

# Growth determination of tropical marine fishes by means of otolith interpretation and length frequency analysis

Beatriz Morales-Nin

*Instituto de Ciencias del Mar, Paseo nacional S/N, Barcelona 08003, Spain.*

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## Abstract

Age and growth of four tropical marine fish species: *Lethrinus choerorhynchus*, *Lutjanus kasmira*, *Nemipterus furcosus* and *Scomberomorus brasiliensis*, were determined by means of otolith interpretation and length-frequency analysis. The results showed the presence of annual rings in the studied species. These rings were consistently interpreted and their annual periodicity tested by means of various methods. The annuli are composed of distinct daily increments, of different thickness depending of the otolith area. Growth determination by means of length-frequency analysis was problematic in some species due to the lack of clear modal classes (in the length distributions). The joint analysis of the age and the length-frequency data improved the estimation of growth parameters, and allowed the selection of results that were biologically acceptable.

**Keywords :** Growth, tropical fish, otolith microstructure, length frequency analysis.

*Détermination de la croissance de poissons marins tropicaux au moyen de l'analyse des fréquences de tailles et de l'interprétation de lecture d'otolithes.*

## Résumé

L'étude de la croissance et de l'âge de quatre espèces de poissons marins tropicaux: *Lethrinus choerorhynchus*, *Lutjanus kasmira*, *Nemipterus furcosus* et *Scomberomorus brasiliensis* a été faite au moyen de l'analyse des fréquences de tailles et de lectures d'otolithes. Ces otolithes présentent des anneaux annuels chez les espèces étudiées. Ces anneaux se distinguent clairement et leur périodicité annuelle a été testée à l'aide de diverses méthodes. Les annuli sont formés du dépôt journalier de microstries d'épaisseur variable selon la zone de l'otolithe considérée. La détermination de la croissance au moyen de l'analyse des fréquences de tailles est rendue délicate chez certaines espèces par le manque de classes modales distinctes. L'analyse conjointe de l'âge et de la fréquence des tailles des captures améliore l'estimation des paramètres de croissance et permet la sélection des résultats ayant une signification biologique.

**Mots-clés :** Croissance, poissons tropicaux, microstructure de l'otolithe, analyse des fréquences de tailles.

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## INTRODUCTION

The estimation of growth in tropical marine fishes has long been considered problematic due to the supposed lack of annual rings in their hard structures

(scales, otoliths and vertebrae) 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 (Mohr, 1921).

However, it was realized during the 1960s and 1970s that tropical marine fishes generate annual rings

in their hard parts under a wide range of conditions. Also, it was found that growth could be estimated for many tropical fish stocks by analysis of seasonal growth rings on otoliths (Bayagbona, 1963; Poinard and Troadec, 1966; Longhurst and Pauly, 1987; Morales-Nin, 1989; *inter al.*).

While spawning of tropical fishes is often more prolonged than that in temperate fishes, it is usually concentrated in one or two periods each year. The fluctuations in fish spawning are only partially responsible for recruitment fluctuations. The occurrence during larval and juvenile life of recruitment windows (Bakun *et al.*, 1982) can vary seasonally even when egg production is constant. These recruitment fluctuations then generate the modes which make it possible to analyze length-frequency data (Pauly, 1984).

Pannella's discovery (1971) of the daily periodicity of the very fine striations within otoliths, previously described by Hickling (1931), offered a new growth determination method. Daily growth increments have been applied to determine growth rates (Shubnikov, 1976), to establish the duration of the larval stage of coral fishes (Victor, 1982), and to determine fishes growth (Brothers, 1979; Ralston, 1985).

In this contribution, length-based methods and otolith-based methods are jointly applied to determine growth of various tropical marine species important to the fisheries of their respective areas. The species were selected to represent different types of data sets obtained by different fishing techniques (table 1).

Table 1. — Data related to the studied species.

<i>Lethrinus choerorhynchus</i> (Lethrinidae)	
NW Australia	
Length frequencies collected September 1982 (D. W. Whitelaw, CSIRO Marine Laboratories, pers. comm. 1986).	
95 pairs of otoliths collected September 1982 (D. W. Whitelaw, CSIRO Marine Laboratories, pers. comm. 1986).	
<i>Lutjanus kasmira</i> (Lutjanidae)	
Oahu, Hawaii	
171 otoliths collected along 1986.	
Length frequencies from 1978-1979 (J. D. Parrish, Hawaii Cooperative Fishery Research Unit, pers. comm. 1986) and 1987 (S. Ralston, Southwest Fisheries Center, pers. comm. 1987).	
<i>Nemipterus furcosus</i> (Nemipteridae)	
NW Australia	
80 pairs of otoliths collected September 1982 (D. W. Whitelaw, CSIRO Marine Laboratories, pers. comm. 1986).	
Length frequencies (D. W. Whitelaw CSIRO Marine Laboratories, pers. comm. 1986).	
<i>Scomberomorus brasiliensis</i> (Scombridae)	
Fortaleza (Brazil)	
Length frequency collected throughout 1968 (Costa and Pavia 1969)	
40 otoliths collected 1968 (Costa and Pavia 1969) (J. Fontelhes-Filho, Universidade Federal Ceara, pers. comm. 1986).	

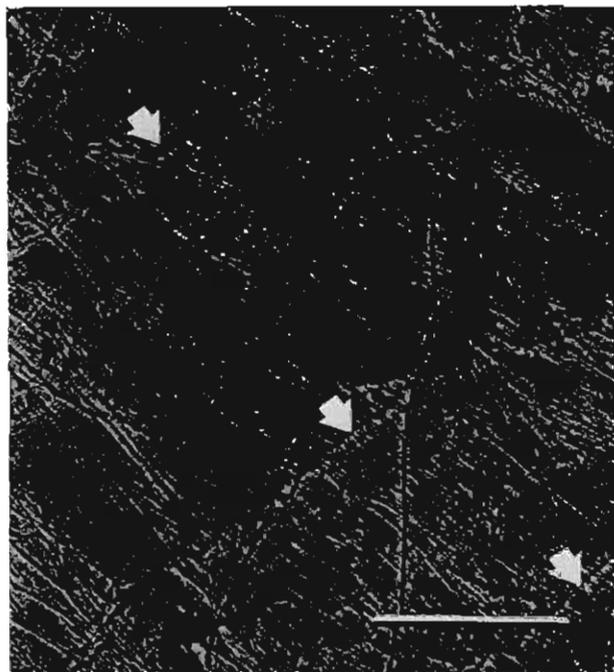


Figure 1. — Scanning electron micrograph showing the regular increment pattern in an otolith of *Lethrinus choerorhynchus*. The increments are composed of an incremental unit and a discontinuous unit appearing as a groove. Rhythmic growth patterns were well developed (white arrows), scale bar 3  $\mu$ m.

## MATERIAL AND METHODS

A total of four species from the Southwest Atlantic and the Central and Southeast Pacific, covering pelagic and demersal habitats, has been studied (table 1). The following procedures were applied when suitable material was available.

### Otolith studies

Otoliths of the studied species were stored dry in paper envelopes with a code number. The sagittal otoliths were read whole, against a black background and immersed in glycerol, using a compound microscope. As a rule, each otolith was read three times and the consistency of the otolith interpretation was determined by the average percentage error (APE) index (Beamish and Fournier, 1981).

The annual nature of the annulus present in the otoliths was determined using three methods:

1. The increments laid down in each ring were enumerated in the samples studied with a scanning electron microscope (SEM). A *t*-test was used for comparing the mean number of increments laid down in each annual period (comprising a hyaline and an opaque ring) and the number of days elapsed. The daily nature of the increments was assumed due to the occurrence of daily rings in most marine species

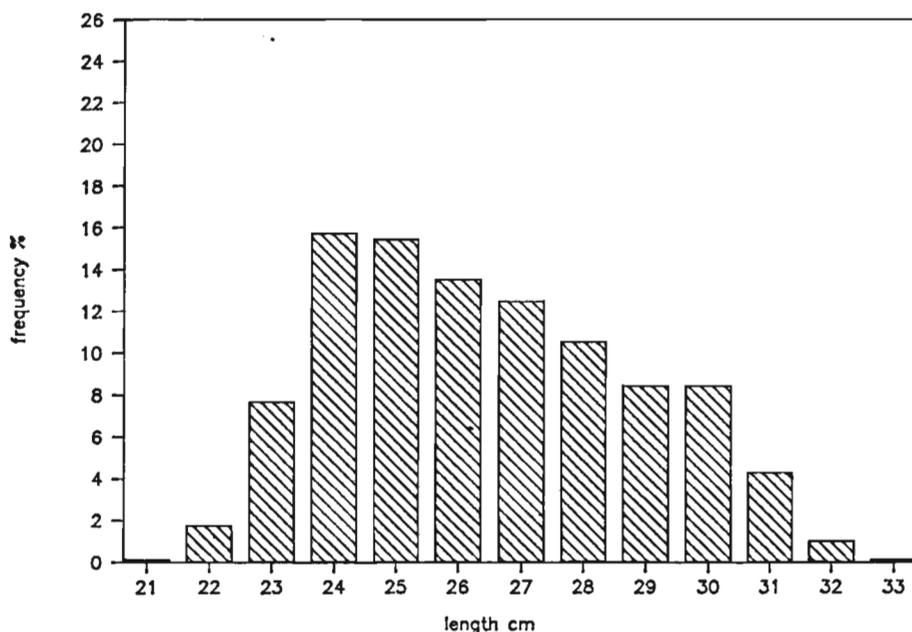


Figure 2. — *Lethrinus choerorhynchus* length frequency data.

(Campana and Neilson, 1985). The rings on the otolith edge were not used to avoid the underestimation of the age caused by the loss of increments due to the otolith grinding process.

2. When the available otolith sample covered a year, the evolution of the annulus on the otolith edge during the year were used to determine the period of formation.

3. Further validation of the otolith-based results was obtained by length frequency analysis.

January 1st was used as an arbitrary birth date to transform the coincident otolith interpretations into age-length relationships. The age-length matrix thus obtained for each species was employed to fit a von Bertalanffy growth curve (Allen, 1966).

Some otoliths ( $n=5$  for each species) were also studied for microstructural growth increments. The otoliths were ground and polished until the nucleus plane was reached. Then, the sections were washed and acid-etched with HCl 0.1 N during 30-45 secondes to reveal daily growth increments. The sections were glued to scanning electron microscope (SEM) stives, gold coated and observed with a Hitachi S-570 SEM.

The occurrence of banding patterns grouping 7, 14 or 28 daily increments, which is generally attributed to the action of tidal cycles (Pannella, 1974; 1980), was considered to provide further support of the daily nature of the observed increments (Campana and Neilson, 1985).

### Length-based studies

Size groups presumed to represent age classes in the available length-frequency data were identified by means of the method of Bhattacharya (1967), and this was followed by the application of modal class progression analysis (Gayanilo *et al.*, 1988).

The regression model of Weatherall *et al.* (1987) was used to obtain a first estimate of  $L_{\infty}$ . The von Bertalanffy growth curve was then fitted to the available sets of length-frequency data using the ELEFAN I program (Pauly and David, 1981; Gayanilo *et al.*, 1988).

This program restructures length-frequency data in an attempt to identify the peaks corresponding to cohorts independently of the height or shape of the peaks themselves. The frequency ( $F_i$ ) of each length class  $i$  ( $i=1$  to  $n$ ) is divided by the moving average ( $MA_i$ ) over five length classes. The values

$$FA_i = F_i / MA_i$$

identify peaks ( $FA_i > 1$ ) and troughs ( $FA_i < 1$ ). The average adjusted frequency value  $FA$  is computed, and the final transformation consists of the division of each  $FA_i$  by  $FA$  and 1 is subtracted:  $F'_i = FA_i / FA - 1$ . The frequency consists then of a series of peaks (presumably corresponding to age classes), troughs ( $-1 < F'_i < 0$ ) and of points with  $F'_i = -1$ , corresponding to the original zero values.

In a set of restructured length frequency samples, a number of peaks is found within each of the samples. If it is assumed that each peak corresponds to a distinct age class, then any growth curve going

Table 2. — Age length relationships obtained from otolith reading.

*Lethrinus choerorhynchus*

Length (cm)	Age (year)			
	2	3	4	5
23	5			
25	7	1		
27	7	17	3	1
29		19	16	2
31		4	12	3
33			1	2
Mean (cm)	25.2	28.2	29.6	30.5
s. d. (cm)	1.6	1.3	1.4	2.0
N	19	41	32	8

*Nemipterus furcosus*

Length (cm)	Age (year)				
	0	1	2	3	4
7	1				
9	2				
11	4				
13	4				
15		1	2		
17	1	6	1		
19		6	8		
21		3	1	4	
23			4	9	4
25				4	6
27				1	1
Mean (cm)	11.5	18.3	19.5	23.2	24.4
s. d. (cm)	2.5	1.7	2.5	1.6	1.2
N	12	16	16	18	11

*Lutjanus kasmira*

Length (cm)	Age (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
Mean (cm)	16.7	21.5	24.1	26.0	27.7	31.1
s. d. (cm)	1.7	2.4	2.5	1.6	1.6	2.4
N	21	70	45	19	7	8

*Scomberomorus brasiliensis*

Length (cm)	Age (years)								
	1	2	3	4	5	6	7	8	9
20	1								
22									
24									
26									
28									
30	1								
32	1	1							
34	3								
36		1							
38		1	1						
40									
42									
44		2	2						
46			2		2				
48				1					
50				1		1			
52									
54				1					
56				1					
58				1	1				
60									
62							1		
64					1	1			
66					1	1			
68						1		1	
70									1
72									1
74									
76									1
78									
80									1
Mean (cm)	30.7	38.8	42.0	51.2	54.4	60	60	68	74.5
s. d. (cm)	5.5	5.2	2.4	4.2	9.6	9	0	0	4.4
N	6	5	5	5	5	4	1	1	4

through a certain peak will be able to "hit" (intersect) only one of the length classes constituting this peak. Thus, by definition, the maximum sum of positive point values that can be accumulated by a growth curve fitted to a set of  $ns$  samples equals the sum of the highest values of all  $np$  peaks in all  $ns$  samples. This sum is called (ASP)=available sum of peaks.

Any growth curve passing through a restructured length frequency matrix will "hit" a number of points within this matrix. Adding up the restructured frequency values corresponding to these points, the value (ESP)=explained sum of peaks, is obtained.

The goodness of fit of a growth curve passing through a restructured length frequency data matrix can be thus determined by means of the number of hits in relation to the total number of available peaks. The ratio  $ESP/ASP$  can be used to assess the goodness of fit, but following Gayanilo *et al.* (1988), we use here  $R_n = (10^{ESP/ASP})/10$ , because  $0 < R_n < 1$  and hence  $R_n$  is roughly similar to a coefficient of determination ( $r^2$ ) (Brey and Pauly, 1986). The curve interconnecting the largest number of peaks is considered

to explain the positions of these peaks as the result of individual growth of the studied species.

An initial set of parameters is improved in successive runs trying to optimize the  $R_n$  value. When a range of growth parameters is tested, a narrow area with high values should be determined. The best parameter combination is obtained with a repetitive procedure.

The inclusion of length-at-age data in the length frequency analysis implies considering complex mathematical problems related to the estimation of  $t_0$  (age at length 0) (Brey and Pauly, 1986). Therefore, the length at age data obtained from the age-length determinations are re-expressed so as to resemble tagging-recapture data. Annual growth increments were calculated from successive lengths at age as if they were recaptures one year later. In some analyses these increments were weighted in proportion to the abundance of the age class in the age-length relationship. Also, a deterministic routine which picks the growth increments closest to the mean increment for each length interval and then moves outward, was also



Figure 3. — Scanning electron micrograph of a *Lutjanus kasmira* otolith showing the rhythmic growth patterns (white arrows), scale bar 1.5  $\mu$ m.

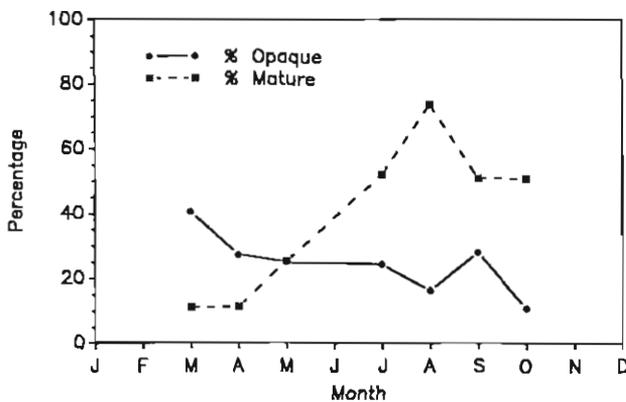


Figure 4. — Evolution during the year of the opaque ring on the edge of *Lutjanus kasmira* otolith. The split line indicates the percentage of mature fish (from development to post-spawning) in the same period.

used in the growth increment selection (Brey and Pauly, 1986).

The growth increments and the length frequency data were analyzed jointly using the ELEFAN V computer program (Gayanilo *et al.*, 1988), which is based on an approach developed by Morgan (1987). The growth curve which provides the best fit to both the length composition and the age-length data sets will be the curve which maximizes  $R_m = R_n + r^2$ , where

Table 3. — Decomposition of length frequency data using the method of Bhattacharya (1967) as implemented in the complete ELEFAN (Gayanilo *et al.*, 1988).

<i>Lethrinus choerorhynchus</i>				
Age Group	Mean (cm)	s. d.	N	Separation index (*)
1	24.25	1.06	288.5	—
2	27.16	1.22	268.4	2.544
3	30.01	1.08	114.0	2.463

<i>Lutjanus kasmira</i>				
Age Group	Mean (cm)	s. d.	N	Separation index (*)
1	14.46	0.58	100.0	—
2	17.44	1.62	305.0	2.703
3	23.52	1.74	358.9	3.617
4	28.15	0.84	65.4	3.587
5	31.09	0.61	4.5	4.031

<i>Nemipterus furcosus</i>				
Age Group	Mean (cm)	s. d.	N	Separation index (*)
1	12.70	1.42	88.5	—
2	16.38	1.14	87.8	2.871
3	18.83	0.91	110.8	2.378
4	24.33	1.79	387.0	4.061
5	27.91	0.64	59.7	2.933

<i>Scomberomorus brasiliensis</i>				
Age Group	Mean (cm)	s. d.	N	Separation index (*)
1	44.37	4.73	2,249.3	—
2	56.13	8.75	636.8	1.744
3	70.23	3.81	92.6	2.244
4	88.76	3.54	8.1	5.083

(\*) Separation index >2 to be meaningfully separated.

$r^2$  is the proportion of the variance of the growth increments that is explained by the growth parameters in question.

Since  $K$  and  $L_\infty$  are correlated, the growth performance index,  $\Phi = \log_{10} K + 2 \log_{10} L_\infty$  (Pauly, 1979) was used to compare the growth parameters obtained.

## RESULTS

### *Lethrinus choerorhynchus*

The otoliths of this species showed a recurrent pattern of diffuse growth rings. A thin opaque ring was laid down in the otolith before a slow growth period started causing the formation of a hyaline ring.

Table 4. — Response surface of  $R_n$  values ( $M \times 1,000$ ) in the *Lethrinus choerorynchus* length frequency data and growth increments; note the plateau with  $R_n > 0.985$ .

K (year <sup>-1</sup> )	$L_\infty$ (cm)										
	25	26	27	28	29	30	31	32	33	34	35
0.70	575	586	529	985	996	998	997	997	998	714	714
0.62	575	586	530	521	997	997	998	997	997	997	714
0.54	575	577	586	525	999	997	997	998	997	714	997
0.46	575	577	586	583	531	997	997	997	997	714	714
0.38	997	576	577	585	587	529	529	529	997	997	997
0.30	997	576	577	577	587	584	529	529	529	511	714

## Lutjanus kasmira

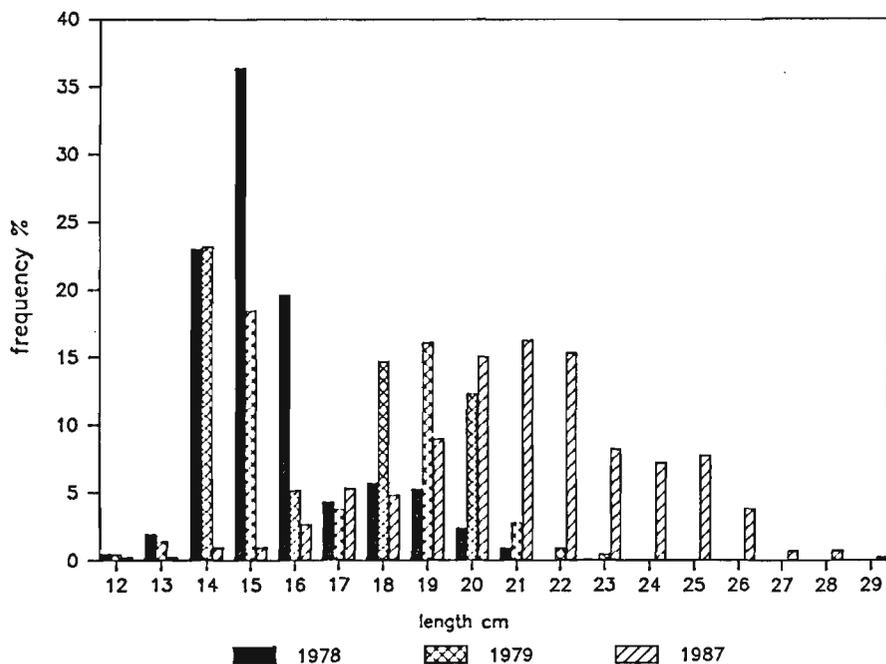


Figure 5. — *Lutjanus kasmira* length frequency data.

The daily nature of the increments laid down in the otoliths of this species is supported by the presence of growth patterns composed of 7, 14 and 28 increments. The pattern of deposition in this species was regular (fig. 1) with relatively thick increments (1.5–5  $\mu\text{m}$  depending on the otolith area). The enumeration of increment was supported, when possible, by the age determined by means of annual rings.

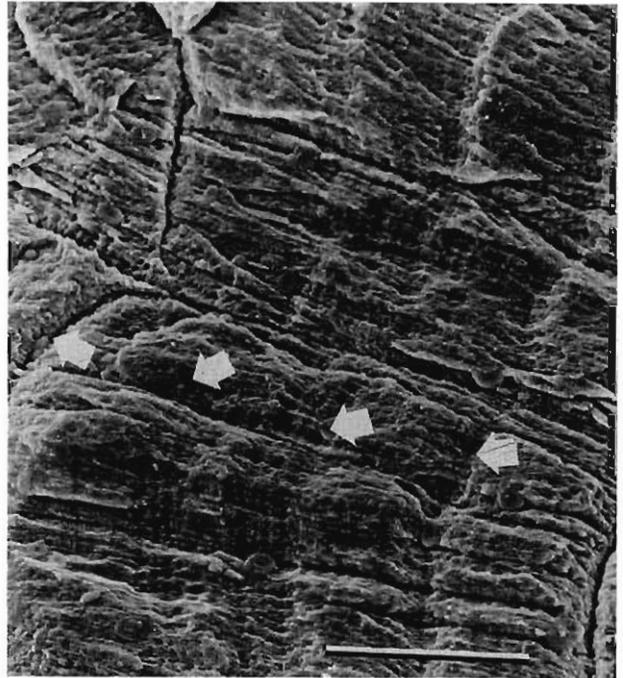
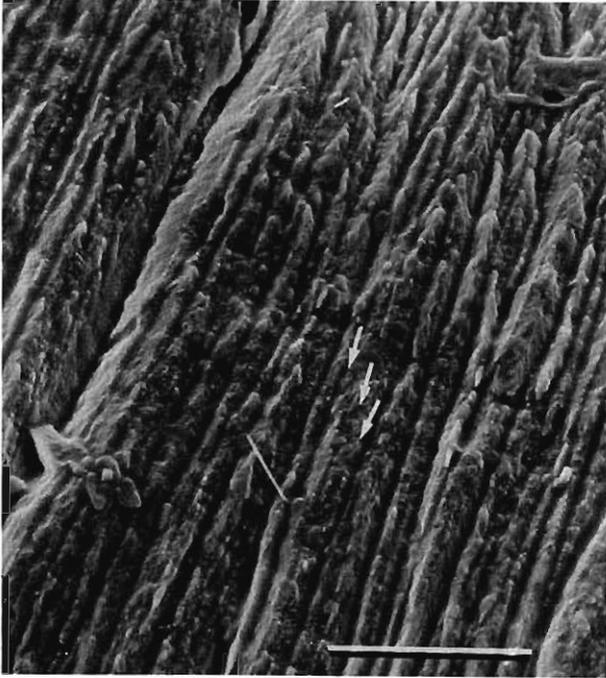
The low value of the APE index (APE=3.36%) demonstrated the consistency of the age determinations. All the otoliths were interpretable. The age-length relationship that was obtained is included in table 2. The growth parameters calculated from otolith interpretation are included in table 7.

Modal progression analysis (table 3) of the length frequency data (fig. 2) showed the presence of at least 3 age classes in the length distributions. The mean length-at-age for the first two groups is similar to the otolith results. However, the last two (or more) ages could not be separated.

The  $L_\infty$  estimate obtained through the method of Wetherall *et al.* (1987) was  $L_\infty = 32.3$  cm. An attempt was made to improve the estimate using the ELEFAN procedure. However, the response surface analysis showed a wide range of parameter combinations fitting the length distribution equally well (table 4). The transformed length-frequency data led to a plateau of equal values of  $R_n$ . This situation was not improved when the age-length increments were incorporated in a joint analysis. Thus, growth determination was not possible using these methods.

### *Lutjanus kasmira*

Otoliths of *Lutjanus kasmira*, when observed with a dissecting microscope, showed a concentric pattern of broad translucent and diffuse opaque rings. The hyaline rings were composed of thin increments (fig. 3) (0.8  $\mu\text{m}$  on average), while the opaque rings were composed of thicker increments (2.15  $\mu\text{m}$  on



**Figure 6.** — Scanning electron micrograph of the increments (arrows) laid down in the nuclear area of a *Nemipterus furcosus* otolith, scale bar 2  $\mu\text{m}$ .

**Figure 7.** — Scanning electron micrograph of the increments laid down in a hyaline annulus (between arrows) of a *Nemipterus furcosus* otolith, scale bar 2  $\mu\text{m}$ .

**Figure 8.** — Scanning electron micrograph of the rhythmic growth patterns (arrows) in a *Nemipterus furcosus* otolith, scale bar 3  $\mu\text{m}$ .

average). Rhythmic growth patterns of 7, 14 and 28 increments were frequent, supporting the assumption of a daily nature of the increments.

The number of increments laid down in each growth period was not significantly different from the number of days in one year (*t*-test). The occurrence of opaque margins in the otolith (*fig. 4*) during the year also showed the formation of a single pair of hyaline and opaque rings per year.

Once the annual periodicity of the rings was established and the consistency of the otolith interpretation tested (APE = 4.01%), the age-length relationship was

determined (*table 2*). All the otoliths were interpretable.

The modal progression analysis of the pooled length frequency data found five age classes in the length distribution (*table 3*).

The growth parameters (*table 7*) determined by means of the length-frequency (*fig. 5*) varied considerably, depending on which data were used. This was due the fish depth-related length distribution and to the presence of recruit fish in the 1979 sample. The results of the analysis of the length frequency data and of the joint analysis of the age-length data

Table 5. — Growth increments for *Nemipterus furcosus* determined: A, by means of a deterministic routine; B, from length-at-age estimated by otolith interpretation; C, from mean length-at-age estimated by modal progression analysis.

L1 (*) (cm)	t1 (*)	L2 (*) (cm)	t2 (*)	L1 (cm)	t1	L2 (cm)	t2
A							
10.60	0.71	17.20	1.71	19.90	2.71	24.50	3.71
10.60	0.71	17.20	1.71	20.20	2.71	22.40	3.71
10.60	0.71	18.60	1.71	20.20	2.71	25.20	3.71
10.60	0.71	18.60	1.71	20.30	1.71	19.20	2.71
10.60	0.71	19.50	1.71	21.00	1.71	19.00	2.71
10.60	0.71	19.50	1.71	21.20	1.71	19.00	2.71
11.70	0.71	17.20	1.71	21.20	2.71	21.50	3.71
11.70	0.71	18.50	1.71	21.20	2.71	21.60	3.71
12.00	0.71	17.20	1.71	21.20	2.71	24.50	3.71
12.00	0.71	18.50	1.71	22.40	3.71	25.10	4.71
12.00	0.71	19.50	1.71	22.80	3.71	24.00	4.71
12.40	0.71	18.50	1.71	23.70	3.71	25.80	4.71
12.40	0.71	19.50	1.71	23.70	3.71	26.10	4.71
12.80	0.71	17.20	1.71	24.00	4.71	32.70	5.71
12.80	0.71	21.20	1.71	24.50	3.71	24.60	4.71
13.50	0.71	17.20	1.71	24.50	3.71	24.60	4.71
13.50	0.71	22.50	1.71	24.60	4.71	32.70	5.71
14.00	0.71	17.20	1.71	25.00	3.71	25.20	4.71
14.00	0.71	22.50	1.71	25.10	3.71	25.20	4.71
17.20	1.71	16.30	2.71	25.10	4.71	32.70	5.71
17.60	2.71	23.70	3.71	25.20	4.71	24.50	5.71
17.60	2.71	25.10	3.71	25.20	4.71	32.70	5.71
19.00	2.71	25.00	3.71	25.80	4.71	24.50	5.71
19.50	1.71	19.90	2.71	25.80	4.71	32.70	5.71
19.50	1.71	19.90	2.71	26.10	4.71	24.50	5.71
19.50	1.71	21.20	2.71	26.10	4.71	32.70	5.71
19.50	1.71	23.00	2.71	26.50	4.71	24.50	5.71
19.50	1.71	23.00	2.71	26.50	4.71	32.70	5.71
19.90	2.71	24.50	3.71				
B							
12.70	0.90	16.38	1.20	16.38	1.20	24.33	2.20
24.33	2.20	27.91	3.20				
C							
24.25	0.70	27.16	1.89	27.16	0.70	30.01	1.89

(\*) L1=length at age t1; L2=length at age t2.

are shown in table 7. The use of the age data lowered the K value obtained, making the estimation more similar to the otolith results. However, the use of the 1987 age data to analyze the length frequency data of previous years offered poor results, probably due to the different age structure of the samples.

### *Nemipterus furcosus*

The otoliths of this species showed clear growth rings. The low APE index (APE=3.78%) confirmed the consistency of the otolith interpretation. However, only 91.25% of the otoliths could be interpreted. The age-length relationship obtained is shown in table 2.

The increments laid down in the otoliths of the species are regular and thick in the nuclear area (average 3  $\mu\text{m}$ ) (fig. 6). The increments laid down during periods of low growth rates are thinner (average 1  $\mu\text{m}$ ) (fig. 7). The growth patterns confirmed the daily periodicity of the increments (fig. 8). In the otoliths where the complete increment sequence was obtained the number of increments confirmed the age estimated by the growth rings.

The growth parameters obtained from the age-length relationship calculated by otolith interpretation (table 2) are included in table 7.

Modal progression analysis (table 3) suggested the presence of 5 age groups in the length composition (fig. 9), thus validating the otolith results.

The  $L_{\infty}$  value obtained from Wetherall *et al.* (1987) plot ( $L_{\infty}=29.9$  cm) was similar to the value obtained from the analysis of the length frequency data. The  $L_{\infty}$  estimate decreased when the age-length data (table 5) were introduced in the analysis (table 6). The best fit was obtained with the growth increments determined by MPA, but the wide range of similar  $R_n$  values difficulted the selection of one set of growth parameters.

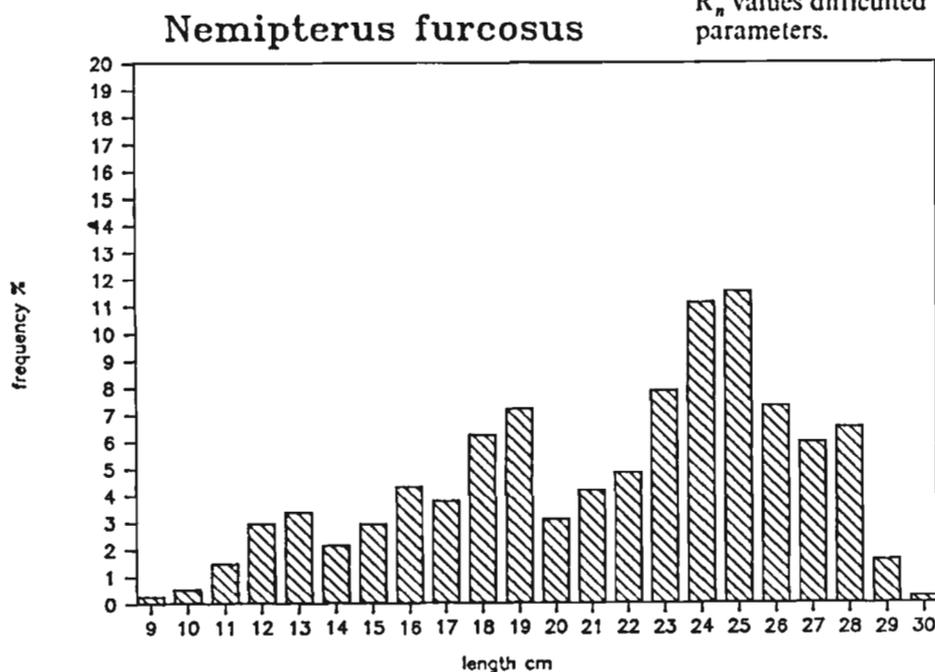


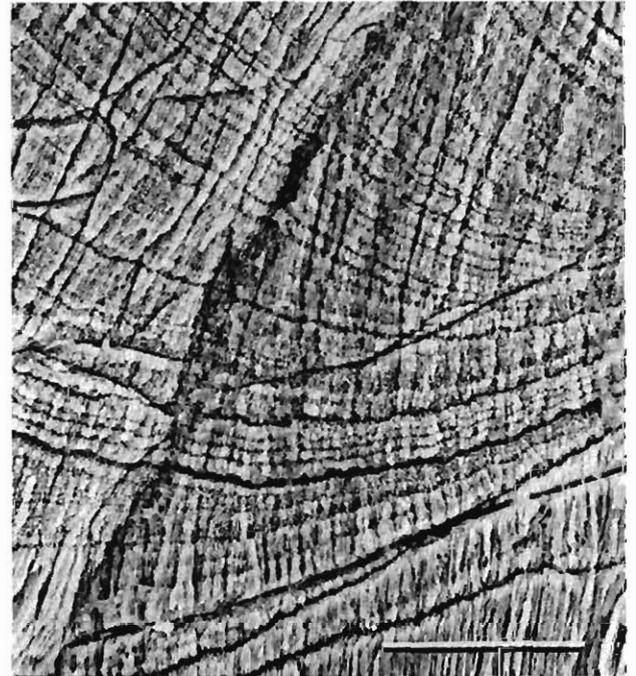
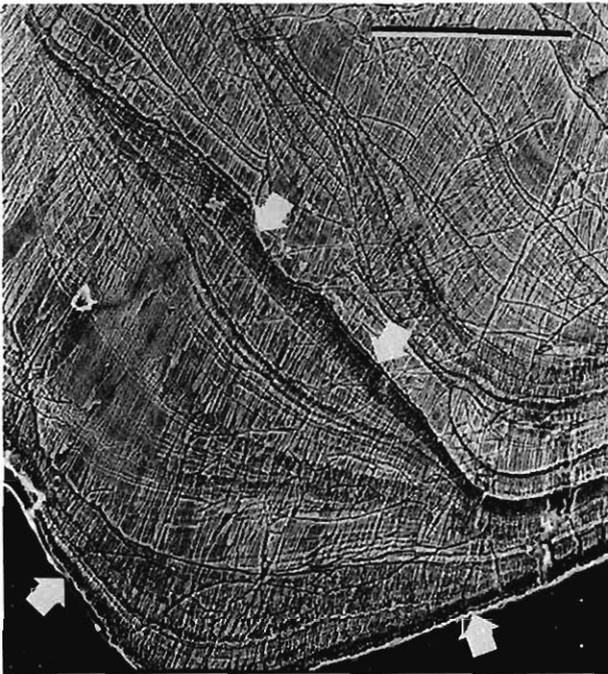
Figure 9. — *Nemipterus furcosus* length frequency data.

**Table 6.** — Response surface of  $R_n$  ( $M \times 1,000$ ) values in the *Nemipterus furcosus* length frequency data analysis with age imput. Each set of analysis was carried out respectively with the growth increment sets A and C of table 5.

A											
K ( $\text{year}^{-1}$ )	$L_{\infty}$ (cm)										
	23	23.8	24.6	25.4	26.1	26.9	27.7	28.4	29.2	30.0	30.8
0.40	116	143	160	146	119	121	147	120	112	131	—
0.44	157	160	130	101	106	110	106	137	145	111	—
0.49	174	142	107	101	127	103	106	144	121	127	—
0.53	155	107	101	138	133	102	105	147	138	132	—
0.58	116	107	138	117	152	101	103	103	195	144	—
0.62	116	139	139	140	146	102	135	178	157	192	—
0.67	104	138	167	140	127	129	121	168	184	138	—
0.71	152	167	140	140	106	118	124	217	184	138	—
0.76	151	152	140	110	106	116	154	213	126	129	—
0.80	181	152	107	110	102	129	150	137	123	107	—

C											
0.60	605	605	605	650	582	582	582	575	552	552	543
0.58	605	605	605	605	650	582	582	575	575	552	552
0.56	593	593	605	605	650	582	582	575	576	552	552
0.54	593	593	593	605	605	650	650	582	575	575	576
0.52	593	593	593	605	605	649	650	650	575	575	575
0.50	579	593	593	593	593	605	648	650	650	638	638
0.48	540	547	593	593	593	593	593	648	638	638	633
0.46	540	540	547	593	593	593	586	621	638	638	638
0.44	533	540	556	547	593	593	593	586	621	621	638
0.42	533	540	556	547	593	593	586	621	621	621	638



**Figure 10.** — Scanning electron micrograph showing the annulus in a *Scomberomorus brasiliensis* otolith. The hyaline rings (slow growing periods) (between arrows) are composed of thinner increments, scale bar 7.5  $\mu\text{m}$ .

**Figure 11.** — Increments laid down in a *Scomberomorus brasiliensis* otolith during a fast growing period, scale bar 1.76  $\mu\text{m}$ .

## Scomberomorus brasiliensis

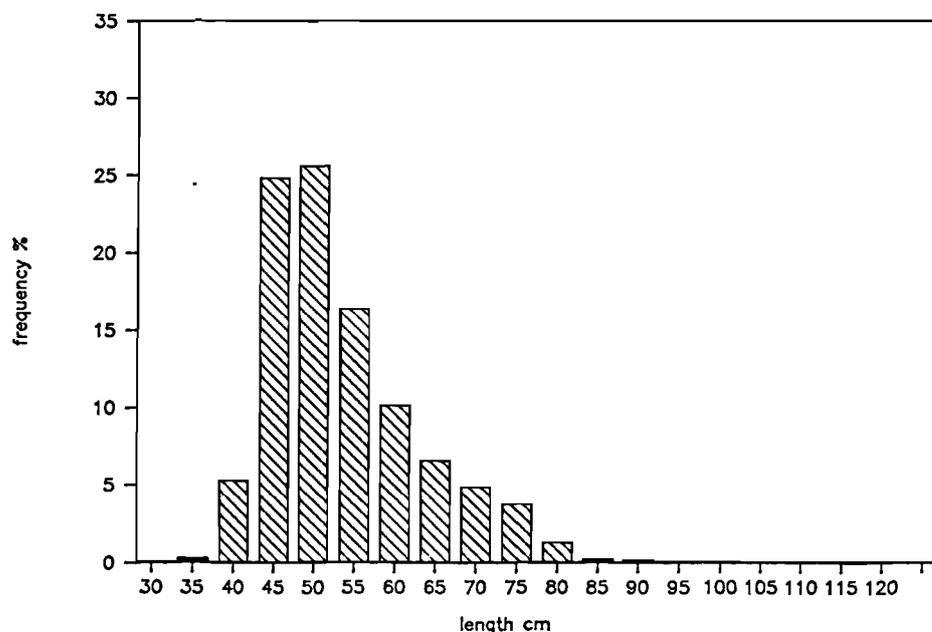


Figure 12. — *Scomberomorus brasiliensis* length frequency data.

Table 7. — Growth parameters determined for the studied species.

Species	$L_{\infty}$ (cm)	K (years <sup>-1</sup> )	$\phi$ (*)
<i>Lutjanus choerorhynchus</i>			
otoliths	32.59	0.43	2.66
ELEFAN I	31.0	0.64	2.78
ELEFAN V	32	0.40	2.61
<i>Lutjanus kasmira</i>			
otoliths	33.71	0.27	2.48
pooled length frequency			
ELEFAN I	28.11	0.37	2.46
ELEFAN V	28.89	0.34	2.45
1978/79 length frequency			
ELEFAN I	24.80	0.29	2.25
ELEFAN V	23.56	0.63	2.54
1987 length frequency			
ELEFAN I	33.0	0.67	2.86
ELEFAN V	29.87	0.41	2.56
<i>Nemipterus furcosus</i>			
otoliths	26.7	0.45	2.54
ELEFAN I (**)	29.9	0.42	2.57
ELEFAN V			
A	28.44	0.71	2.79
B	26.95	0.54	2.59
C	26.65	0.55	2.59
<i>Scomberomorus brasiliensis</i>			
otoliths	100.48	0.11	3.05
ELEFAN I	108.50	0.25	3.48
ELEFAN V	105.20	0.18	3.29

(\*)  $\phi = 2 \log_{10} L_{\infty} + \log_{10} K$ .

(\*\*) Analysis with the growth increments in table 5.

### *Scomberomorus brasiliensis*

The otoliths of this species showed a clear growth pattern. Although the presence of nuclear rings made difficult the selection of the first annual ring, the low APE index (6.23%) showed consistency in the age interpretation.

The annuli appeared clearly in the SEM observations (fig. 10) so that, it was possible to count the number of increments in each one. The hyaline annuli were composed of thin increments and numerous growth discontinuities, while the opaque rings (fig. 11) were composed of thick well-defined increments. The mean number of increments in the hyaline ring was close to the time in days reported for their formation (Ximenes, 1981), and the number in each growth cycle was not significantly different from the mean number of days in one year (*t*-test). The age length relationship obtained is shown in table 2.

The modal progression analysis (table 3) applied to the length frequency (fig. 12) data failed to detect all the age classes present in the length distribution. The obtained growth parameters are shown in table 7.

## DISCUSSION

In all the studied species, annual rings were found in the otoliths and it was possible to determine their temporal significance by means of some validation methods: temporal evolution of the marginal otolith structures, number of daily increments laid down in

the rings, and modal length progression analysis. The amount of subjectivity involved in selecting the true annuli was low, as the small value of the APE index showed.

The length-based methods require representative length frequency data, covering the complete length range of the species. When only a limited length range is used, the growth estimations will be biased; this occurred here in conjunction with growth determination in *Lutjanus kasmira*. Thus, the suitability of the length frequency analysis depends on the structure of the available length frequency data. The progression of the modes gives the absolute rate of growth (centimetre per year) only over the part of the range of sizes within which clear modes can be distinguished. The length overlap in older age classes, caused by the deceleration of growth and by the increasing variability within age classes, often made separation of size/age groups of older fish difficult. In such cases, the fast-growing younger age classes might define clear modes at the left of the histograms, which can support the age determination, but in older fishes the method frequently could not be used to separate the age classes known to occur in the length composition.

In some cases clear modes are absent in the length frequency, as was found in *L. choerorynchus*. Conse-

quently, the selection of a combination of growth parameters fitting the length distribution is impossible.

The incorporation of age-at-length data into a length frequency analysis generally improves the identification of best growth parameters. The degree of usefulness of the length-at-age data in describing the growth curve may depend on the variability of length at any age and the consistency of the length composition and the length-at-age data. When the length frequency data and the ages used do not correspond to the same period and area, the estimated growth parameters are inconsistent, as shown here in *Lutjanus kasmira* when the age data from 1987 was employed in the joint analysis with length data of previous years.

The method of conversion of age-at-length data into growth increments and the weighting factors are essential in such joint estimation of growth parameters. The best fit might depend on the length distribution and the age data structure. Generally, the goodness of fit indexes showed a poor relation between the growth increments and the length frequency data. Even if the incorporation of the growth increments improved the analysis, the problems of the joint analysis of age and length data deserve further study.

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