Age and growth of yellowfin tuna (*Thunnus albacares*) in the western equatorial Atlantic, using dorsal fin spines

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Abstract

Lengths of 6758 yellowfin tuna, *Thunnus albacares* (*T. albacares*), were measured (42–191 cm FL) from 1992 to 2000 off northeastern Brazil ($0–12°S/30–41°W$). Age and growth were estimated from seasonally formed bands on the first dorsal spines of 380 specimens (45–191 cm FL) obtained from 1998 to 2000. Von Bertalanffy growth parameters were estimated from the observed length-at-age, from back-calculated lengths, and from a combination of back-calculated lengths and observed lengths. This last method was chosen for describing the species' growth; parameters were $L_\infty = 230.7$ cm, $K = 0.267$, and $t_0 = -0.081$ year. Marginal increment ratio and spine edge characterization suggested the annual deposition of two bands. Mean MIR values increase from November to April and from June to September, whereas translucent edges predominate in May and October, when new band formation is supposed to start. Overall, spines showed one to six complete bands with a well-developed absorbed area. The estimated reading error (IAPE) between two examiners was 9% for the overall sample. Size at maturity corresponded to an age of 3.4 years and the oldest individual in the sample was 6.5 years (191 cm FL). Fish lengths (35,469), taken from the International Commission for the Conservation of Atlantic Tuna–ICCAT database and measured in the area $20°S–05°N$ from 1975 to 1994, were analyzed leading to results similar to those produced from reading spines. Comparisons with von Bertalanffy parameters from the literature indicated statistical differences among all growth curves, with exception of that presented for the northern Atlantic. Average fish lengths decreased from 1975 to 1994, and only 25% of individuals in landings were larger than the size at maturity.

1. Introduction

The yellowfin tuna, *Thunnus albacares* (*T. albacares*), have been studied extensively due to their economic importance and abundance in the fisheries of the southern Atlantic Ocean. Most of the available information comes from the eastern-southern

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Atlantic and pertains to age and growth (Le Guen and Sakagawa, 1973; Fonteneau, 1980; Myabe, 1983; Bard, 1984; Draganick and Pelczarski, 1984; Manooch and Hinkley, 1991), reproduction (Albaret, 1977; Capisano and Fonteneau, 1991; Vieira, 1991), distribution and migration (Stretta et al., 1990; Fonteneau, 1991), and stock structure (Bard and Scott, 1991).

Likewise, in the western southern Atlantic, where the yellowfin tuna have been exploited since the 1950s, studies have focused on reproduction (Zavala-Camin, 1978), larvae distribution (Matsuura and Sato, 1981), feeding (Zavala-Camin, 1981) and abundance indexes (Travassos, 1999). Fish lengths and catch effort data are reported annually by member countries to the International Commission for Conservation of Atlantic Tuna (ICCAT), where periodic stock assessments are carried out.

Based on data collected from longline, no reproductive activity has been observed in the area from 0–10°S/30–40°W, and the catch is primarily composed of sub-adults or resting females (Lessa et al., 1993). This concurs with the information from southern Brazil (27–33°S) where no reproductive activity has been detected (Zavala-Camin, 1978). Similarly, at the São Pedro–São Paulo Archipelago (0° 59′N/30° 0′W), no spawning activity has been observed between January and April, based on specimens captured with handlines. In a survey of pelagic fishes, conducted from 1992–1997, yellowfin tuna represented 40% of the catch in the equatorial Brazilian EEZ (Travassos, 1999), which is regarded as a feeding ground where migratory yellowfin, on their way to spawning sites, prey on flying-fish, *Cypselurus cyanopterus* (Lessa et al., 1999). Some juveniles (∼45 cm FL), however, have been caught around the São Pedro–São Paulo Archipelago by artisanal fisheries.

Age and growth parameters for yellowfin tuna from the eastern-southern Atlantic have been estimated by analyzing length frequencies (Le Guen and Sakagawa, 1973; Fonteneau, 1980), tag recoveries (Myabe, 1983; Bard, 1984) and calcified structures (Yang et al., 1969; Draganick and Pelczarski, 1984; Manooch and Hinkley, 1991). Similarly, in the western Atlantic, assessments of age and growth were conducted using length–frequency analysis from Venezuela (Gaertner and Pagavino, 1991), and daily microstructures in otoliths in the northern Atlantic (Driggers et al., 1999).

According to Bard and Scott (1991), this species constitutes a single stock in the Atlantic, with adults migrating from east to west. This assumption, based on tag-recoveries, is widely accepted as the most likely. Mitochondrial DNA research (Scoles and Graves, 1993) supports the global stock hypothesis, and differences in life histories (e.g. growth rates) among yellowfin tuna between oceans may be attributed to varying environmental factors (Driggers et al., 1999).

This study was conducted as part of the Renewable Resources Assessment Programme (REVIZEE) aimed at providing information on the Brazilian Exclusive Economic Zone (EEZ). Its purpose is to supply information on age, growth and stock structure for *T. albacares* caught in the equatorial western-southern Atlantic, using dorsal spines and length–frequency analysis. This information is needed to construct age-based models that can be used to manage the species.

2. Material and methods

A sample was collected in landings of commercial longliners, research vessels, and from artisanal fisheries between 1992 and 2000. Commercial and research vessels were equipped with Japanese-style multifilament longlines (Suzuki et al., 1977), and operated in the area between 0–2°S/30–41°W and around the São Pedro–São Paulo Archipelago (0°59′N/30°0′W). The artisanal fleet used hand lines near the shelf break off northeastern Brazil (Fig. 1). While sampling artisanal landings, livers removed from most of the young individuals (<60 cm FL) were examined to distinguish between *T. albacares* and *Thunnus obesus* (*T. obesus*), according to Collette and Nauen (1983) criteria based on striations on the liver surface.

The spiniform rays of the first dorsal fin on 380 individuals, representative of full range of fish size were collected from 1998 to 2000 and were excised, frozen, and stored in either 4% formaldehyde and alcohol for up to 6 months. After being air-dried for 24–48 h, spine lengths were measured (cm), and cross-sections were taken between 5 and 30% of the spine length above the condyle. These spine portions were embedded in polyester resin and sectioned using a low-speed saw. The sections closest to the condyle, ranging from 0.75
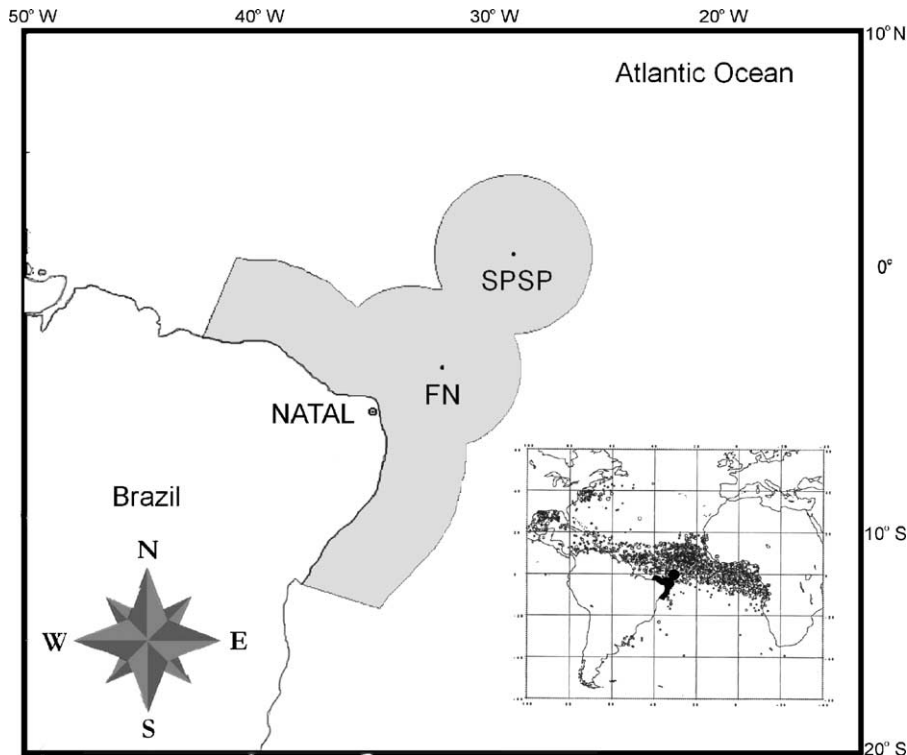
Fig. 1. Location of fishing ground for yellowfin tuna, *Thunnus albacares*, off northeastern Brazil. (Black area: Brazilian Exclusive Economic Zones-EEZ, SPSP: São Pedro and São Paulo Archipelago, FN: Fernando de Noronha Archipelago, insert: distribution area for the species in the Atlantic Ocean).

to 1 mm in thickness, were found to provide the best contrast of growth zones. These were mounted on glass slides with a synthetic resin and viewed with transmitted light using a binocular microscope equipped with an ocular micrometer. Measurements were made under 10× magnification (1 micrometer unit = 1.0 mm).

The spine diameter was defined as the horizontal distance to the outside margin above the posterior notch, where the least band curvature occurred. To avoid errors due to the loss of material from the vascularized core area, measurements were taken from the outside edge of each translucent zone to the opposite edge of the cross-section (Antoine et al., 1983) (Fig. 2). Proportionality between the structure and individual fish size was verified through relationships between the spine diameter (micrometer unit, m.u.) and fork length (cm). Linear and curvilinear equations were tested using a regression analysis.

Opaque zones, assumed to represent fast growth, were separated by translucent zones, which were often present in clusters or groups of two or more and were interpreted as representing periodic events indicative of slow growth, as with other tuna species (Cayré and Diouf, 1983; Compéan-Jimenez and Bard, 1983; Megalofonou, 2000). A single translucent zone (or tight cluster of zones) and the associated opaque zone together were assumed to represent one growth band (Megalofonou, 2000). According to the last named author, zones were considered doubled if the distance between them was less than the distance to the preceding and following translucent zone. The total number of translucent zones, which were counted when they were continuous around the perimeter of the section, was assigned in each spine. Sections were read twice at different times by two readers and counts were made without knowledge of the individual size and previous count. Whenever counts differed between
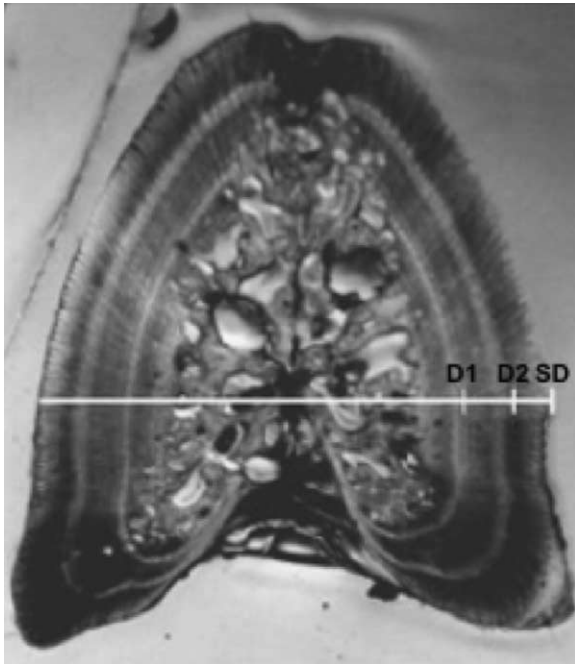
Fig. 2. Cross-section of first dorsal spine of yellowfin tuna, *Thunnus albacares* (102.0 cm) showing the measurements taken (*D*1: diameter to the first band; *D*2: diameter to the second band; SD: spine diameter).

readers, a third reading was done. In cases where disagreement persisted, the section was discarded.

The index of percentage error (IAPE) (Beamish and Fournier, 1981) was calculated to compare reproducibility of age determination between two readings:

$$\text{IAPE} = \frac{100}{N} \sum_{j=1}^{N} \left[\frac{1}{R} \sum_{i=1}^{R} \frac{|X_{ij} - X_j|}{X_j} \right],$$

where N is the number of fish aged, R is the number of readings, X_{ij} is the ith age determination of the jth fish, and X_j is the mean age calculated for the jth fish.

Marginal increment ratio (MIR) analysis was performed using 257 specimens collected from 1999 to 2000, to determine the time of band formation using the following equation (Natanson et al., 1995):

$$\text{MIR} = \frac{(\text{SD} - D_n)}{(D_n - D_{n-1})}$$

where SD is the spine diameter, D_n is the diameter to the last complete band and D_{n-1} is the diameter to

the penultimate complete band. The mean MIR (S.D.) were plotted monthly in order to locate periodic trends in band formation. An analysis of variance (ANOVA) was used to detect significant differences throughout the course of the year and Tukey tests were performed to demonstrate which months differed from the others.

The edge-characterization analysis was used to determine the time period of growth-band formation (Newman and Dunk, 2003). Under transmitted light, a narrow light zone (MIR = 0), a narrow light zone (0.1 < MIR < 0.4) and a broad dark zone (MIR > 0.4) were observed throughout the year.

To estimate fork lengths at previous ages, back-calculation was conducted using the Fraser–Lee equation (Natanson et al., 1995):

$$L_t = \left(\frac{D_n}{\text{SD}} \right) \times (L_c - a) + a$$

where L_t = the fork length at the deposition of nth ring, a = correction factor corresponding to the intercept, D_n = distance between the ring and the spine edge, SD = the spine diameter, and L_c = fork length at capture.

Length at previous ages was estimated using back-calculation for all bands visible in the spines. To circumvent the problem of a central vascularized area that increases with size, the number of lost bands was estimated from obervations of their position and number in spines of young specimens as has been done for *Euthynnus alletteratus* (*E. alletteratus*), *T. thynnus*, and *T. obesus* (Cayré and Diouf, 1983; Compéan-Jimenez and Bard, 1983; Sun et al., 2001). The final location of specimens in a given age class was done correcting for lost bands.

The FISHPARM program (Prager et al., 1987) was used, allowing parameters to be estimated without transforming the data into linear form. The Von Bertalanffy Growth Function (VBGF) (von Bertalanffy, 1938) was fitted to data:

$$L_t = L_\infty \left[1 - e^{-k(t-t_0)} \right]$$

where L_t = the predicted length at age t, L_∞ = the mean asymptotic fork length, K = the growth constant (year^{-1}), and t_0 = the theoretical age at which the fish would have been zero length. Analyses of variances (ANOVA) were carried out using observed, back-calculated, and the combination of observed and

back-calculated lengths to detect the VBGF that best fitted length-at-age data.

Using an age-length key based on 380 specimens, for which spines were read, the age composition of the sample was evaluated (Bartoo and Parker, 1983).

Length–frequency data of 35,469 specimens from the ICCAT database, collected from 1975 to 1994 in the area between $05°$N–$20°$S, were divided into 4 cm intervals. Lengths ranging from 60 to 190 cm FL were analyzed monthly in four samples, each with five years. Length–frequency analyses (LFA) were conducted using the FAO-ICLARM Stock Assessment Tools (FISAT) program (Gayanilo et al., 1994), in which the automatic search option of the ELEFAN routine was employed. The initial value of L_{∞} was 170 cm FL that is lower than the maximal observed length in the sample (step size $\pm$ 0.05); the lowest K value used was 0.2 (step size $\pm$ 0.005). The best combinations of parameters were those providing the highest R_n goodness-of-fit index. Five-year length–frequency distributions were compared using ANOVA.

Following procedures described by Stéquert et al. (1996), the growth pattern obtained in the present study was graphically compared to several others available in literature, generated through length–frequency and hard-structure analyses (Yabuta et al., 1960; Yang et al., 1969; Manooch and Hinkley, 1991; Stéquert et al., 1996; Driggers et al., 1999). Also, lengths-at-age were compared using bivariate Hotellings' T^2 test (Cerrato, 1990).

3. Results

Of a total sample comprising 6758 individuals (42 to 191 cm FL) (Fig. 3), spine sections were taken from 380 individuals ranging from 45 to 191 cm FL. Spines, collected between 1998 and 2000, presented a central vascularized area, which increased in specimens larger than 70 cm FL. Overall, spines showed one to six complete bands in each section with a well-developed absorbed area. However, the precision estimation provided an average IAPE of 9% for the overall sample, with values ranging from 0 to 14% for bands 1–6.

Relationships between spine diameter and fork length were estimated using linear and curvilinear models. Both led to similar determination coefficients (r^2 = 0.90; n = 380; P < 0.05). Once tested by ANOVA, F values were of the same magnitude and observed dispersion of residuals indicated that either of these models is appropriate for describing the relationship, as no tendency in distribution was detected (Table 1, Fig. 4). For the sake of simplicity, the linear model was chosen for back-calculations (Fig. 5).

Marginal increment ratios reach minimum values twice a year, in May and October (Fig. 6). ANOVA was carried out after testing for homogeneity. It indicated that there are significant differences throughout the year (P < 0.05), suggesting that two translucent zones are deposited in spines annually. The Tukey test indicated differences between February and October, March and October.
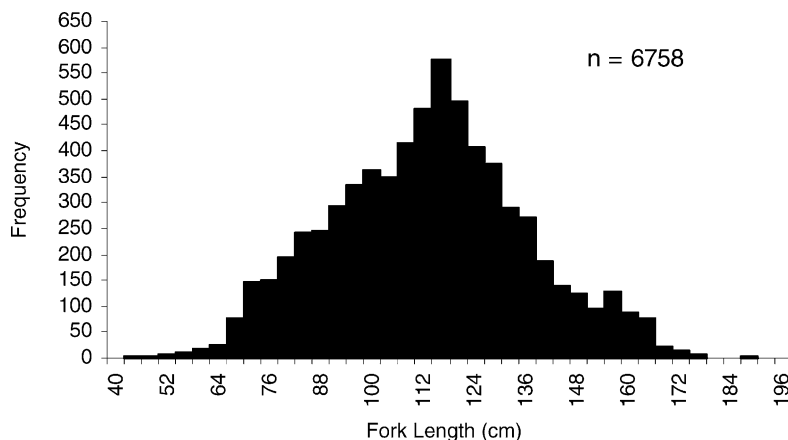

Fig. 3. Length–frequency distribution of yellowfin tuna, *Thunnus albacares*, caught by research vessels and by the brazilian commercial fleet off northeastern Brazil, from 1992 to 2000.

Table 1
Relationship between spine diameter and fork length at capture for yellowfin tuna, *Thunnus albacares*. F is calculated from the ANOVA for testing the model, r^2 is the determination coefficient

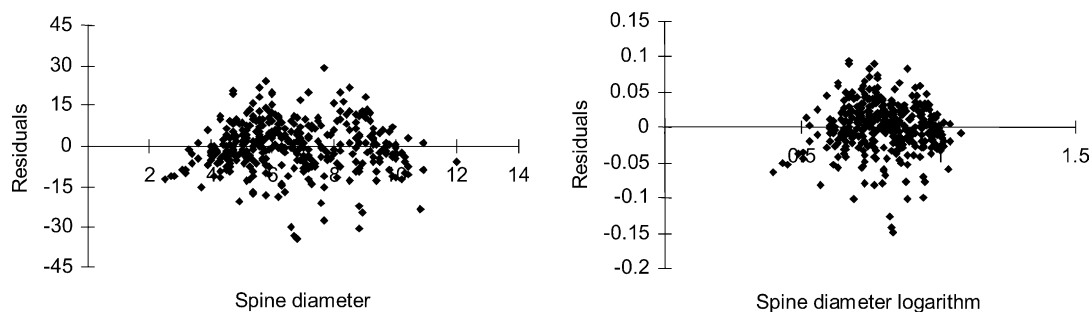| Model	Equation	Intercept	Slope	r^2	F
Linear	$y = a + bx$	20.94	14.65	0.901	3460.47
Curvilinear	$\ln y = \ln a + b \ln x$	3.18	0.84	0.903	3347.52

Fig. 4. Plots of residuals from the ANOVA performed for relationships between the spine diameter and fork length for yellowfin tuna, *Thunnus albacares*, off northeastern Brazil.

Furthermore, monthly categorization of spine edge indicated that the highest frequency of translucent zones (narrow light zones) occurred in May and October (Fig. 7). These months were also those where the lowest number of opaque zones (broad dark zones) appeared in the sample, suggesting growth band deposition twice a year.

Observed and back-calculated lengths-at-age are shown in Table 2. Growth rates from back-calculated lengths-at-age were 48.2 cm year^{-1} in the first year and 38.7 cm year^{-1} through maturity, gradually decreasing to 9.9 cm year^{-1}, when individuals are 6 years old.
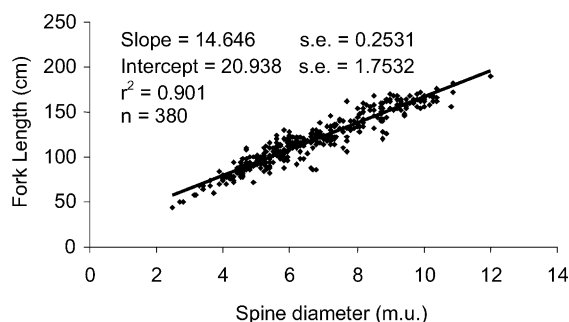

Fig. 5. Linear relationship between the spine diameter and fork length for yellowfin tuna, *Thunnus albacares*, off northeastern Brazil.

VBGF parameters, estimated using back-calculated mean lengths, observed length-at-age and a combination of both are shown in Table 3. VBGF obtained from back-calculated lengths and in combination with observed length for 0.5-year-old specimens (not available in the observed length sample) yielded close parameters and F values of the same magnitude (Table 3, Fig. 8). The most varying results were those derived from observed lengths-at-age according to the F test.

The maturity size of 140 cm FL (Fontana and Fonteneau, 1978; Hazin, 1993) was reached at 3.4 years in both sexes. The oldest individual used for the back-calculated growth curve and for the curve based on observed length-at-age was 6.5 years old (191 cm FL).

The age composition for the overall sample (6758 individuals), based on the age/length key, indicated that 25% were adults corresponding to sizes greater than 140 cm FL (>3.4 years) (Fig. 9).

The analysis of the ICCAT sample, composed of 35,469 fishlengths (60–190 cm FL) collected from 1975 to 1994 (05°N–20°S), compared 5-year periods, and indicated that the mean and maximum sizes decreased gradually as exploitation developed (Table 4). The ANOVA test indicates that these changes were statistically significant ($P < 0.05$).
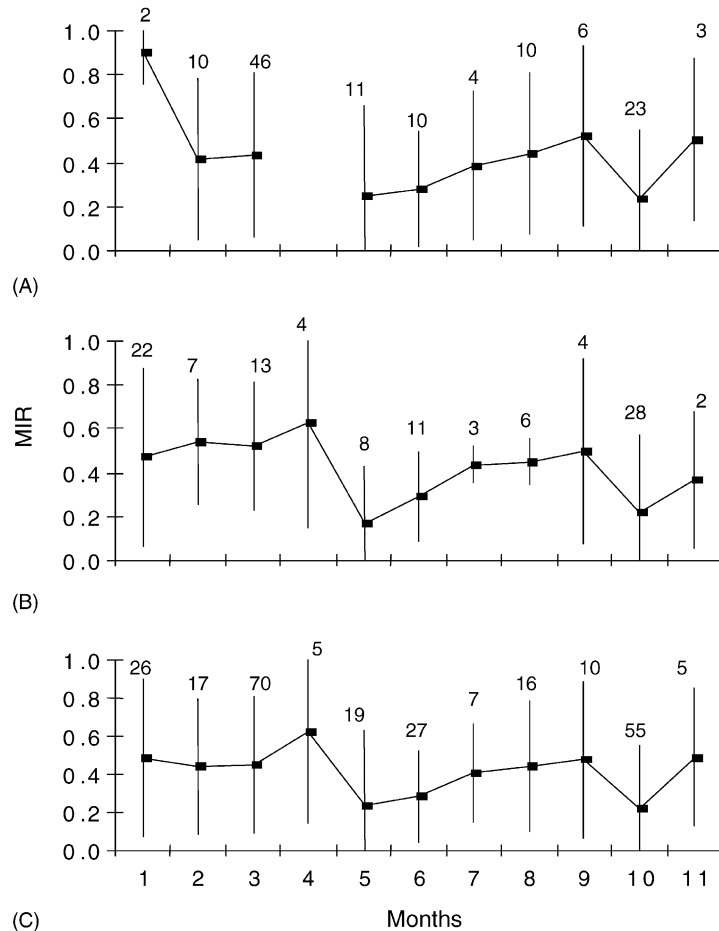
Fig. 6. Mean marginal increment ratios (MIR ± S.D.) by month for yellowfin tuna, *Thunnus albacares*, from northeastern Brazil. (A) age groups 1 and 2, (B) age groups 3 and 4, and (C) all age groups combined.
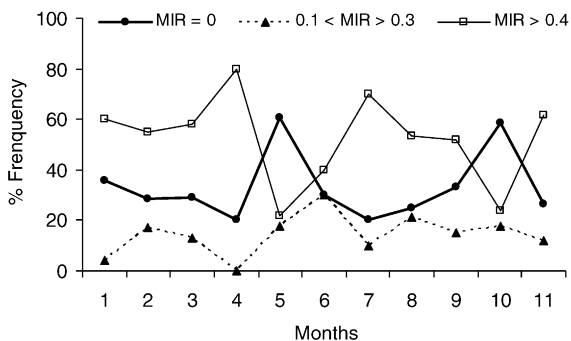

Fig. 7. Categorization of edges by month for yellowfin tuna, *Thunnus albacares*, from northeastern Brazil. Lines correspond to narrow ligth zone (MIR = 0), narrow dark zone (0.1 < MIR < 0.4) and broad dark zone (MIR > 0.4).

Parameters of the VBGF were also obtained on the basis of length–frequency analysis. Samples were examined monthly for each 5-year period (Table 3). Overall, the ELEFAN routine generated parameters similar to those obtained using hard structures (Fig. 10, Table 3). The assumption of two different cohorts in each sample allowed most peaks of reestructured data to be included in growth curves. One of these cohorts is presumed to hatch in the first half of the year and another in the second half.

Length-at-age estimated using VBGF by different authors was compared, graphically suggesting that growth estimated in the present study does not differ greatly from that estimated by Yang et al. (1969), Stéquert et al. (1996) and Driggers et al. (1999)

Table 2

Back-calculated (*a*) and observed (*b*) length at age *t* (mean, S.D.) for yellowfin tuna, *Thunnus albacares*, collected off northeastern Brazil

(a) Back-calculated

T	N	0.5	1	1.5	2	2.5	3	3.5	4	4.5	5	5.5	6	6.5
		3	129	230	241	148	77	90	75	41	5	3	2	1
1	10	42.9	47.0											
1.5	28		49.1	68.6										
2	115		48.6	73.4	92.5									
2.5	101			74.2	95.5	115.6								
3	29				96.9	118	131.8							
3.5	19				119	134.3	141.5							
4	34					134.8	143	151.1						
4.5	37						138	149.4	161					
5	2			Lost rings				156	164.8	172				
5.5	1						142	158.2	166	171	174			
6	1						142.01	157.1	166.5	171	179	181.1		
6.5	1									173	182.5	182.2	191	
Mean		42.9	48.2	72.1	95	117.5	133.7	141.3	154.4	164.6	171.8	175.3	181.7	191
S.D.		0	1.1	3.0	2.7	1.7	1.6	1.9	3.9	2.5	1.0	4.3	0.8	0
(b) Observed														
Means		–	48.4	72.4	95.1	118.7	133.9	143.7	155.6	164.7	172	176	181	191
S.D.		–	3.0	7	7.9	5.3	2.7	3.1	3.3	3.0	1.4	0	0	0

Table 3

Von Bertalanffy parameters derived from (A) back-calculated length-at-age; (B) observed length-at-age; (C) observed length-at-age combined with back-calculated length for age 0.5; and (D) by length–frequency (ELEFAN) using the FISAT package for analyzing the ICCAT data (05°N–20°S) on yellowfin tuna, *Thunnus albacares*. *F* is calculated from the ANOVA for testing the adjustment

Method	Period	Cohort	L_∞	S.E.	K	S.E.	T_0	S.E	F
A			233.2	11.578	0.258	0.043	−0.098	0.127	348.52
B			209.4	3.897	0.368	0.021	0.306	0.166	273.25
C			230.8	15.090	0.267	0.041	−0.081	0.126	342.88
D	75–79	1	235.0		0.300				
		2	231.0		0.270				
	80–84	1	233.0		0.275				
		2	237.0		0.279				
	85–89	1	234.0		0.295				
		2	235.0		0.280				
	90–94	1	236.0		0.290				
		2	229.0		0.285				

Table 4

Mean size comparisons for different exploitation periods derived from the analysis of the ICCAT database on yellowfin tuna, *Thunnus albacares*. *F* is calculated from the ANOVA and S.D. is the standard deviation of means

Period	*n*	Mean	S.D.	*F*
75–79	13985	136.1	18.4	185.72
80–84	9846	132.2	15.0	
85–89	5987	132.6	15.7	
90–94	4651	125.8	20.6	

(Fig. 11). However, when statistically compared, significant differences were found among all of them ($P <$ 0.05), with exception of that by Driggers et al. (1999).

4. Discussion

According to Scoles and Graves (1993), there is a single global stock of yellowfin tuna, since no genetic difference has been found between oceans. This im-
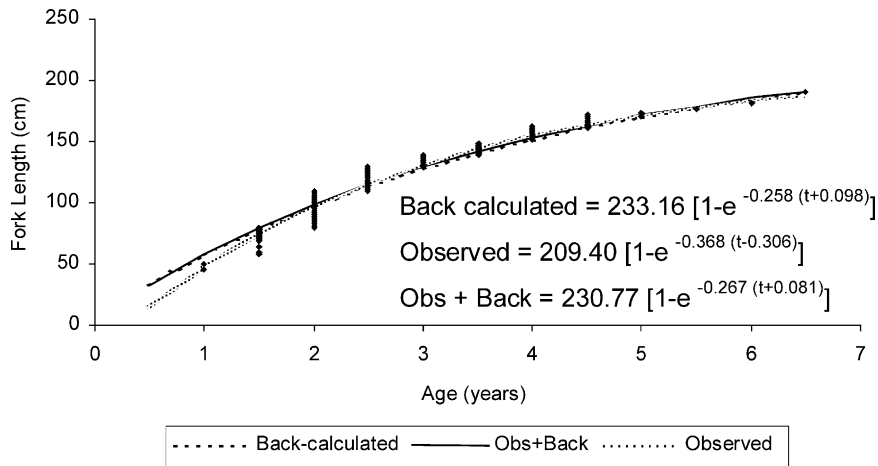
Fig. 8. Von Bertalanffy growth curves generated from (a) mean back-calculated lengths; (b) observed length-at-age and (c) observed length-at-age combined with the back-calculated value for age 0.5 for both sexes of the yellowfin tuna, *Thunnus albacares*. Black dots are individual length-at-age.
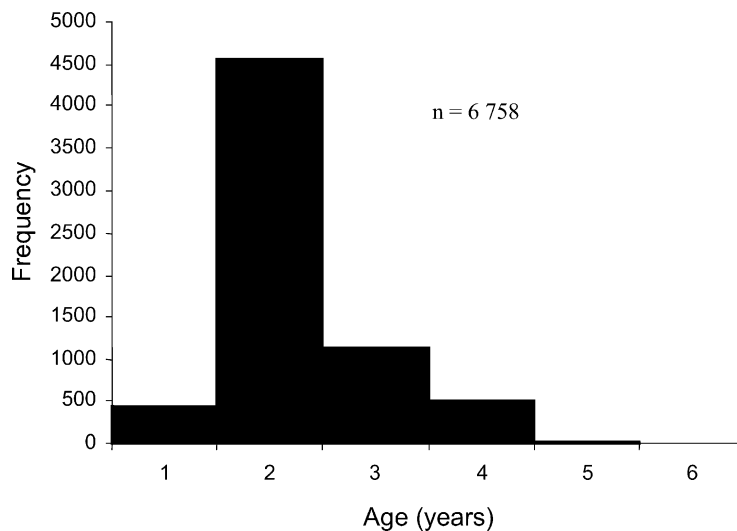

Fig. 9. Age composition of the overall sample of the yellowfin tuna, *Thunnus albacares*, collected off northeastern Brazil (1992–2000).

plies that it is reasonable to expect similar growth rates in different areas, as stated by Stéquert et al. (1996). Accordingly, after graphically comparing several curves generated for different oceans, the latter authors concluded that there was an overall similarity, despite differences in parameters amongst all VBGF.

Graphical comparisons of the growth pattern in the present study with those derived by different authors led to similarities with that of the Indian Ocean (Stéquert et al., 1996) and the northern Atlantic Ocean (Driggers et al., 1999), both based on otolith microstructure, despite distinct VBGF parameters (Fig. 11). In contrast, other growth curves generated for the Atlantic using hard structures supplied the most varying results (Manooch and Hinkley, 1991), suggesting different growth rates in
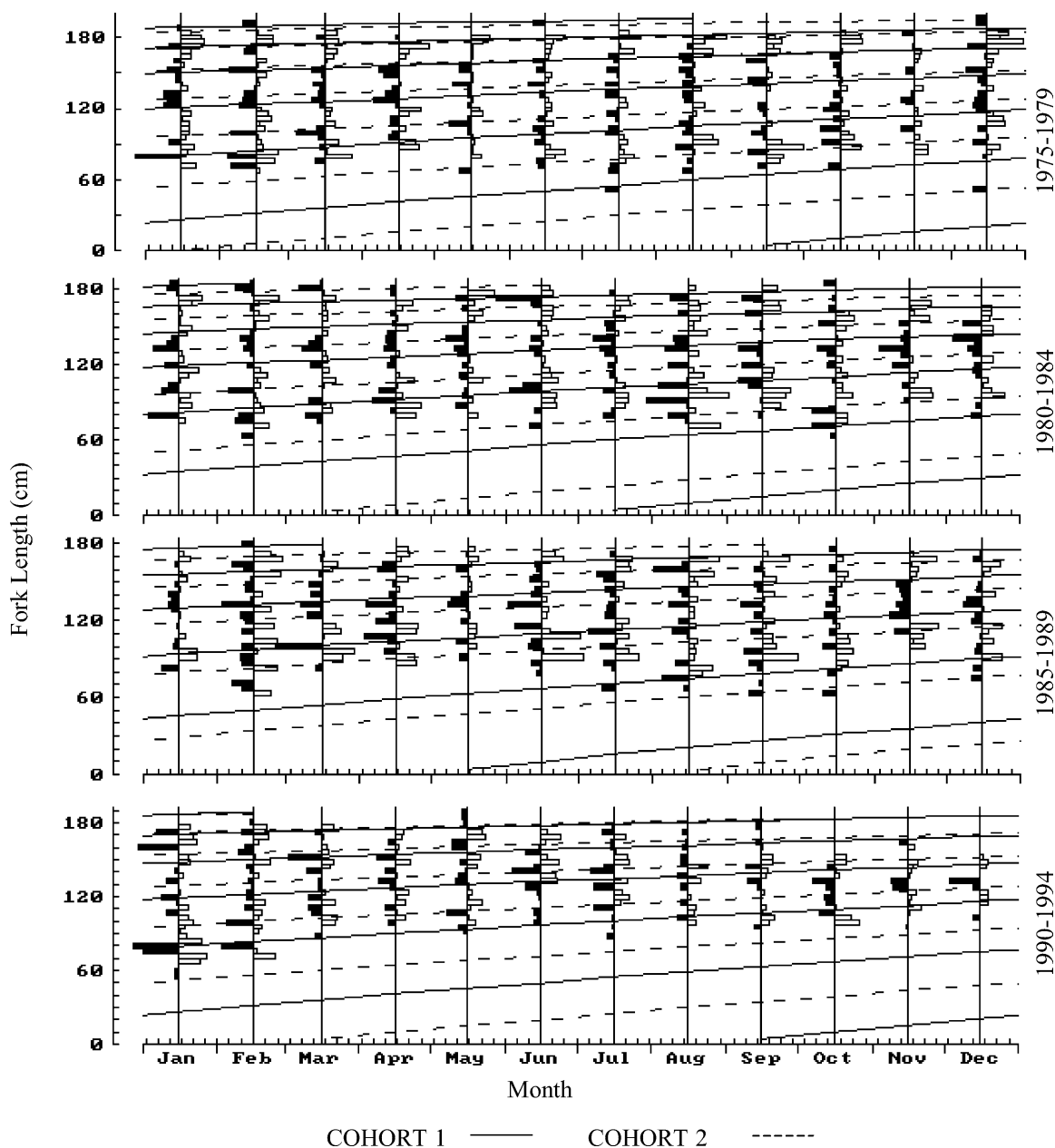
Fig. 10. Restructured length–frequency data for yellowfin tuna, *Thunnus albacares*, from the ICCAT data collected between 05°N to 20°S by commercial longliners (1975–1994) with superimposed growth curve estimated by the ELEFAN routine. Lines indicate cohorts resulting from different recruitments.

different areas. The small size of samples used by the latter authors and the different hard structures employed perhaps explain the dissimilarities found. However, the growth pattern in the present study, comparable to that generated from a microstructure analysis,

corroborates that the dorsal spine analysis is a robust and less time-consuming method, providing reliable results. In defiance of graphical similarities, when statistically compared, significant differences were found among all of them, with exception for
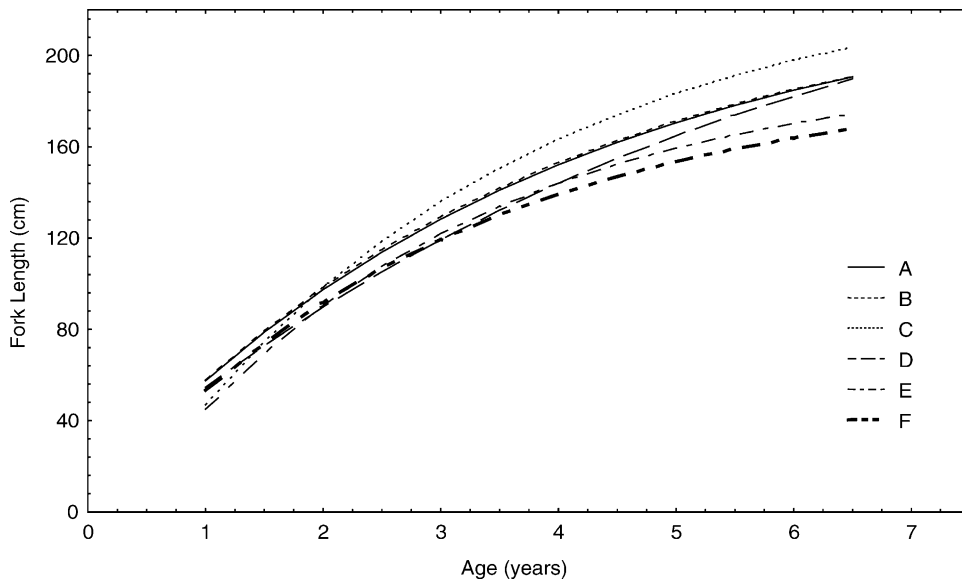
Fig. 11. Comparisons of growth curves established for yellowfin tuna, *Thunnus albacares*, by several authors. (A) Back-calculated; (B) observed + back-calculated; (C) Driggers et al, 1999; (D) Stéquert et al, 1996; (E) Yang et al, 1969; (F) Yabuta et al, 1960.

that by Driggers et al. (1999), derived for the northern Atlantic.

Considering results from the published literature, VBGF parameters estimated by different methods and even by the same method, showed discrepancies for both L_∞ and K values. For example, growth curves based on tagging-recoveries in the Atlantic provided L_∞ and K values of 132.54 cm/0.47 and 142.63 cm/0.304, respectively (Bard et al., 1991). With regard to the L_∞, these sets of parameters are unrealistic, since they were estimated for local fisheries (Gulf of Guinea or Venezuela) where: (1) only juveniles were represented; (2) lengths did not approach maximum values known to be attained by the species (208 cm FL, Collette and Nauen, 1983) and (3) lengths were lower than the maximum recorded in local catches by different gears. Similarly, K values were all extremely dissimilar and, according to criteria set forth by Musick et al. (2000), they sometimes indicate a rather slow growth ($K = 0.035$, Le Guen and Sakagawa, 1973), or contrarily, a rather fast growth ($K = 0.884$, Gaertner and Pagavino, 1991) for the same area. It is important to understand the consequences of assigning unreliable growth parameters to a fully exploited stock, as predictions of fish populations from models rely heavily on input data, including age and growth. According to

Potts and Manooch (2002), if samples used in aging studies are not representative of the entire population, model predictions can lead to faulty management decisions.

Length–frequency analysis (LFA) used in the present study as a verification method, is frequently criticized for (1) the overlap of length modes leading to age underestimation; (2) schools based on size rather than on age; (3) spawning not occurring during a discrete period of the year; (4) cohorts developing under different environmental conditions with different growth rates; (5) size–frequency deficiencies where year classes may be absent or underrepresented (Everhart and Youngs, 1992; Driggers et al., 1999) and (6) gear selectivity and seasonal sampling (Fonteneau, 1980). Despite these criticisms, it is proper to assess age and growth using length frequencies available at ICCAT made up of data gathered over time, as in the present account, assuming that some of the potential biases are present. Results were found coherent and compatible with those generated from hard structures.

Back-calculated hatching dates indicated that the yellowfin tuna spawns year round (Driggers et al., 1999) with a peak in September–March. Also, in the Gulf of Guinea, considered to be the main spawning site in the southern eastern Atlantic, spawning occurs

within this period, from December to March (Albaret, 1977; Capisano and Fonteneau, 1991). Juveniles stay in the Gulf until reaching 60–80 cm and then migrate westward where they grow to maturity, returning to the Gulf of Guinea for spawning. At Cape Verde, a secondary spawning ground, catches obtained from June to October are composed of juveniles around 50 cm (Vieira, 1991) or 1-year-old according to our estimations. It can therefore be speculated that the successful use of LFA in the present study may, in fact, mean that individuals produced in two spawning peaks at different halves of the year prevail in samples, leading the program to identify two cohorts.

The analysis of marginal increments, although showing significant differences throughout the year, was statistically inconclusive in respect to two annual deposition periods assumed to take place in May and October. However, the edge characterization analyzes clearly supported this assumption, showing two peaks of highest frequency of translucent zones in the same months. This is in accordance with the patterns of two annual band depositions proposed by Yang et al. (1969) using scales. These authors demonstrated that bands are deposited in March/April and September/October. Translucent bands, formed in pairs on a yearly basis, were also found for *T. thynnus* and *T. alalunga* (Compéan-Jimenez and Bard, 1983; Gonzales-Garcés and Fariña Perez, 1983, respectively) being related to migrations.

Summing up, dorsal spines that are easier to collect during landings and less time-consuming for preparation, are also suitable structures for *T. albacares* ageing. VBGF parameters generated in the current study by back-calculation, observed length-at-age, and LFA were all considered appropriate for describing growth and produced similar theoretical growth parameters. However, accepting criticisms for LFA and limitations of back-calculation procedures (Cailliet, 1990), the VBGF derived from the combination of observed and back-calculated lengths for age 0.5 was chosen to represent growth for the species.

Although the Brazilian coast is not a spawning ground, small specimens have been caught around the São Pedro–São Paulo Archipelago using handlines. It is possible that young spawned in the Gulf of Guinea are transported to this Archipelago by the southern Equatorial Current, which carries water westward and is stronger in the fourth quarter of the year (Travassos et al., 1999), concurring with the peak of spawning for the species.

Regarding mean sizes throughout the entire period (1975–1994), it is worth noting that mean lengths have decreased significantly over time, indicating that fisheries may be removing large individuals from the population. The mean size in samples has decreased in the whole area (Table 4) and is now below mean size at maturity. Similarly, Hazin (1993), analyzing data from northeastern Brazil, observed that the size of the yellowfin tuna has continuously decreased since the 1950s, and in 1993, 90% of the catch were smaller than 140 cm.

The pattern of exploitation developed for *T. albacares* needs to be based on accurate growth information because the stock is considered fully exploited. In this regard, development of responsible management strategies is required to prevent the yellowfin tuna stock from suffering the same fate as that of the bluefin tuna and swordfish (Driggers et al., 1999).

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