

## Age and growth of *Lutjanus kasmira* (Forskål) in Hawaiian waters

B. MORALES-NIN\* AND S. RALSTON†‡

\**Instituto de Ciencias del Mar, Paseo Nacional s/n, 08003 Barcelona, Spain and †Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, Hawaii 96822-2396, U.S.A.*

(Received 14 March 1989, Accepted 20 September 1989)

The growth of Hawaiian taape, *Lutjanus kasmira*, was studied by examining otoliths and by analysing length–frequency distribution. Annual hyaline and opaque markings were visible in whole mounts of sagittae, which were verified by enumeration of daily increments with a scanning electron microscope (SEM) and through marginal increment analysis. The von Bertalanffy growth curve was fitted to the data, resulting in:

$$T.L. = 34.0 \{1 - \exp[-0.29(t + 1.37)]\}$$

where T.L. is total length (cm) and  $t$  is age (years). SEM observations revealed that the slow-growth hyaline zones were composed of daily increments too small (0.4–0.8  $\mu\text{m}$ ) to be resolved optically. Thus, age estimates derived by numerically integrating otolith growth rate data obtained with a light microscope showed a negative bias, resulting in overestimation of growth rates. Parameter estimates obtained from three different types of length–frequency analysis were also unstable. This was due, at least in part, to differences in the size composition of fish sampled with different fishing gears and from different depths.

The growth rate registered in Hawaii falls within the reported growth coefficients of lutjanids, whereas it is one of the highest in the Pacific and clearly higher than a deep-water lutjanid species growth in Hawaii. Probably, this high growth rate may have been enhanced by the relative lack of competitors in the depauperate Hawaiian marine fish community.

Key words: growth; otolith; daily growth rings; Lutjanidae; Hawaii.

### I. INTRODUCTION

With its great isolation from other island ecosystems, the Hawaiian Archipelago is known for its relatively depauperate nearshore marine fish fauna. One of the most striking features of this community is the complete absence of native shallow-water snappers (Lutjanidae) and groupers (Epinephelinae), two ubiquitous taxa occurring on shallow reefs elsewhere in the tropical Indo-Pacific. As a consequence, a number of attempts have been made to introduce these commercially valuable fishes to Hawaii. The most successful of these has been taape, *Lutjanus kasmira* (Forskål), which was first released from the island of Oahu late in the 1950s (Randall, 1960); within 10 years it had spread to all other major islands of the archipelago.

Taape were first legally fished in 1966, and landings have increased rapidly, with a reported commercial catch of 36 700 kg in 1981. The present population is quite large and, based upon a trophic analysis of gut contents (Oda & Parrish, 1981), the introduction of taape is thought to have adversely affected populations of native

‡Present address: Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, 3150 Paradise Drive, Tiburon, CA 94920, U.S.A.

species. Beyond this single study, however, the population dynamics and community ecology of *taape* in Hawaii have not been studied, despite its remarkable population growth and increased importance to local fisheries.

The study of tropical fish growth has been a persistent problem due to poorly developed growth marks in the hard parts of most species and what, characteristically, are extended periods of spawning activity (Brothers, 1980). A broad reproductive period tends to obscure the distinction among cohorts in length–frequency data. Therefore, we studied *taape* growth using several independent approaches, including both otolith and length–frequency analysis. The general problem of determining age in tropical species is also discussed in the light of our more specific findings relating to the growth of *taape* in Hawaiian waters.

## II. MATERIALS AND METHODS

In 1987, *taape* were sampled at several fish markets on Oahu and during a cruise of the R/V Townsend Cromwell<sup>1</sup>. In the laboratory the total length (T.L., cm) and sex of each fish was determined. The monthly percentage of sexually mature females (i.e. vitellogenesis to post-spawning inclusive) was determined to assess the timing of the spawning season.

### OTOLITH STUDIES

Sagittae were extracted from all specimens, cleaned, and stored dry in vials. Although some of the otoliths ( $N=15$ ) were examined with a scanning electron microscope (SEM), most were studied with light microscopes, both dissecting and compound. When observed with a dissecting microscope under reflected light in a black Petri dish while immersed in a dense clarifying medium such as glycerine, *taape* otoliths show a concentric pattern of opaque and translucent rings. These rings are generally believed to be deposited during periods of fast and slow growth, respectively (Williams & Bedford, 1974). We studied the periodicity and timing of ring formation through marginal increment analysis, i.e. the percentage of otoliths having opaque margins was plotted for each month sampled. Once the annual periodicity of the rings was confirmed, an age–length relationship was estimated by fitting the von Bertalanffy growth equation to the data using Marquardt's algorithm.

For SEM study the otoliths were sagittally sectioned and preparations were glued to SEM staves with colloidal silver and polished with 0.3- $\mu\text{m}$  alumina. The otolith surface was then cleaned and etched 40 s with 1% HCl, washed, and dried overnight in an oven at 80° C to reduce electric charges during observation. Finally, samples were sputter-coated with gold-palladium and viewed with a Hitachi S-570 SEM at the Instituto de Ciencias del Mar using 15 kV tension. Using magnification, the rings were seen to be composed of differentiated daily growth increments (Pannella, 1971). The number of increments in a growth cycle (i.e. one opaque ring and its adjacent translucent ring) was compared with the number of days in a year, to evaluate the periodicity of ring formation.

An additional otolith subsample ( $N=31$ ) was prepared for study with compound light microscopy. These were embedded in casting resin and 0.7- $\mu\text{m}$  sections were cut through the frontal plane (focus to most distal portion of postrostrum). Samples were polished and mounted on glass slides with Euparal for observation. The otoliths were viewed using a semi-automatic image analysis system (Biosonics Optical Pattern Recognition System\*). Daily increment widths were measured to estimate the growth rate of the otolith at specific sites along the focus-postrostrum growth axis. The exact location of each site was determined by measuring the distance to the otolith focus. Numerical integration of the data provided estimated of age (years) at fixed 500- $\mu\text{m}$  increments in length to the otolith. Otolith length was then used to predict T.L. with an equation obtained by regressing the natural logarithm of T.L. on the logarithm of the radial length of the otolith. The weighted T.L. and age data were then fitted to the von Bertalanffy growth equation using non-linear

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

regression. Ralston & Williams (1989) provide a detailed description and evaluation of this method, which depends upon a close coupling between somatic and otolith growth.

The Hotelling's  $T^2$  multivariate statistical procedure (Bernard, 1981) was used to test the differences in growth between the Hawaiian taape and taape in other areas where it is indigenous.

#### LENGTH-FREQUENCY ANALYSIS

Three sets of data were used in the length-frequency analysis. Two were collected off Oahu in July 1978 and April 1979 (samples 1978 and 1979) by scuba divers setting a bottom gill net near a school of taape at 15 m depth and herding the fish into the net (J. D. Parrish, Hawaii Cooperative Fishery Research Unit, Honolulu). The third was collected by hook-and-line fishing in 40 m of water during a research cruise in September 1987 off the island of Niihau (sample 1987).

The regression method of Wetherall *et al.* (1987) was used to obtain a first estimate of  $L_{\infty}$ . The von Bertalanffy growth curve was then fitted to the three length-frequency data sets using the ELEFAN I procedure (Pauly & Gaschutz, 1979).

An additional combined analysis of otolith and length-frequency data was performed, wherein mean T.L. at annulus statistics obtained from examination of translucent and opaque marks in the otoliths were restructured to resemble tag-recapture data. Annual growth increments were calculated from successive lengths at age as if they were recaptures 1 year later. Deterministic selection of the growth increments by the ELEFAN V computer program (Brey & Pauly, 1986) was used to jointly analyse the length-frequency and otolith data, following the approach used by Morgan (1987).

### III. RESULTS

#### OTOLITH STUDIES

Taape otoliths, when observed with a dissecting microscope, showed a concentric pattern of broad translucent (i.e. hyaline) and diffuse opaque rings. Slight movements of the light source helped in differentiating and visualizing the two types of rings. Under the SEM the microstructure of the two classes of rings (translucent and opaque) was revealed; translucent rings were composed of narrow increments that were often characterized by discontinuities and irregularities, whereas the wider opaque rings were formed by thicker more consistently patterned increments.

The translucent zones with thin discontinuous increments were probably caused by periods of low growth in response to either environmental or physiological stress (Pannella, 1980). In taape, periods of slow growth often resulted in the formation of 70–90 very thin increments, with an average width of 0.8  $\mu\text{m}$  in juvenile fish (s.d. 0.45  $\mu\text{m}$ ) and an average thickness of 0.4  $\mu\text{m}$  (s.d. 0.30  $\mu\text{m}$ ) in mature fish [Fig. 1(a),(b)]. In contrast, daily increments laid down during periods of rapid growth were thicker. At these times the mean width of increments was 2.15  $\mu\text{m}$  (s.d. 1.05  $\mu\text{m}$ ) in juvenile fish and 1.2  $\mu\text{m}$  (s.d. 0.65  $\mu\text{m}$ ) in adult fish. These were arranged in higher-order rhythmical growth patterns of 3, 7, 14, and 28 increments [Fig. 1(c)]. Transitions between the two growth phases were usually abrupt.

In some samples a small group of seven thin but well-marked increments was laid down in the midst of a fast-growth zone [Fig. 1(d)]. In others this sharply defined but narrow seven-increment group was located at the start of a slow-growth period.

To determine the periodicity of the translucent and opaque rings, the number of increments in one presumptive annual period (one fast and one slow growth ring)

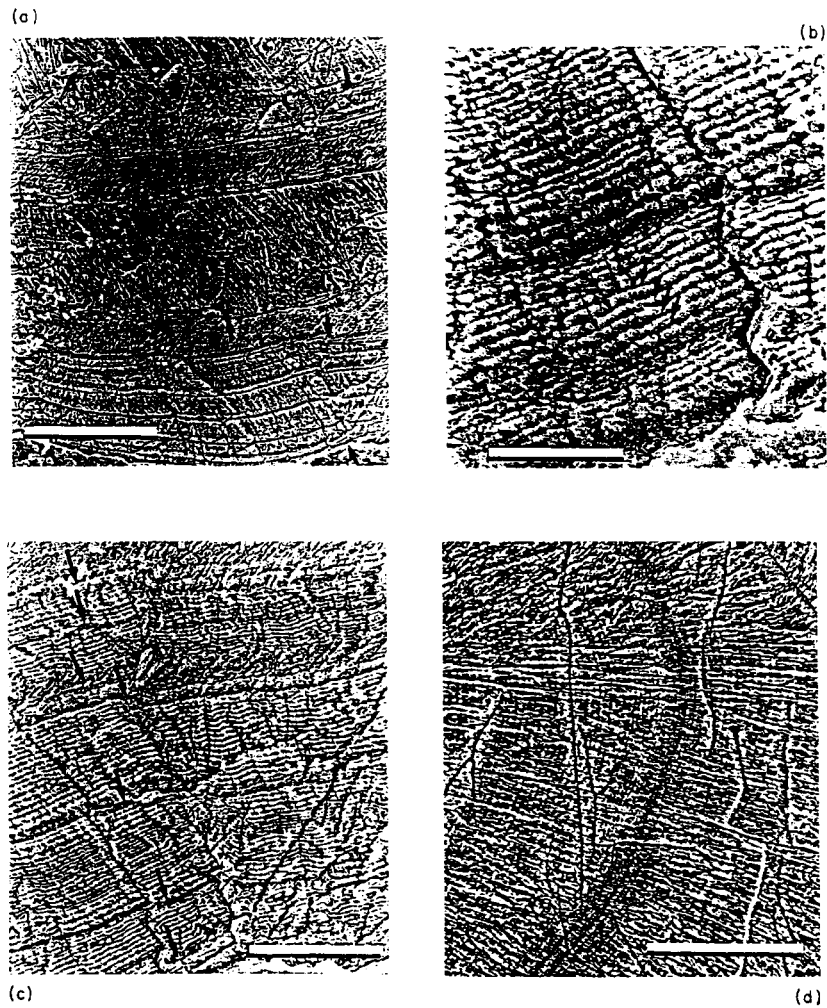


FIG. 1. Scanning electron micrographs of a taape otolith showing (a) fast (between arrows) and slow growth zones (scale bar = 75  $\mu\text{m}$ ), (b) thin increments (arrows) composed of discontinuous units (small arrows) and continuous units, laid down during a slow growth period (scale bar = 7.5  $\mu\text{m}$ ), (c) higher-order periodical growth patterns (arrows) (scale bar = 20  $\mu\text{m}$ ), and (d) thin increments standing out in a regular growth pattern (scale bar = 30  $\mu\text{m}$ ).

were enumerated. The mean number of increments was not significantly different from the number of days in a year (mean = 363, S.D. = 20.3,  $t = 0.1220 < t_{0.05}$ , d.f. = 15).

The occurrence of opaque margins on the otoliths (corresponding to periods of fast growth) was greatest during March (Fig. 2). As the spawning season advanced and the incidence of mature gonads increased, opaque margins became less evident in our samples, and there was an apparent slowing of growth. Although our samples were taken during only a portion of the year (March–October), and

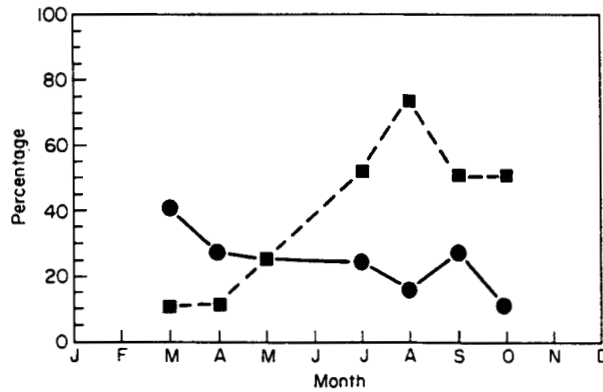


FIG. 2. Alteration of the taape otolith margin over the period of study, showing the monthly percentage of otoliths with opaque margins (% opaque, ●—●). Also shown is the seasonal representation of maturing females (% mature, ■- -■).

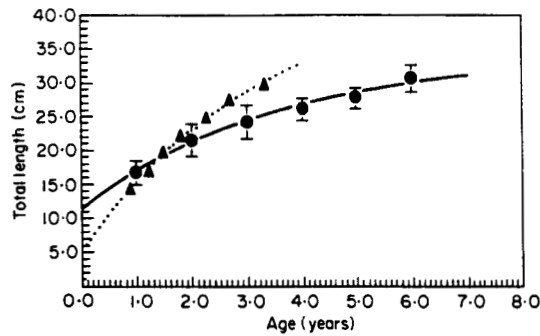


FIG. 3. Estimated von Bertalanffy growth curves obtained from the study of taape otolith annual marks (—●—) and increment microstructure widths (▲...). Error bars represent  $\pm 1.0$  s.d.

opaque margins were sometimes difficult to detect due to translucency of the otolith, these data are consistent with the hypothesis that one opaque and one translucent ring were formed per year, i.e., the marks were annuli. Moreover, the data suggest that the opaque ring began to form at some time between November and March.

Once the annual periodicity of the rings was verified, the age of the fish was determined by enumerating the marks and considering 1 July as the standard birthdate. The resulting relationship between age and length is shown in Table I. These data were fitted to the von Bertalanffy equation and the growth parameters estimated (Fig. 3; Table II).

The size of the 31 otoliths sectioned and measured for increment widths was well correlated with body size. A double logarithmic regression relating otolith length

TABLE I. Hawaiian *Lutjanus kasmira* age-length relationship obtained by reading hyaline/opaque zones in otoliths

Total length (cm)	Age class (years)					
	1	2	3	4	5	6
13	1					
14	1					
15	3					
16	5					
17	2	3				
18	6	6				
19	3	4	2			
20		14	2			
21		10	3			
22		7	4			
23		11	6	1		
24		6	7	3		
25		7	10	3	1	
26			5	5		
27		2	1	2	2	1
28			4	4	2	
29			2	1	1	1
30					1	1
31						2
32						1
33						2
<i>N</i>	21	70	46	19	7	8
<i>T.L.</i>	16.7	21.5	24.2	26.1	27.7	30.8

and *T.L.* was significant ( $r^2 = 0.83$ ), allowing prediction of *T.L.* from the radial length of the otolith (Fig. 4).

A total of 1915 estimates of otolith growth rate were obtained from measuring daily increment widths. These data were collected at otolith lengths as large as 6250  $\mu\text{m}$ . Otolith growth rate rose rapidly, followed by a slow decline as otolith length increased (Fig. 5). Growth rate variance was roughly proportional to the square of the mean, a result used in developing statistical weights for each estimate of *T.L.* at age (Ralston & Williams, 1989).

A full summary of otolith growth by 500- $\mu\text{m}$  intervals in otolith length is presented in Table III. The radial length of the otolith upon completion of growth through an interval was used to predict the corresponding *T.L.* with the regression presented in Fig. 4. To avoid extrapolating the regression to otolith lengths smaller than those actually measured, predictions were made only for otolith lengths greater than 3000  $\mu\text{m}$ . The resulting length-at-age data were fitted to the von Bertalanffy equation and the growth parameters estimated (Fig. 3; Table II).

The available data on taape growth in the Mariana Islands and American Samoa, determined by the same increment width method (Ralston & Williams, 1988*a,b*), proved to be significantly different from taape growth rate in Hawaii (Table IV).

TABLE II. Growth parameters of Hawaiian *Lutjanus kasmira* estimated from otoliths and length frequency analysis

Method	Sample	$L_{\infty}$ (cm)	$K$ (year <sup>-1</sup> )	$t_0$ (years)
Otoliths				
Annual rings	1987	34.0	0.29	-1.37
Increment width	1987	42.9	0.33	-0.37
Length frequency				
Wetherall <i>et al.</i>	1987	32.3	—	—
	1978/79	24.1	—	—
	pooled	32.3	—	—
ELEFANI	1987	33.0	0.67	—
	1978/79	24.8	0.29	—
	pooled	28.1	0.37	—
ELEFAN V	1987	29.9	0.41	—
	1978/79	23.6	0.63	—
	pooled	28.9	0.34	—

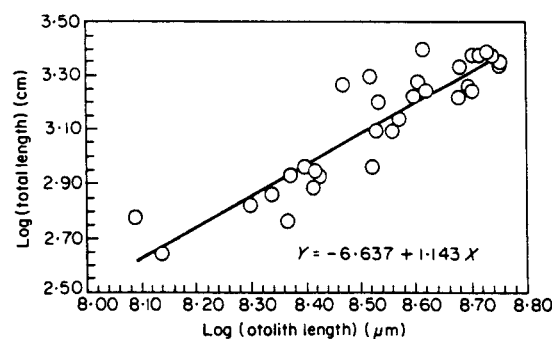


FIG. 4. The relationship between taape otolith size (radial length from focus to postrostrum) and total fish length.

#### LENGTH-FREQUENCY ANALYSIS

The length ranges sampled by the two different fishing gears (gill net and hook-and-line) were very different. In shallow water, only small fish were caught, while in the hook samples from deep water the fish were substantially larger (Fig. 6). Moreover, the 1979 gill net sample showed a substantial increase in the number of fish in the smallest length categories, relative to the 1978 net sample; this suggests that a major recruitment episode occurred in shallow water during early winter.

Estimates of  $L_{\infty}$  were obtained by application of the regression method of Wetherall *et al.* (1987) to the length-frequency data (Table II). Due to the absence

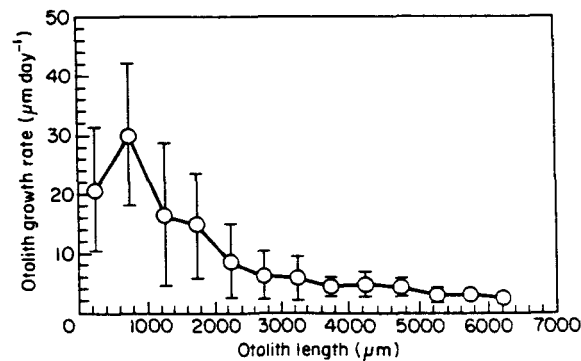


FIG. 5. Relationship between taape otolith growth rate and otolith length in 500- $\mu\text{m}$  intervals.

TABLE III. Summary of otolith length, otolith growth rate, mean age, and total length for Hawaiian *Lutjanus kasmira*

Otolith length interval ( $\mu\text{m}$ )	<i>N</i>	Mean otolith growth rate ( $\mu\text{m day}^{-1}$ )	Interval duration (days)	Age (years)	Predicted total length (cm)	Statistical weight
0-500	146	20.83	24.0	0.066	—	—
500-1000	45	30.10	16.6	0.111	—	—
1000-1500	126	16.59	30.1	0.194	—	—
1500-2000	166	14.72	34.0	0.287	—	—
2000-2500	159	8.66	57.7	0.445	—	—
2500-3000	181	6.34	78.9	0.661	—	—
3000-3500	124	5.77	86.7	0.898	14.8	1.00
3500-4000	99	4.39	113.9	1.210	17.2	0.97
4000-4500	270	4.85	103.1	1.492	19.7	0.95
4500-5000	226	4.24	118.0	1.815	22.2	0.94
5000-5500	183	3.08	162.4	2.260	24.8	0.93
5500-6000	157	3.12	160.3	2.699	27.4	0.91
6000-6500	33	2.37	211.3	3.277	30.0	0.90

of large fish in the shallow-water gill net samples taken in 1978/79, the estimate of  $L_{\infty}$  obtained with these data was lower (24.1 cm T.L.) than for either the 1987 deep-water hook-and-line sample alone or the entire pooled length-frequency data set (32.3 cm T.L.).

Regression method estimates of  $L_{\infty}$  were then used as starting points for the ELEFAN I procedure. Parameter estimates obtained with ELEFAN I varied considerably, depending on which data were used (Table II). Final values of  $L_{\infty}$  ranged from 24.8 to 33.0 cm T.L., whereas estimates of  $K$  ranged from 0.29 to 0.67 year<sup>-1</sup>.



TABLE IV. Results of the multivariate test between measured growth of taape in Hawaii, in American Samoa and in Mariana Archipelago. Entries include the pooled, estimated, variance-covariance matrix ( $S$ ) and its inverse ( $S^{-1}$ ), the calculated  $T^2$  statistic and the critical  $F_0$

<i>Hawaii-Samoa</i>							
$S$	8.103823	-0.16625	-0.70014	$S^{-1}$	7.76461	560.8541	-44.7389
	-0.16625	0.00359	0.01626		560.854	43083.31	-3739.08
	-0.70014	0.01626	0.08244		-44.7389	-3739.08	370.063
$P_1 - P_2 = i10.05$	0.0442	1.5728		$F_0 = 2.605$			
				$T^2 = 347.9052$			
<i>Hawaii-Mariana</i>							
$S$	19.6352	-0.47458	-2.46353	$S^{-1}$	-0.00992	-0.1402	-0.4581
	-0.4735	0.00256	0.00944		-0.16219	1271.3	-245.67
	2.4635	0.00951	0.05050		-0.45380	-246.03	43.676
$P_1 - P_2 = i-12.7$	0.215	1.686		$F_0 = 2.605$			
				$T^2 = 23.4335$			

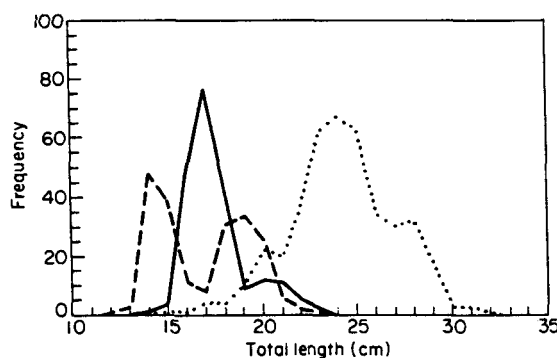


FIG. 6. Taape length frequency distributions. The 1978 (—) and the 1979 (---) samples were obtained in shallow water (15 m) with gill nets. The 1987 sample (...) was drawn from deep water (40 m) with hook-and-line gear.

Reconstructed annual growth rates were derived for the joint analysis of length-frequency and otolith data. These were restricted to lengths appropriate to the length-frequency data used (i.e.  $T.L. \leq 23$  cm for the gill net samples obtained in 1978/79). Under this constraint, the ELEFAN V program produced estimates of the von Bertalanffy growth parameters given in Table II. As with the other length-frequency analyses, the 1978/79 data produced the lowest estimate of  $L_{\infty}$  (23.6 cm T.L.) and, correspondingly, the estimate of  $K$  was the highest ( $0.63 \text{ year}^{-1}$ ).

The growth performance index ( $\phi = \log_{10} K + \{2 * \log_{10} L_{\infty}\}$ ) (Pauly & Munro, 1983) was calculated for each of the eight entries in Table II where both the  $K$  and  $L_{\infty}$  parameters were estimated. Values ranged from 2.25 (ELEFAN I applied to the 1978/79 sample) to 2.86 (ELEFAN I applied to the 1987 sample), with a mean of  $\phi = 2.55$  and s.d. = 0.19.

#### IV. DISCUSSION

The opaque and translucent rings found in taape otoliths were laid down with annual periodicity, allowing age determination with relative ease. Examination of otolith microstructure by SEM revealed the existence of very thin ( $0.4 \mu\text{m}$ ) bipartite growth increments that, due to their small size, were below the resolving threshold of a light microscope (Campana *et al.*, 1987; Jones & Brothers, 1987). The narrow translucent rings deposited during periods of slow growth were largely composed of these very thin increments. Therefore, translucent slow growth regions did not display a full complement of increments when viewed with a light microscope.

The increment width method (Ralston & Miyamoto, 1983; Ralston, 1985; Ralston & Williams, 1989) is based upon measuring the widths of daily increments at specific sites along a predefined axis of otolith growth. In theory, all daily increments, from focus to otolith margin, need not be visible to employ this technique. Although regions of the otolith characterized by ill-defined microstructure have previously been attributed solely to preparation defects (Ralston, 1985), these areas can also occur when increments are so small that they cannot be resolved with a conventional light microscope (Campana *et al.*, 1987; Jones & Brothers, 1987). In this situation, a sample of increment widths obtained by light microscopy would not be representative, resulting in the overestimation of otolith growth rates (Table III) and the underestimation of age. This kind of error may explain the discrepancy (Fig. 3) between estimates of asymptotic length ( $34.0$  v.  $42.9$  cm T.L.) and growth coefficient ( $0.29$  v.  $0.33$  year<sup>-1</sup>) derived from the two methods of otolith analysis.

Mizenko (1984) also used a light microscope in his study of *L. kasmira* otoliths from Western Samoa, and reported the existence of regions lacking clear increment microstructure. Increments smaller than  $0.8 \mu\text{m}$  (the practical limit of resolution with light microscopy) are not uncommon in tropical species (Morales-Nin, 1988). These findings illustrate the advantage of previewing otolith microstructure with SEM before attempting to age tropical species with a light microscope. If the latter is effective at resolving the smallest daily increments, one can proceed using either whole counts or the increment width method.

As an alternative approach, Ralston & Williams (1988a, 1989) advocated use of the regression method of Wetherall *et al.* (1987) to estimate the  $L_{\infty}$  parameter of the von Bertalanffy growth equation. Increment widths obtained from juvenile stages, where microstructure is more easily resolved, can then be used to estimate  $K$  and  $t_0$ , constrained by the estimated value of  $L_{\infty}$  obtained from the regression method.

Analysis of length-frequency data showed that parameter estimates were strongly affected by which sample was analysed. The pooled data produced results most similar to those obtained with otoliths, although in this situation the goodness-of-fit of the ELEFAN I program was poor (ESP/ASP = 0.110). The fit

was much better when independently-obtained otolith growth rates were incorporated into the calculations of ELEFAN V ( $ESP/ASP = 0.437$ ). These findings indicate that if a species has a bathymetric and/or geographical distribution that is heterogeneous with respect to length structure (e.g. Fig. 6), length-frequency samples may not be representative of the whole population. The difficulty is knowing when this occurs and correcting for it.

The estimation of growth in tropical marine fish has long been considered problematic due to the supposed lack of annual rings in their hard structures and their 'continuous' spawning which was assumed to render impossible the analysis of the growth of tropical fish based on the study of length-frequency data. Although biological and environmental conditions combine to make taape age and growth determination difficult, the multi-approach used herein made it possible to determine age and growth avoiding the subjectivity generally involved in age interpretation.

The presence of daily growth rings in the otoliths is, presumably, related to the diurnal changes in taape activity levels. Taape feed actively in rocky areas at night, while staying in sandy shallower areas at day (J. D. Parrish pers. comm.). These daily activity levels might be related to concomitant changes in the oxygen budget of the tissues. Thus, high activity levels during feeding, sustained high-speed swimming etc. will induce changes in the fluids surrounding the otoliths, and must result in alterations of the chemistry of the outermost layer of the otolith. Probably the discontinuous increment layer is laid down during the activity periods.

Seasonal growth cycles in tropical fish might be related to physiological changes induced by the influence of temperature, feeding regime and reproductive cycle. The evidence presently available suggests that a seasonal temperature difference of 2–3° C might be sufficient to cause ring formation (Morales-Nin, in prep.). The Hawaii nearshore marine system shows small temperature fluctuations which might be related to changes in taape growth rate. Seasonal changes in feeding regime do not seem evident in taape (Oda & Parrish, 1981), while the reproductive cycle appears to be related to the ring formation (Fig. 2). During the maturity period the metabolic energy seems to be diverted from growth, causing the formation of thin increments which are in turn reflected in hyaline seasonal growth rings.

Growth of taape in the Hawaiian Islands is rapid in comparison to the Mariana Islands (Ralston & Williams, 1988a) where the species is indigenous. Our estimates of growth rate are similar to those obtained in New Caledonia by Loubens (1980) and in American Samoa by Ralston & Williams (1988b). Moreover, our calculations of growth performance index indicate that taape is, relatively speaking, a fast-growing species of snapper (Manooch, 1987).

Taape in Hawaii shows a growth rate superior to that ( $K \text{ year}^{-1} = 0.146$ ) of the deep-water Hawaiian lutjanid *Pristipomoides filamentosus* (Ralston & Miyamoto, 1983). The very successful introduction of taape into the Hawaiian nearshore marine ecosystem, which had been entirely lacking in snappers and groupers, may have been due to its fast growth rate which, in turn, might have been enhanced by a lack of close competitors and predators.

We thank J. D. Parrish, Hawaii Cooperative Fishery Research Unit, Honolulu for providing the 1978–79 samples, J. M. Fortuño, Instituto de Ciencias del Mar for helping with SEM observations and sample processing, and H. Williams of the Honolulu Laboratory, National Marine Fisheries Service for assistance with the increment width method.

The study was made in 1987–88 as a part of B.M-N's FAO André Mayer Fellowship 'Tropical fish aging by means of otolith microstructure'.

### References

- Bernard, D. R. (1981). Multivariate analysis as means of comparing growth in fish. *Can. J. Fish. Aquat. Sci.* **38**, 233–236.
- Brey, T. & Pauly, D. (1986). Electronic length–frequency analysis: a revised and expanded user's guide to ELEFAN O, 1 and 2. *Ber. Inst. Meeres.* Christian-Albrecht Univ. Kiel. No. 149. 76 pp.
- Brothers, E. B. (1980). Age and growth studies on tropical fishes. In *Stock Assessment for Tropical Small-scale Fisheries* (S. B. Saila & P. M. Roedel, eds), pp. 119–136. Kingston, RI: International Center for Marine Resource Development, University of Rhode Island.
- Campana, S. E., Gagné, J. A. & Munro, J. (1987). Otolith microstructure of larval herring (*Clupea harengus*): image or reality? *Can. J. Fish. Aquat. Sci.* **44**, 1922–1929.
- Jones, C. & Brothers, E. B. (1987). Validation of the otolith increment aging technique for striped bass, *Morone saxatilis*, larvae reared under suboptimal feeding conditions. *Fish. Bull., U.S.* **85**, 171–178.
- Loubens, G. (1980). Biologie de quelques especes de poisson du lagon néo-Calédonien. I. Détermination de l'age (otolithométrie). *Cah. ORSTOM, Sér. Océanogr.* **16**(3 and 4), 263–283.
- Manooch, C. S., III (1987). Age and growth of snappers and groupers. In *Tropical Snappers and Groupers: Biology and Fisheries Management* (J. J. Polovina & S. Ralston, eds), pp. 329–374. Boulder, CO: Westview Press, Inc.
- Mizenko, D. (1984). The biology of western Samoan reef-slope snapper (Pisces: Lutjanidae) populations of: *Lutjanus kasmira*, *Lutjanus rufolineatus*, and *Pristipomoides multidens*. Unpubl. M.S. thesis, Univ. Rhode Island. 66 pp.
- Morales-Nin, B. (1988). Caution in the use of daily increments for ageing tropical fishes. *Fishbyte (ICLARM)* **6**(2), 5–6.
- Morgan, G. R. (1987). Incorporating age data in length-based stock assessment methods. In *Length-based Methods in Fishery Research* (D. Pauly & G. Morgan, eds), pp. 137–146. ICLARM Conference Proceedings 13. Manila, Philippines: International Center for Living Aquatic Resource Management.
- Oda, D. & Parrish, J. D. (1981). Ecology of commercial snappers and groupers introduced to Hawaiian reefs. In *The Reef and Man* (E. D. Gomez, C. E. Birkeland, R. W. Buddemeier, R. E. Johannes, J. A. Marsh, Jr. & R. T. Tsuda, eds), pp. 59–67. Proceedings of the Fourth International Coral Reef Symposium Vol. 1. Quezon City, Philippines: Marine Science Center, University of the Philippines.
- Pannella, G. (1971). Fish otoliths: daily growth layers and periodical patterns. *Science, Washington DC* **173**, 1124–1127.
- Pannella, G. (1980). Growth patterns in fish sagittae. In *Skeletal Growth of Aquatic Organisms: Biological Records of Environmental Change* (D. C. Rhoads & R. A. Lutz, eds), pp. 519–560. New York: Plenum Press.
- Pauly, D. & Gaschutz, G. (1979). A simple method for fitting oscillating length growth data, with a program for pocket calculator. *ICES CM 1979/G:24*. 26 pp. (mimeo.).
- Pauly, D. & Munro, J. L. (1983). Once more on the comparison of growth in fish and invertebrates. *Fishbyte (ICLARM)* **2**(1), 21.
- Ralston, S. (1985). A novel approach to aging tropical fish. Int. Center Living Aquat. Resour. Mgmt Manila, Philippines. *ICLARM Newsletter* **8**(1), 14–15.
- Ralston, S. & Miyamoto, G. T. (1983). Analysing the width of daily otolith increments to age the Hawaiian snapper, *Pristipomoides filamentosus*. *Fish. Bull., U.S.* **81**, 523–535.
- Ralston, S. & Williams, H. A. (1988a). Depth distributions, growth, and mortality of deep slope fishes from the Mariana Archipelago. *U.S. Dept Commerce, NOAA Tech. Memo NMFS, NOAA-TM-NMFS-SWFC-113*. 47 pp.

- Ralston, S. & Williams, H. A. (1988b). Age and growth of *Lutjanus kasmira*, *Lethrinus rubrioperculatus*, *Acanthurus lineatus*, and *Ctenochaetus striatus* from American Samoa. *Southwest Fish. Cent. Honolulu Lab., Natl Mar. Fish. Serv., NOAA, Admin. Rep. H-88-18*. 11 pp.
- Ralston, S. & Williams, H. A. (1989). Numerical integration of daily growth increments: an efficient means of aging tropical fishes for stock assessment. *Fish. Bull., U.S.* **87**(1), pp. 1-16.
- Randall, J. E. (1960). New fishes for Hawaii. *Sea Frontiers* **6**, 33-43.
- Wetherall, J. A., Polovina, J. J. & Ralston, S. (1987). Estimating growth and mortality in steady state fish stocks from length-frequency data. *Length-based Methods in Fishery Research* (D. Pauly & G. Morgan, eds), pp. 53-74. ICLARM Conference Proceedings 13. Manila, Philippines: International Centre for Living Aquatic Resource Management.
- Williams, T. & Bedford, B. C. (1974). The use of otoliths for age determination. In *The Ageing of Fish* (T. B. Bagenal, ed.), pp. 114-123. Old Woking, Surrey: Unwin Brothers.
-