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

(Elasmobranch Fisheries – Oral)

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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) during December 1993–June 1997. Ninety-five specimens were obtained from commercial fishery catches, and vertebrae were examined from 20 males, 61 females, and 14 unidentified organisms. Vertebrae were examined using five different techniques to enhance the visibility of growth rings: i) using alizarin red stain, ii) crystal violet staining, iii) "X" rays, iv) silver nitrate stain, and iv) without staining. Validation of temporal growth rings formation was done by the indirect method of the marginal increment (MI) analysis. An isometric relationship was found between *centrum* growth and length, 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 year-old (256.0 cm TL), and the oldest male was 23 year-old (243.0 cm TL). We estimated the von Bertalanffy growth parameters for the species (L_∞ = 256.4 cm TL, k = 0.1397^{-yr} and t_0 = -1.935), for males (L_∞ = 248.4 cm TL, k = 0.1692^{-yr} and t_o = -1.03), and for females (L_∞ = 262.1 cm TL, k = 0.1235^{-yr} 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 large size.

Key words: Age, Ageing methods, Growth, Vertebral bands, *Carcharhinus leucas*.

Introduction

In the Gulf of Mexico, 33 main species of sharks are commercially exploited (30,000 t). The sixth most important for its volume of capture, 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), age and growth data are scarce (Thorson and Lacy, 1982; Branstetter and Stiles, 1987). In this paper, age and growth of the bull shark from the southern Gulf of Mexico is reported to further contribute to the knowledge on the population dynamics of *C. leucas*.

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 measured as the straight-line distance between perpendiculars with caudal fins in a natural position (Branstetter and

Stiles, 1987). Maturity of males and females was determined using morphological and gonadal characteristics (degree of clasper calcification and rotation for males; uterine development, the presence of developing or ripe ovarian eggs or the presence of uterine embryos, for females).

For age and growth analysis, a section of the vertebral column, under the first dorsal fin, was removed. 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, 1995) to facilitate the mechanical removal of the neural arch, apophysis, and remaining connective tissue. A sagittal section was cut from centrum with an Isomet cutter 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 were 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) using alizarin red stain, ii) crystal violet staining, iii) "X" rays, iv) silver nitrate stain, and iv) without staining. The alizarin red method was used since proved to be an easy and simple way to give good results, enhancing the rings in vertebrae of *C. leucas* having ≥15 bands.

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 prove that all the vertebrae have the same number of rings, two vertebral columns (from one male and one female) were analyzed. The number of rings every fifth vertebra were counted. Preliminary results showed that the number of rings was the same trough out the vertebral column ($p > 0.05$) and that the best vertebra to use for age determination is the one located under the first dorsal fin since its radius has the greater 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, 1995). Samples were not included in the analysis if, after a fourth count, they were above this limit. Final age estimates are 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 then related to TL through linear regression analysis (Killam and Parsons, 1989). 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. 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

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

Vertebrae of 20 males, 61 females, and 14 unidentified organisms were analyzed. Exact agreement of ring counts was reached on 70% of readings. The 2.37% APE indicates that aging had a relatively high level of precision. Age estimations ranged from 4 to 23 years in males of *C. leucas* (144 cm ≤ TL ≤243 cm), and from 5 to 28 years in females (157 cm ≤ TL ≤256 cm). Age–length (TL, cm) relationships are shown in Table 1.

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:

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

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, validating the annual periodicity of bands. Apparently the annulus is formed at birth since unborn sharks did not have an embrionary 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 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 higher 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, hence a wide range of sizes is attained (Fig. 6).

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 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 sub-estimated 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 is difficult to reveal all the growth bands but several papers on this subject do not report 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-rays 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 exposition times of the X-rays.

An isometric relationship between centrum growth and total length was found. Sharks of many genera show this pattern (Cailliet *et al*., 1983; Gruber and Sout, 1983, Pratt and Casey, 1983). The equation obtained by Branstetter and Stiles (1987, Y = 11.2X + 50.6) shows that this relationship varies geographically as a result of the differential growth rates of *Carharhinus leucas*.

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 elasmobrach 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 arrive at age 23, attaining sizes of 271 ± 8.5 cm TL and 254 cm TL. Branstetter and Stiles (1987), in the northern Gulf, found that the older female of this species was 24.2 years old (268 cm TL), while the older male was 21.3 years old (245 cm TL).

The k estimates of the von Bertalanffy growth model were 0.12^{-yr} for females, and 0.16^{-yr} for males. Branstetter and Stiles (1987) estimated, for the northern Gulf of Mexico population, that $k = 0.076^{-yr}$. Typical values for k in various species of carcharinids fall in the range 0.05-0.2 (Simpfendorfer, 1993). 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). The velocity at which L_∞ is reached, results in competitive advantages for sharks. A faster growth rate is likely to improve the individual competitive ability, since larger individuals have advantages over smaller ones in order to acquire and process the environmental and reproductive resources and helps them to withstand fishing pressures, compared to slow-growing populations.

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 this value to be 18 years for 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 rates 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.

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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.

"Age group"	Males			Females		
	Total length (cm)	SD	n	Total length (cm)	SD	n
"Unborn"	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

Table 2. Von Bertalanfy 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

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)	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 (Kg)	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 waters	Synopsis of world data	Indian River, Florida	Northern Gulf of Mexico	Gulf of Mexico

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

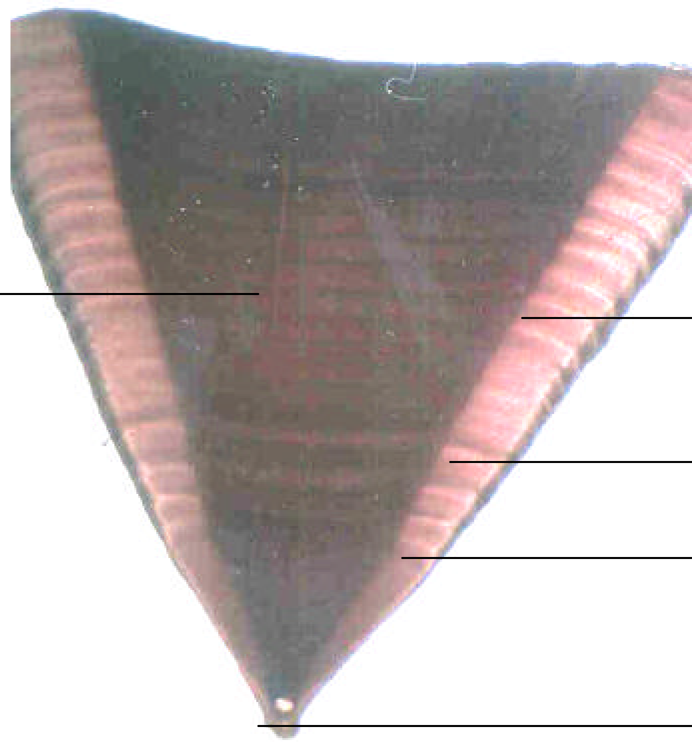

Fig. 1. One half of a sagittal section of a centrum of bull shark, *Carcharhinus leucas* showing the growth marks used to estimated ages.

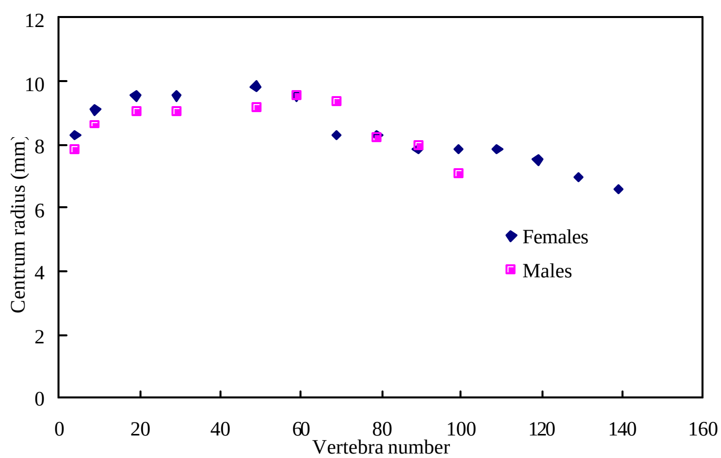

Fig. 2 . Centrum radius at different locations along the vertebral column of bull shark, *Carcharhinus leucas* from the southern Gulf of Mexico.

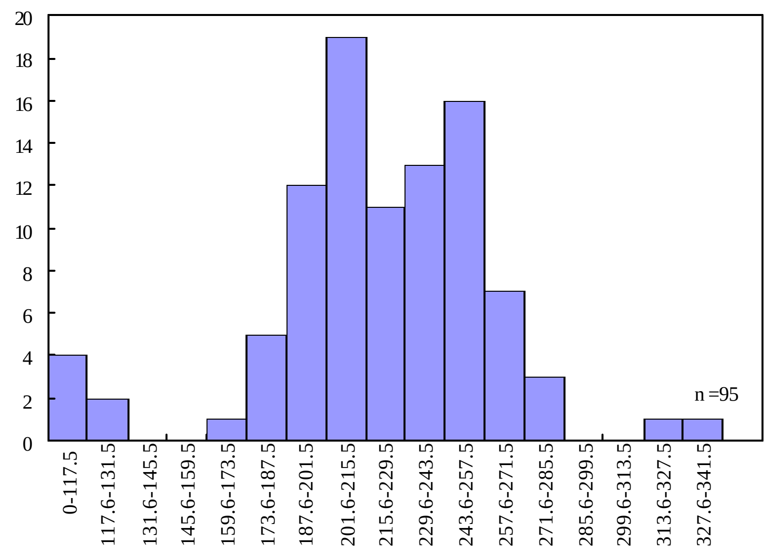

Fig. 3. Catch-length distribution of bull shark, *Carcharhinus leucas* from the southern Gulf of Mexico.

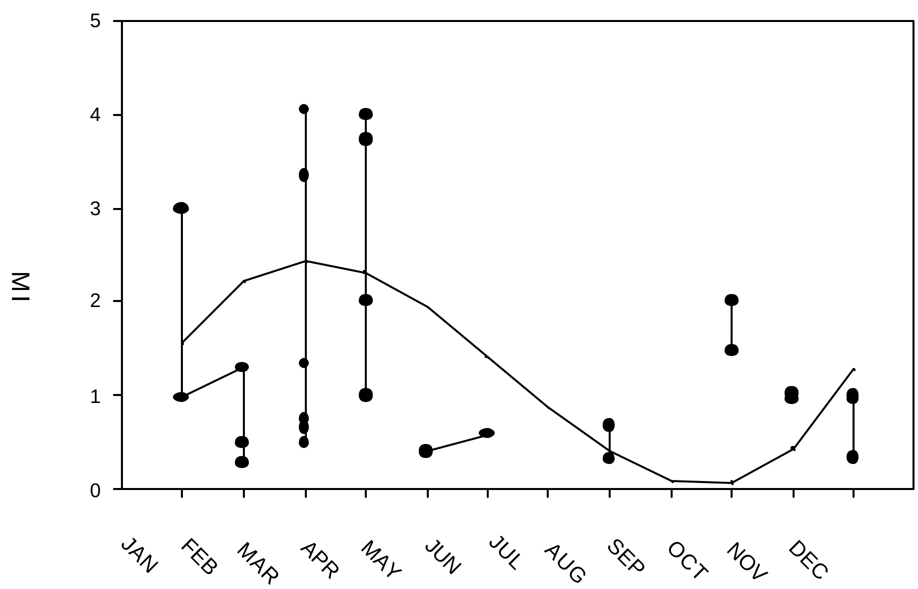

Fig. 4. Monthly analysis of Marginal Increment (MI) data for bull shark, *Carcharhinus leucas* from the southern Gulf of Mexico. ¾ Third order polynomial fit.

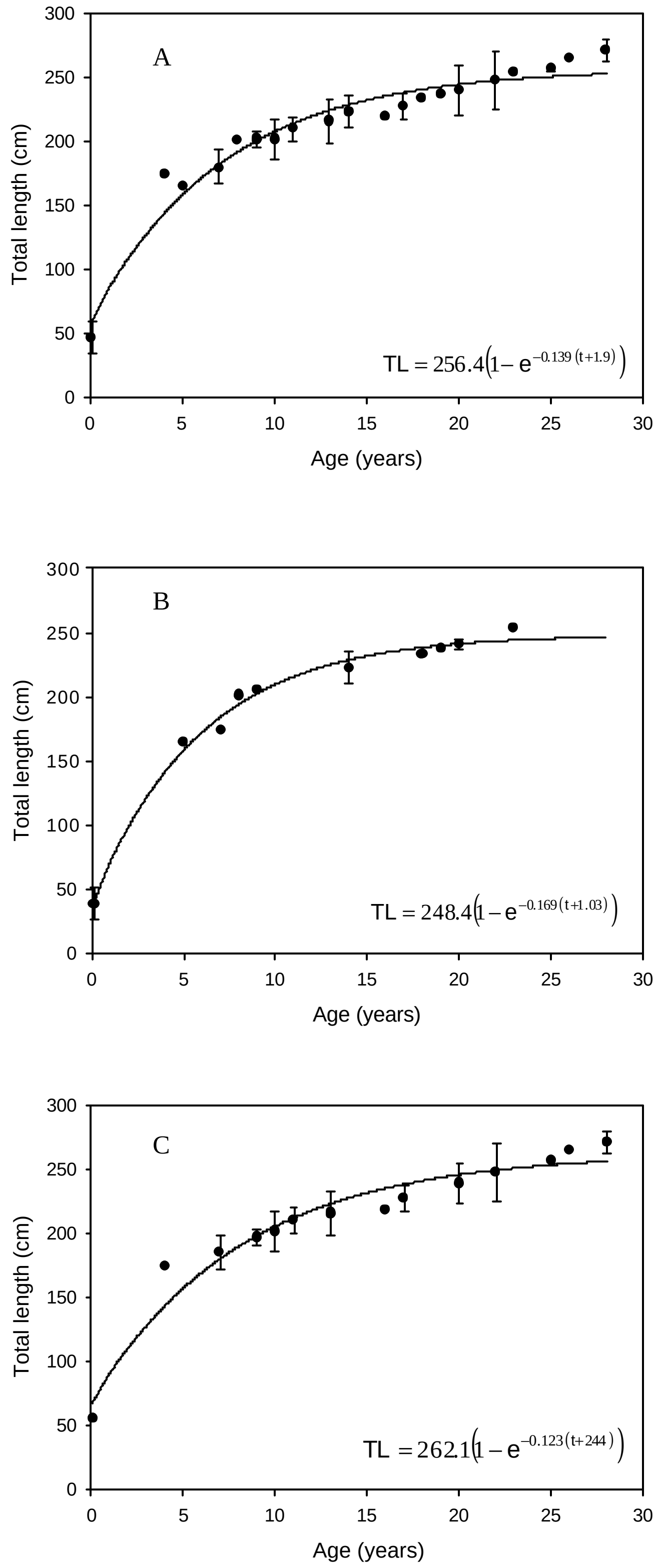

Fig. 5. Von Bertalanffy growth curve of bull shark, *Carcharhinus leucas* from the southern Gulf of Mexico. A: sexes combined; B: males; C: females.

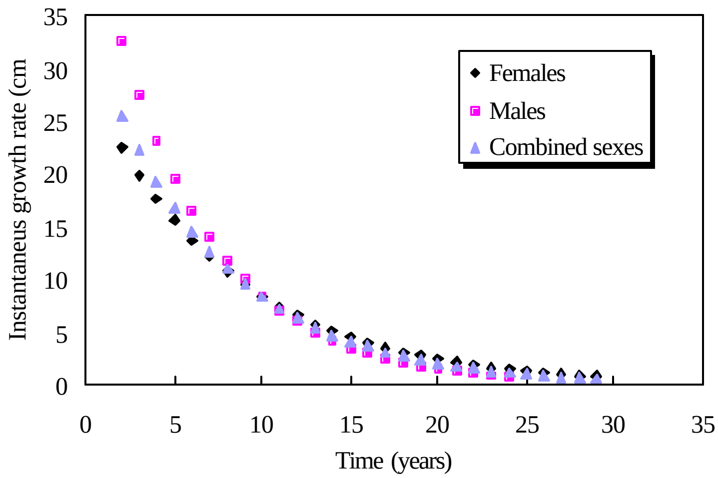

Fig. 6. Instantaneous growth rate of bull shark, *Carcharhinus leucas* from the southern Gulf of Mexico.