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AGE AND GROWTH OF SKIPJACK TUNA, *KATSUWONUS PELAMIS*, AND YELLOWFIN TUNA, *THUNNUS ALBACARES*, AS INDICATED BY DAILY GROWTH INCREMENTS OF SAGITTAE

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ABSTRACT

Counts of the daily growth increments on otoliths provided the means for establishing growth curves for central Pacific skipjack tuna, *Katsuwonus pelamis*, up to 3 years old and for central Pacific yellowfin tuna, *Thunnus albacares*, up to 2 years old. The data indicated three stanzas of linear growth for 51 skipjack tuna ranging in size from 3 to 80 cm fork length. Estimated daily growth rates were 1.6 mm/day for fish up to a length of about 27.0 cm; 0.8 mm/day for fish between 27.0 and 71.4 cm; and 0.3 mm/day for fish between 71.4 and 80.3 cm. Growth data for 20 eastern Pacific skipjack tuna ranging in size from 38 to 65 cm fork length suggested that skipjack tuna in the eastern Pacific grew at a slower rate than those from the central Pacific.

Age determinations of 14 central Pacific yellowfin tuna suggested possibly two stanzas of linear growth. Estimated growth rates are 1.4 mm/day for fish up to a length of 64.2 cm and 0.9 mm/day for fish between 64.2 and 93.0 cm. Growth curves from this study were compared with published growth curves based on other methods.

The validity of daily growth increments was tentatively determined by observations on skipjack and yellowfin tunas held in captivity. Agreement of our growth curves with those of previous studies on the same stock of tunas using other growth estimating techniques also suggests that our aging technique is acceptable. However, the day-to-growth increment relation and the effect of various variables on the formation of growth increments of tunas need to be investigated further.

The many studies on age and growth of skipjack tuna, *Katsuwonus pelamis*, have primarily utilized three basic methods. Brock (1954), Schaefer (1961), Kawasaki (1965), Joseph and Calkins (1969), Yoshida (1971), Marcille and Stequert (1976a), and Diaz[3] determined growth rate and estimated the age of skipjack tuna by examining modal progression in length-frequency distributions. Yamashita and Waldron (1959), Shaefer et al. (1961), Clemens and Roedel (1964), Rothschild (1967), and Joseph and Calkins (1969) used data from tagged skipjack tuna to determine growth rates. Wild and Foreman (1980) estimated the growth rate of eastern Pacific skipjack tuna from the recapture fork length, the known period of growth, and the linear change in an otolith dimension following a tetracycline injection which was used to estimate length at marking. Marks on hard parts such as vertebrae and dorsal spines were interpreted to determine age and growth of skipjack tuna by Aikawa and Kato (1938), Yokota et al. (1961), Shabotiniets (1968), Batts (1972), and Chi and Yang (1973). Numerous reviews have been written on the subject and the lack of agreement on the aging and growth rate of skipjack tuna has frequently been noted.

Likewise, many studies have been conducted on age and growth of yellowfin tuna, *Thunnus albacares*. Moore (1951), Yabuta and Yukinawa (1957), Hennemuth (1961), Davidoff (1963), Diaz (1963), Le Guen et al. (1969), Yang et al. (1969), Le Guen and Sakagawa (1973), and Marcille and Stequert (1976b) have estimated age and growth rate by the analysis of modal progression in either length or weight frequencies. Blunt and Messersmith (1960), Schafer et al. (1961), and Bayliff[4] used results of their tagging experiments to determine the growth rate of yellowfin tuna in the eastern Pacific. Wild and Foreman (1980) estimated the growth rate of eastern Pacific yellowfin tuna by

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[3] Diaz, E. L. 1966. Growth of skipjack tuna, *Katsuwonus pelamis*, in the eastern Pacific Ocean. Unpubl. rep., 18 p. Inter-Am. Trop. Tuna Comm., La Jolla, Calif.

[4] Bayliff, W. H. 1973. Observations on the growth of yellowfin tuna in the eastern Pacific Ocean derived from tagging experiments. Unpubl. rep., 26 p. Inter-Am. Trop. Tuna Comm., La Jolla, Calif.

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their tetracycline-otolith method. Aikawa and Kato (1938), Nose et al. (1957), Yabuta et al. (1960), Tan et al. (1965), and Shabotiniets (1968) interpreted marks on scales, dorsal spines, and the centrum of vertebrae to estimate age and growth. These studies were performed on commercial-sized fish (>2 kg); growth during early life (<2 kg) has yet to be examined.

Pannella's reports (1971, 1974) provided circumstantial evidence that the smallest discernible growth increments in the sagittae (otoliths) of fish are deposited daily. More recent studies provide direct evidence that these growth increments are diel phenomena in sagittae of temperate (Brothers et al. 1976; Taubert and Coble 1977; Barkman 1978) and tropical (Struhsaker and Uchiyama 1976; Wild and Foreman 1980) species of teleosts. In the study of the short-lived engraulid *Stolephorus purpureus*, the information gained from the reading of sagittae was utilized in the construction of a growth curve for the first 190 d after yolk-sac absorption (full life cycle) (Struhsaker and Uchiyama 1976). In the present paper, growth curves are presented for central Pacific skipjack tuna to an age of about 3 yr, based on a sample of 51 fish, and for yellowfin tuna to about 2 yr, based on 14 fish. Counts on sagittae from 20 skipjack tuna from the eastern Pacific and 5 skipjack tuna from Papua New Guinea are also given. The results are discussed in relation to earlier age and growth studies of these species.

METHODS

Otolith Preparation and Counting

The central Pacific skipjack and yellowfin tunas were caught in the vicinity of the Line Islands and Hawaii. All specimens >20 cm FL (fork length) are samples taken from commercial fisheries or caught by trolling. Specimens <20 cm FL are from stomach contents of troll-caught skipjack tuna and regurgitations of a seabird, *Sula* sp., after it landed on the deck of a research vessel.

Juvenile skipjack tuna from stomach contents were identified by vertebral counts and skeletal characters given by Godsil and Byers (1944) and Gibbs and Collette (1967). In one case, only the anterior portion of a juvenile skipjack tuna was collected; standard length (SL) was estimated from the length of the precaudal vertebrae using the equation given by Yoshida (1971). A small (7.0 cm FL) yellowfin tuna specimen was tentatively identified on the basis of skeletal characters given by Matsumoto et al. (1972) and descriptions of *Thunnus* livers by Godsil and Byers (1944) and Gibbs and Collette (1967).

The caudal rays were missing from most tuna specimens collected from stomachs. Fork lengths were estimated by increasing standard lengths by 3.3% (Matsumoto[5]).

Heads from which the sagittae were not immediately removed after collection were frozen or preserved in 75% isopropanol.

In tunas <100 cm FL, we obtained the sagittae by splitting or cutting the skull along the sagittal plane and teasing them from the semicircular canals. With experience, the cut could be made without damaging either of the sagittae. We cleaned the sagittae by teasing or brushing off the sacculus and nerve endings. Sagittae that were not mounted immediately were stored in distilled water or 40% isopropanol, but were then mounted within a year.

After removal and cleaning, sagittae from tunas >45 cm FL were etched in a 1% solution of HCl for 3-5 min. The otoliths were then rinsed with several changes of water, mounted in Euparal,[6] and, in most cases, permitted to clear for 4 wk or more. Short lengths of monofilament line prevented contact of the otolith with the glass cover slip.

Increment counts were made from the core,[7] the center of the nucleus, to the tips of the rostrum, antirostrum, and postrostrum (terminology of Messieh 1972) for most sagittae. On sagittae from fish >60 cm FL, counts were made only to the rostrum and postrostrum. When the edge of the rostrum and postrostrum was fringed with irregular projections, counts were made on the projections leading to the point. Specimens were examined at magnifications of 200-800×. A microscope with a zoom feature was found to be useful, as the width of daily increments varied.

Counting increments in whole mounted otoliths becomes progressively more difficult with increasing specimen size. Experience is best obtained by beginning with otoliths from young fish and progressing through older fish. The initial counts en-

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[5] W. M. Matsumoto, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812, pers. commun. October 1974.

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

[7] Terminology agreed upon at the Otolith Workshop, Scripps Institution of Oceanography and Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, Calif., 12-16 July 1976.

able the investigator to determine the best path to follow from the core to the edge of the otolith. Eventually, the counts either converge on a value or repeated identical counts are obtained. The number of counts required to determine age is dependent on the readability of the otolith. An average of about 20 counts was made for fish >1 yr old. We found that yellowfin tuna sagittae were easier to read than those of skipjack tuna. In yellowfin tuna, the increments are wider and can be examined at a lower magnification (200×), which provides a broader view and greater depth of field. The increment counts on 15 skipjack tuna and 3 yellowfin tuna sagittae were verified by a second reader whose counts were within 9% (5.4% average deviation) of the original counts except for one which was 17% off the original count.

Statistical Analysis

The parameters of linear growth stanzas were determined by the use of LINFIT, a computer program (Kamer[8]) which used the ordinary least squares procedure to fit two or three straight lines to bivariate data. Join points, also known as break points, are the places where one regime ends and another begins; these are assumed to exist. The range of the explanatory variable in which the join points are expected to occur must be designated. Given the range for these join points, the program performs the ordinary least squares procedure on each possible combination of regimes. The resulting output indicates the partitioning scheme, the intercept and slope of each fitted line representing a regime, the residual sum of squares for each regime, the combined residual sum of squares for the model, and the values of the dependent and explanatory variables at the join points. The linear growth stanzas used in this paper were selected under the following conditions: 1) minimized combined residual sum of squares for the model and 2) each join point associated with a partitioning scheme has a value for the explanatory variable which lies between the last data value in the regime to the left and the first data value in the regime to its right.

On the assumption that the maximum number of increments approximates the age of the fish in days, we calculated a growth curve for central Pacific skipjack tuna, eastern Pacific skipjack tuna, and central Pacific yellowfin tuna for comparison with other studies. The von Bertalanffy growth parameters were estimated on an annual basis using the computer program BGC3 (Abramson 1971).

ESTABLISHING THE GROWTH INCREMENT-DAY RELATION

The only direct evidence we have that a number of growth increments equal the same number of days came from the serendipitous opportunity to examine skipjack and yellowfin tunas under known captive conditions. These fishes were not held under strict experimental conditions and their primary use was not for aging studies; however, a detailed record on the amount of food consumed by each fish during the experiment was maintained. The experiment was similar to that used for nehu, *S. purpureus* (Struhsaker and Uchiyama 1976), and was carried out at the Kewalo Research Facility of the Honolulu Laboratory.

The stress of being hooked, transported, and confined in the community tanks at the Kewalo Research Facility, as well as the taking of little or no food during the first week of captivity, probably all contributed to the formation of a check mark on the otolith (Figure 1a, b). When the tuna were sufficiently recovered to feed normally, they received a daily ration which apparently was adequate to maintain life but inadequate for normal increment formation. Perhaps very thin increments were formed during this period, which might have added prominence to the check mark. When these tunas were fed to satiation throughout the day, the widths of the increments increased and became countable.

Under low magnification (200×), growth increments formed on the edge of a sagitta during the experiment were not as well defined as those of a tuna captured in the wild. The increments appeared thinner than normal when examined under high magnification (400×). For this reason, a sagitta was first examined under low power (200×) to locate the check mark and then examined under high power (400×) to enumerate the growth increments formed during the experimental feeding period. Although growth increments occurred all along the periphery of the sagitta, the full array of increments corresponding

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[8] Kamer, G. A computer program for fitting straight lines to regimented data. Manuscr. in prep. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, Hawaii.

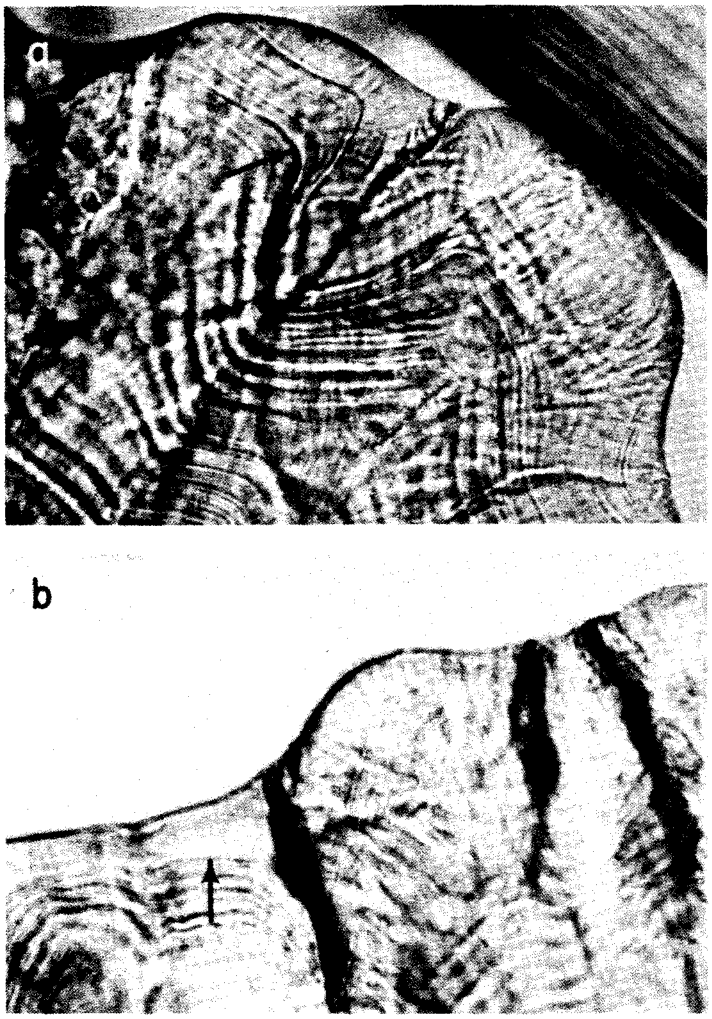

FIGURE 1.—Check mark, indicated by arrow, separates the environmentally marked increments from previous growth increments at a) tip of skipjack tuna sagitta rostrum; b) postrostrum of same skipjack tuna sagitta.

to the feeding period formed primarily on the tips of the rostrum and postrostrum (Figure 1a, b).

The highest count attainable corresponded with the number of days the tuna were fed to satiation, thus confirming the growth increment-day relation (Table 1). The number of increments formed after the check mark usually exceeded the number of feeding days because the tunas continued to live beyond the feeding period. During this latter period, the tunas either received a daily ration or starved. Great care was taken to avoid double counting of an increment where the sagitta was thin. The observations on these specimens were not long term and conditions were not fully controlled. Therefore, these data are considered tentative and in need of replication by rigorous experimental methods.

Wild and Foreman (1980) were able to show a 1:1 (day-to-growth increment) relationship for yellowfin tuna, 40-110 cm FL. However, their day-to-growth increment relation for skipjack tuna was significantly <1:1. Although an experiment where the fish lived in its natural environment was highly desirable, there was no control over variables and a record of variables which the fish might have encountered was unavailable.

Variables such as the amount of food a fish consumes (Struhsaker and Uchiyama 1976; Methot

TABLE 1.—Experimental data on marked daily growth increments in skipjack and yellowfin tunas.

Experimental animals	Fork length (cm)	Feeding period	Date of death per sampling	Length of feeding period (d)	No. of marked increments
Skipjack tuna 3	48.3	23 Aug.-22 Sept.	6 Oct.	30	33
Skipjack tuna 4	45.3	9-14 Oct.	27 Oct.	5	7
Skipjack tuna 5	49.3	15-22 Oct.	27 Oct.	7	8
Skipjack tuna 6	45.0	19-30 Oct.	4 Nov.	11	14
Yellowfin tuna 1	52.2	2-26 Aug.	4 Sept.	24	24
Yellowfin tuna 2	52.0	20 Aug.-19 Sept.	29 Sept.	30	31

and Kramer 1979), temperature (Taubert and Coble 1977; Methot and Kramer 1979), and age of fish (Pannella 1971; Brothers et al. 1976) have been demonstrated to affect the formation of daily growth rings on the sagitta. In our experiments with nehu, skipjack tuna, and yellowfin tuna, the amount of daily ration appeared to have an influence on otolith growth increments. Fishes fed once daily did not have clear otoliths with countable growth increments. Only when the fishes were fed to satiation throughout the day were countable growth increments formed. In the experiment on the effect of winter conditions on the formation of growth increments by Taubert and Coble (1977), the green sunfish, *Lepomis cyanellus*, lowered their activity level and fed less when the temperature fell below 10° C. Wild and Foreman (1980) also suggested that the difference in their results between yellowfin and skipjack tunas may have been due to feeding, citing the differences in the occurrence of full stomachs in the yellowfin and skipjack tunas from the Revillagigedo Islands area examined by Alverson (1963). Thus, it is evident that there is need for further research on the variables affecting day-to-growth increment relation of tuna otoliths.

RESULTS AND DISCUSSION

Skipjack Tuna

A plot of fork length versus age for 51 central Pacific tuna indicated three linear stanzas of growth (Figure 2). A least squares procedure was used to compute the lines of best fit for each stanza (Figure 2, Table 2). Von Bertalanffy growth parameters were also calculated (Figure 2). As there are no means available to statistically compare the von Bertalanffy growth curve, which has three parameters, with the three linear growth stanzas, which have a total of six parameters, the comparison was performed by examining the distribution of residuals (Figure 3). The residuals for the linear growth stanzas were distributed randomly about the x-axis, signifying a good fit (run's test: $Z = 0.39678$, $P \approx 0.6892$). On the other hand, the residuals for the von Bertalanffy curve oscillated about zero and were largest at breakpoints between linear stanzas and at the midpoint of the stanzas, thus suggesting a deviation from randomness (run's test: $Z = -3.32287$, $P<0.001$). Therefore, the linear stanzas appeared to be the preferable growth curve.

TABLE 2.—Length-age regression parameters for the three linear growth stanzas of skipjack tuna: N = number of data and RSS = residual sum of squares.

Stanzas	N	Intercept	Slope	RSS	Intersections	
					Years	Fork length (cm)
1	11	0.0552	58.4167	3.0910		
					0.4616	27.0192
2	35	13.6402	28.9853	17.6038		
					1.9921	71.3812
3	5	51.6918	9.8838	0.2761		
Total RSS				20.9709		

It was noted earlier that the series of three linear growth lines appeared to provide a better fit to our data than the von Bertalanffy growth curve. However, since many of the earlier growth studies use the von Bertalanffy growth curve, it is of interest to compare the von Bertalanffy growth curve of this study with those of other growth studies on the central Pacific skipjack tuna stock (Figure 4). Growth rate estimates by Rothschild (1967) using corrected data of 35 long-term tag returns, by Joseph and Calkins (1969) using Rothschild's uncorrected data, and by Skillman[9] using 356 tag returns obtained during a 2-yr period, were all less than the rate obtained in this study. Brock (1954) analyzed the modal progression in length-frequency distributions obtained over a 5-yr period, and derived a growth curve similar to ours. Both curves show similar growth

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[9] Skillman, R.A. Estimates of von Bertalanffy growth parameters for skipjack tuna, *Katsuwonus pelamis*, from capture-recapture experiments in the Hawaiian Islands. Manuscr. in prep. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, Hawaii.

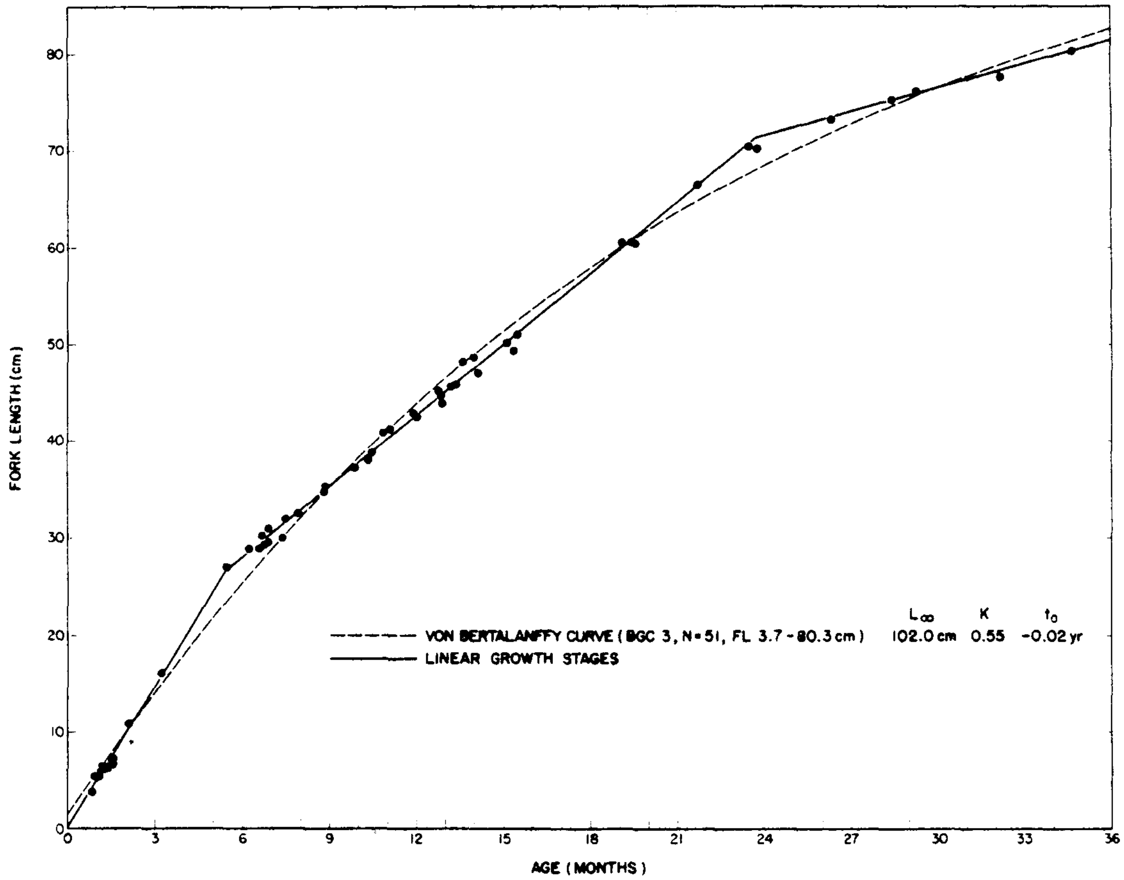

FIGURE 2.—Growth curve of skipjack tuna in the central Pacific as determined by otolith examination. Linear growth stanzas determined by LINFIT (see text). For parameters of growth stanzas, see Table 2.

rates up to 65 cm FL; beyond 65 cm FL, Brock's curve departs from ours and approaches an asymptote more rapidly. The difference in the growth rates above 65 cm may be due to two factors which would affect the modes of large (>6.8 kg) skipjack tuna: differential fishing or total mortality and temperature requirements of skipjack tuna. Barkley et al. (1978) hypothesized that large (>6.8 kg) skipjack tuna required cooler water than small skipjack tuna and therefore could tolerate the warmer surface water for relatively short periods. If so, the catchability of large skipjack tuna would be altered in the surface fishery and length-frequency modes of large skipjack tuna would be underestimated. Our otolith age determinations are not affected by these factors.

Otolith readings were also used to examine the age-length relationship of eastern Pacific skipjack tuna (Figure 5). Of the 20 specimens examined, 11 were caught off Baja California, Mexico. The other nine were caught in the eastern Pacific west of the Inter-American Tropical Tuna Commission's Yellowfin Regulatory Area. Most of these nine specimens had age-length relationships similar to those of fish caught off Baja California, but several had relationships similar to specimens taken in the central Pacific. Indications are that skipjack tuna in the eastern Pacific Ocean off Baja California grew at a slower rate than those in the central Pacific.

Our eastern Pacific skipjack tuna growth curve was compared with those of earlier studies from the eastern Pacific (Figure 5). A growth curve based on the progression of modes in length frequencies (Joseph and Calkins 1969) is similar to our curve; both show good agreement between 40

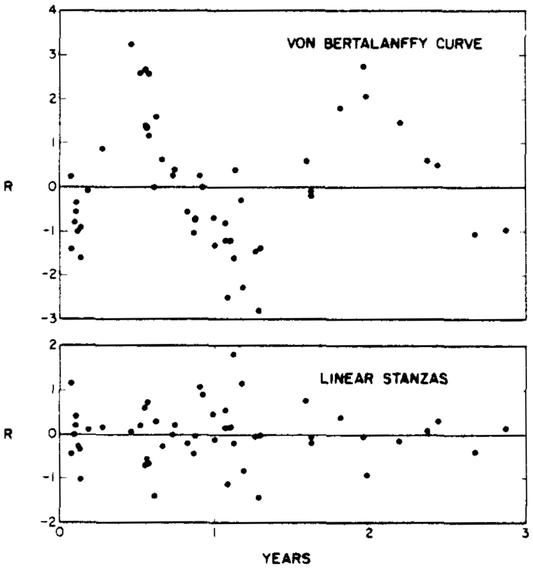

FIGURE 3.—Plot of residuals from von Bertalanffy growth curve and linear growth stanzas of central Pacific skipjack tuna shown in Figure 2.

and 65 cm FL. Growth curves determined from tagging data (Schaefer 1961; Joseph and Calkins 1969) showed slower growth.

The sagittae of five skipjack tuna from Papua New Guinea waters were examined (Figure 6). These fish grew more slowly than those from the central Pacific area.

Central Pacific Yellowfin Tuna

Two distinct stanzas of growth are evident for the sample of 14 central Pacific yellowfin tuna (Figure 7). Linear growth is apparent for about the first 14 mo of life, after which time the data suggest either the beginning of another linear growth phase or an asymptotic growth process. A segmented model with two linear phases was fitted to the data (Table 3). A von Bertalanffy growth equation was also fitted to the data and the following growth parameters were obtained: $L_\infty = 170.3$ cm; $K = 0.3864$, and $t_0 = 0.0366$ yr. Plots of residuals on age for both the segmental model and the von Bertalanffy growth curve were

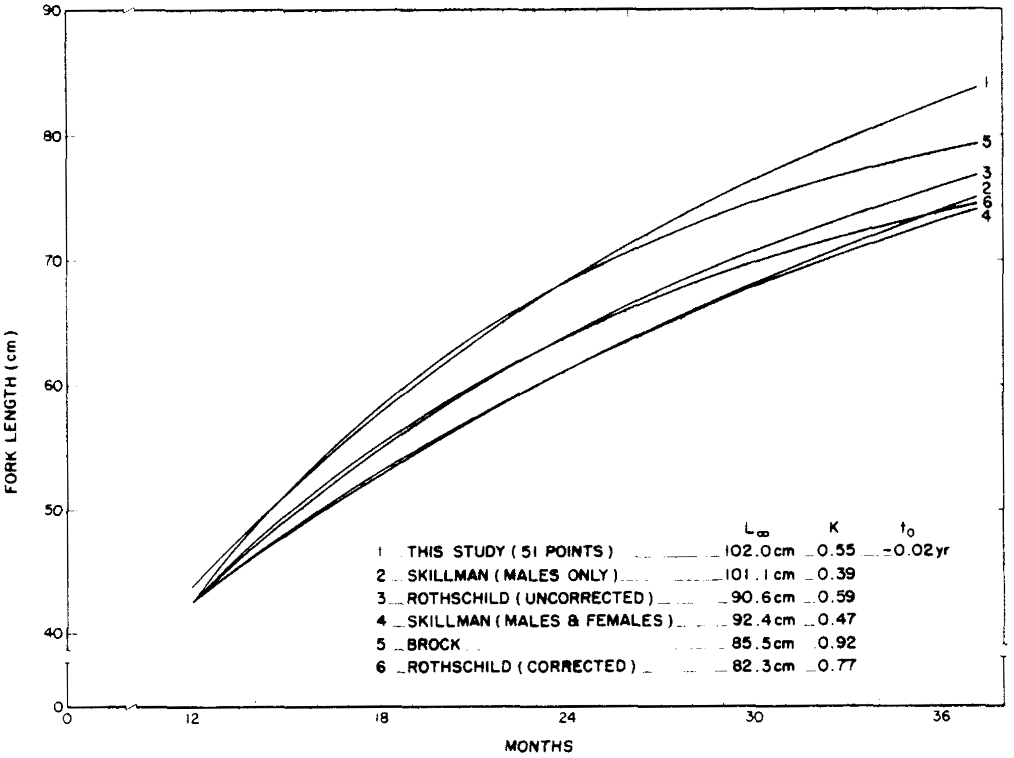

FIGURE 4.—A comparison of von Bertalanffy growth curves determined for central Pacific skipjack tuna (for full references, see text).

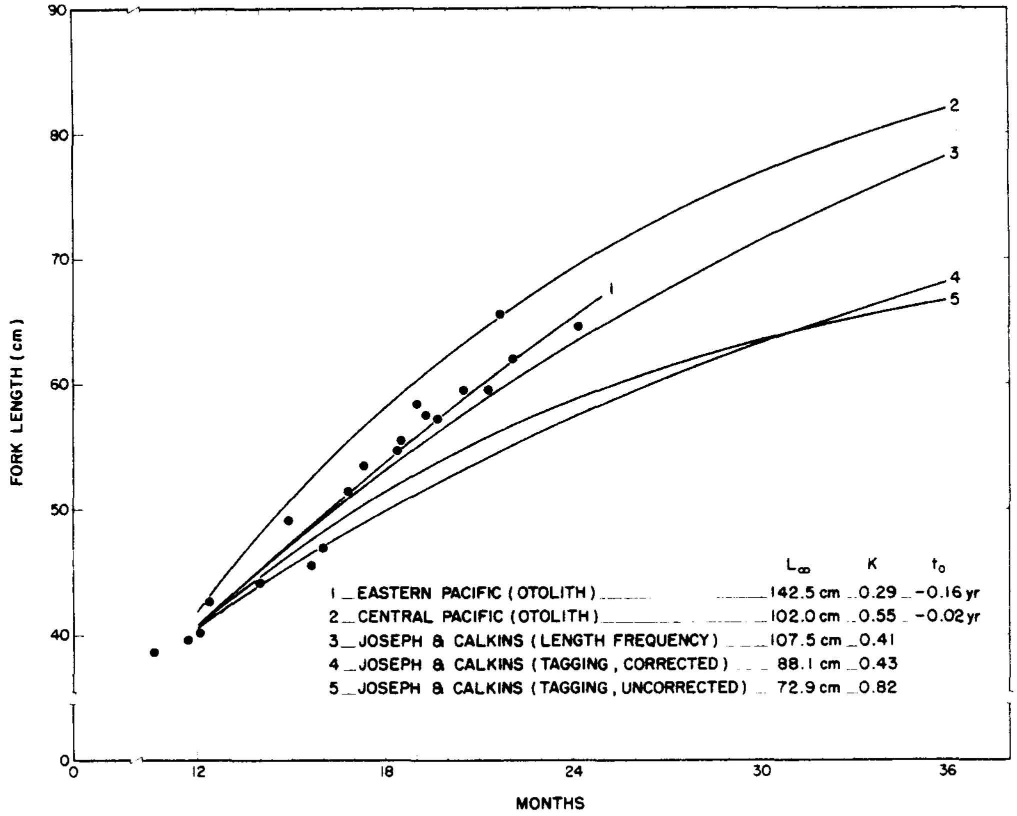

FIGURE 5.—The von Bertalanffy growth curve of skipjack tuna in the eastern Pacific as determined by otolith examination and its comparison with von Bertalanffy growth curves of previous studies from that area and the central Pacific (for full reference, see text).

TABLE 3.—Length-age regression parameters for the two linear growth stanzas of central Pacific yellowfin tuna: N = number of data and RSS = residual sum of squares.

					Intersections	
Stanzas	N	Intercept	Slope	RSS	Years	Fork length (cm)
1	10	0.8831	52.5837	5.7430	1.2047	64.2304
2	4	25.5653	32.0954	0.4620		
Total RSS				6.2050		

compared (Figure 8). As with skipjack tuna, the von Bertalanffy model gives a poorer fit than the linear segmental model. Although the probability for the distribution of residuals to be randomly distributed along the von Bertalanffy curve was significant at $P = 0.05$ (run's test, table of critical values: $r = 7$, $n_1 = 7$, $n_2 = 7$), clustering of pluses and minuses occurred. The run's test for the linear segmental model also showed randomness ($r = 9$, $n_1 = 6, n_2 = 8$; table of critical values, $P < 0.05$), and was an improvement over the von Bertalanffy curve with the increase in the number of runs from 7 to 9.

The results of our study on yellowfin tuna within the size range examined agree with most earlier studies for this species from the eastern and central Pacific Ocean. The results of aging by scales (Yabuta et al. 1960) and modal progression in length-frequency distributions (Hennemuth 1961) are given for comparison (Figure 6). It has been suggested that growth of yellowfin tuna in the eastern Pacific between the lengths of 50 and 100 cm is linear and that growth rates are 0.6-1.0 mm/d (Inter-American Tropical Tuna Commission 1972, 1974).

CONCLUSIONS

Daily growth information provides much greater insight into the growth patterns of teleost

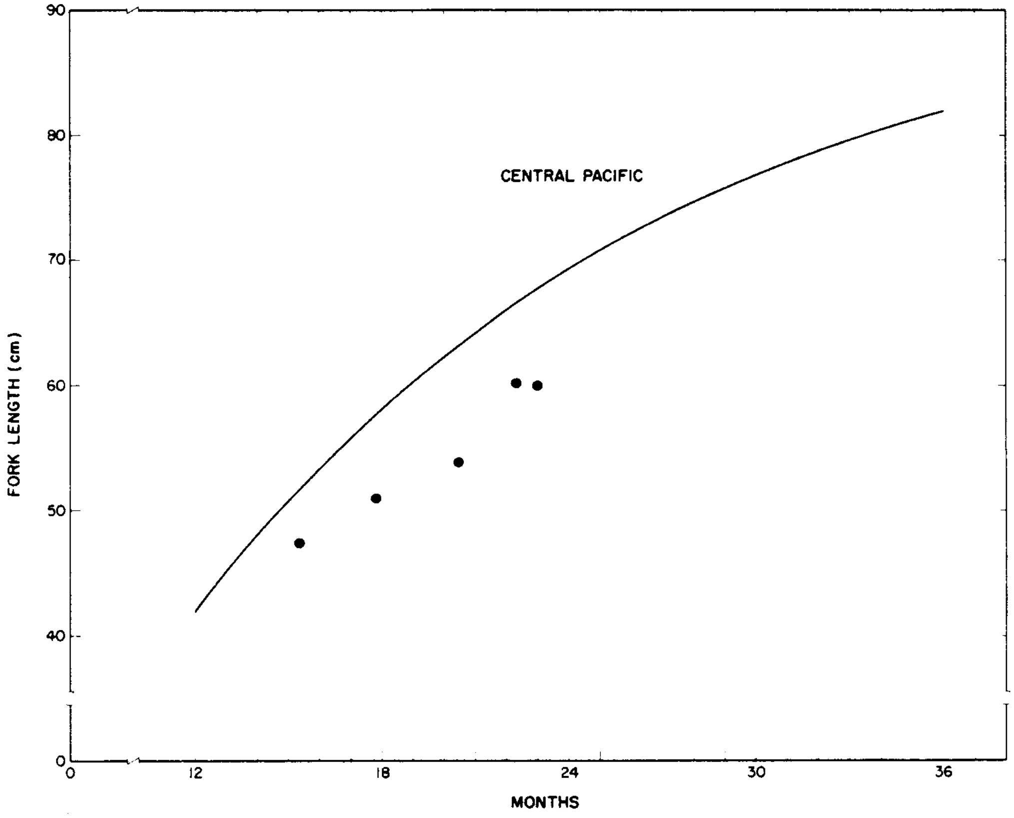

FIGURE 6.—Age determinations (points) of skipjack tuna from Papua New Guinea and comparison with the von Bertalanffy growth curve of central Pacific skipjack tuna derived in this paper.

fishes than can be gleaned using traditional annual techniques. Data presented here suggest three stanzas of linear growth for central Pacific skipjack tuna ranging in size from 3 to 80 cm FL, and that central Pacific yellowfin tuna from 7 to 93 cm FL have at least one stanza of linear growth.

Our assumption that the growth increments on the sagittae of skipjack and yellowfin tunas are deposited daily was supported by the deposition of experimentally induced increments on the sagittae of captive fishes and the relatively good agreement of our skipjack tuna and yellowfin tuna growth curves with those of previous studies utilizing other growth estimating techniques such as progression of modes in length-frequency distributions and interpretation of other hard parts. Growth studies on tunas based on tagging experiments have usually slower growth rates.

Otolith readings on specimens from three different areas suggest that there are geographical variations.

Estimation of growth rates from daily growth increments on sagittae is subject to at least two possible sources of error. One is that increments may not be deposited due to variables such as an inadequate ration, diet, temperature, age of fish, or during some physiologically stressful activity, such as reproduction. This is apparently the case for three species of boreal gadoids investigated by Pannella (1971). Another source is differential error during increment counting. If fewer rings are counted than actually exist, this, in addition to nondeposition of daily increments, would result in overestimation of growth rate.

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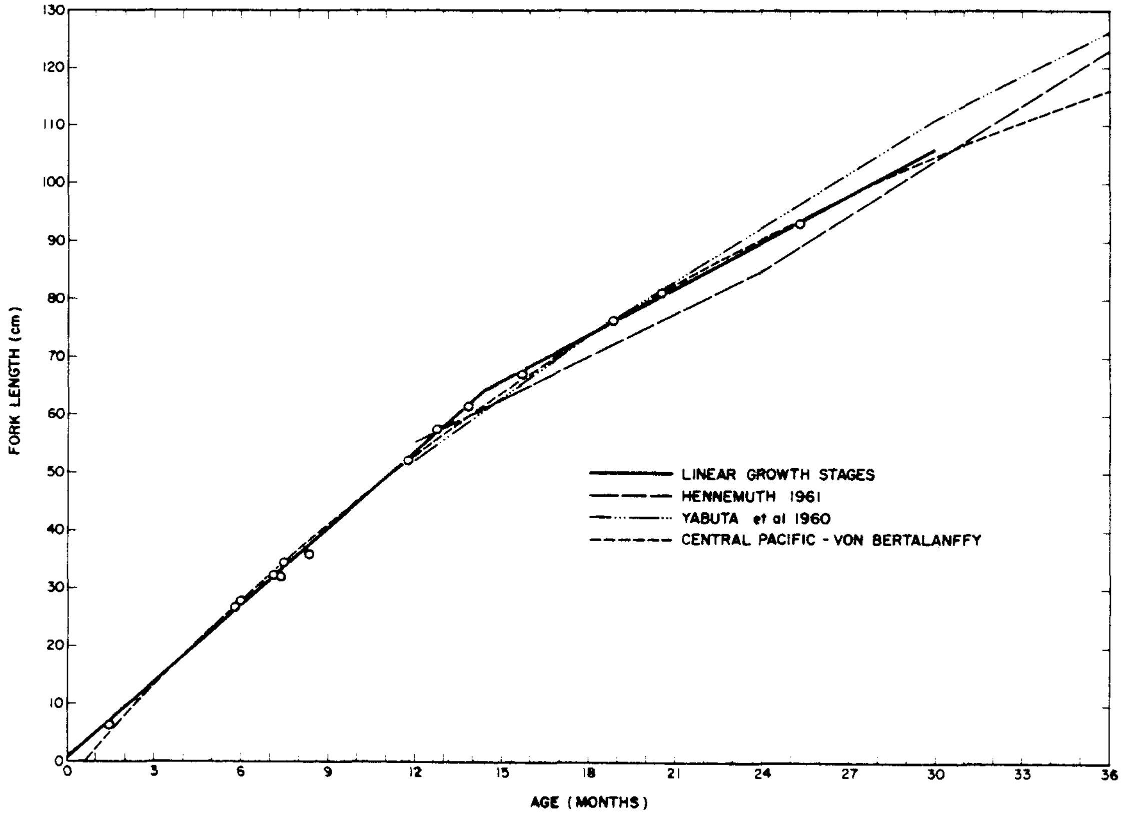

FIGURE 7.—Growth curve of yellowfin tuna in the central Pacific as determined by otolith examination and compared with growth curves of previous studies from that area and the eastern Pacific. Linear growth stanzas determined by LINFIT (see text). For parameters of growth stanzas, see Table 3.

pen and Howard O. Yoshida for their editorial help. We are especially indebted to Gary L. Kamer and Jeffrey J. Polovina for assisting with the statistical problems encountered. Marian Y. Y. Yong assisted with the data processing and Glen H. Sugiyama verified some of the age determinations. We are grateful to Sherry Steffel for sharing her data on feeding records and otoliths of skipjack and yellowfin tunas from her experiment.

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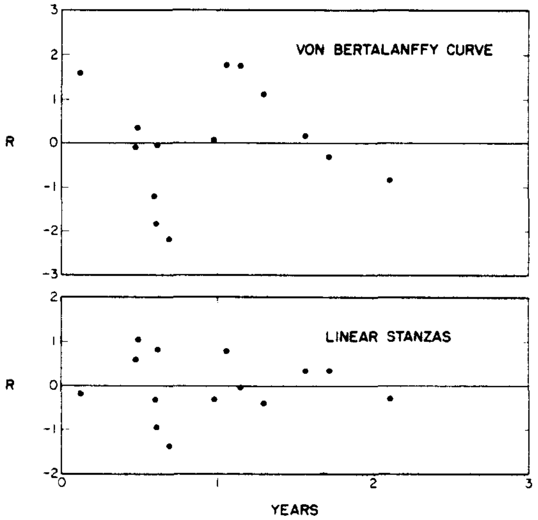

FIGURE 8.—Plots of residuals from von Bertalanffy growth curve and linear stanzas of central Pacific yellowfin tuna shown in Figure 7.

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