

Abstract.—Microincrements of otoliths of 151 yellowfin tuna, *Thunnus albacares*, caught in the western Indian Ocean by French and Mauritian purse seiners were used to establish growth curves. On the basis of comparisons among several otolith preparations (transverse or oblique sections, acetate replicas of the external face) and two methods of examination (light microscopy and scanning electron microscopy), we chose to observe transverse otolith sections in light microscopy to estimate age in days.

The von Bertalanffy growth curve, $FL = 272.7 (1 - e^{-0.176(t + 0.266)})$, where FL = fork length in cm and t in years, is very similar to those obtained by other investigators. It does not support the hypothesis that yellowfin tuna of the eastern Atlantic Ocean and the western Indian Ocean have two growth stanzas. Back-calculated dates of spawning show that yellowfin tuna spawn successfully throughout the year, but principally between November and March.

Age and growth of yellowfin tuna, *Thunnus albacares*, from the western Indian Ocean, based on otolith microstructure*

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Numerous studies have been conducted on the age and growth of yellowfin tuna, *Thunnus albacares*, in the tropical oceans using three techniques: 1) length-frequency analyses (Moore, 1951; Hennemuth, 1961; Davidoff, 1963; Le Guen and Sakagawa, 1973; Marcille and Stéguert, 1976; Fonteneau, 1980; Gascuel et al., 1992; Marsac¹); 2) tagging (Bard, 1984; Bayliff, 1988); and 3) observation and interpretation of marks on calcified structures such as scales (Yabuta et al., 1960; Huang et al., 1973), vertebrae (Aikawa and Kato, 1938; Romanov and Korotkova²), dorsal spines (Shabotiniets, 1968), or otoliths (Wild and Foreman, 1980; Uchiyama and Struhsaker, 1981; Wild, 1986; Yamanaka³).

Only a few age and growth studies have been conducted in the Indian Ocean, and the results have been contradictory. There are presently two hypotheses concerning yellowfin tuna growth. The first suggests that growth follows a von

Bertalanffy model (von Bertalanffy, 1938), with growth rates from 2.9 to 3.4 cm per month for individuals between 60 and 70 cm. These studies were based on the analysis of length-frequency distributions

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¹ Marsac, F. 1991. Growth of Indian Ocean yellowfin tuna estimated from size frequencies data collected on French purse seiners. FAO, Indo-Pacif. Tuna Prog., Workshop on stock assessment of yellowfin tuna in the Indian Ocean, Coll. Vol. of Working Documents TWS/91/17, 8 p.

² Romanov, E. V., and L. P. Korotkova. 1988. Age and growth rates of the yellowfin tuna (*Thunnus albacares*) (Bonaterre, 1788) (Pisces, Scombridae) in the northern part of the Indian Ocean, determined by counting the rings of vertebrae. FAO, Indo-Pacif. Tuna Prog., Coll. Vol. of Working Documents TWS/88/38, p. 68-73.

³ Yamanaka, K. L. 1990. Age, growth, and spawning of yellowfin tuna in the southern Philippines. FAO, Indo-Pacif. Tuna Prog. Working Paper 90/WP/21, 87 p.

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Fishery Bulletin 94:124-134 (1996).

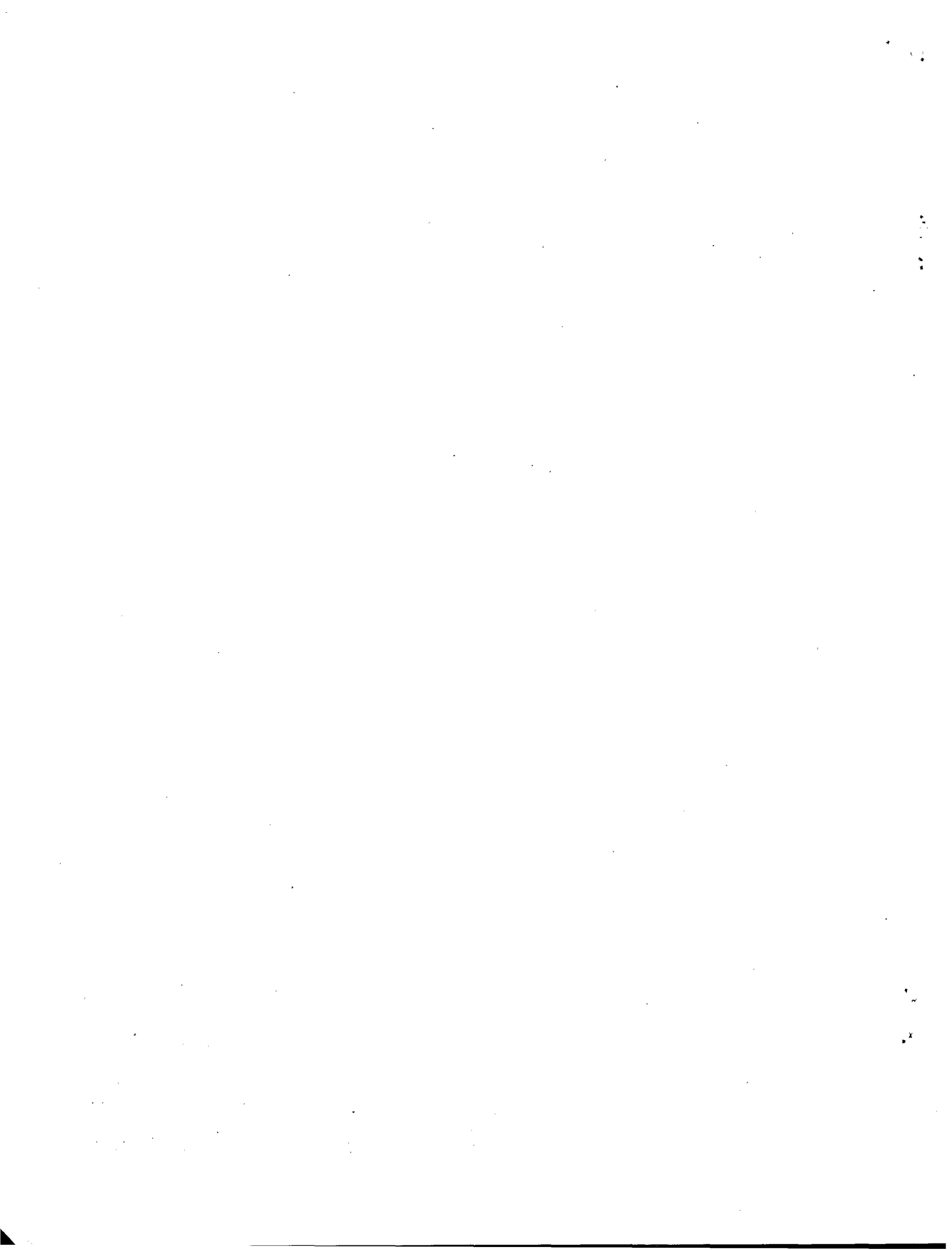
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(Marcille and Stéguert, 1976; Maldeniya and Joseph⁴; Anderson⁵) or seasonal growth marks on calcified structures (Yabuta et al., 1960; Huang et al., 1973). The second hypothesis, also based on length-frequency analysis, suggests that there are two different growth periods, a slow period for young fish (1.5 cm/month for fork length [FL] below 60 cm) and a faster period for larger fish with FL >60 cm (Marsac and Lablache⁶; Marsac¹). The objective of the present study is to test these two hypotheses by estimation of the ages (based on counting daily microincrements on otoliths) of yellowfin tunas in the Indian Ocean.

Materials and methods

Sampling

Sagittal otoliths were collected from fish caught in the western Indian Ocean (between lat. 5°N to 15°S and long. 42°E to 72°E). Otoliths were extracted either directly on board French purse seiners based in Mahé (Seychelles) or at the Port Louis tuna cannery (Mauritius) from fish caught by Mauritian purse seiners. A total of 674 yellowfin between 28 and 154 cm fork length (measured to the nearest half centimeter from the tip of the snout to the fork of the tail) were collected between May 1989 and November 1990. The sagittae were removed with forceps, rinsed, dried, and then stored in heat-welded, numbered plastic bags.

Otolith preparation

A subsample of 170 otolith pairs were chosen on the basis of fish-size frequency. Otoliths were cleaned in sodium hypochlorite (household bleach), rinsed with distilled water, and dried. They were then prepared

according to the methods described in Secor et al. (1992). All terminology corresponded with that of the otolith glossary in Kalish et al. (1994). The right otolith was embedded in polyester resin (Embed 812), and a transverse section (Fig. 1) was made with a low-speed Buehler Isomet saw to obtain a slice containing the primordium. For 33 individuals, the left otolith was also embedded and sectioned in an oblique plane (Fig. 1). In each case, the slice was attached to a microscope slide with Crystalbond thermoplastic glue and then ground with wet sandpaper (400, 600, and 1,200 grit) and polished on a polishing plate with water and aluminium powder (0.3 µm) until the primordium was reached. The microscope slide was then placed on a hot plate for a few seconds to soften the glue and to turn the section: the primordium was then in direct contact with the microscope slide. The section was polished on the other side until a thin section of 75–100 µm maximum was obtained. The surface of this section was partially decalcified with 5–7% EDTA (tri-sodium-ethylenediaminetetraacetic acid, pH=7.2–7.6) to emphasize the increments used to estimate the age.

For 33 individuals ranging from 28.5 and 135 cm, we counted with the aid of light microscopy the number of daily increments on the transverse section of one otolith and the number of daily increments on the oblique section of the other. The results were compared to determine whether the interpretation of transverse sections tended to underestimate age as suggested by Wild and Foreman (1980). For 10 individuals ranging from 30 and 130 cm, we estimated age by counting the microincrements on acetate replicas of the external surface of the otoliths as in Wild and Foreman (1980). The results of the acetate replica counts were then compared with those of the transverse sections.

⁴ Maldeniya, R., and L. Joseph. 1985. On the distribution and biology of yellowfin tuna from the western and southern waters of Sri Lanka. FAO, Indo-Pacif. Tuna Prog., Coll. Vol. of Working Documents TWS/85/21, p. 51–61.

⁵ Anderson, R. C. 1988. Growth and migration of juvenile tuna (*Thunnus albacares*) in the central Indian Ocean. FAO, Indo-Pac. Tuna Prog., Coll. Vol. of Working Documents TWS/88/21, p. 28–39.

⁶ Marsac, F., and G. Lablache. 1985. Preliminary study of the growth of yellowfin estimated from purse seiner data in the western Indian Ocean. FAO, Indo-Pacif. Tuna Prog., Coll. Vol. of Working Documents TWS/85/22, p. 91–110.

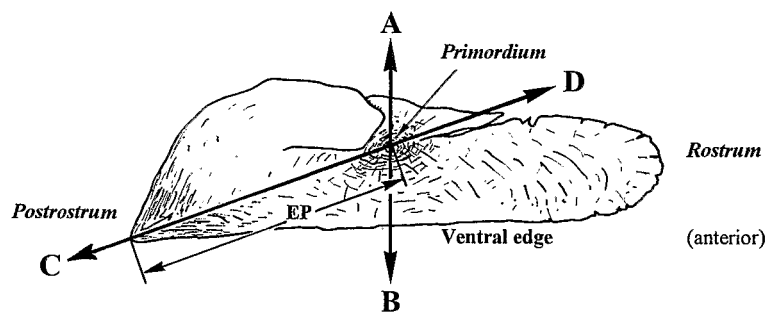


Figure 1

Drawing of a typical right yellowfin tuna, *Thunnus albacares*, sagitta. (A–B) Transverse section axis. (C–D) oblique section axis. EP = external path.

Age reading

Microincrements were counted on transverse sections of yellowfin tuna otoliths under a light microscope (1,000×) with an Olympus microscope BX 40 with a MPL 100× dry objective. Only 151 preparations were readable from the 170 fish because some were broken during grinding or too deeply etched by EDTA. The reading of microstructures was always made on the external part of the transverse sections along the ventral limb.

Each transverse section was chosen randomly and microincrements were counted at three different times by the same reader without knowledge of the sample identification or previous counts. After the readings, 16 sections were prepared for observation on a scanning electron microscope (SEM). A photographic series was made along each section (800×) to obtain the whole reading area and to count the number of microincrements. These results were then compared with those obtained from the light microscope reading.

Growth

Several growth models exist to describe the relationship between fish size (FL in cm) and age (t in year = number of increments/365). Among the most used models, three of them (von Bertalanffy, Gompertz, and Richards) were tested. The equations of these models are as follows:

$$\text{von Bertalanffy model: } FL_t = FL_\infty (1 - e^{-K(t-t_0)})$$

$$\text{Gompertz model: } FL_t = FL_\infty \exp(-ae^{-Kt})$$

$$\text{Richards model: } FL_t = FL_\infty / (1 + e^{(-Kt+b)})^m$$

when FL_t = fork length at age t ;
 FL_∞ = asymptotic fork length;
 K = coefficient of growth;
 t_0 = theoretical age for $FL = 0$; and
 a , b , and m = parameters.

Results

The fork lengths of the fish that had readable otoliths are shown in Figure 2. On the transverse section (Fig. 3), we observed that the microstructures are more visible in the layer (50–60 μm of thickness) which is located immediately under the otolith surface and that interpretation on the internal face is difficult because the microstructures tend to be obscure (Fig. 4).

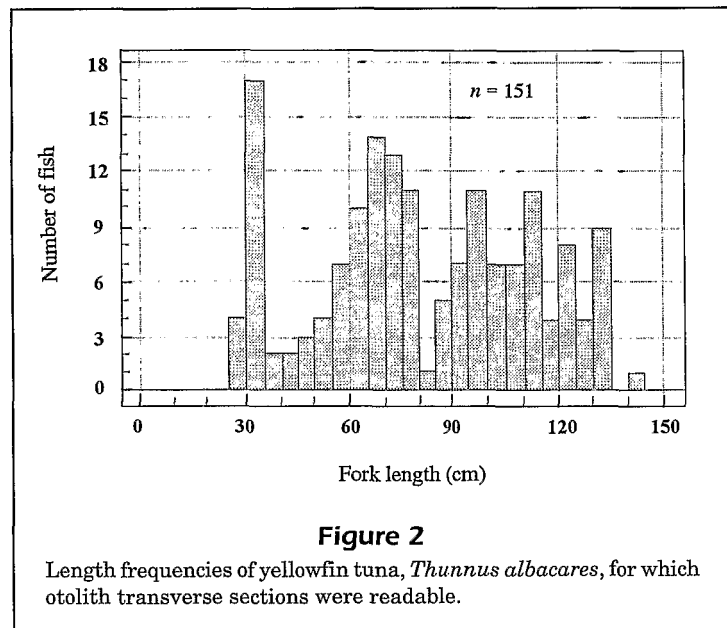


Figure 2

Length frequencies of yellowfin tuna, *Thunnus albacares*, for which otolith transverse sections were readable.

Comparison of methods

The relationship between the numbers of microincrements on the transverse section and on the oblique section was highly significant ($r=0.992$, $P<0.05$, $n=33$) (Fig. 5). The slope of the regression was not different from one ($t=-0.943$, $P>0.05$, $df=31$), and the intercept was not different from zero ($t=0.266$, $P>0.05$, $df=31$). Therefore, transverse sections were used for the age readings.

Counts of microincrements on the transverse section under a light microscope (400×) compared to counts from SEM on the same section were significantly different for fish larger than 100 cm fork length ($t=-4.643$, $P>0.05$, $df=18$). To determine whether the difference was the result of the magnification used, we compared counts for 16 transverse sections under a light microscope (1,000× magnification) and a SEM with a comparable magnification (1,000×) (Fig. 6). The slope of the relationship was not different from one ($t=-0.426$, $P>0.05$, $df=14$), and the intercept was not different from zero ($t=0.246$, $P>0.05$, $df=14$). These results suggest that these two techniques give comparable counts. Therefore, subsequent analyses were based on counts from the light microscope (1,000×).

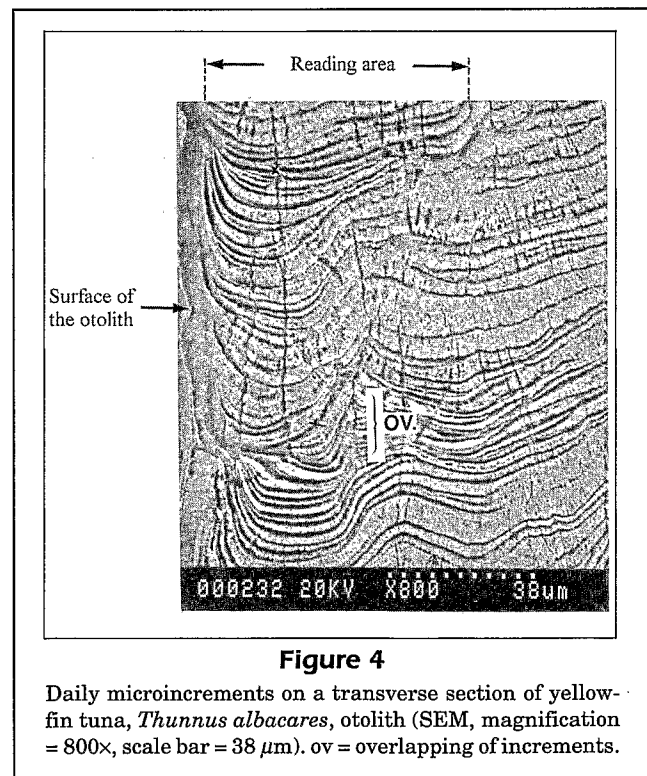
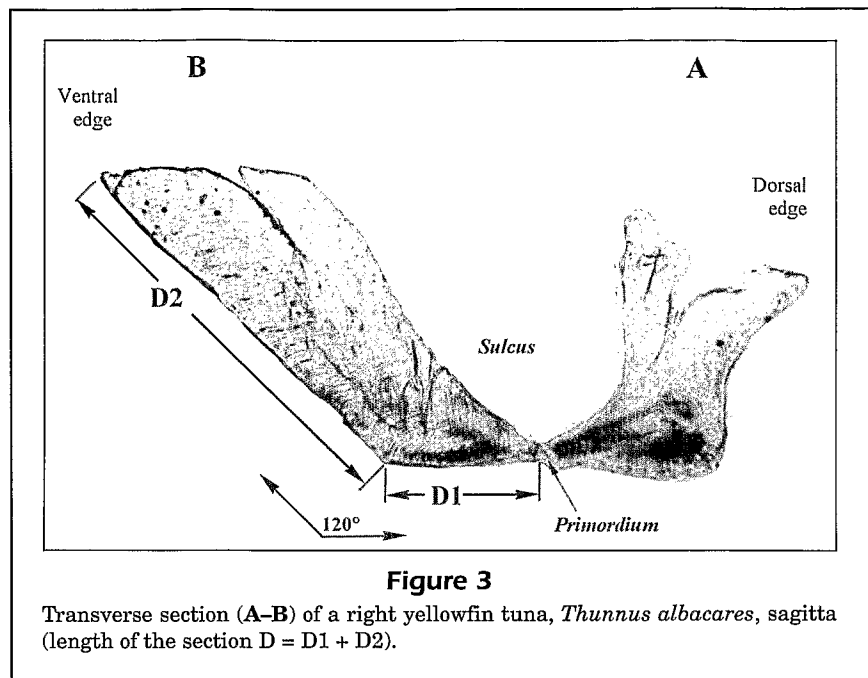
As the relationship between microincrement counts from acetate replicas and transverse sections could not be established for the same otolith, we plotted the results (age versus fork length) obtained from 10 individuals for which age was determined by replicas directly on the age versus fork length relationship estimated on the 151 transverse sections (means

of 3 counts) corresponding to our sample (Fig. 7). For acetate replica readings, the standard error of the counts is quite small (Table 1), and for counts on transverse sections, the coefficient of variation of Chang (1982) is acceptable ($CV=2.802\%$, $n=151$).

Transverse sections observed with the SEM clearly show that some increments overlap inside the otolith (Fig. 4). These increments cannot be seen on the external face even after acid etching for acetate replication. This overlap does not seem to appear on oblique sections where increments are more evenly spaced. In addition, the plane of growth of the otolith changed when viewed in a transverse plane (Fig. 8). From this plane (Fig. 3), the ventral surface of the otolith grows at an angle of about 120° to the original plane of growth which contains the primordium. The direction of otolith growth changes before the fish reaches 28 cm fork length. For all individuals, the distance between the primordium and the top of this angle (D1, Figs. 3 and 8) has a stable value ($D1=644 \mu\text{m} [\pm 4 \mu\text{m}]$). Then, the otolith growth depends only on the plane of growth of D2 (Figs. 3 and 8). This change in growth direction occurs, on average, 50 (± 5) days after the date of hatching ($n=151$). Because of this change, the use of back-calculation can be complicated. Because ages obtained with the acetate replica technique were similar to those based on transverse sections, we used the ages based on transverse sections for this study. All the observations described above (comparisons between oblique and transverse sections, replicas, light microscope, and SEM) show that the observation of microstructures on transverse sections of yellowfin tuna otoliths with a light microscope are suitable to estimate age in days.

Growth

The estimations of parameters were calculated by using the nonlinear regression procedure and are summarized in Table 2. The fits of each of these models are highly significant ($P < 0.01$). For the three models, F -ratios of ANOVA (respectively 14,698, 14,799, and 10,960) and r^2 values (0.974 for each of them) are very similar to one another (Table 2). We used the von Bertalanffy growth curve to express our results and to compare with results obtained by other



investigators because this model is the most widely used.

The model was also applied to males ($n=63$) and to females ($n=61$) separately. Males and females were similar in size at any given age (Table 3). ANCOVA

for both male and female adjusted relationships of fork length to age indicated no significant differences in the slope ($F_{(1, 120)}=1.270$, $P>0.05$) or intercept ($F_{(1, 121)}=0.359$, $P>0.05$).

The mean growth rate of yellowfin tuna in the Indian Ocean, based on this study, is approximately 2 mm/day for fish measuring 30 cm (FL), 1.3 mm·day⁻¹ for length between 60 and 80 cm, and 1 mm·day⁻¹ for fish larger than 110 cm.

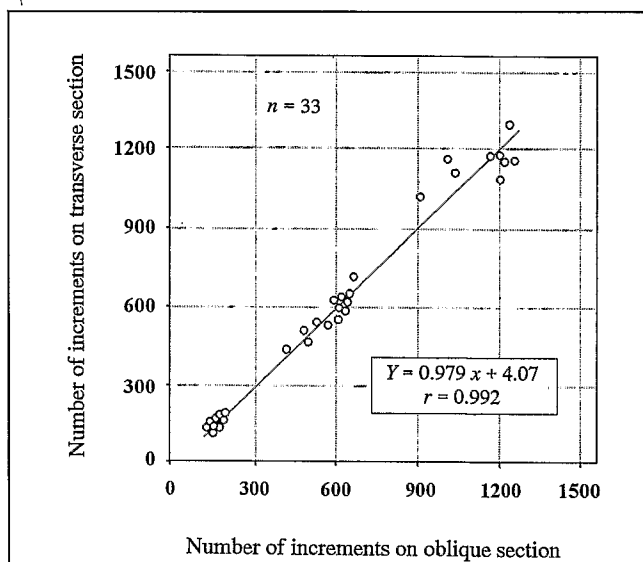


Figure 5

Comparison between the number of increments read on transverse and on oblique sections of yellowfin tuna, *Thunnus albacares*, otoliths.

Date of hatching

Spawnings occurred throughout the year, but mainly from October through March. If we compare the monthly development of the number of births (back-calculated from age estimations) and the variation of the gonad index (GI) established by Hassani and Stéquent,⁷ there is a similarity in development for reproduction (Fig. 9). Analysis of correlation yields a significant correlation ($r=0.997$, $P<0.05$, $n=12$) between these two data sets. The months of hatching established from otolith estimations correspond to the months of the maximum reproductive activity determined from GI's.

Discussion

Choice of otolith preparation method

Age readings of yellowfin tuna previously have been made either directly on the external surface of the otolith or on the acetate replica of this surface (Wild and Foreman, 1980; Wild, 1986). Using the external surface of the otolith etched with 0.5N HCl, Wild and Foreman (1980) showed that the age reading should be done on the primordium-postrostrum axis (EP, Fig. 1) for interpreting the increments. They concluded that age was underestimated when the pri-

⁷ Hassani, S., and B. Stéquent. 1990. Sexual maturity, spawning and fecundity of the yellowfin tuna (*Thunnus albacares*) of the western Indian Ocean. Document presented at the FAO expert consultation on stock assessment of tuna in the Indian Ocean; Bangkok, Thailand, 2-6 July 1990. FAO, Indo-Pacif. Tuna Prog., Coll. Vol. of Working Documents TWS/90/68, p. 91-104.

Table 1

Results of the microincrement readings on acetate replicas of the external otolith face of yellowfin tuna, *Thunnus albacares*, otoliths. I_n = number of increments for the n th reading. I = mean of the increment numbers. SE = standard error

FL (cm)	I1	I2	I3	I4	I5	I6	I_n	SE
35.0	195	197	198	194	197	196	196.2	0.60
49.5	310	307	311	308	306	310	308.7	0.80
59.5	405	406	401	403	405	407	404.5	0.88
66.0	518	532	522	515	523	526	522.7	2.44
75.0	561	559	550	551	557	552	555.0	1.88
78.5	623	644	635	627	631	624	630.7	3.23
99.0	809	814	802	804	803	818	808.3	2.67
99.5	852	861	848	850	860	872	857.2	3.67
118.0	1,148	1,155	1,137	1,151	1,143	1,132	1,144.3	3.56
130.5	1,211	1,224	1,208	1,220	1,222	1,233	1,219.7	3.71

mordium-ventral edge axis (Fig. 1) was used. This underestimation was as high as 17% for larger individuals. The irregularity of microincrement structure and its overlapping (Fig. 4) may explain the differ-

ence observed by Wild and Foreman (1980) between their readings on the surface of the otolith along the oblique and those on the transverse axis.

The results of the present study show that the microincrements can also be counted on a transverse or oblique otolith section which crosses the primordium. We obtained similar results with all three techniques. Because transverse otolith sections are easier to prepare and have excellent statistical replicability (CV <5%), they were used to count the microincrements and estimate the age of yellowfin tuna from the Indian Ocean. However, our results suggest that under light microscopy, a magnification of 1,000× must be used.

Validation of the age estimations

Wild and Foreman (1980) have shown that one daily microincrement is formed each day on the otolith of the yellowfin tuna from the eastern Pacific. If the same phenomenon occurs in the western Indian Ocean, comparable results should be found in this area with other methods. In order to verify indirectly our age estimations, we used the results of mark-recapture studies (Cayré and Ramcharrun⁸; Yesaki and Waheed⁹) and of length-frequency analyses of young individuals for which cohorts are easily recognized (Marcille and Stéquert, 1976).

In a tagging experiment carried out in the southwest Seychelles Islands area and in the Mozambique channel (Cayré and Ramcharrun⁸), three individuals (FL=67, 73, and 67 cm) were recaptured after liberty at sea for 252, 411, and 613 days, respectively after marking. They presented a mean growth rate of 27.3 cm·yr⁻¹. A tagging experiment in the Maldives (Yesaki and Waheed⁹) resulted in a mean growth rate of 2.4 cm·mo⁻¹ for the 37 recaptured fish that were at liberty for more than 29 days after marking. The growth rates obtained in these two experiments were similar to those of the present study. Following the young yellowfin tuna cohorts caught by Japanese pole-and-line tuna boats along the northwest coast of Madagascar (Marcille and Stéquert, 1976), the mean growth rate of 40

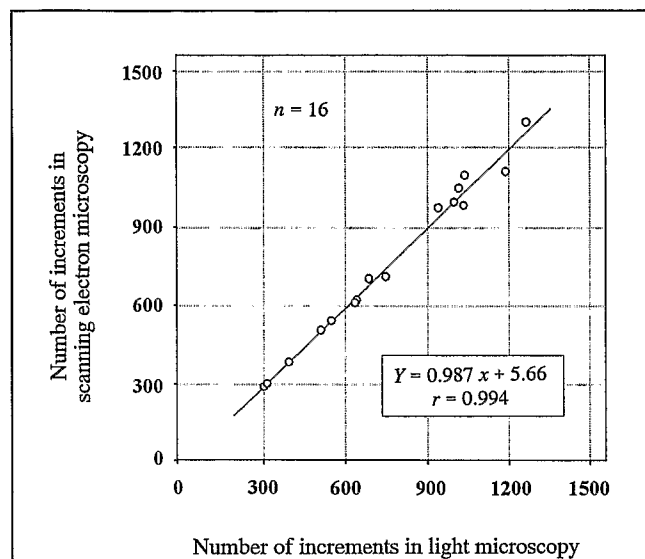


Figure 6

Comparisons between the number of increments estimated on transverse section of yellowfin tuna, *Thunnus albacares*, otoliths with the light microscope and the SEM.

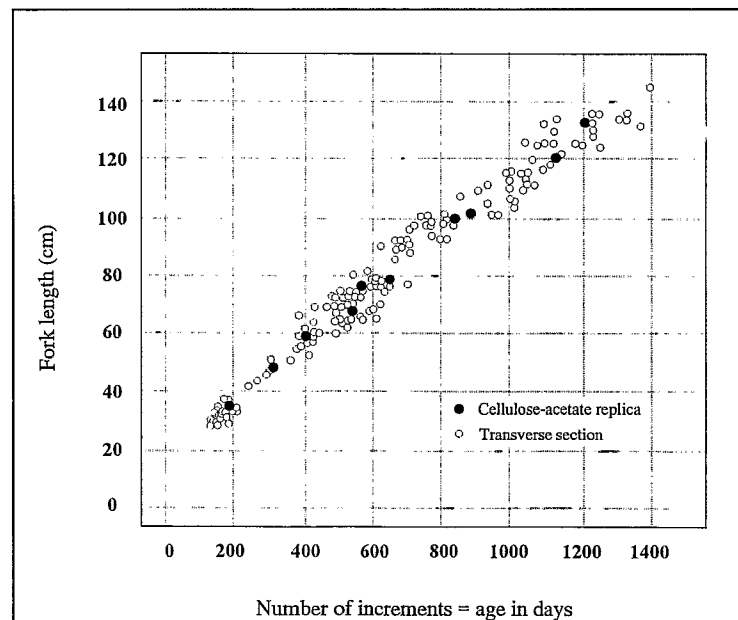


Figure 7

Comparison between the number of increments on yellowfin tuna, *Thunnus albacares*, otoliths estimated from acetate replicas and the number of increments estimated from transverse sections.

⁸ Cayré, P., and B. Ramcharrun. 1990. Results of the tagging operations conducted within the Regional Tuna Project (Indian Ocean Commission) in 1988 and 1989. FAO, Indo-Pacif. Tuna Prog. Coll. Vol. of Working Documents TRW/90/61, p. 63-85.

⁹ Yesaki, M., and A. Waheed. 1992. Results of the tuna tagging program conducted in the Maldives during 1990. FAO, Indo-Pacif. Tuna Prog. Working Paper 92/WP/24, 18 p.

to 70 cm individuals was about 34 cm·yr⁻¹. The slopes corresponding to those growth rates, when plotted against the growth curve of the present study, show close agreement (Fig. 10). These comparisons demonstrate that 1) the microincrements on otoliths are deposited on a daily basis and 2) the ages of young tuna (FL ≤ 100 cm) estimated from otoliths are correct.

Comparative study of yellowfin tuna growths

The growth curve obtained for yellowfin tuna from the western Indian Ocean is similar to those obtained by different investigators in other oceans and using other age estimation methods. The use of skeletal

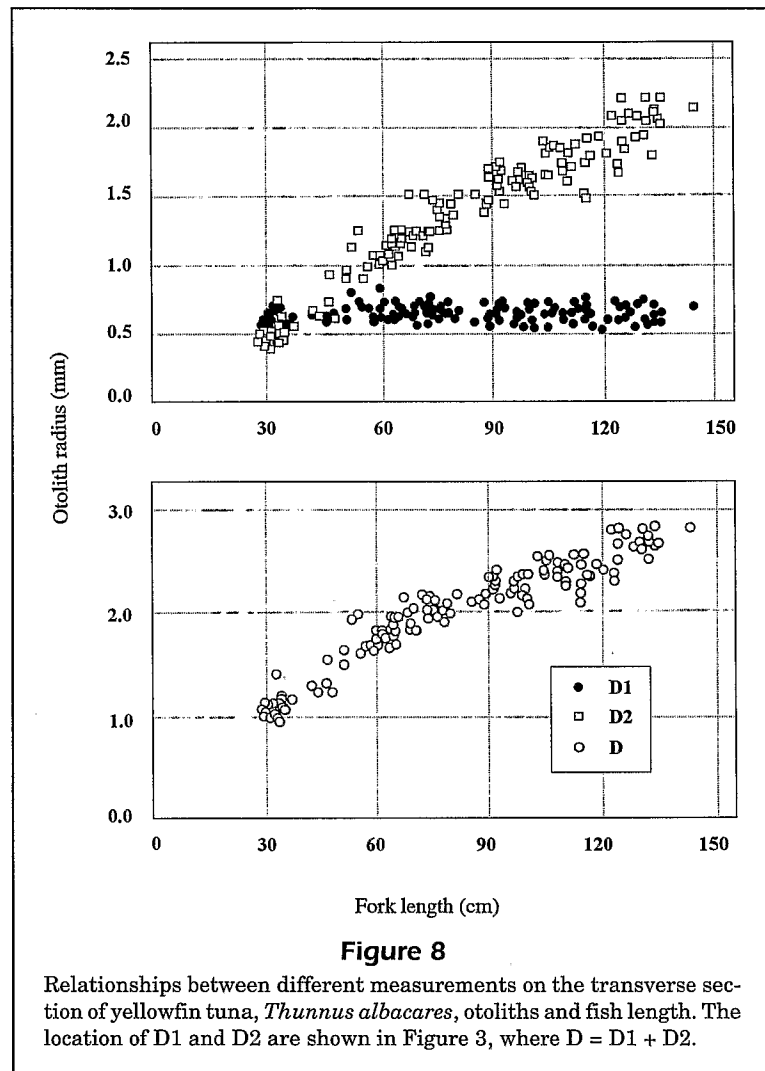


Table 2

Estimated parameters of the growth models for yellowfin tuna, *Thunnus albacares*, (all sexes, n=151) in the western Indian Ocean (FL in cm, t_0 in years). Est. = estimated value; SE = standard error.

	von Bertalanffy			Gompertz			Richards			
	FL_{∞}	K	t_0	FL_{∞}	a	K	FL_{∞}	K	b	m
Est.	272.7	0.176	-0.266	165.7	2.131	0.629	160.8	0.698	1.450	6.675
SE	28.9	0.027	0.050	5.2	0.039	0.033	13.1	0.204	5.269	19.604

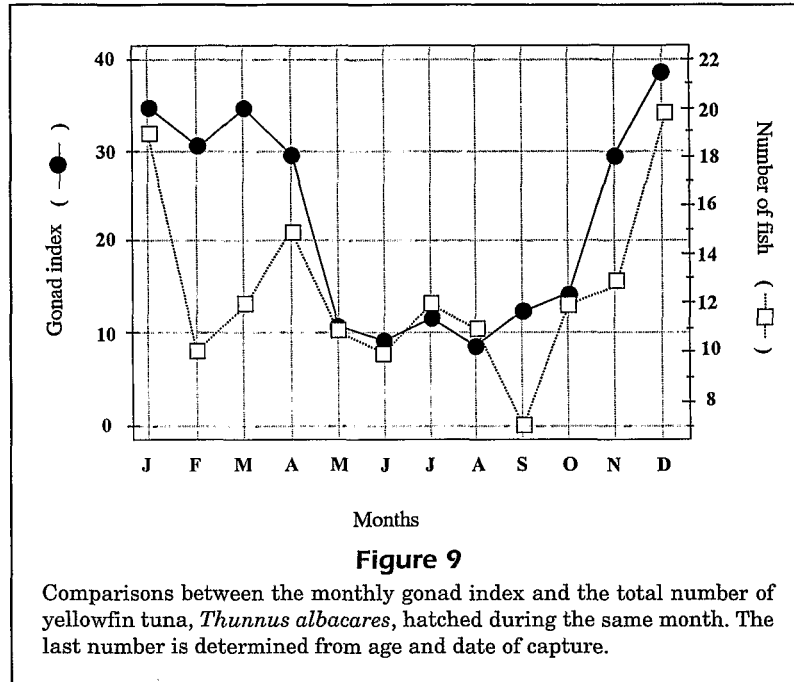


Table 3
Length (in cm) at different ages for yellowfin tuna, *Thunnus albacares*, predicted by the von Bertalanffy growth model.

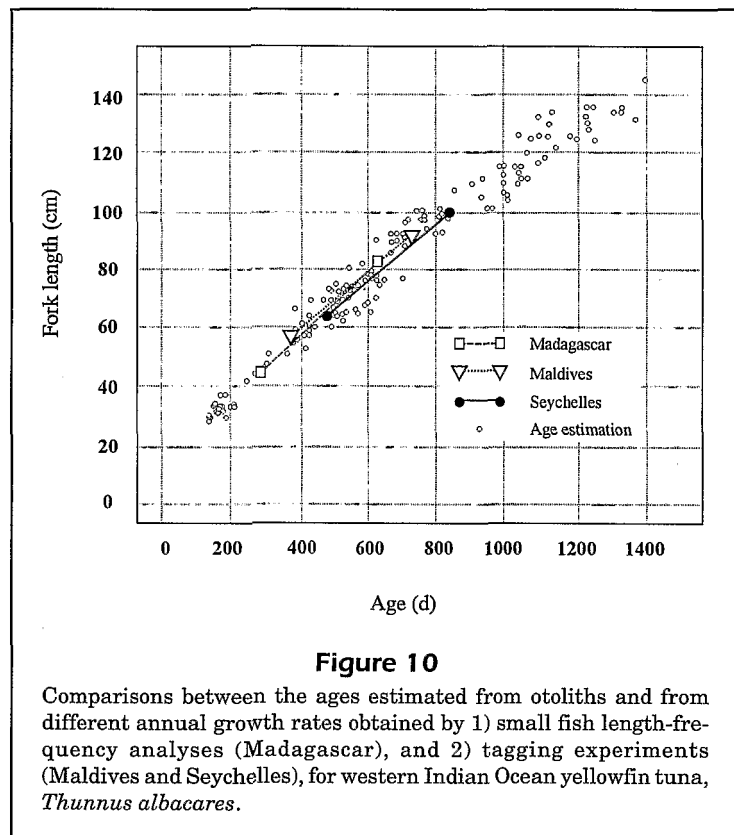
	Age (yr)							
	0.5	1	1.5	2	2.5	3	3.5	4
All individuals	34.4	54.5	74.4	89.7	105.1	119.2	132.2	144.0
Females	—	54.3	73.1	90.1	105.2	118.0	131.2	142.2
Males	—	53.5	72.3	89.7	105.7	120.4	134.0	146.5

bony structures in the Pacific (Yabuta et al., 1960) or in the Indian Ocean (Huang et al., 1973) gave results similar to ours (Fig. 11A). Studies conducted on length-frequency analyses have also led to comparable results. The results for the Pacific yellowfin tuna of Hennemuth (1961) are close to those of the present study. The growth estimation of Le Guen and Sakagawa (1973) for the eastern Atlantic shows slight differences for young individuals: until 2 years of age, young yellowfin tuna grow more slowly than those from the Indian Ocean; however, after 2 years of age, growth is the same for eastern Atlantic and Indian Ocean populations. Two growth stanzas have been observed in the western Atlantic (Capisano and Fonteneau, 1991; Gascuel et al., 1992) and in the Indian Ocean (Marsac¹), but we did not observe the accentuated inflection in the growth of juveniles reported by these studies.

A comparison of our results with other estimates based on otoliths yields similar growth models (Fig. 11B). Age estimates given by Yamanaka³ for the

smallest fish in the Philippines (FL between 25 and 50 cm) are equal to those of the small yellowfin tuna caught by the French purse seiners in the Indian Ocean. The length of our smallest fish (6 months old) is only a few centimeters larger than that proposed by Uchiyama and Struhsaker (1981) for the Pacific but is exactly the same for individuals older than 1 yr. The growth curve established by Wild (1986) for eastern Pacific yellowfin tuna shows growth rates slightly greater than those of the western Indian Ocean, but for 2-yr-old individuals, the lengths are equal (FL=90 cm).

For the Indian Ocean, however, studies of yellowfin tuna growth rates yield contradictory results. Growth rates calculated in the present study are similar to those obtained in the small-scale fisheries of the Maldives (Anderson⁵) and Sri Lanka (Maldeniya and Joseph⁴) but are significantly different from those obtained for the same Indian Ocean population landed by French purse seiners (Marsac¹; Marsac and Lablache⁶). Differences in length are



observed for each age except for 1-yr-old and 2.5-yr-old individuals (Fig. 11C). That these studies assume there is only one period of reproduction that occurs annually during a short duration of time (November to March) and that individuals are sexually resting during the remainder of the year may explain the discrepancy. Recent hormone analyses (unpubl. data, senior author) and estimated dates of hatching show that yellowfin tuna of the western Indian Ocean spawn throughout the year. It is clear that the major reproductive period is between November and March, however some of the population spawns from July to September. A similar observation has been noted for the eastern Pacific populations of yellowfin tuna.¹⁰ For the Indian Ocean population, there is agreement between the spawning period estimated from the otolith readings and the condition of the female gonad index during the year. This observation supports the assumption of daily deposition of microincrements.

The growth rates estimated in the present study are high at the beginning of the life cycle until 1 yr and regularly decrease with time to reach 1 mm-day⁻¹, which is consistent with growth estimates for most

species of fish and other stocks of yellowfin tuna. This contradicts the growth model for the same stock landed by the French purse seiners presented by Marsac¹: the young fish have linear growth, until they reach 60 cm, and then grow faster in accord with the von Bertalanffy growth model. A uniform growth model is also reasonable because yellowfin tuna from the Atlantic and Pacific oceans show no significant genetic differences (Scoles and Graves, 1993).

The present study introduces some new information about the growth of yellowfin tuna in the western Indian Ocean; that is to say, growth is regular, following a classical von Bertalanffy model without stanzas. Nevertheless, some problems remain unsolved. For example, we collected no fish smaller than 28 cm (from larvae until 28 cm size, i.e. for the first 5–6 months of life) and very few large individuals (>140 cm). The problem is more complex in collecting small fish: analysis of the stomach contents of more than 1,000 adult tunas or other predators did not yield any small individuals as has been possible for adult tunas in the Pacific Ocean (Uchiyama and Struhsaker, 1981). In fact, we do not know where the small Indian Ocean yellowfin tuna live or how to capture them in order to collect their otoliths. Once these otoliths are obtained, an important first study would concern otolith growth itself to determine the correspondence between life cycle

¹⁰ Schaefer, K. 1993. Inter-American Tropical Tuna Commission, Scripps Institution of Oceanography, 8604 La Jolla Shores Drive, La Jolla, CA 92037-1508. Personal commun.

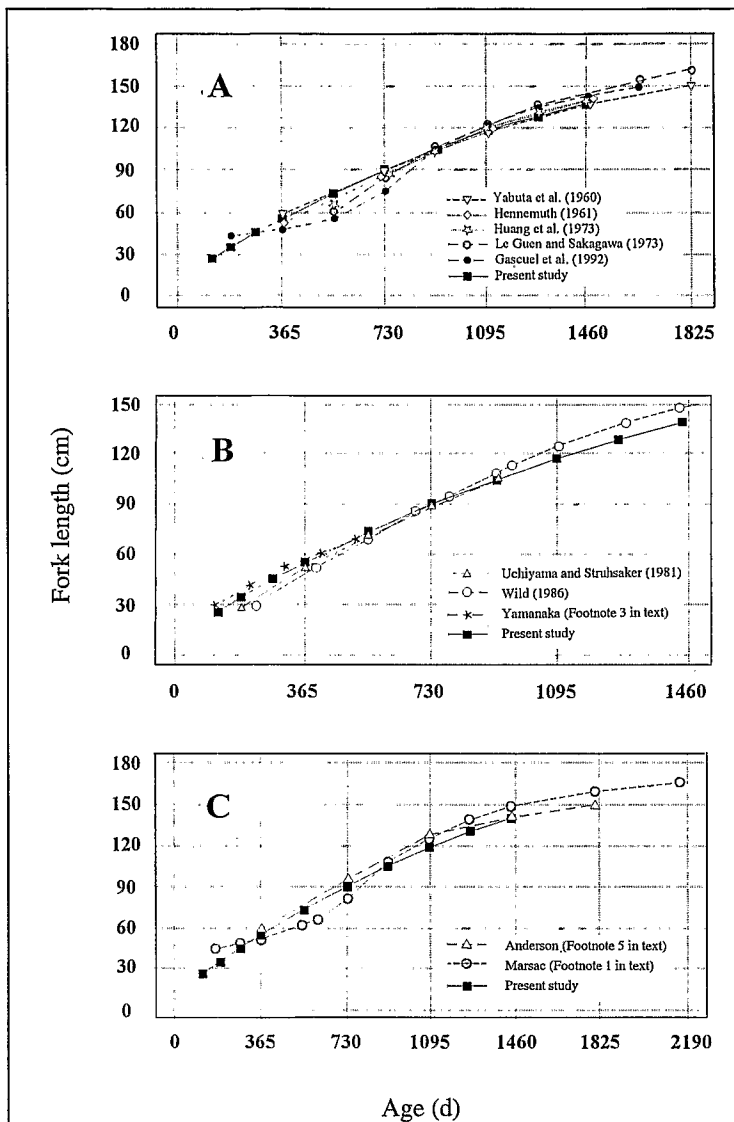


Figure 11

Comparisons of yellowfin tuna, *Thunnus albacares*, growth curves established by several investigators: (A) Atlantic and Pacific Oceans with different age estimation methods; (B) otolith daily increment readings; (C) Indian Ocean with different methods of age estimation.

events and the change in otolith growth direction (D1-D2 boundary). Regular samplings of small individuals and the analysis of daily microincrements could avoid difficult interpretations in the length-frequency analyses during the first months of growth.

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