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Age and Growth of the Bull Shark, *Carcharhinus leucas*, from Southern Gulf of Mexico

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Abstract

Age and growth of bull shark, *Carcharhinus leucas,* was investigated in the southern Gulf of Mexico (Veracruz and Campeche, Mexico) from December 1993 through June 1997. Ninety-five specimens were obtained from commercial fishery catches, and vertebrae were examined from 20 males, 61 females and 14 individuals unidentified to sex. Vertebrae were examined using five different techniques to enhance the visibility of growth rings: i) alizarin red stain, ii) crystal violet stain, iii) X-ray, iv) silver nitrate stain, and v) without staining. Verification of temporal growth ring formation was done by the indirect method of marginal increment analysis. An isometric relationship was found between growth and length of centrum, is described by a linear equation. Age-at-maturity was 10 years (204 cm total length, TL) for females and 9-10 years (190-200 cm TL) for males. The oldest female was 28 (256.0 cm TL), and the oldest male was 23 (243.0 cm TL). The von Bertalanffy growth parameters were estimated for the species (L_∞ = 256.4 cm TL, k = 0.1397 per year and t_o = -1.935), for males (L_∞ = 248.4 cm TL, k = 0.1692 per year and t_o = -1.03), and for females (L_∞ = 262.1 cm TL, k = 0.1235 per year and t_o = -2.44). Sexual differences for each particular growth curve were found, L_∞ being the parameter that showed the greatest difference between males and females; females attain a larger size.

Key words: Age, ageing methods, *Carcharhinus leucas*, growth, length maturity, vertebrae

Introduction

In the Gulf of Mexico, 33 main species of sharks are commercially exploited (30 000 tons). The sixth most important by volume captured (approximately, 700 tons) is the bull shark, *Carcharhinus leucas*, contributing 2% of the catch in the region (Rodríguez de la Cruz *et al*., 1996). This is a coastal, estuarine, riverine and lacustrine shark usually found near-shore in marine habitats. This species has a widespread distribution along the continental coast of all tropical and subtropical seas, and travels far up warm rivers into freshwater lakes (Compagno, 1984). Although information on its freshwater biology is documented by Thorson *et al*. (1966) and Thorson (1971; 1972), information on age and growth data are scarce (Thorson and Lacy, 1982; Branstetter and Stiles, 1987). In this paper, age and growth of the *C. leucas* from the southern Gulf of Mexico are reported to further contribute to the knowledge on the population dynamics.

Materials and Methods

Bull sharks (n = 95) were obtained from the commercial fishery catches in coastal and shelf waters of Veracruz and Campeche, Mexico, from December 1993 through June 1997. Total length (TL, ±0.5 cm) of individuals was

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measured as the straight-line distance between perpendiculars from the snout to the tip of the caudal fin with the caudal fin in a natural position (Branstetter and Stiles, 1987). Maturity of males and females was determined using morphological and gonadal characteristics (for males the degree of clasper calcification and rotation; for females the uterine development, presence of developing or ripe ovarian eggs or presence of uterine embryos).

For age and growth analyses, a section of the vertebral column was removed from under the first dorsal fin. Vertebrae were then preserved in 70% isopropyl alcohol (Branstetter and McEachran, 1986). Individual centra were submersed in a 5.25% solution of sodium hypochlorate for 10–40 minutes (Wintner and Cliff, 1996) to facilitate the mechanical removal of the neural arch, apophysis and remaining connective tissue. A sagittal section was cut from centrum with an Isomet saw equipped with a diamond-bordered blade. Thin laminae (thickness 0.4 ± 0.1 cm) were obtained and mounted on glass microscope slides with clear epoxy resin for viewing under transmitted light.

Ring-enhancing methods

Vertebrae having <15 bands could be counted without any staining technique but those with a greater number of rings presented some problems. In these cases, five methods to enhance visibility of growth rings were tested: i) alizarin red stain, ii) crystal violet stain, iii) X-rays, iv) silver nitrate stain, and v) without staining. The alizarin red method proved to be a simple way to enhance the rings.

Distinct marks (annuli), as illustrated by Bransttetter and Stiles (1987) were visible in the intermedialia of the centra (Fig. 1). A growth ring was defined as a pair of opaque (more mineralized) and translucent bands. To confirm that all the vertebrae from one animal have the same number of rings, complete vertebral columns from two specimens (from one male and one female) were analyzed. The number of rings on every fifth vertebra was counted. Preliminary results showed that the number of rings was the same throughout the vertebral column (P >0.05) and that the best vertebrae to use for age determination were the ones located under the first dorsal fin, since their radius has the greatest magnitude (Fig. 2).

Ring counts

Three non-consecutive counts, in which the reader had no knowledge of the identity or characteristics of specimens, were made. The average percentage error index (APE, Beamish and Fournier, 1981) was used as an estimate of count reproducibility. An upper limit in the APE was set at 20% for each vertebra (Wintner and Cliff, 1996). Samples were not included in the analysis if, after a fourth count, they were above this limit. Final age estimates were the average of at least three readings.

Centrum analysis

The radius of each centrum was measured from the focus to the distal margin of the corpus calcareum under a binocular dissecting microscope equipped with an ocular micrometer, and the radius was then related to TL through linear regression analysis (Killam and Parsons, 1989).

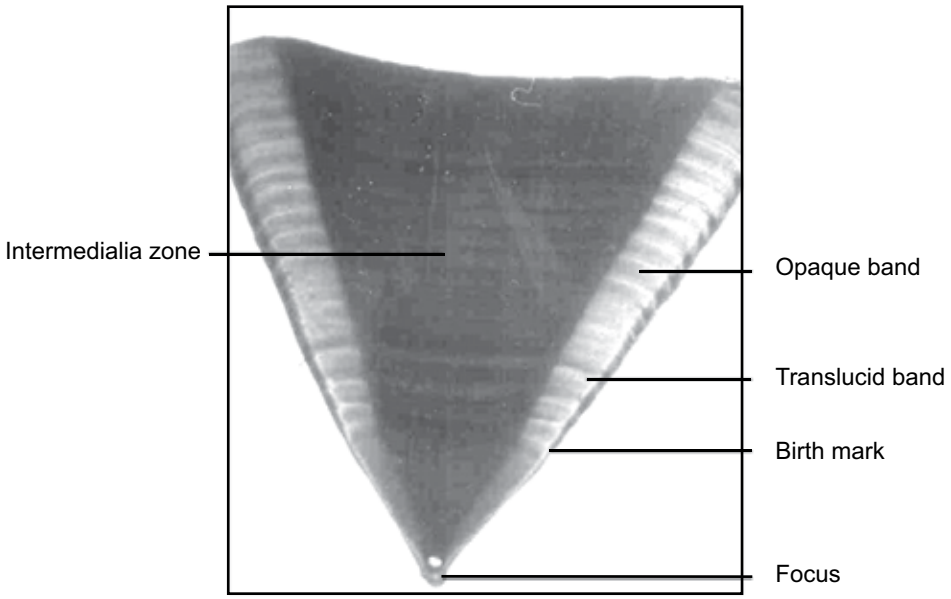

Fig. 1. One half of a sagittal section of a centrum of bull shark, *Carcharhinus leucas*, showing the growth marks used to estimated ages.

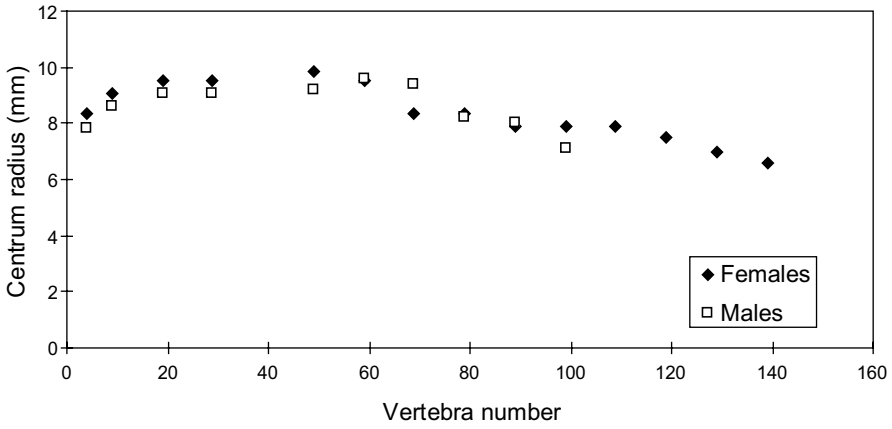

Fig. 2. Centrum radius at different locations along the vertebral column of bull shark, *Carcharhinus leucas*, from the southern Gulf of Mexico

Differences between regression lines of data belonging to males and females were tested with an analysis of covariance (Zar, 1999). The periodicity of the formation of the rings was assessed by examining the margins of vertebrae using the marginal increment analysis (MI) calculated by the following equation (Chen *et al.*, 1990; Galluci *et al*., 1996; Kwang-Ming *et al*., 1998):

$$MI = \frac{R - r_b}{r_b - r_{b-1}}$$

where R is the centrum radius, and r_b and r_{b-1} are the radii of the last and one before the last annuli, respectively. Time-series of monthly MI data was analyzed using a third order polynomial smoothing to obtain the time of annulus formation.

Growth

The von Bertalanffy growth model was fitted with a computerized algorithm (FISHPARM; Prager *et al*., 1987) using observed age-length data (11 data for males and 42 data for females, respectively; Table 1). Hotelling's T^2 test (Bernard, 1981) was used to compare growth curves of the two sexes. This test assumes that estimations of L_∞, k and t_o for both groups (males and females) were obtained from two normal distributions of joint probability with three variables and one common variance.

Results

The length distribution of the bull shark *Carcharhinus leucas* captured during the sampling period is shown in Fig. 3. Three main modes can be observed: the first one includes individuals ≤131.5 cm TL, the second includes the range 159.6 to ≤285.5 cm TL, and the last one, individuals ≥313.6 cm TL.

Vertebrae of 20 males, 61 females, and 14 specimens unidentified to sex were analysed, included 3 embryos. Exact agreement of ring counts was reached on 70% of readings. The 2.37% APE indicated that aging had a relatively high level of precision. Age estimates ranged from 5 to 23 years in males of *C. leucas* (TL range 165–254 cm), and from 4 to 28 years in females (174–271 cm). This information was used to calculate von Bertalanffy parameters (Table 1), for these analyses, embryo data were not used.

The relationship between centrum radius (mm) and TL was linear. Since no differences in the regression lines of sexes were detected (P >0.05), data were pooled and the following equation was calculated:

$$TL = 14.42X + 28.43 \, (n = 75; r^2 = 0.89)$$

where X = centrum radius.

Monthly analysis of MI data is shown in Fig. 4. Polynomial smoothing showed that MI values have a peak in early spring, while low values are present in the fall suggesting that band deposition takes place at this time of the year, verifying the annual periodicity of bands. Apparently, the annulus is formed at birth since unborn sharks did not have an embryonic mark.

In Fig. 5, growth curves of *C. leucas*, as described by the von Bertalanffy growth model fit with observed data (Table 1), are shown.

Table 2 contains the values of the growth parameters, their standard errors, and coefficients of variation calculated with the Prager *et al*., (1987) method for both sexes and population. The results of the multivariate

TABLE 1. Age-length (TL, cm) relationship of the bull shark, *Carcharhinus leucas*, from the southern Gulf of Mexico. Standard deviations (SD) and sample size (*n*) are shown.

	Males			Females		
Age-group	Total length (cm)	SD	*n*	Total length (cm)	SD	*n*
embryo	39.0	12.7	2	55.0		1
4				174.0		1
5	165.0		1			
7	174.0		1	185.5	13.4	2
8	201.0		1			
9	206.0		1	196.8	6.3	5
10				201.3	15.1	3
11				209.7	9.5	6
13				215.6	16.7	4
14	223.0	12.7	2			
16				219.0		1
17				226.8	10.0	5
18	234.0		1			
19	237.0		1			
20	241.0	4.2	2	238.8	15.1	4
22				247.3	22.5	3
23	254.0		1	253.67	21.1	3
25				256.0	1.4	2
26				265.0		1
28				271.0	8.5	2

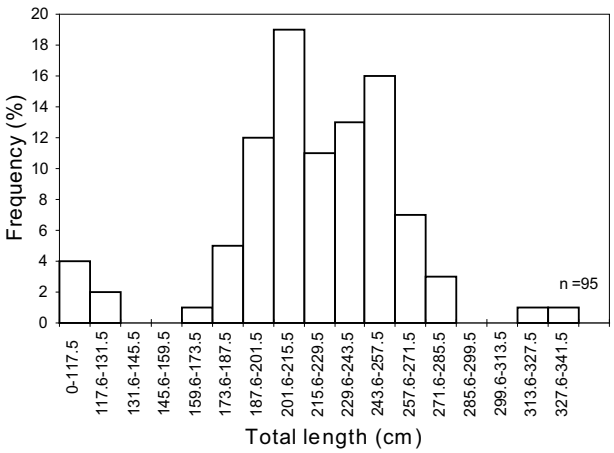

Fig. 3. Length distribution of 95 bull sharks, *Carcharhinus leucas*, sampled in the southern Gulf of Mexico December 1993–June 1997.

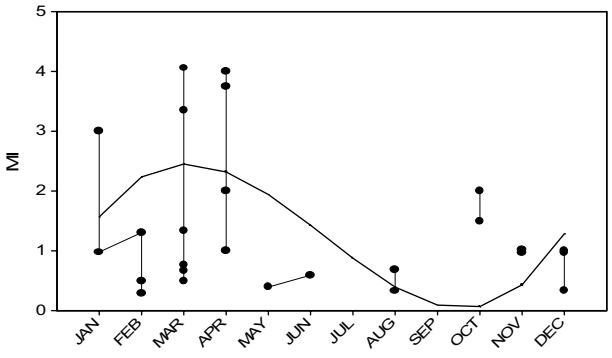

Fig. 4. Monthly analysis of Marginal Increment (MI) data for bull shark, *Carcharhinus leucas*, from the southern Gulf of Mexico. – Third order polynomial fit.

analysis show that males and females grow differently. The calculated T^2 value is significant (P <0.05). L_∞ is the parameter that showed the highest differences between sexes (Table 3).

Age at maturity was 10 years (204 cm TL) for females and 9–10 years (190–200 cm TL) for males. Growth rates of *C. leucas* are high during the first ten years of life, until males and females reach sexual maturity. After maturity is reached, growth varies widely among individuals of the same age (Fig. 6).

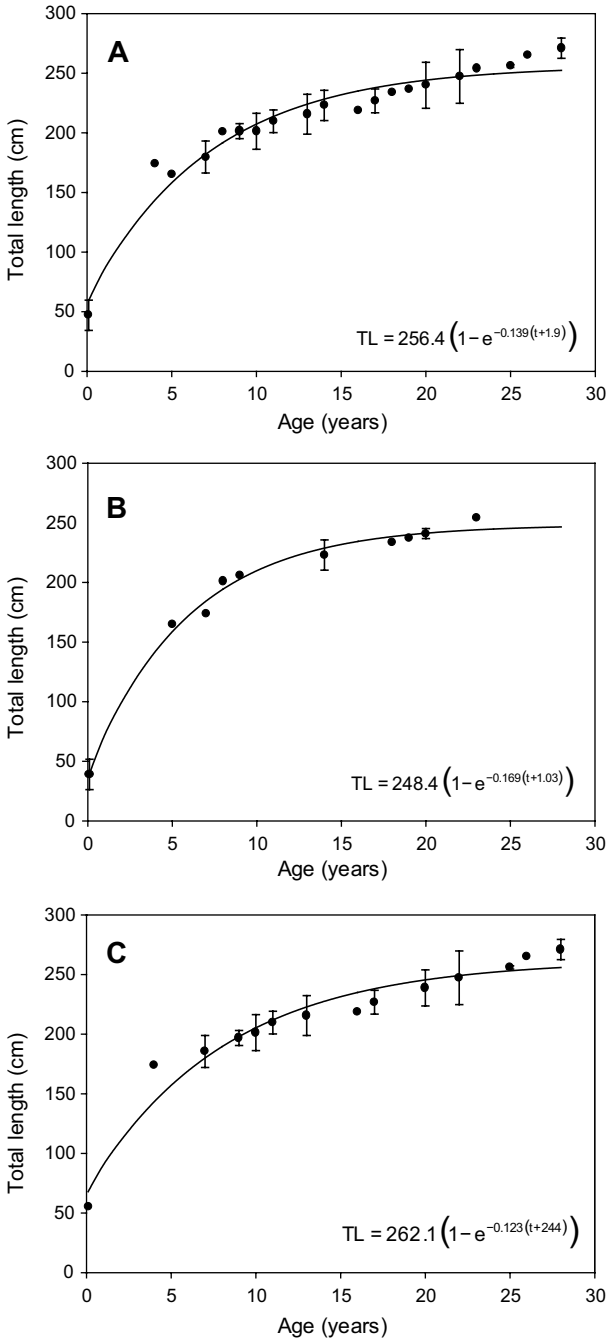

Fig. 5. Von Bertalanffy growth curve of bull shark, *Carcharhinus leucas*, from the southern Gulf of Mexico. (**A**) sexes combined; (**B**) males; (**C**) females.

Discussion

The fishery of the bull shark in the southern Gulf of Mexico is focused to individuals in the length range between 201 cm and 215 cm TL. 72% of these organisms were mature sharks.

In this work, we tried several techniques to enhance the visibility of bands in centra. The alizarin red method was used since it proved to be an easy and simple way to give good results, enhancing the rings in vertebrae of *C. leucas* having ≥15 bands (Fig. 1). Nonetheless, some of the data obtained in this study may have been underestimated because the distance between bands in older sharks was small due to the slow growth rates. Francis and Mulligan (1998), in their study on the age of the school shark *Galeorhinus galeus*, reported that it was difficult to discern all the growth bands but several other papers on this subject have not reported this limitation (Caselman, 1983; Casey *et al.*, 1983; Schwartz, 1983; Cailliet *et al*., 1985; Brown and Gruber, 1988; Casey and Natanson, 1992).

In previous works, the X-ray method was used to enhance growth bands in the blue shark *Prionace glauca*, the thresher shark *Alopias vulpinus*, and the shortfin mako *Isurus oxyrinchus* (Caillet *et al.,* l983, Yudin and Cailliet, 1990). In our case, this technique was not useful and additional technical work is needed to improve exposure times of the X-rays.

An isometric relationship between centrum growth and total length was found as seen in other shark species (Cailliet *et al.*, 1983; Gruber and Stout, 1983; Pratt and Casey, 1983).

Marginal increment analysis of annuli demonstrated that a growth band, consisting of one calcified opaque zone and one translucent zone, is formed with an annual periodicity. Factors that mediate the differential rate of calcium deposition in elasmobranch centra are not known. Changes in temperature and diet (Stevens, 1975), and stress-related activities such as migration (Pratt and Casey, 1983) have been suggested.

Our results show that females of *C. leucas* in the southern Gulf of Mexico reach 28 years of age, while males attain age 23, attaining sizes of 271 ±8.5 cm TL and 254 cm TL, respectively. Branstetter and Stiles (1987), in the northern Gulf, found that the oldest female of this species was 24.2 years (268 cm TL), while the oldest male was 21.3 years (245 cm TL).

The *k* estimates of the von Bertalanffy growth model were 0.12 per year for females, and 0.16 per year for males. Branstetter and Stiles (1987) estimated for the northern Gulf of Mexico population that $k = 0.076$ per year. Typical values for *k* in various species of carcharinids fall in the range 0.05–0.2 (Simpfendorfer, 1993). Due to the paucity of samples in the 0–5 age group, this rate may

TABLE 2. Von Bertalanffy estimated growth parameters for bull shark, *Carcharhinus leucas*. Standard error (SE), Coefficient of variation (CV) in percent, and sample size (*n*), are shown.

	Females	Males	Combined sexes
L_∞	262.1	248.4	256.4
SE	8.78	5.02	6.49
CV (%)	0.03	0.02	0.02
k	0.1235	0.1692	0.1397
SE	0.02	0.01	0.02
CV (%)	0.15	0.09	0.12
t_o	-2.44	-1.03	-1.935
SE	0.74	0.24	0.56
CV (%)	-0.30	-0.23	-0.29
n	11	43	54

TABLE 3. Hotelling's T^2 test (Bernard, 1981) for bull shark, *Carcharhinus leucas.*

T^2 = 298.345			
Growth parameters	Critical values	Confidence intervals	F_o values
L_∞	-13.7	-13.36 a -14.03	493.42
k	0.0457	0.38 a -0.29	1.80
t_o	1.41	1.74 a 1.075	0.049

be an overestimate. Most carcharhinid species studied to date have been found to have slow growth rates and to mature after several years (Thorson and Lacy, 1982; Schwartz, 1983; Simpfendorfer, 1993).

According to our data, age at maturity of *C. leucas* in the southern Gulf of Mexico was 9–10 years. Branstetter and Stiles (1987) found 14–15 years for males and 18+ years for females of the same species inhabiting the northern Gulf of Mexico. Since biological parameters of this species vary according to different localities, in Table 4 we present a summary of available information.

The fishing pressure due to increasing commercial exploitation of *Carcharhinus leucas* in the southern Gulf of Mexico is likely to reduce the abundance of this species as a consequence of its relatively low growth rate and late maturity. As pointed out by Branstetter and Stiles (1987), the combination of these *K*-selected characteristics must be taken into account to regulate the fishery of the bull shark, if we consider that life history pattern of elasmobranchs make this group more vulnerable to over fishing because they have slow growth, large adult size, and late reproduction (Hoening and Gruber, 1990).

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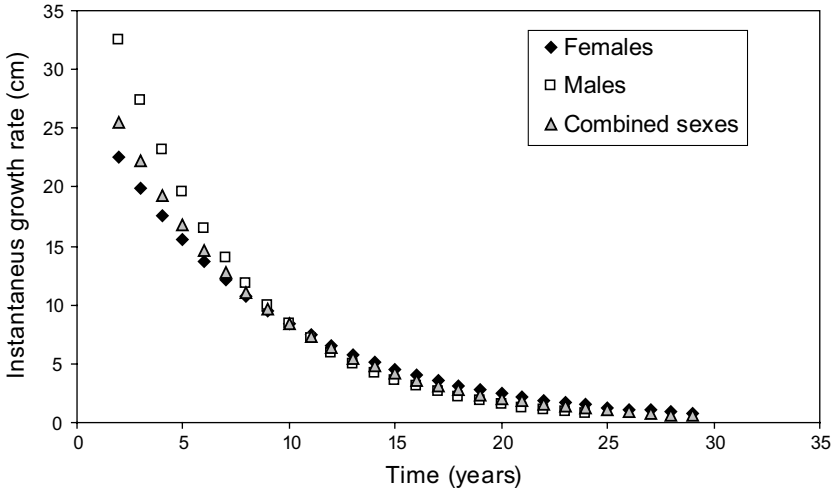

Fig. 6. Instantaneous growth rate of bull shark, *Carcharhinus leucas*, from the southern Gulf of Mexico.

TABLE 4. Information on the biology of the bull shark, *Carcharhinus leucas*.

	Branstetter (1981)	Castro (1983)	Compagno (1984)	Snelson *et al*. (1984)	Branstetter and Stiles (1987)	Rodriquez de la Cruz *et al*. (1996)
Average total length (cm)	NA	F = 240 M = 225	NA	NA	F = 242–268 M = 213–245	206.2
Maximum length (cm)	NA	350	340	NA	F = 268 M = 245	F = 334
Average weight	NA	F = 130 M = 95	NA	NA	NA	NA
Maximum age (years)			14		F = 24 M = 21	
Length-at-maturity (cm)	F = 228 M = 217	200	250	F = 249	F = >225 M = 210–220	F = 204 M = 190–200
Age-at-maturity (years)			6		F = 18+ M = 14–15	
Gestation time (month)	NA	10–11	10–11	NA	10–11	10–11
Time of birth	April–May	April–June	Spring–Summer	May–June	June–August	May–June
Pup size (cm)	75	75	56–81	60–80	75	78
Number of pups	3–6	NA	1–13	NA	NA	1–22
Location	Northern Gulf Of Mexico	North American	Symposis of world data	Indian River, Florida	Northern Gulf of Mexico	Gulf of Mexico

NA: Not available; F: female; M: male.

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