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Age, growth and stock structure of the oceanic whitetip shark, *Carcharhinus longimanus*, from the southwestern equatorial Atlantic

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Abstract

Between November 1992 and November 1997, 258 specimens (71.0–250.0 cm-TL) of *Carcharhinus longimanus* were collected off northeastern Brazil (Brazilian EEZ). Vertebral sections from 110 individuals, 44 males (71.0–235.5 cm), 60 females (81.0–230.0 cm) and six of undetermined sex (120.5–187.2 cm) were analyzed. Mean MIR analysis showed that one band is formed annually starting in August. Male and female growth is similar, back-calculated von Bertalanffy parameters were $L_{\infty} = 325.4$ cm, K = 0.075 yr⁻¹ and $t_0 = -3.342$ yr⁻¹ for both sexes, whereas observed length-at-age parameters were $L_{\infty} = 284.9$ cm; K = 0.996 yr⁻¹, and $t_0 = -3.391$ yr⁻¹. Observed length-at-age described growth better than back-calculated lengths. Maturity is reached for both sexes at 180.0–190.0 cm, or 6–7 year-old individuals. The overall sample ranged from a recently born male from the 0 age-class (71.0 cm) to a 17 year-old female (250.0 cm). Growth rates are 25.2 cm yr⁻¹ in the first free-living year, 13.6 cm yr⁻¹ from ages 1 to 4, 9.7 cm yr⁻¹ for adolescents of age 5 and 9.10 cm yr⁻¹ for mature individuals. The size-range of the overall sample is similar to others collected in different locations worldwide. The species follows the *K*-selected pattern like most elasmobranchs. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Sharks; Elasmobranchs; Carcharhinus longimanus; Carcharhinus maou; Southern Atlantic; Age and growth

1. Introduction

The oceanic whitetip shark, Carcharhinus long-imanus (Poey, 1861), previously described as Carcharhinus maou (Lesson, 1830), is an epipelagic, strictly oceanic species caught in longline fisheries for tuna in tropical and warm-temperate waters around the world (Compagno, 1984). In the Western Atlantic, the species ranges from Maine (USA) to Argentina (from 45°N to 40°S), but is most abundant in the tropics

(from 20°N to 20°S). It has also been captured in the Central and Eastern Atlantic from Madeira (Portugal) to the Guinea Gulf. Its abundance increases with increasing distance from land, and it is one of the most common species in tuna longline catches, occurring with *C. falciformis* and *Prionace glauca* at temperatures above 20°C (Compagno, 1984).

Although common in fisheries, occurring particularly off oceanic islands, or in continental areas where the shelf is very narrow, the population dynamics and structure of the species has received little attention. *C. longimanus* is now considered in the IUCN redlist in the lower risk (near threatened) category (IUCN,

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unpublished), subjected to high levels of bycatch and a target in some fisheries. Fishing pressure of the species is expected to increase in the future because its fins are highly prized in trade.

Information on this species includes taxonomic descriptions (Bigelow and Schroeder, 1948; Springer, 1950; Garrick, 1982; Compagno, 1984, 1988) and natural history (Backus et al., 1956; Strasburg, 1958, Fourmanoir, 1961; Randall, 1963; Gohar and Mazhar, 1964; Linewaever and Backus, 1970; Bass et al., 1973; Guitar Manday, 1975; Cadenat and Blache, 1981). An age and growth study, as yet unpublished, was carried out in the Pacific by Saika and Yoshimura in 1985.

In general, this placental viviparous species is said to attain a maximum size of 395.0 cm. However, the most common sizes are below 300.0 cm (Compagno, 1984). Maturity is reached between 175.0 and 198.0 cm in males and about 200.0 cm in females. An assumed size at birth is 60–65 cm and gestation lasts about 1 year (Bass et al., 1973).

A survey of pelagic fishes was conducted using a research vessel from 1992 to 1997 in the southwestern equatorial Atlantic, within limits of the Brazilian Economic Exclusive Zone (EEZ) in the context of the Renewable Resources Assessment Programme (REVIZEE), where the species represented 29% of all elasmobranch catches. The oceanic whitetip shark was, among elasmobranchs, the second most abundant, outnumbered only by Prionace glauca. Specimens collected during the survey were used in the present account which attempts to fill gaps in knowledge supplying information on age, growth and stock structure required for age-based methods that can be used for the management of the species. Age was determined and validated by vertebral analysis and growth parameters were estimated by statistical fit to the von Bertalanffy growth function.

2. Materials and methods

Between November 1992 and November 1997 a sample comprising 258 specimens (71.0–250.0 cm) of *C. longimanus* was collected by a research vessel equipped with a longline. The gear was similar to that traditionally used by Japanese tuna longline fishery, which consisted of about 30 km of line and 100

baskets containing 6 hooks each. In all, 197 sets were performed beyond the 1000 m isobath.

The studied area ranged from 1°N to 9°S latitude and 40°W to 30°W longitude, corresponding northeastern sector of the EEZ (Fig. 1). The northeastern shelf is narrow and the distance between the coast and the 200 m isobath, considered the limit between shelf and slope, is 30 mile on average. Surface water temperature ranges from 26°C to 28°C.

Sex, total length (cm) and a set of five or six vertebrae were removed from below the first dorsal fin of each specimen. Total length (cm), was measured in the natural position (without depressing the tail to be in line with body axis), according to Garrick (1982). When length is mentioned hereafter, we always refer to total length and terminology on vertebrae by Caillet et al. (1983).

After being cleaned of excess tissue, vertebrae were fixed in 4% formaldehyde for 24 h and preserved in 70% ethanol. Because of the concavity, a slice including the focus was sectioned sagitally (Caillet et al., 1983) and then, embedded in polyester resin. These sections, about 7 mm thick, were polished with 100–400 grit wet sandpaper until sections less than 1 mm thick were obtained.

Initially, 10 sections stained with alizarin red-S (Gruber and Stout, 1983) were compared to sections of the same set impregnated by silver nitrate (Stevens, 1975) and also to unstained sections, always from the same individuals, in order to define the method that best contrasted narrow and broad rings.

In the first procedure, sections were immersed overnight in an aqueous solution of alizarin red-S and 0.1% NaOH in a ratio 1:9 and then rinsed in running tap water. In the second, sections were immersed in a solution of silver nitrate and exposed to ultraviolet light for about 5 min. Excess silver was removed in water and fixation by soaking in sodium thiosulphate (5%) was employed. In sections stained either by alizarin red-S or impregnated with silver nitrate, narrow rings became dark-red and dark-brown, respectively.

Bands, in unstained sections, consisted of a translucent (narrow) and an opaque (broad) ring, and were counted in each vertebrae using transmitted light and distances from the focus to the margin of each narrow ring were recorded. Unstained sections were considered the best for ring observation in the study material.

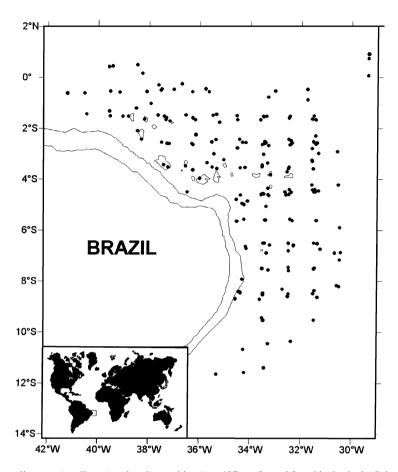


Fig. 1. Location of the sampling area (small map) and station position (n = 197) performed for whitetip shark, C. longimanus, { } {collected off northeastern Brazil.

Distances from the focus to the outer edge of the section, or vertebral radius, was measured using a binocular dissecting microscope equipped with an ocular micrometer. Measurements were made with a 8X magnification (1 micrometer unit = 0.8 mm).

Sections from the same specimen were read twice, each reading at different times and always by the same reader. All counts were made without knowledge of the individual size and previous count. Whenever the counts differed between the two readings, a third reading was done for back-calculation of size-at-age.

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

IAPE =
$$1/N \sum (1/R \sum (|X_{ij} - X_j|/X_j)100$$
,

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

To determine the time of formation of bands in vertebrae, a marginal increment analysis was performed using the equation for marginal increment ratio (MIR) calculations (Natanson et al., 1995).

$$MIR = (VR - R_n)/(R_n - R_{n-1}),$$

where VR is the vertebral radius, R_n the last complete band and R_{n-1} is the penultimate complete band.

Mean MIR \pm s.d. was plotted monthly in order to locate periodic trends in band formation. Data were tested for normality and variance analysis (ANOVA)

was performed to detect significant differences throughout the year.

Lengths at previous ages were back-calculated from vertebral measurements using a modification of the Fraser–Lee equation proposed by Campana (1990), which considers the biologically derived intercept. The biological intercept was defined by the author as the fish and structure sizes at which proportionality of fish and the structure growth is initiated. So, vertebrae may be used for aging and proportional back-calculation (Campana, 1990; Sminkey and Musick, 1995).

$$L_a = L_c + [(O_a - O_c)(L_c - L_0)/(O_c - O_0)],$$

where L_0 is size of the fish at the biological intercept, O_0 the size of vertebrae at the biological intercept, L_a the length-at-age a, O_a the distance from focus to band a, L_c the length at capture, and O_c is the vertebral radius at capture.

The size at the biological intercept (L_0) was 71.0 cm, which is the size of the smallest specimen in the sample. The size of vertebrae at the biological intercept (O_0) , was the corresponding size of their vertebrae (2.24 mm). For back-calculation, the biological intercept was 71.0 cm for both sexes.

The FISHPHARM programme (Prager et al., 1987), which implements Marquardt's algorithm, allowing parameters to be estimated without transforming the data into linear form, was used. von Bertalanffy growth functions (VBGF) (von Bertalanffy, 1938) were fitted to back-calculated and observed length-at-age data.

$$L_t = L_{\infty}[1 - e^{-K(t-t_0)}],$$

where L_t is predicted length-at-age t, L_{∞} the mean asymptotic total length, K the growth rate constant (yr^{-1}) , and t_0 is the theoretical age at which the fish would have been zero length.

Growth data (total length vs. number of rings) were linearized for each sex separately and resulting regressions were compared.

Also, Bernard (1981) multivariate analysis, based on Hotelling's T^2 , was performed for comparing male and female back-calculated growth curves by testing the hypothesis that differences between male and female vertebral growth curves were not significant.

The age composition of the sample was determined using the inverse von Bertalanffy growth equation as presented by Sparre et al. (1989):

$$t_{(L)} = t_0 - 1/K \ln(1 - L/L_{\infty}).$$

Data were tested for heteroscedascity and then linear regressions were compared using ANCOVA (Zar, 1996). All statistical inferences were made at a significance level of 0.05, except those related to Bernard's method where 0.01 was used.

3. Results

A sample composed of 258 individuals (121 males: 71.0–235.0 cm and 137 females: 80.0–250.0 cm) was collected in the study area (Fig. 2). Vertebral sections from 110 individuals, 44 males (71.0–235.5 cm), 60 females (81.0–230.0 cm) and 6 of undetermined sex (120.5–187.2 cm) were analyzed without stains.

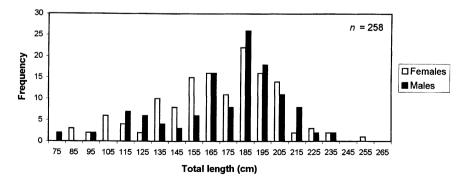


Fig. 2. Length-frequency distribution for male and female whitetip shark, *C. longimanus*, caught off northeastern Brazil between 1992 and 1997.

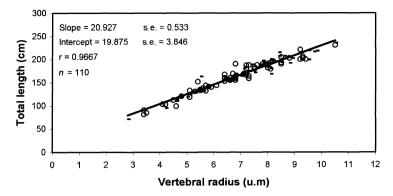


Fig. 3. Relationship between vertebral radius and total length (shown parameters of the equation and standard errors) for the whitetip shark, *C. longimanus* off northeastern Brazil. Black dots are males, empty circles are females and full circles are undetermined sex.

Differences for VR vs. TL regression equations between sexes were not significant (ANCOVA, P > 0.05) (Zar, 1996). The VR vs. TL regression for the overall sample showed a linear relationship ($r^2 = 0.93$; n = 110) (Fig. 3).

The precision estimation, calculated using two readings, provided results ranging from 0% to 7.3%. This involved ages from 1 to 13 with an entire sample mean of 3.0%.

The mean MIR \pm s.d. reaches the maximum value in July and the minimum in August with low mean values recorded from September to December. In contrast, from May to July increasing values of mean MIR are evident (Fig. 4). Differences in mean MIR are significant (ANOVA, P=0.0062) throughout the year. This pattern suggests that the formation of bands starts in August, after the abrupt fall in mean MIR values. Unfortunately, no samples were obtained in March during the entire study period. This, however, does not impede the definition of the time formation of the new band.

In almost all instances the mean back-calculated length-at-age was smaller than mean observed length-at-age for both sexes (Table 1). Linearized observed size-at-age data when compared by sex did not show significant differences (ANCOVA, P > 0.05). Also, on the basis of back-calculated length-at-age, male and female growth curves were estimated separately and then compared by Bernard (1981) multivariate analysis, which did not indicate significant difference in growth between sexes.

$$S = \begin{vmatrix} L\infty & K & t_0 \\ 156.95 & -0.0816 & -2.1591 \\ 0.00004 & 0.0012 \\ 0.0079 & t_0 \end{vmatrix}$$

$$T^2 = -1186.51, \qquad T_{0.013,100}^2 = -12.179.$$

Since there were no differences between sexes in male and female growth, data were treated together, incorporating the 6 individuals of undetermined sex. Mean back-calculated length-at-age for both sexes for

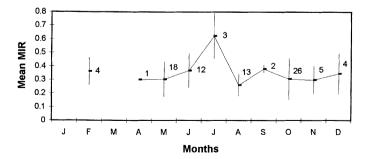


Fig. 4. Mean vertebral MIR by month for the whitetip shark, C. longimanus. Vertical bars are standard deviation of mean.

Table 1 Mean back-calculated (\pm s.d.) and mean observed length-at-age data (\pm s.d.) for male and female whitetip shark, *C. longimanus*, collected off northeast Brazil

| t | Females | | Males | | | | | |
|----|--------------------|--------------------|-------------------|--------------------|--|--|--|--|
| | $BC (cm) \pm s.d.$ | OL (cm) \pm s.d. | $BC(cm) \pm s.d.$ | OL (cm) \pm s.d. | | | | |
| 0 | 71.42 ± 1.34 | 85.67 ± 5.03 | 71.19 ± 1.38 | 71 | | | | |
| 1 | 90.62 ± 1.12 | 103.23 ± 0.4 | 89.71 ± 1.77 | 95 | | | | |
| 2 | 108 ± 1.96 | 115.83 ± 13.98 | 107.56 ± 2.38 | 114.33 ± 4.51 | | | | |
| 3 | 124.13 ± 3.22 | 138.35 ± 8.38 | 123.95 ± 3.21 | 136.8 ± 15.42 | | | | |
| 4 | 138.28 ± 3.75 | 145.67 ± 6.66 | 138.95 ± 3.45 | _ | | | | |
| 5 | 151.68 ± 4.8 | 163.37 ± 9.94 | 153.03 ± 3.63 | 162.3 ± 8.12 | | | | |
| 6 | 163.42 ± 5.15 | 174.51 ± 11.16 | 166 ± 4.38 | 178 ± 8.6 | | | | |
| 7 | 173.71 ± 5.3 | 187.08 ± 5.14 | 177.34 ± 4.31 | 189 ± 10.14 | | | | |
| 8 | 182.91 ± 4.87 | 190.17 ± 6.24 | 187.2 ± 2.32 | 193.82 ± 13.54 | | | | |
| 9 | 191.5 ± 6.43 | 201.4 ± 6.02 | 196.51 ± 2.54 | 199.67 ± 7.02 | | | | |
| 10 | 198.76 ± 7.71 | 207 ± 12.12 | 208.01 ± 2.62 | _ | | | | |
| 11 | 205.77 ± 10.91 | 200 | 216.91 ± 2.13 | 217.5 ± 1.32 | | | | |
| 12 | 221.74 | _ | 226.95 | _ | | | | |
| 13 | 227.94 | 230 | 233.36 | 235.5 | | | | |

ages from 0 to 13 and mean observed length-at-age for the same ages, except age 12, are shown in Table 2. From back-calculated lengths a mean rate of 13.60 cm yr $^{-1}$ was calculated for the first four years; 9.7 cm for 5–7 years and 9.10 cm yr $^{-1}$ after maturity.

VBGF obtained on the basis of back-calculated length-at-age and observed length-at-age yielded varying parameters (Fig. 5). For deriving parameters from observed length-at-age, the corresponding back-calculated length (i.e., 224.3 cm) for age 12 was used,

Table 2 Back-calculated and observed length-at-age data (cm) for combined sexes of the whitetip shark, *C. longimanus* off Northeastern Brazil

| t | n | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|-------------------------------|----|------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| | | 110 | 106 | 102 | 94 | 82 | 78 | 61 | 48 | 33 | 17 | 9 | 6 | 6 | 2 |
| Back-calculated length-at-age | | | | | | | | | | | | | | | |
| 0 | 4 | 69.2 | | | | | | | | | | | | | |
| 1 | 4 | 70.8 | 89.4 | | | | | | | | | | | | |
| 2 | 8 | 72.3 | 90.6 | 108 | | | | | | | | | | | |
| 3 | 12 | 70.3 | 91.4 | 110.8 | 128.9 | | | | | | | | | | |
| 4 | 4 | 71 | 90.1 | 108.3 | 124.2 | 138.9 | | | | | | | | | |
| 5 | 17 | 71.5 | 91.2 | 109 | 125.8 | 141.9 | 155.8 | | | | | | | | |
| 6 | 13 | 70.9 | 90.7 | 109.1 | 126.2 | 142.1 | 156 | 168.1 | | | | | | | |
| 7 | 15 | 72.1 | 91.5 | 109.4 | 126 | 142.3 | 157 | 170.8 | 182.6 | | | | | | |
| 8 | 16 | 71 | 89.7 | 106.8 | 123.3 | 139 | 153 | 165.8 | 177.3 | 187.8 | | | | | |
| 9 | 8 | 71.2 | 89.6 | 106.4 | 121.9 | 136.7 | 150.2 | 162.4 | 173.7 | 184.9 | 194.6 | | | | |
| 10 | 3 | 71 | 89.3 | 105.5 | 120.2 | 134.3 | 146.9 | 159.5 | 171.5 | 182.7 | 191.7 | 200.8 | | | |
| 11 | 4 | 72.5 | 89.7 | 105.9 | 120 | 134.2 | 147.3 | 159.8 | 171.8 | 182.8 | 192.8 | 202.2 | 211.1 | | |
| 12 | | | | | | | | | | | | | | | |
| 13 | 2 | 69.9 | 87.8 | 104.6 | 121.4 | 136.1 | 150.8 | 163.4 | 176 | 187.6 | 198.1 | 207.5 | 215.9 | 224.3 | 230.6 |
| Mean TL | | 71.1 | 90.1 | 107.6 | 123.8 | 138.4 | 152.1 | 164.4 | 175.5 | 185.2 | 194.3 | 203.5 | 213.5 | 224.3 | 230.6 |
| SD | | 0.92 | 1.09 | 1.92 | 2.95 | 3.25 | 8.86 | 4.35 | 4.17 | 2.48 | 2.78 | 3.55 | 3.45 | 0 | 0 |
| Observed length-at-age | | | | | | | | | | | | | | | |
| t | | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
| Mean TL | | 82 | 101.2 | 115.8 | 137.4 | 144.6 | 163 | 175.1 | 188.2 | 192 | 200.7 | 207 | 213.1 | | 232.7 |
| SD | | 8.41 | 4.13 | 9.67 | 10.93 | 5.86 | 8.86 | 9.89 | 8.31 | 10.75 | 5.97 | 12.12 | 8.82 | 2 | 3.89 |

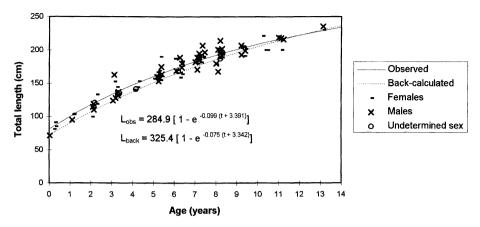


Fig. 5. von Bertalanffy growth curve generated from mean back-calculated lengths and observed length-at-age for both sexes of whitetip shark, *C. longimanus*, -, x and o represent individual observed length-at-age.

due to the lack of mean observed lengths for this age class.

The youngest specimen, still with a visible umbilical scar, was a 71.0 cm male not showing any complete band in vertebral sections. Back-calculated length-at-age ranged from 71.1 cm for age 0 to 230.6 cm for age-class 13, with relatively low standard deviations for both sexes (Table 2). Growth rate, from back-calculated length-at-age was 25.2 cm yr⁻¹ from birth to the first ring corresponding to 38.7% of the birth length, assuming 70.0 cm as the length at birth (Bigelow and Schroeder, 1948).

From the study sample size at maturity is 180.0–190.0 cm for both sexes (pers. obs.) corresponds to 7–8 and 6–7 year-old individuals, using back-calculated and observed length-at-age VBGF, respectively. The

oldest specimen whose vertebrae were used for back-calculated growth curve was a 14 year-old 235.5 cm male, whereas the oldest female (230.0 cm) was 13 year-old. Lee's phenomenon (Ricker, 1980), a tendency for back-calculated lengths of older fish in the early years of life to be systematically lower than those of younger ones at the same age, was not evident.

The study of age composition for the overall sample (n=258 individuals) (Fig. 2) indicated that 27% of the specimens were older than 6–7 years, considered the age at maturity, corresponding to sizes larger than 180.0-190.0 cm. Moreover, considering sexes separately, 32% of males and 22% of females corresponded to the adult part of the sample. In general, the male sample is composed of individuals ranging from 0 to 14 year-class and females from 0 to 17 years.

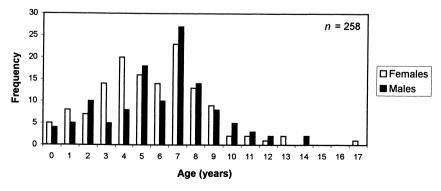


Fig. 6. Age composition of the sample of whitetip shark, C. longimanus collected off northeastern Brazil.

Modal age class indicated complete recruitment to fishery at age 7 for both males and females, where 50 specimen are located (Fig. 6).

4. Discussion

Several techniques have been used for enhancing the pattern of bands in elasmobranch vertebrae (Cailliet et al., 1983), among them the most common methods are Alizarin stains and silver nitrate impregnation employed in *P. glauca, Sphyrna lewini* (Griffith and Smith, 1834), *C. falciformis* and *Negaprion brevirostris* (Stevens, 1975; Schwartz, 1982; Gruber and Stout, 1983; Bonfil et al., 1993). These techniques, however, were not found to increase the contrast between rings in the current study. Accordingly, satisfactory results were obtained for sections without stains for *Galeocerdo cuvieri* (Peron and Le Sueur, 1822) (Branstetter et al., 1987) and *C. plumbeus* (Nardo, 1827) (Sminkey and Musick, 1995).

Significant differences in mean MIR throughout the year provided support for the annual deposition of one band, as has been shown for most carcharhinids like *C. falciformis*, *C. plumbeus*, *C. obscurus*, etc. (Bonfil et al., 1993; Natanson et al., 1995: Sminkey and Musick, 1995). Mean MIR values approaching 0.9 were recorded in July with low values around 0.2 starting in August. This pattern shows high mean MIR values followed by an abrupt decrease, suggesting that the band is completely formed in July and a new band begins to form in August, when the lowest values were recorded. The lack of data in March is not thought to have hampered the mean MIR interpretation.

Both Bernard (1981) multivariate analysis and ANCOVA performed with linearized size-at-age data showed no significant differences between male and female growth. Considering identical growth rates, the fact that females attain larger sizes than males may be attributed to differential mortality between sexes, or to reduced growth in males after maturity. The same pattern, as yet unexplained, has been shown for other species such as *C. obscurus* and *C. plumbeus* (Natanson et al., 1995; Sminkey and Musick, 1995).

Mean back-calculated length-at-age values are lower than mean observed length-at-age as indicated in Tables 1 and 2. Differences are due to capture after the deposition of the last band, as also for *C. falci-*

formis (Bonfil et al., 1993). Higher values of observed length-at-age brought about a lower value for L_{∞} and a slightly higher value for the K parameter.

In a previous study by Saika and Yoshimura (unpublished), L_{∞} values from 270.0 to 300.0 cm and K ranging from 0.04 to 0.09 were estimated for both sexes. The upper limit of these results does not differ greatly from ours, as a L_{∞} of 325.4 cm and a K of 0.075 yr⁻¹, were determined from back-calculated lengths and $L_{\infty}=284.9$ cm and K=0.099 yr⁻¹ were obtained from observed length-at-age.

Considering the reliability of L_{∞} , observed length-at-age provided a result closer to the maximum lengths in captures ($L_{\rm c_{max}}$) than back-calculated length-at-age. Thus, there have been recordings of $L_{\rm c_{max}}=270.0$ cm off Africa (Bass et al., 1973), $L_{\rm c_{max}}=270.0$ cm off Australia (Stevens, 1975), $L_{\rm c_{max}}=250.0$ cm in the Pacific Ocean (Saika and Yoshimura, unpublished), and in 1996 $L_{\rm c_{max}}=245.0$ cm in the Indian Ocean and $L_{\rm c_{max}}=240.0$ cm in the southeastern Atlantic (Stretta et al., 1996) of the same order of $L_{\rm c_{max}}=250.0$ cm in the present study.

Although, back-calculated growth parameters have been generally accepted as best describing growth in previous studies on elasmobranchs (Bonfil et al., 1993; Natanson et al., 1995; Sminkey and Musick, 1995) due to the robustness of the method which greatly increases the amount of information from each specimen (Bonfil et al., 1993), parameters obtained on the basis of observed length-at-age were considered more consistent with maximal lengths, whereas L_{∞} derived from back-calculated length-at-age extrapolates $L_{\text{c}_{\text{max}}}$ by 30%.

Natanson and Kohler, 1996, analyzing observed size-at-age for the dusky shark, concluded that growth slows considerably after maturity as demonstrated by high values of standard deviation of mean lengths. Such a pattern, common in Carcharinids, is extreme in the dusky shark, in which the same size may vary by 15 years, rendering unreliable the prediction of age after maturity from a given length using the VBGF. This situation, occurs to a lesser extent for *C. long-imanus* and despite limitations, the inverse von Bertalanffy growth equation was used to infer the age composition of the sample, considered a more appropriate method than age-length keys (Kimura, 1977).

Bigelow and Schroeder (1948) estimated that young individuals were born at about 65.0–70.0 cm and Bass

et al. (1973), with their southern African sample, estimated the birth size at 60.0–65.0 cm. Garrick (1982) observed full-term embryos from Hawaii at 60.0–61.0 cm long. The smallest specimen caught in the wild in the present study was 71.0 cm long, showing fresh umbilical scars, thus suggesting that 70.0 cm may be assumed as the birth size in the area as proposed by Bigelow and Schroeder (1948). Based on this observation, 71.0 cm was used as L_0 in the present study.

Considering the maximum length at birth of 70.0 cm, a growth rate > 35% of the birth length is attained during the first free-living year. Newborns showing visible umbilical scars with the first band not yet completely formed were caught, suggesting that females give birth in this study area. Data presented here indicate that the birth translucent ring (age 0) is laid down at or shortly after birth, as demonstrated by back-calculated length-at-age. This pattern is confirmed by the newborns caught in August which did not present any complete band in vertebrae.

The inclusion of the oceanic whitetip shark in the IUCN redlist in 1998 as "near threatened" with observations that it is subject to high levels of bycatch and to some target fisheries is in accordance with the findings of several authors, among them Compagno (1984), Taniuchi (1990) and Bonfil (1994). Taniuchi (1990) states that it is abundant in pelagic fisheries carried out by American and Japanese fleets. Also, in the Indian Ocean, where Taiwanese and Korean fleet operate, research vessels obtained important catches. In the southern Atlantic where Brazilian (Hazin et al., 1990) and Brazilian-leased vessels (from USA, Taiwan, Spain) targeting swordfish and tuna are in operation, fin landings sampling indicates that the species is the third most abundant in catches (pers. observation).

Bigelow and Schroeder (1948) mentioned that the maximum length effectively measured was 350.0 cm in 1940s, perhaps exceptionally attaining 395.0 cm. This length seems to have never been measured, although is also stated by Compagno (1984). It is implied from the general context that under an increasing fishing pressure the length composition of the species may have been altered since the accounts from the late forties. Thus, the scarcity of individuals larger than 270.0 cm in catches obtained worldwide, as referred above, may be due to fisheries which have reduced the mean length and maximum sizes. The

small number of old (and large) fishes in catches may be the result of their actual small representation in the population. This is expected in populations under fishing pressure (Sparre et al., 1989), mainly considering that it is fully recruited to fisheries earlier than the age at maturity and may be highly vulnerable to overfishing due to *K*-selected characteristics which includes a long gestation period, low fecundity and slow growth. Special attention should be paid to the oceanic whitetip shark, which, like all other elasmobranchs, may possess no means of compensating for reductions in its population (Anderson, 1990).

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References

Anderson, E.D., 1990. Estimates of large shark catches in the Western Atlantic and Gulf of Mexico, 1960–1986. In: Pratt, H., Gruber, S., Taniuchi, T. (Eds.), Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries. NOAA Technical Report NMFS circular 90, pp. 443–454.

Backus, R.H., Springer, S., Arnold Jr, E.L., 1956. A contribution to the natural history of the white-tip shark *Pterolamiops long-imanus*. Deep Sea Res. 3, 178–188.

Bass, A.J., Aubrey D', D.J.D., Kitnasamy, N., 1973. Sharks of the east coast of Southern Africa. I. Genus Carcharhinus (Carcharhinidae). S. Afr. Assoc. Mar. Biol. Res. Invest. Rep. 38, 100.

Beamish, R.J., Fournier, D.A., 1981. A method for comparing the precision of a set of age determinations. Can. J. Fish. Aquatic. Sci. 38, 982–983.

- Bernard, D.R., 1981. Multivariate analysis as a means of comparing growth in fish. Can. J. Fish. Aquatic Sci. 38, 233– 236.
- von Bertalanffy, L., 1938. A quantitative theory of organic growth. Human Biol. 10, 181–213.
- Bigelow, H.B., Schroeder, W.C., 1948. Fishes of the Western North Atlantic, Lancelets, Cyclostomes, Sharks, Memoirs of Sears Foundation for Marine Research. Number I, 576 pp.
- Bonfil, R., 1994. Overview of world elasmobranch fisheries. FAO Fisheries Technical Paper 341, 119.
- Bonfil, R., Mena, R., Anda, D., 1993. Biological parameters of commercially exploited silky shark, *C. falciformis*, from the campeche bank, Mexico. NOAA Technical Report NMFS Circular 115, 73–76.
- Branstetter, S., Musick, J.A., Colvocoresses, J.A., 1987. A comparison of the age and growth of the tiger shark, *Galeocerdo cuvieri*, from off Virginia and from the northwestern gulf of Mexico. Fishery Bull. 85(2), 269–279.
- Cadenat, J., Blache, J., 1981. Requins de Méditerranée et d'Atlantique. Faune Tropicale. ORSTOM 21, 330.
- Caillet, G., Martin, K.L., Kusher, D., Wolf, P., Welden, B.A., 1983.
 Techniques for enhancing vertebral bands in age estimation of California elasmobranchs. In: Prince, E.D., Pulos, L.M. (Eds.),
 Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks.
 NOAA Technical Report NMFS 8, pp. 157–165.
- Campana, S.E., 1990. How reliable are growth back-calculations based on otoliths? Can. J. Fish. Aquatic Sci. 44, 1922–1929.
- Compagno, L.J.V., 1984. FAO Species Catalogue, vol. 4: Sharks of the world, part 2; Carcharhiniformes. FAO Fish. Synopsis, vol. 125, pp. 251–655.
- Compagno, L.J.V., 1988. Sharks of the order Carcharhiniformes. Princeton University Press, Princeton, NJ, p. 486.
- Fourmanoir, P., 1961. Requins de la côte de Madagascar. Mem. Inst. Sci. Madagascar (Ser. F) 4, 1–81.
- Garrick, J.A.F., 1982. Sharks of the genus *Carcharhinus*. NOAA Tech. Rep. NMFS circular, 194 pp.
- Gohar, H.A.F., Mazhar, F.M., 1964. The elasmobranchs of the northwestern Red Sea. Publ. Mar. Biol. Stn. Alghardaga 13, 3–143.
- Gruber, S., Stout, R., 1983. Biological materials for the study of age and growth in tropical marine elasmobranch, the Lemon Shark, Negaprion brevirostris (Poey). In: Prince, E.D., Pulos, L.M. (Eds.), Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks. NOAA Technical Report NMFS circular 8, pp. 193– 205.
- Guitar Manday, D., 1975. Las pesquerias pelago-oceanicas de corto radio de acción en la région noroccidental de Cuba. Ser. Oceanol. Acad. Cienc. Cuba 31, 26.
- Hazin, F.H.V., Couto, A.A., Kihara, K., Otsuka, K., Ishino, M., 1990. Distribution and abundance of pelagic sharks in the southwestern equatorial Atlantic. J. Tokyo Univ. Fish. 77(1), 51–64.

- Kimura, D.K., 1977. Statistical assessment of the age-length key. J. Fish. Res. Board Can. 34, 317–324.
- Linewaever, T.H., Backus, R.H., 1970. The Natural History of Sharks. J.B. Lippencott Company, Philadelphia, 256 pp.
- Natanson, L.J., Casey, J.G., Kohler, N.E., 1995. Age and growth estimates for the dusky shark, *C. obscurus*, in the western North Atlantic Ocean. Fish. Bull. 93, 116–126.
- Natanson, L., Kolher, N.E., 1996. A preliminary estimate of age and growth of the dusky shark *C. obscurus* from the South-West Indian Ocean, with comparisons to the Western North Atlantic population. S. Afr. J. mar. Sci. 17, 217–224.
- Prager, M.M., Saila, S.B., Recksiek, C.M., 1987. FISHPARM: a microcomputer program for parameter estimation of nonlinear models in fishery science. Dep. Oceanography, Old Dominion University, Norfolk, VA. Technical Report 87-10, pp. 1–37.
- Randall, J.E., 1963. Dangerous sharks of the western Atlantic. In: Gilbert, P.E., Garrick, J.A.F., Schultz, L.P. (Eds.), Sharks and Survival. D.C. Heath and company, Boston, 361 pp.
- Ricker, W.E., 1980. Cacul et interprétation des statistiques biologiques des populations de poissons. Bull. Fish. Res. Board Can., 409pp.
- Schwartz, F.J., 1982. Shark ageing methods and age estimation of scalloped hammerhead, *Sphyrna lewini* and dusky *C. obscurus*, sharks based on vertebral rings counts. In: Prince, E.D., Pulos, L.M. (Eds.), Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks. NOAA Technical Report NMFS circular 8, pp. 167– 173.
- Sminkey, T.R., Musick, J.A., 1995. Age and growth of the sandbar shark, *C. plumbeus*, before and after population depletion. Copeia 1995(4), 871–883.
- Sparre, P., Ursin, E., Venema, S.C., 1989. Introduction to tropical fish stock Part 1. Manual. FAO Fisheries Technical Paper no. vol. 306(1). Rome, 337 pp.
- Springer, S., 1950. A revision of North American sharks allied to the genus *carcharhinus*. Am. Mus. Novit. 1451, 13.
- Stevens, J.D., 1975. Vertebral rings as a means of age determination in the blue shark *Prionace glauca* L. J. Mar. Biol. Assoc. UK 55, 657–665.
- Strasburg, D.W., 1958. Distribution, abundance and habits of pelagic sharks in the central Pacific Ocean. US Fish. Wildl. Serv. Fish. Bull. 58, 335–361.
- Stretta, J.M., Molina, A.D., Ariz, J., Domalain, G., Santana, J.C., 1996. Les espèces associées aux pêches thonières tropicales. Programme BIOECO/93/05. Institut Français pour le Développement en Coopération-ORSTOM/Instituto Espagnol de Oceanografia-IEO. Deuxième et Quatrième parties, 286 pp.
- Taniuchi, T., 1990. The role of elasmobranch in Japanese Fisheries.
 In: Pratt, H., Gruber, S., Taniuchi, T. (Eds.), Elasmobranchs as
 Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries. NOAA Technical Report
 NMFS circular 90, pp. 415–426.
- Zar, J.H., 1996. Biostatistical Analysis, Third ed. Prentice-Hall, Englewood Cliffs, NJ, 662 pp.