolith Growth Rate and Specimen Age

After otoliths had cleared, they were read with a compound binocular microscope using transmitted light at a magnification of 400X. The distance in microns (μm) between the focus and the postrostral margin, representing the total length (L) of the otolith along the postrostral radius, was measured with a
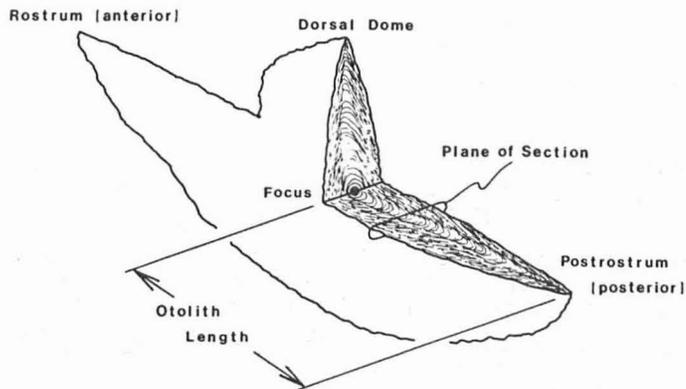
FIGURE 1.—Schematic of an otolith from *Pristipomoides filamentosus* with specific points of reference discussed in the text.
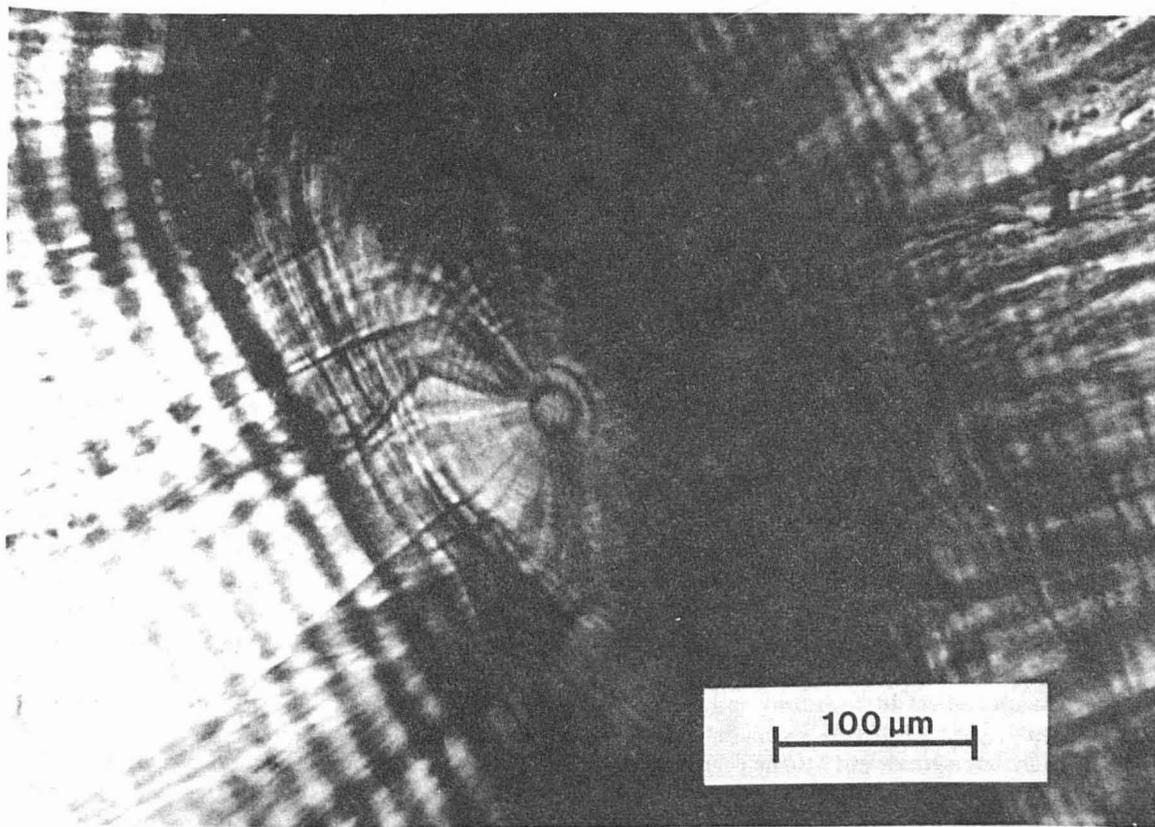
FIGURE 2.—Photomicrograph through the nuclear core region of an otolith from *Pristipomoides filamentosus*. Note increments become compressed in this area.

calibrated ocular micrometer (Fig. 1). Readings were then made at selected points along the postrostral growth axis, wherever increment microstructure was clearly viewed. At such locations the average width of increments was determined by counting the number of increments visible ($\bar{x} = 15.95$, SD $= 11.24$) and by measuring the radial length of the short segment in which the increments were observed. In addition, the distance between the midpoint of the sample region and the otolith focus (ℓ) was measured along the

same postrostral growth axis. As many readings as possible were made from each preparation ($\bar{x} = 31.9$), subject to the constraint that counts be made only in regions where increments were clear.

Data were summarized for each specimen by computing the ratios of segment length in μm to the number of increments included at each specific segment examined in the preparation. These figures represent the average increment width at given points in the otolith. Under the assumption that one increment forms each day, it is possible to approximate the otolith growth rate on a size-specific basis as follows:

$$\frac{\Delta \ell}{\Delta \text{ increments}} = \frac{\Delta \ell}{\Delta t} \simeq \frac{d\ell}{dt}$$

where $\Delta \ell$ is the change in length (μm) of the otolith over a given subregion, and Δt is the change in time (days). The finite approximation to the differential was always computed on a sufficiently small scale of time and length.

Given the series of ordered pairs, $\dfrac{d\ell}{dt}$ at otolith length ℓ, it is possible to evaluate the functional relationship between these quantities, $\dfrac{d\ell}{dt} = f(\ell)$, and to estimate the parameters of the function using regression analysis. The regression equation can then be solved by separation of variables and treated as a definite integral, bounded by the focus and the total length (L) of the otolith at death, providing an explicit estimate of age in days (T). That is:

$$\int_{t=0}^{T} dt = \int_{\ell=0}^{L} [f(\ell)]^{-1} d\ell. \tag{1}$$

Size at Maturity

Samples of opakapaka gonads were obtained from throughout the Hawaiian Archipelago. Sampling was haphazard with respect to both time and location. Gonads were preserved in 10% Formalin until examined, when they were weighed to the nearest gram after excess moisture had been removed by blotting with a paper towel. Sex was determined by microscopic examination of smeared gonadal tissues, and ovaries were staged according to the following classification:

Stage I. Inactive ovary
    a) egg diameters 75-100 μm
    b) transparent primary oocytes in ovary
    c) nucleii faintly visible
    d) eggs ovoid

Stage II. Developing ovary
    a) egg diameters 100-325 μm
    b) some opaque eggs in ovary
    c) nucleii clearly visible
    d) eggs wedge-shaped
Stage III. Gravid/spawning ovary
    a) egg diameters 325-850 μm
    b) presence of oil globules
    c) evidence of yolk granules
    d) eggs ovoid

RESULTS

Typical looking increments are found in the sagittae of opakapaka (Fig. 3). In this SEM photograph the distinct incremental growth of the otolith is readily apparent, with a structure similar to that described in previous descriptions of daily increments. Discernible under high magnification is a more deeply etched, discontinuous zone which transects the radial growth of aragonite crystals found in the incremental zone (Hickling 1931; Pannella 1971, 1974, 1980; Blacker 1975; Brothers et al. 1976; Timola 1977; Dunkelberger et al. 1980; Mugiya et al. 1981; Tanaka et al. 1981; Watabe et al. 1982; Radtke footnote 3).

Tetracycline Validation

Photomicrographs of a sagittal section through the otolith of one of the three experimental fish injected with oxytetracycline are presented in Figure 4. In the upper photograph the specimen was illuminated with ultraviolet light, clearly showing the fluorescing tetracycline checkmark. The lower photograph shows the same specimen illuminated with visible light. A discontinuity coincident with the tetracycline label is evident. We interpret this latter checkmark to be due to exposure to acetazolamide and handling trauma. The close coincidence of the two marks allowed us to positively identify the experimentally induced checkmark in all six specimens.

The results of marginal increment counts from these fish are summarized in Table 1. Several sections were taken from each otolith, although not all preparations were readable. Furthermore, because the quality of all sections was poor, multiple counts of each section were made. The figures under the heading "Number of marginal increments" represent the range of counts.

It is evident from these data that the number of increments deposited on the otoliths after marking was quite similar to the number of days elapsed after the fish were marked. Since these fish were stressed dur-
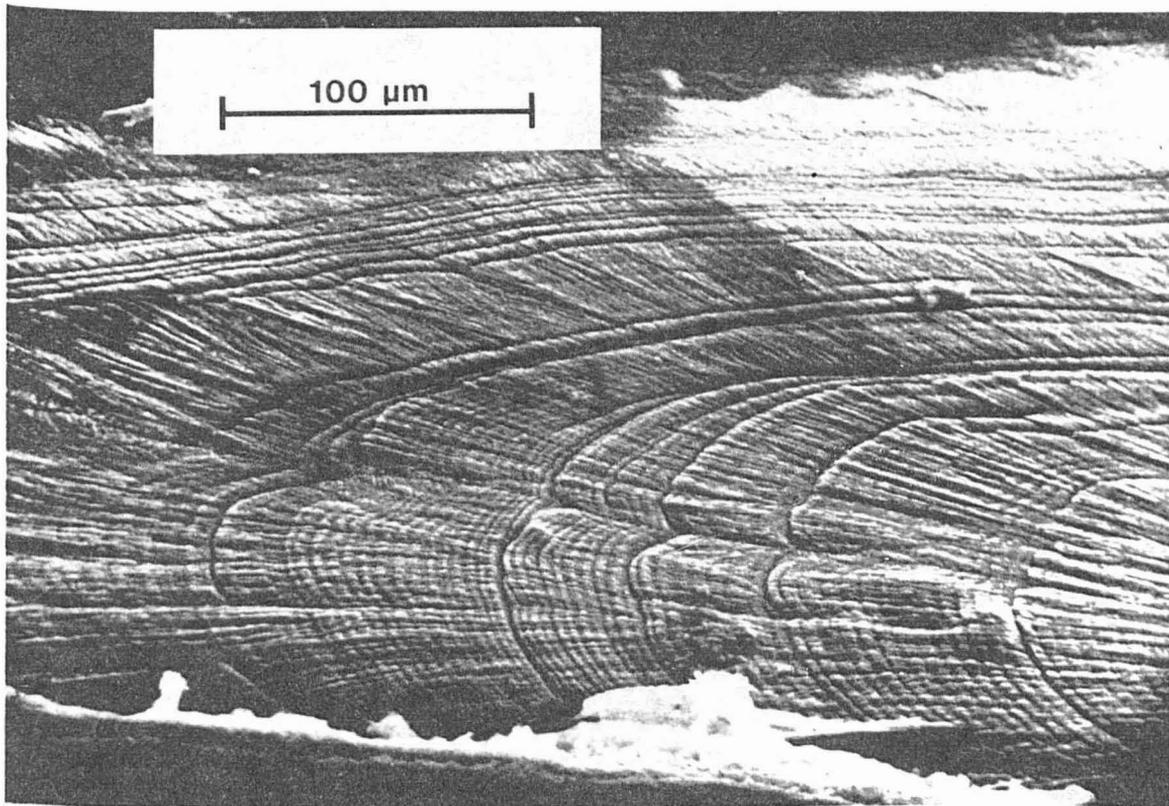
FIGURE 3.—A scanning electron microscope (SEM) photograph of a sagitta from *Pristipomoides filamentosus*, showing radial development of aragonite crystals transected by incremental and discontinuous zones.

ing captivity and did not feed for 2 d after treatment, we interpret these as confirming results. During the course of the experiment a 1:1 correspondence was maintained between increments and days, demonstrating the presence of daily marks rather than features entrained to other periodicities (e.g., subdaily marks).

Otolith Growth

Due to the likelihood of allometric relationships, it is important to distinguish between the growth of the otolith and the growth of the whole fish. Figure 5 shows that the slope of the log-linear power function regression of otolith length on fork length, based on measurements from 66 individuals, is significantly <1 ($\beta = 0.6286$, $t = -14.12$, df $= 64$). This is typical of many fish species (Hickling 1933; Templeman and Squires 1956; Blacker 1974; but see Taubert and Coble 1977) and implies that the growth rate of opakapaka otoliths $\left(\frac{d\ell}{dt}\right)$ is not related in a simple linear fashion to somatic growth rate.

TABLE 1.—The results of marginal increment counts on tetracycline- and acetazolamide-marked otoliths of *Pristipomoides filamentosus*.

Specimen no.	Days marked	Number of marginal increments
E-1, Section D	27	24-27
E-2, Section B	38	33-39
Section C		35-38
E-3, Section F	38	30-31
E-4, Section A	38	30-32
Section B		30-38
E-5, Section A	38	37-39
Section C		30
E-6, Section C	39	27-30
Section D		35-39

A total of 81 sagittae from 68 individuals were examined with light microscopy for presence of daily increments. In 13 cases both left and right otoliths from the same individual were viewed. These 81 samples provided 2,957 separate estimates of otolith growth rate along the postrostral growth axis. Initially the data were pooled to elucidate the functional relationship between otolith growth rate and otolith length. The results are presented in Figure 6.

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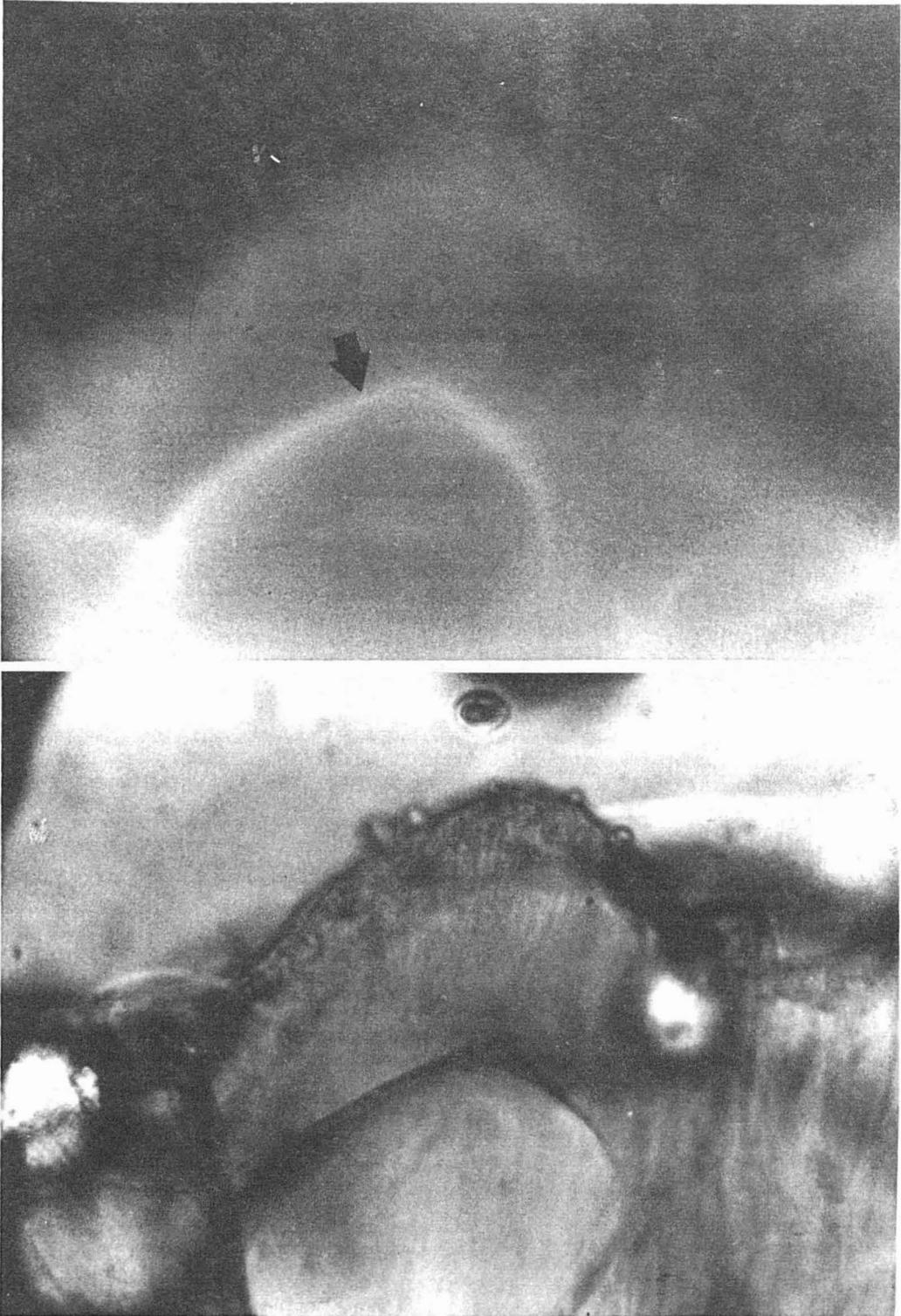
FIGURE 4.—(top) Photomicrograph of a tetracycline-marked otolith of *Pristipomoides filamentosus*, illuminated by ultraviolet light. Note checkmark at arrow. (bottom) Photomicrograph of the same sample illuminated under visible light. 300× magnification.
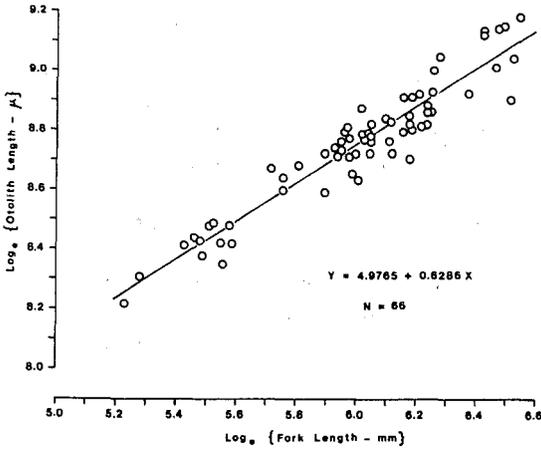
FIGURE 5.—Relationship between otolith length and fork length in *Pristipomoides filamentosus*.

There is pronounced curvilinearity in the data, as well as heteroscedastic variance. The von Bertalanffy growth model (Ricker 1979) asserts that somatic growth rate in length is a linear decreasing function of length, with the X-intercept defining the asymptotic upper bound on growth (L_∞). The observation that the growth-rate curve of opakapaka otoliths is a concave (upwards), monotonic decreasing function of otolith length (Fig. 6) is consistent

with this notion, given the previously deduced allometric relationship between fork length and otolith length.

Growth-rate data were logarithmically transformed to linearize the trend line and stabilize the variance (Fig. 7). It is evident that once the otolith reaches about 6,000 μm in length, an alteration occurs in the rate (slope) at which log-transformed growth rate declines, maintaining a higher rate than would be expected otherwise. This noticeable change in slope is apparently due to attainment of reproductive maturity.

Of those female opakapaka collected during the summer spawning season (Kikkawa 1980; Ralston 1981), the incidence of gravid/spawning ovaries is strongly dependent upon fish size (Fig. 8). These data indicate that female opakapaka reach reproductive maturity at about 40 cm FL. Fish this length have otoliths about 6,250 μm long (Fig. 5). Thus the distinct change in trend of otolith growth rate coincides closely with maturation. Males show a similar pattern of gonad maturation (Ralston 1981).

Based on these observations, it is likely that periods of episodic growth commence in opakapaka otoliths with the onset of maturity. That growth dynamics should improve at this time, as suggested by a moderation in the decline of log-transformed otolith

FIGURE 6.—Relationship between otolith growth rate (increment width) and otolith size in *Pristipomoides filamentosus*. Points represent means bracketed by standard deviations. Sample sizes are given above each length class.
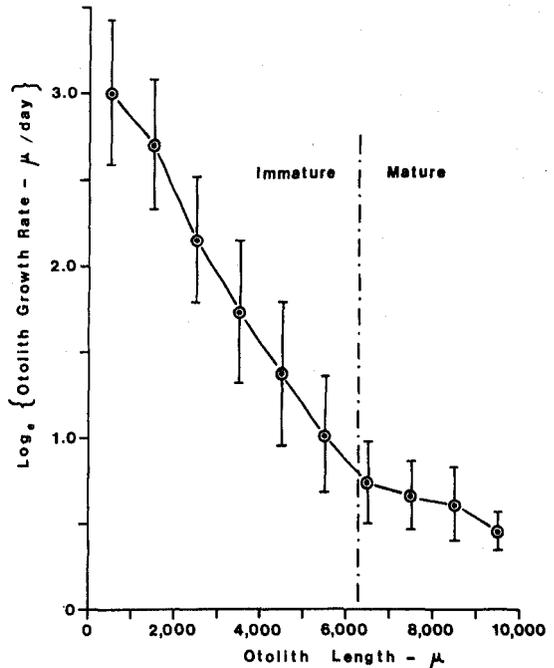
FIGURE 7.—Linearization of otolith growth rate data by logarithmic transformation for *Pristipomoides filamentosus*. Points represent means bracketed by standard deviations.

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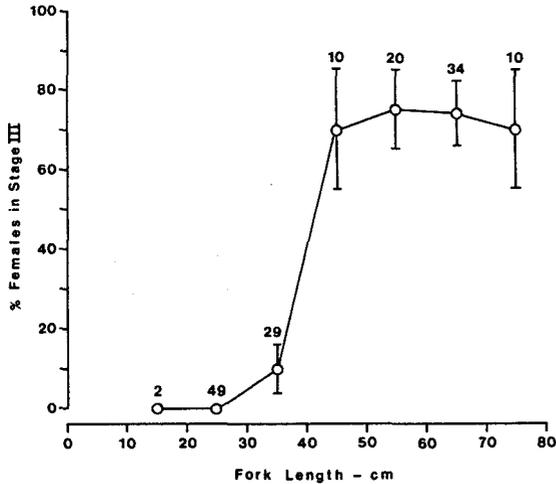
FIGURE 8.—Maturation in *Pristipomoides filamentosus* female. Stage III represents gravid/spawning individuals. Only samples collected during the spawning season are presented. Points represent means bracketed by standard deviations. Sample sizes are given above each length class.

growth rate, is completely counterintuitive to our understanding of the trade offs involved in optimizing growth and reproductive processes. Rather, it is more likely that episodic growth leaves an incomplete time record in the otolith (i.e., increments are not deposited) while concurrently, changes in otolith length are tightly coupled to changes in fork length (see Figure 5 where $r^2 = 0.899$). The resulting process would tend to underestimate Δt and thus to overestimate $\frac{d\ell}{dt}$. This hypothesis of interrupted otolith growth could explain the anomalous trend in otolith growth rates; consequently, we have regarded all data from otolith lengths $>6,000$ μm to be equivocal. We excluded these points from the remaining analyses, reducing the data set by 13% (2,957 ordered pairs to 2,577).

It is evident from Figure 7 that for otoliths $\leq 6,000$ μm the logarithmic transformation was effective in linearizing the trend line and in stabilizing the variance, allowing the formulation of an analytical model describing the functional relationship between $\frac{d\ell}{dt}$ and ℓ. We write

$$\log_e \left(\frac{d\ell}{dt} \right) = \alpha - \beta\ell + \varepsilon \qquad (2)$$

where ℓ is otolith length in μm, t is time in days, α and β are model parameters, and ε is a normal random variable with mean zero and finite variance. When this model is cast in the form of Equation (1) and integrated, the solution is

$$\hat{T} = (e^\alpha\beta)^{-1} (e^{\beta L} - 1) \qquad (3)$$

where T is the estimate of age in days, and L is the total length of the otolith along the postrostral radial axis. Thus, to estimate the age of a sample specimen, one need only acquire estimates of α, β, and L.

Von Bertalanffy Growth Curve

A regression of log-transformed otolith growth rate against otolith length (Equation (2)) was performed for each of the 81 otolith samples. The age of each specimen was then estimated by Equation (3).

The fork length of the sample specimens is plotted against the point estimate of age in Figure 9. Because 13 of the 81 determinations were duplicates based on left and right otoliths from the same fish, and 4 of the remaining preparations had excessive coefficients of variation ($\geq 20\%$), only 64 points are presented. These data were fitted to the von Bertalanffy growth model (Ricker 1979) using a nonlinear regression routine (NLIN Procedure) (Statistical Analysis System 1979). In this three-parameter formulation, L_∞ signifies the asymptotic upper bound on growth in length, K is an instantaneous growth-rate constant, and t_0 is a scaling factor equal to the X-intercept. When the model was freely fitted to the data, an unrealistically low estimate of L_∞ resulted (Table 2, solid line in Figure 9). As part of a related study in
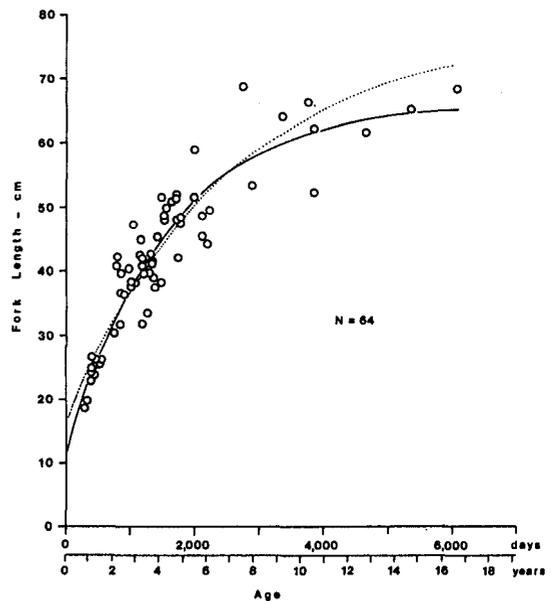
FIGURE 9.—Estimated growth curve for *Pristipomoides filamentosus*. Solid line represents a freely fitted von Bertalanffy curve whereas the L_∞ parameter was constrained to 78.0 cm in the fit of the dotted line.

TABLE 2.—Parameter estimates from the von Bertalanffy model fitted to 64 integrated age estimates of *Pristipomoides filamentosus*.

Parameter	Estimate	Standard error	Units
Freely fitted			
K	0.235	0.034	yr^{-1}
t_o	−0.807	0.298	yr
L_∞	66.4	28.15	cm
Constrained ($L_\infty \approx 78.0$ cm)			
K	0.146	0.010	yr^{-1}
t_o	−1.67	0.327	yr

which more than 2,500 opakapaka were measured, many fish exceeded 70 cm FL. Consequently, the 64 data points were refitted to the model with L_∞ constrained to a value of 78 cm FL, the largest specimen we have observed (Table 2, dotted line in Figure 9).

Analysis of Size-Frequency Distributions

The data presented in Figure 10 represent three length-frequency distributions of opakapaka sampled at French Frigate Shoals in the Hawaiian Islands. All three samples were taken on different dates but at the same position on the west side of the atoll (lat. 23°47'N, long. 166°22'W). In each distribution a large mode of small fish is plainly visible. If one accepts the premise that these small fish represent a
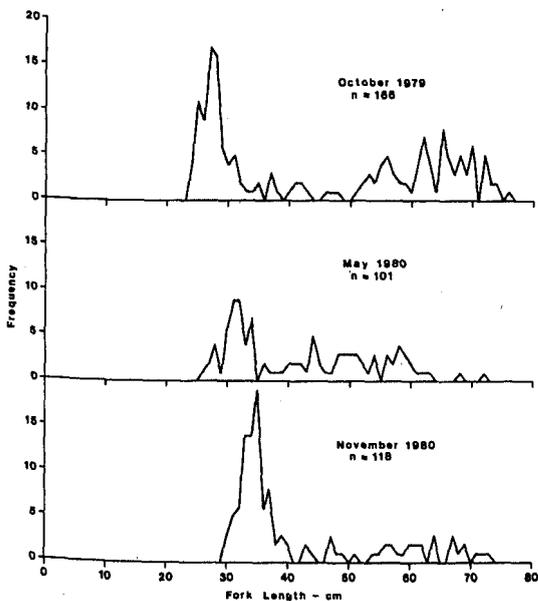
single cohort of juveniles, these data afford the opportunity to estimate their size-specific growth rate by examining the progression of modes in time (Ricker 1975; McNew and Summerfelt 1978).

The simplified calculations presented in Table 3 show that these fish grew, on the average, at the rates of 0.020 cm/d during the winter growth period (October-May), 0.022 cm/d during the summer growth phase (May-November), and an average 0.021 cm/d over the entire year (October 1979-November 1980). If we compute the expected size-specific (31 cm FL) growth rate of these fish, based upon the fit of the integrated otolith age data to the von Bertalanffy model (Table 2, Fig. 9), we predict growth rates of 0.023 and 0.019 cm/d for the freely fitted and the constrained versions of the model, respectively. These results compare favorably with the modal growth rates, further substantiating our age estimates.

TABLE 3.—Growth rate calculations for *Pristipomoides filamentosus* based on size-frequency distributions. Samples from French Frigate Shoals, Hawaiian Islands.

		Sample no.	
	I	II	III
Date:	16 Oct. 1979	27 May 1980	3 Nov. 1980
Modal size (FL cm):	27.0	31.5	35.0
Samples compared	I-II	II-III	I-III
Elapsed time (d)	223	160	383
Change in length (cm)	4.5	3.5	8.0
Growth rate (cm/d)	0.020	0.022	0.021

DISCUSSION

Elsewhere we have shown that the increment thickness model presented here provides reasonably precise age estimates from a purely statistical standpoint (Ralston and Miyamoto 1981). The frequency distribution of coefficients of variation of T is centered on 6%, with 67 of the 81 values $\leq 10\%$. Thus, a typical preparation provides an age estimate for which the 95% confidence interval is about $\pm 12\%$ of the estimate. Furthermore, the regression technique is an effective means of accounting for variation in otolith growth rates. The frequency distribution of r^2 values for the 81 regressions had a median value of 78% (Ralston and Miyamoto 1981).

Several explicit and implicit assumptions, however, underlie the aging method presented here. It is important to address these at this time and to review to what extent they may or may not be justified. One important assumption is that it is appropriate to use the interpolative power of the regression Equation (2) to predict otolith growth rates in intermediate regions where increment microstructure is unclear. This

FIGURE 10.—Length-frequency distributions of *Pristipomoides filamentosus* sampled at French Frigate Shoals, Hawaiian Islands (lat. 23°47'N, long. 166°22'W).

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assumption implies that similar processes occur in regions of the otolith that appear somewhat different superficially. We feel it is not an unreasonable assumption, however, because one can usually enhance the quality of a preparation by increasing the amount of time and care devoted to it, bringing out distinct increments in regions which otherwise would remain uninterpretable. For example, Radtke (footnote 3) has shown that the core area of opakapaka otoliths requires substantially more etching time than does the marginal zone. He improved the quality of his samples by employing differential etching times, a tedious but effective technique. Wild and Foreman (1980) used similar methods in their study. Presumably, the visual quality of a preparation is largely limited by the ability of the investigator to unveil its contents.

A second and more important assumption is that it is reasonable to extrapolate the growth of a sexually mature fish based on its individual pattern of growth prior to gonad maturation. Because all data gathered at otolith lengths >6,000 μm were deleted, age estimates obtained from Equation (3) are bound by this constraint. We have argued that otolith increments become equivocal chronometers past maturity, due to interrupted growth. Both Pannella (1971) and Wild and Foreman (1980) reached similar conclusions in their studies of red hake, *Urophycis chuss*, and skipjack tuna, *Katsuwonus pelamis*, respectively. Significantly, in the latter study growth interruptions were not evident in yellowfin tuna, *Thunnus albacares*, and almost all specimens were of immature size (Schaefer et al. 1963). Not only has maturation been implicated in interrupting otolith growth, but also reduced food (Irie 1960; Methot and Kramer 1979; Uchiyama and Struhsaker 1981) and low temperature (Irie 1960; Taubert and Coble 1977). It is apparent from these studies that any factor which arrests the growth of the whole fish, temporarily or otherwise, can lead to errors in the time chronicle of daily increments (Pannella 1980). Clearly, if the additional energy burden incurred at sexual maturity is substantial (sensu Gadgil and Bossert 1970), extrapolation beyond 6,000 μm may be an unrealistic exercise and growth rates of large fish may in fact be overestimated. However, it is pertinent to note that the proportions in opakapaka of both ovarian and testicular tissues relative to total body weight are not great, ranging from 1 to 4% among Stage III females and slightly less among males (Ralston 1981). Furthermore, most models of fish growth currently in use (e.g., von Bertalanffy and Gompertz models) do not treat maturity as a growth singularity, i.e., a time when the pattern of growth changes. In spite of their relative simplicity, these models have adequately described fish growth dynamics in a surprisingly large number of situations (Ricker 1979). Undoubtedly this is because fine scale departures from model growth (e.g., seasonal trends) are averaged out when treating a lifespan measured in years. Finally, the procedure we have used involves extrapolating, at most, 68% beyond the range of the data (6,000-10,000 μm). In most cases, the amount we extrapolated was far less. Nonetheless, this particular assumption is critical and yet remains unresolved. Additional research on this topic is essential.

At the other extreme, by applying a linear model to the data (Equation (2)), we have assumed that otolith growth rate is greatest as otolith length approaches zero. This is unrealistic (see, for example, Pannella 1974; Brothers and McFarland 1981). The average width of increments actually decreases very near the focus (Fig. 2). We evaluated the extent of bias introduced by this computational simplification, however, by comparing age estimates derived from both analytical (Equation (3)) and complete numerical integration of all the otolith growth-rate data, broken down by 100 μm size classes. The largest absolute difference between the two types of age estimates was 18 d. This was for the youngest of fish, as might be expected, and indicates that the analytical method provides a poor approximation for fish <1 mo old. However, because our results are intended to describe growth over the entire size range of opakapaka, measured on a time scale of years, and because the difference between the two estimates becomes progressively smaller among the larger fish, we consider this a negligible error.

A final assumption is that one increment forms each day in preproductive individuals. We have presented evidence that validates this assumption, at least for fish 30-34 cm FL, in the form of in vivo marking of otoliths with tetracycline. Furthermore, evidence from the field (Fig. 10) also strongly supports this conclusion, again for immatures (27-35 cm FL). A final assessment of this assumption can be made by comparing the growth of opakapaka, as developed here, with studies available in the literature on lutjanid growth.

Researchers have long recognized the interdependence of growth parameters. Beverton and Holt (1959) presented values of K and L_∞ computed from the von Bertalanffy growth model and noted an inverse relationship between these parameters. Similarly, Cushing (1968) presented graphs relating growth parameters for several large taxonomic categories (e.g., Clupeoidei, Gadiformes, Salmonoidei, etc.). Pauly (1979) has attempted to quantify the relation-

ship between asymptotic weight (W_∞ or the weight of an individual at length L_∞) and K by developing the concept of the auximetric grid. He has argued that the logarithm of the product of K and W_∞ is relatively uniform for families of fishes. That is

$$P = \log_{10} (KW_\infty)$$

where P can be considered characteristic of taxa.

A review of the lutjanid growth literature allowed us to estimate P for lutjanids by computing the arithmetic average of the eight P values presented in Table 4 ($\bar{P} = 3.03$). An estimate of the asymptotic weight of opakapaka is 7,670 g (Ralston 1981). Using these two figures, we calculate an estimate of K for opakapaka to be 0.140 yr^{-1}. This figure compares very favorably with the estimate of K obtained from the constrained fit of the von Bertalanffy model to otolith data from immature fish presented earlier (0.146 yr^{-1}). The results of our marking experiments, length-frequency data, and literature comparisons all support the conclusion that increments are formed daily in subadult opakapaka (up to 3 yr old).

After considering all of the assumptions that underlie our analysis, we conclude that the results presented in Figure 9 accurately reflect the growth of opakapaka. Other investigators (Moffitt 1980; Radtke footnote 3) have presented growth curves for opakapaka, also based on otolith microstructure, but which show somewhat faster growth, especially for large, mature fish. Both studies were based upon complete counts of growth increments. We attribute the differences between our estimates and theirs to growth interruptions confounding the otolith time record in adults. These earlier studies neglected to entertain this possibility, an oversight which could lead to serious underestimates of age.

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TABLE 4.—Growth relationships among the Lutjanidae with application of the auximetric grid (Pauly 1979).

Species	K (yr^{-1})	W_∞ (g)	P[1]	Source
Lutjanus apodus	0.180	3,774	2.83	Munro 1974
L. bohar	[2]0.106	9,100	2.99	Talbot 1960
L. campechanus	0.162	13,480	3.34	Nelson and Manooch 1982
L. johnii	[2]0.135	—	—	Druzhinin 1970
L. malabaricus	[2]0.064	13,600	2.94	Druzhinin 1970
L. purpureus	0.090	—	—	Menezes and Gesteira 1974
L. sanguineus	0.142	10,597	3.18	Lai and Liu 1974
	0.148	12,469	3.27	Lai and Liu 1974
L. synagris	[2]0.101	—	—	Druzhinin 1970
Ocyurus chrysurus	0.250	3,600	2.95	Munro 1974
Rhomboplites aurorubens	0.198	2,800	2.74	Grimes 1978

[1]$P = \log_{10}(KW_\infty)$.
[2]Estimated from Walford plots of size-at-age data.

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