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## Age and growth of the daggernose shark, *Isogomphodon oxyrinchus*, from northern Brazil

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**Abstract.** Age and growth of the daggernose shark, *Isogomphodon oxyrinchus*, from northern Brazil were determined from 105 vertebral sections stained with alizarin red-S representing 46 males, 52 females and 7 specimens of unknown sex (58.4 to 141 cm-TL) and verified with length–frequency analysis of 1135 specimens (632 females and 503 males, 58–160 cm). Marginal increments did not show significant differences throughout the year, and it was assumed that one band is formed annually. Different tests provided varying results for growth curve comparisons between sexes; the curves were similar, despite biological differences. von Bertalanffy growth parameters estimated from back-calculated mean lengths, observed mean lengths-at-age and length–frequency analysis were of the same magnitude. Parameters generated from observed length-at-age were chosen for describing growth for the species:  $L_{\infty}$  171.4 cm,  $k$  0.12 year<sup>-1</sup> and  $t_0$  -2.612 years. The largest female aged from vertebrae was 12 years old, whereas the largest male was aged at 7 years. Neonates, ~42.3 cm, showed one band in the vertebrae, formed at birth, or soon thereafter. Males are mature at 103 cm or 5–6 years and females at 115 cm or 6–7 years.

**Resumo.** A idade e o crescimento do cação quati, *Isogomphodon oxyrinchus*, do norte do Brasil foi determinada usando 105 vértebras seccionadas e coradas com alizarina vermelha-S de 46 machos, 52 fêmeas e 7 exemplares de sexo indeterminado (58,4–141 cm-CT). Análise de distribuição de frequência de comprimentos de 1135 indivíduos (632 fêmeas e 503 machos, 58–160 cm) foi utilizada como método de verificação. Os incrementos marginais não mostraram diferenças significativas ao longo do ano, assumindo-se que uma banda é formada anualmente. Com diferentes testes, usados para comparar curvas de crescimento entre os sexos, obteve-se resultados conflitantes; o crescimento foi considerado idêntico entre os sexos, apesar das diferenças biológicas entre machos e fêmeas. Os parâmetros de von Bertalanffy estimados do retrocálculo, comprimentos médios observados e da análise de comprimentos foram semelhantes, tendo sido escolhidos para descrever o crescimento da espécie:  $L_{\infty}$  171,4 cm;  $k$  0,12 year<sup>-1</sup> e  $t_0$  -2,612 years. A maior fêmea cuja idade foi estimada pelas vértebras tinha 12 anos enquanto o maior macho tinha 7 anos. Recém-nascidos de 42,3 cm apresentavam uma banda nas vértebras, formada ao nascer, ou logo depois do nascimento. Machos estão maduros em 103 cm ou 5–6 anos e fêmeas em 115 cm ou 6–7 anos.

### Introduction

The daggernose shark, *Isogomphodon oxyrinchus* (Müller and Henle, 1839), is a viviparous, endemic species of northern South America, found in shallow waters from Venezuela to northern Brazil (Bigelow and Schroeder 1948; Cervigon 1966; Compagno 1984; Lessa *et al.* 1999a). The species range is one of the narrowest known for any elasmobranch

species, with the Maranhão coast as its southernmost limit (Lessa *et al.* 1999a).

Information on the species has focused on taxonomic descriptions (Bigelow and Schroeder 1948; Compagno 1984), abundance (Stride *et al.* 1992), community studies (Lessa and Menni 1994) and reproduction (Lessa 1987; Stride *et al.* 1992; Lessa *et al.* 1999a); nevertheless, age and growth

have not yet been investigated. Overall, length classes corresponding to first maturity for males and females are 103 cm and 115 cm respectively. Birth takes place at ~43 cm, with 8 embryos for the largest litter, a gestation period of about one year and an assumed resting break between pregnancies.

Recently, fisheries directed to the species have developed on the northernmost Brazilian coast using gill-nets ~6000 m long with 18 cm mesh size (Nascimento and Asano 1999). The daggenose shark is mainly caught as by-catch in floating gill-net fishing inside or near the mouths of estuaries, targeting *Scomberomorus brasiliensis* (Collette, Russo and Zavala-Camin) and *Cynoscion acoupa* (Block and Schneider). The species makes up about 10% of the catch of elasmobranchs off Maranhão coast during the dry season (July–November) (Lessa 1986).

Shark collections were conducted off northern Brazil from 1984 to 1987, from 1990 to 1991 and in 1998 with the aim of supplying information on the general aspects required for management in view of the increasing exploitation of coastal sharks in recent years. As a part of this general study, the current work on age and growth of the daggenose shark was undertaken by examination of vertebral rings and through analysis of length frequencies. Growth parameters were estimated by statistical fitting to the von Bertalanffy function.

## Material and methods

Vertebral samples were collected from the artisanal fleet equipped with floating gill-nets (900 m length, 8.0 cm mesh between opposed knots) from 1984 to 1987 and in 1998, off the western Maranhão coast from Turiaçu Bay to Tubarão Bay (Fig. 1). Additionally, a research vessel using gill-nets (1200 m length, 18–30 cm mesh between opposed knots) targeting sharks provided length–frequency data from April 1990 to September 1991. The artisanal fishery and research operations were both conducted in the same area, the latter reaching shallow banks and islands on the external rim of bays and estuaries. All samples were obtained between 6 and 40 m depth (within the 30 m isobath).

Total length (TL, cm) for each specimen was measured according to Compagno (1984) as the 'stretched' length (with tail depressed to be in line with the body axis). Vertebrae excised from below the first dorsal fin were cleaned of excess tissue, stored in 4% formaldehyde for ~24 h and preserved in 70% alcohol, some for up to 6 years. Subsequently, vertebrae were sectioned sagittally (Cailliet *et al.* 1983), immersed in an aqueous solution of alizarin red-S (Gruber and Stout 1983) for ~15 h and then rinsed in running tap water. The terminology used for vertebrae followed Cailliet *et al.* (1983).

Bands presenting a dark-red stained (narrow) ring and a light-red stained (broad) ring were visible in the intermedialia under 12× magnification (1 micrometer unit = 1.2 mm), and were counted in each section. Readings, without knowledge of the length of the specimen, were performed twice by the same reader. Distances from the focus to the margin of each narrow ring and from the focus to the outer edge of the section, or vertebral radius, were measured under reflected light following Branstetter (1987). Whenever counts differed between the two readings, the second reading was considered.

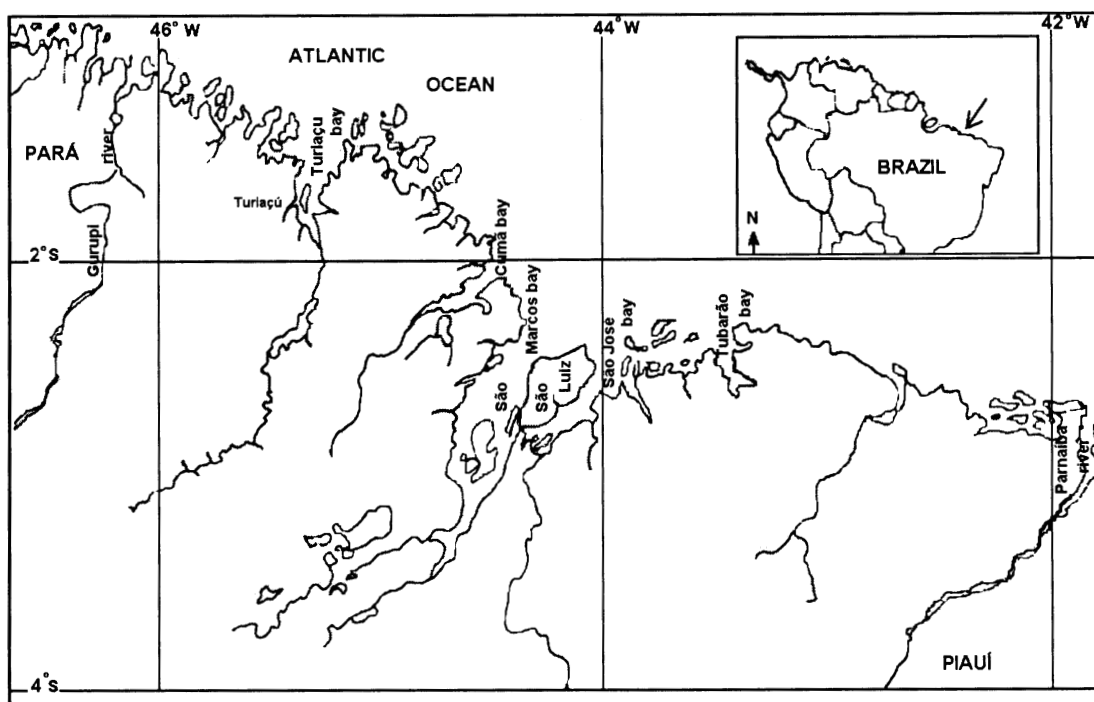


Fig. 1. Site of collection of the daggenose shark, *I. oxyrinchus*, off northern Brazil.

To compare the reproducibility of age determination between the two readings, the index of average percentage error (IAPE; Beamish and Fournier 1981) was estimated using

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

where  $N$  is the number of fish aged,  $R$  is the number of readings,  $X_{ij}$  is the mean age of the  $j$ th fish at the  $i$ th reading, and  $X_j$  is the mean age of the  $j$ th 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):

$$[\text{MIR}] = (V_R - R_n)/(R_n - R_{n-1}),$$

where  $V_R$  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 analysed monthly, in order to locate periodic trends in band formation. MIR values were tested for normality and analysed by variance analysis (ANOVA). Also, characterization of the vertebral edge (Carlson *et al.* 1999) was used for inferences on the period of band formation. Under reflected light, it appeared as (a) a narrow dark band (MIR 0), (b) a narrow light band (MIR 0.1–0.5) and (c) a broad light band (MIR 0.6 to 1).

The relationship between  $V_R$  and TL was calculated by sex, tested for normality and compared by analysis of covariance (Zar 1996). The final regression line with both sexes together did not pass through the origin; this suggests that the Fraser–Lee method was more appropriate for back-calculation:

$$[\text{TL}]_n = (R_n/V_R) ([\text{TL}] - a) + a$$

where  $[\text{TL}]_n$  is the back-calculated length at age  $n$ ,  $R_n$  is vertebral radius at the time of ring  $n$ ,  $V_R$  is vertebral radius at capture, TL is length at capture, and  $a$  is the intercept on the length axis.

A von Bertalanffy growth function was fitted to the data (von Bertalanffy 1938):

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

where  $L_t$  is predicted length at time  $t$ ,  $L_\infty$  is mean asymptotic total length,  $k$  is growth rate constant ( $\text{year}^{-1}$ ) and  $t_0$  is the theoretical age at which fish length is zero.

For obtaining von Bertalanffy parameters, data were analysed by using FISHPARM (Prager *et al.* 1987), which implements Marquardt's algorithm for nonlinear least-squares parameter estimation (Marquardt 1963).

Bernard's (1981) multivariate analysis, based on Hotelling's  $T^2$ , was performed to test the hypothesis that male and female vertebral growth curves were not significantly different. Also employed was Kappenman's method (1981) for comparing growth curves based on the sum of squares of the differences between observed and predicted lengths from a growth model.

Lengths of 1135 individuals (58–160 cm) were divided at 5 cm intervals and analysed by the method of Shepherd (1987) with the Length Frequency Data Analysis Program (LFDA). Initial values of  $L_\infty$  were based on our own data;  $k$  values ranging from 0.07 to 1.8 were entered into the program, which was run repeatedly until the highest score function was obtained. The  $L_\infty$  and  $k$  values were then used to calculate  $t_0$  (Natanson *et al.* 1995):

$$t_0 = t + (1/k) (\ln [L_\infty - L_t] / L_\infty),$$

where  $t_0$  is the time 0 (birth) and  $L_t$  is the mean size at birth.

Back-calculated mean length at age was analysed in order to detect Lee's phenomenon (Ricker 1980), that is the tendency of back-calculated lengths of older fish in the early years to be systematically lower than those of younger ones at the same age.

All statistical inferences were made at a significance level of 0.05, except those related to Bernard's method where 0.01 was used, as indicated. Whenever seasonal aspects of the study area or reproductive features are mentioned, we refer to Lessa (1987) and Lessa *et al.* (1999a).

## Results

The vertebral sample of 105 individuals (46 males, 60.6 to 116 cm; 52 females, 58.4 to 141 cm; and 7 specimens of unknown sex, 67.1 to 106.5 cm) showed a consistent pattern of alternating broad (light-red) and narrow (dark-red) rings stained with alizarin red-S.

The precision estimation provided an average IAPE of 1.74% for the overall sample, with values ranging from 0% to 3.43% for bands 1 to 12.

Differences for  $V_R$  v. TL regression equations between sexes were not significant. A linear relationship was found between  $V_R$  and TL for the overall sample (Fig. 2), indicating that vertebrae are suitable structures for age determination and that direct proportion methods were appropriate for back-calculation.

Mean marginal increment ratios suggest that bands are completely formed by October ( $n = 1$ ) when highest values are reached (Fig. 3). This high value is followed by the lowest mean marginal increments in November, indicating that the new ring may start to form from that point on. However, the small sample in October and the lack of samples in March and May hampered the correct determination of the time of formation of rings. Furthermore, there was monthly variation in categorization of the vertebral edge (Fig. 4), with narrow light edges present almost the year through. Broad light

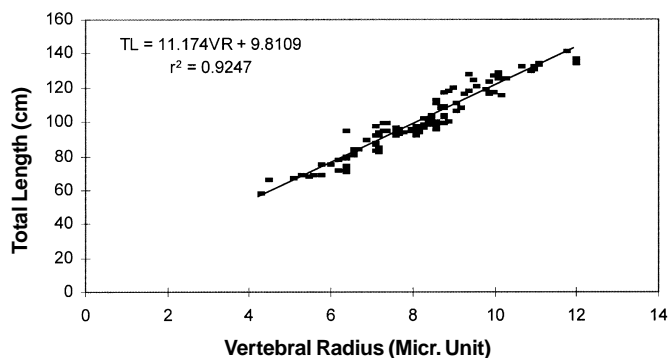


Fig. 2. Relationship between vertebral radius and total length for the daggenose shark, *I. oxyrinchus*, from northern Brazil.

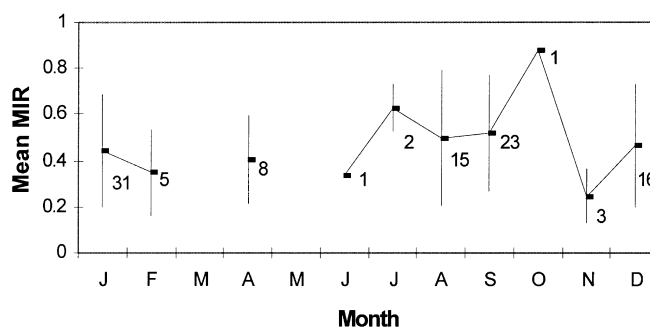
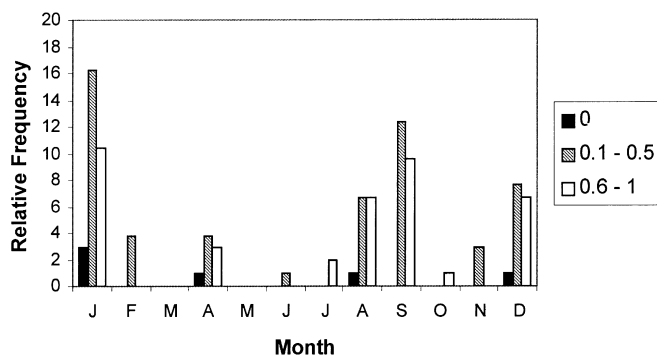


Fig. 3. Mean vertebral marginal increment ratios (MIR  $\pm$  s.d.) by month for *I. oxyrinchus* from northern Brazil.



**Fig. 4.** Categorization of vertebral edges by month for the daggenose shark, *I. oxyrinchus*. Sexes combined.

edges were found from April to January (except July, November and February) and, finally, narrow dark edges were found from August to April. The combination of a higher frequency of broad light edges and narrow dark edges from August to January reinforced the suggestion of the end of the year as the most likely period for the beginning of band formation. However, as ANOVA, carried out after testing mean MIR for normality, did not demonstrate significant differences throughout the year, age was assigned assuming an annual pattern of band deposition. Under this assumption, band counts indicate total age (in years).

With 98 specimens for which sex was known, back-calculated mean lengths were estimated for males and females for bands 0–7 and for 0–12 respectively (Table 1). Also, mean lengths were calculated for observed size at capture, encompassing the same range of bands by sex (Table 1). Observed lengths were larger than back-calculated lengths. These differences were interpreted as the difference between the length at time of ring deposition and length at capture.

von Bertalanffy growth curves estimated from back-calculated lengths were compared between sexes by Bernard's (1981) multivariate analysis and Kappenman's (1981) method, which provided different results: the former indicated significant differences, whereas the latter did not detect any significant difference at all. Given that the mean back-calculated lengths were very similar for male and female (Table 1) and that a graphical comparison suggested that the two sexes were similar, we concluded that growth curves were similar (Fig. 5).

Growth parameters were then obtained for both sexes together, including the seven specimens of undetermined sex. von Bertalanffy curves based on mean observed lengths at capture were also derived, yielding values close to those derived from back-calculated values (Table 2, Fig. 6). In all, these parameters from vertebral analysis were of the same magnitude as those of length–frequency analysis, performed with the LFDA package (Shepherd 1987) using 1135 specimens (632 females, 58–160 cm; 503 males, 60.6 to 127 cm) (Table 2,

**Table 1.** Back-calculated (BC) and observed (OL) length at age  $t$  (mean, s.d.) for male and female daggenose shark, *I. oxyrinchus*, collected off northern Brazil

$t$	Males				Females			
	BC	s.d.	OL	s.d.	BC	s.d.	OL	s.d.
0	42.29	0.74	–	–	42.58	1.28	–	–
1	55.94	1.50	66.10	0	56.20	1.83	58.40	0
2	67.01	0.95	75.20	0	68.21	2.48	70.25	3.57
3	77.28	1.14	79.94	6.20	79.51	2.76	82.13	7.28
4	87.54	1.04	94.51	2.23	89.86	3.13	94.39	6.36
5	95.94	0.49	100.93	5.57	98.83	4.21	98.56	6.24
6	103.46	0.59	105.28	6.51	108.05	4.46	117.21	4.56
7	111.12	0	113.75	3.86	114.72	4.89	122.78	3.85
8	–	–	–	–	120.24	4.09	126.94	1.71
9	–	–	–	–	125.20	3.56	132.07	1.59
10	–	–	–	–	128.89	1.44	–	–
11	–	–	–	–	134.00	2.05	135.15	1.91
12	–	–	–	–	139.89	0	141.00	0

**Table 2.** von Bertalanffy parameters derived from back-calculated and observed length at age by using FISHPARM for both sexes combined and length–frequency data analysis (LFDA) package for the pooled database

Method	$L_{\infty}$	s.e.	$k$	s.e.	$t_0$	s.e.
LFDA	172	–	0.118	–	–2.243	–
Mean back-calculated length	173.8	2.85	0.11	0.004	–2.5	0.086
Mean observed length (without 0)	171.4	0.11	0.121	0.022	–2.612	0.516

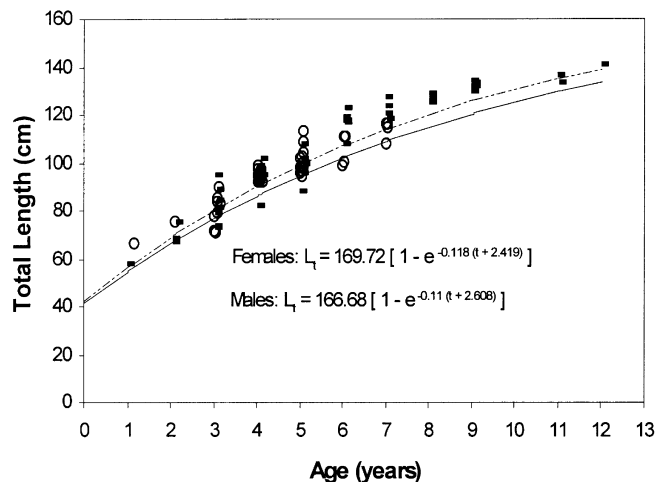


Fig. 5. von Bertalanffy growth curves (male —, female ----) generated from mean back-calculated lengths for male (○) and female (■) daggenose shark, *I. oxyrinchus*, from northern Brazil.

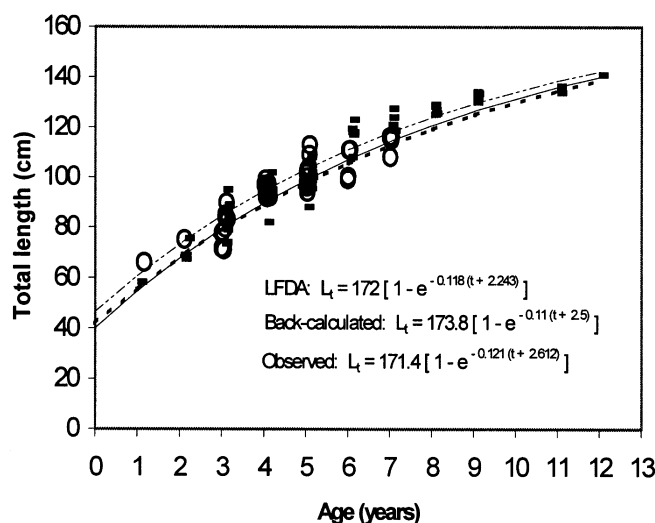


Fig. 6. von Bertalanffy growth curves generated from vertebral data: mean observed length at age, mean back-calculated length at age and length-frequency analysis (LFDA) for combined sexes of daggenose shark, *I. oxyrinchus*. ■, female; ○, male; — LFDA; ---- back-calculated; ..... observed.

Fig. 7). The similarity of  $L_{\infty}$  and  $k$  values derived from different methods confirmed the robustness of the vertebral method.

The largest full-term embryo recorded in the area was 43.2 cm, and back-calculated length for the birth ring was 42.3 cm (Table 3). On average, a growth rate of  $\sim 14$  cm year<sup>-1</sup> from birth at around this size to the first ring laid in vertebrae corresponds to 30% of the birth length. Mean growth rate from ages 1 to 5–6 and 1 to 6–7 when maturity is reached in males (at 103 cm) and females (at 115 cm) respectively is  $\sim 10$  cm year<sup>-1</sup>, decreasing afterwards.

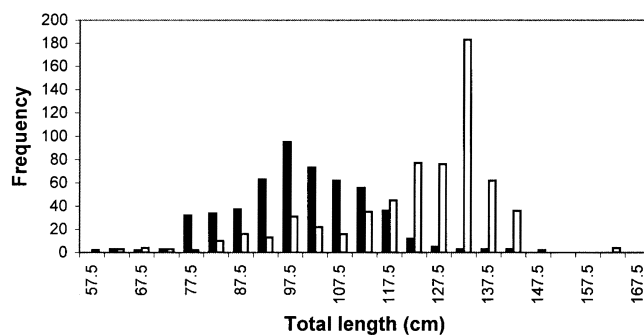


Fig. 7. Length-frequency distribution for male and female daggenose shark, *I. oxyrinchus*, caught off northern Brazil; ■ males; □ females.

In the length frequency sample, the maximum size of 160 cm would correspond to a 20-year-old female and the maximum size of 144 cm to a  $\sim 13$ -year-old male, according to the von Bertalanffy equation. The oldest individuals aged from vertebrae were a 7-year-old male (116 cm) and a 12-year-old female (141 cm).

The tendency of back-calculated lengths of older fish in the early years to be systematically lower than younger ones at the same age was not evident (Table 3). Hence, Lee's phenomenon was not detected.

## Discussion

Despite the suggestion from the mean MIR of fully formed bands in October and new bands starting to form from November (a pattern that agrees with the increasing frequency of broad light edges followed by narrow dark edges from August to April), significant differences were not detected in marginal increments throughout the year. Hence, the periodicity of ring deposition has not yet been ascertained, and this has led to the present assumption of one annual band for the species. Such periodicity is the most common for carcharhinids, among them *C. limbatus*, *C. brevipinna* (Branstetter 1987), *Rhizoprionodon terraenovae* (Branstetter and Stiles 1987), *C. obscurus* (Natanson *et al.* 1995), *C. limbatus* (Wintner and Cliff 1996), *C. falciformis* (Bonfil *et al.* 1993), *C. plumbeus* (Casey and Natanson 1992; Sminkey and Musick 1996), *Negaprion brevirostris* (Gruber and Stout 1983) and *C. longimanus* (Lessa *et al.* 1999b).

For *C. porosus* from the study area, no significant differences were found in marginal increments throughout the year, although the ring seems to form from September to January (Lessa and Santana 1998), which partially coincides with the period of lowest marginal increments for *I. oxyrinchus*. In view of this, Lessa and Santana (1998) speculated that the lack of significant differences in marginal increments might be a consequence of a protracted period of ring formation due to the stable temperatures of the area. In turn, Batista and Silva (1995) suggested, for the same species, that ring differentiation could be a physiological response in coastal waters

**Table 3.** (a) Back-calculated and (b) observed length-at-age data (cm) for combined sexes of the daggenose shark, *I. oxyrinchus*, from northern Brazil

(a)														
<i>t</i>	<i>n</i>	0	1	2	3	4	5	6	7	8	9	10	11	12
		105	105	102	96	78	55	34	22	14	9	9	3	1
1	3	41.77	57.27											
2	6	41.75	54.79	66.03										
3	18	42.21	55.22	66.58	76.76									
4	23	42.59	55.97	68.18	79.17	89.24								
5	21	40.95	54.02	66.01	76.63	86.64	95.52							
6	12	42.74	56.35	68.73	79.79	90.21	99.76	108.01						
7	8	43.01	57.23	69.49	80.18	90.19	99.63	108.35	115.95					
8	5	44.22	58.08	70.32	81.41	91.35	100.36	109.14	117.23	124.39				
9	6	42.89	57.35	69.40	80.89	90.72	100.37	108.53	115.94	122.98	129.10			
11	2	41.38	53.88	64.82	75.25	85.15	93.49	101.31	108.60	115.89	122.24	127.87	132.55	
12	1	42.24	55.56	67.76	78.86	88.85	96.62	104.38	111.04	117.70	124.36	129.90	135.45	139.89
Mean TL		42.34	55.97	67.73	78.77	89.04	97.96	106.62	113.75	120.24	125.23	128.89	134	139.89
s.d.		0.9	1.42	1.81	2.11	2.13	2.75	3.1	3.73	4.09	3.51	1.44	2.05	0
(b)														
Mean TL		–	63.87	70.88	81.3	94.39	100.15	112.35	118.26	126.94	132.07	–	135.15	141
s.d.		–	4.76	3.51	6.56	3.79	5.54	7.7	6	1.71	1.59	–	191	0

during the rainy season (January–June); they explained that salinity can affect growth since lower values (<28 in rainy season v. 33 in dry season) require a higher expenditure of energy for homeostatic equilibrium. Others have speculated that ring formation is related to water temperature (Labelle *et al.* 1993; Liu 1997), change of prey (Stevens 1975) or migration and mating (Pratt and Casey 1983).

In order to compare apparent differences in mean lengths at age by sex, covariance analysis, after linearization, was used for *C. falciformis* (Bonfil *et al.* 1993), *C. limbatus* (Wintner and Cliff 1996), *C. longimanus* (Seki *et al.* 1998) and *Alopias pelagicus* (Liu *et al.* 1999). Furthermore, a *t*-test (Zar 1996, for elevation and slope) was used for *Galeocerdo cuvieri* (Branstetter *et al.* 1987) and the dusky shark (Natanson and Kohler 1996). In turn, growth curves derived from vertebral data have been compared, by sex or between populations, by use of Bernard's multivariate analysis (1981) for *G. cuvieri* (Branstetter *et al.* 1987), *C. plumbeus* (Sminkey and Musick 1995), *C. obscurus* (Natanson *et al.* 1995), *C. longimanus* (Lessa *et al.* 1999) and *C. porosus* (Lessa and Santana 1998), whereas the Kappenman (1981) method was employed in *C. plumbeus* (Sminkey and Musick 1995) and *C. acronotus* (Carlson *et al.* 1999). Gallucci and Quinn reparameterisation (1979) was also used in the case of *C. plumbeus* (Sminkey and Musick 1995).

In some studies, different tests for growth comparisons provided contradictory results. This is the case with *C. plumbeus* (Sminkey and Musick 1995), *C. obscurus* (Natanson and Kohler 1996) and *Thunnus alalunga* (Labelle *et al.* 1993). In the present study, interpretation of contradictory results from the Bernard and Kappenman methods for growth curve comparisons should bear in mind the limitations of the former analysis regarding samples <300 (Cerrato 1981); this

may have distorted results. Cerrato (1981) reported that Bernard's analysis biases results as a result of the combination of all von Bertalanffy parameters ( $L_{\infty}$ ,  $k$  and  $t_0$ ) into a single estimate.

Use of Bernard's analysis on small samples (<300) of *C. obscurus* suggested significant differences in the growth curves derived for males and females (Natanson *et al.* 1995; Natanson and Kohler 1996); however, those authors concluded that differences should not be taken into account, because biological features were similar, both between sexes and between populations, and no other test was used. Also, Labelle *et al.* (1993), studying *Thunnus alalunga*, drew attention to the pitfalls of comparing growth by sex on the basis of von Bertalanffy parameters, and they did not attach any biological significance to differences estimated. In all the above cases, the consensus was to reject statistical results that did not reflect biological differences. Further, Natanson *et al.* (1995) mention Yoccoz (1991), who raised questions as to the validity of judging biological significance on the basis of statistical tests and says that statistical significance is not necessarily indicative of biological significance.

In the present work, following the reasoning by the above-mentioned authors and considering (1) the disparity in size at maturity between sexes (103 cm for males and 115 cm for females), (2) the largest sizes of the sexes (144 cm in males and 160 cm in females), and (3) the different length–weight relationship by sex (Stride *et al.* 1992; Lessa *et al.* 1999a), differences in the growth curves of male and female daggenose sharks would be expected. Also, it is reasonable to presume that different growth would bring about differences in mean length at age (and in growth rates) between sexes, which were actually not evident from back-calculated mean lengths (Table 1).

It seems that the disparity of 12 cm in size at maturity, representing about 1–2 years, was not enough to determine differences in growth between sexes. Thus, comparisons of mean back-calculated lengths by sex (Table 1), similarity between plotted growth curves (Fig. 5) and results of Kappenman's test support identical growth between sexes, because biological differences could not be clearly reflected in growth.

Two sources of error in the present study were the small sample size and the misrepresentation of some size classes by sex. These generally cause differences in growth curves by sex (Cailliet *et al.* 1990). However, no such differences were found.

Still, biases in von Bertalanffy growth parameters and distortions in the shape of growth curves can be caused by long and intensive use of gill-nets, as demonstrated by Walker *et al.* (1998) for *Mustelus antarcticus* off southern Australia. Such effects are referred to as the 'phenomenon of apparent change in growth rate' caused by length-selective fishing mortality (Lee 1912; Ricker 1969). It has the effect of fishers culling a greater proportion of the large (fast-growing) sharks than the small (slow-growing) sharks from the young age-class and of culling a greater proportion of the small (slow-growing) sharks than the large (fast-growing) sharks from the old-classes. Walker *et al.* (1998) demonstrate how the magnitude of growth parameters  $L_{\infty}$  and  $t_0$  tend to increase and  $k$  tends to decrease as gill-net fishing effort increases, and hence explain how these biases, common for sharks in the scientific literature, can occur. In addition, the use of gill-nets to catch sharks for biological sampling from a wild population can cause length-selective sampling bias. This occurs when length–frequency composition of sharks in a sample collected for age determination in any age-class is not representative of length–frequency composition of sharks in that age-class in the wild population (Ricker 1969; Walker *et al.* 1998).

Bigelow and Schroeder (1948) stated that the greatest size measured in daggenose shark (in the natural position) was 152 cm, which is close to the maximum size of 160 cm for the species recorded in the study area in 1990–91 and 1998. The authors commented that 'it is said to attain 180 to 240 cm'. These sizes, however, seem to have never been effectively recorded anywhere. The  $L_{\infty}$  value, estimated from vertebral or length–frequency analysis, compares favourably both to the largest size from length frequency and to the lowest limit of sizes 'said to be attained'.

Cailliet (1990) refers to back-calculation as a verification procedure that provides a qualitative evaluation of how well a calculated curve fits known size information. In this regard, for age-class 0, the mean back-calculated length of 42.3 cm for both sexes in the present study (Table 2) is close to the maximum embryo size for *I. oxyrinchus* observed in the study area, 43.2 cm (Lessa *et al.* 1999a). According to Lessa *et al.* (1999a), birth takes place at the end of the dry season or at the beginning of the rainy season, from January onwards, with the birth ring thought to be formed at birth or soon afterwards. Also, for the smallest specimen, a 58 cm female

showing one band in the vertebrae, the estimated mean back-calculated length for the 1-year-class was 55.9 cm. Thus, the daggenose shark grows by ~30% of the birth length in the first year and the time elapsed between birth and the first ring deposition is about 12 months, considering that the ring starts to form in November.

Length–frequency analysis has been considered inappropriate for ageing elasmobranchs because, since these are slow-growing and long-lived species, the distinction of length modes is difficult beyond the second or third year (Gruber and Stout 1983). Nevertheless, this analysis is widely accepted as a verification method for age studies (Cailliet 1990). It was used for *C. obscurus* and was not found to distinguish length modes well, providing biased results (Natanson *et al.* 1995). Conversely, length–frequency analysis was successfully used as a verification procedure for ageing *C. falciformis* (Bonfil *et al.* 1993), *A. superciliosus* (Liu *et al.* 1997), *C. porosus* (Lessa *et al.* 1998), *A. pelagicus* (Liu *et al.* 1999) and *C. acronotus* (Carlson *et al.* 1999), correlating with vertebral analysis. Thus, the similarity of the values of growth parameters derived by use of these two methods suggests that the age estimation in the present study is reliable.

Values for the von Bertalanffy growth function generated from back-calculation, observed length at age and length frequencies were all considered suitable for describing growth for *I. oxyrinchus*, because they produced similar parameters. However, accepting Cailliet's opinion (1990), the curve generated from observed lengths at age was chosen for representing growth for the species. In this regard, Cailliet says that when back-calculated curves are compared with those from other methods, they provide only a check on the growth model used, and are useful for supplying data on sizes of missing age classes, and for evaluating changes in size-at-age over past time periods.

Branstetter (1990) summarized the life-history of elasmobranchs on the basis of  $k$  and  $L_{\infty}$  values. The daggenose shark is a medium-sized coastal species giving birth to small litters (maximum 8–9 embryos), which grows 30% of the birth length in the first year. A  $k$  value of 0.12 was estimated, reflecting a growth rate similar to *C. acronotus* (Schwartz 1984). That species, like the daggenose shark, occupies littoral zones and is exposed to high levels of predation on juveniles, which may be a major source of mortality. Branstetter (1990) added that an increasing exploitation of adult stocks of fish, as for the daggenose shark, may reduce cohort strength and cause the collapse of populations. Furthermore, the distribution of the endemic species in a reduced geographical area (Lessa *et al.* 1999a), in addition to K-selected traits, may render the daggenose shark vulnerable to overfishing.

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