Age and growth determination of the blacktip shark, *Carcharhinus limbatus*, from the east coast of South Africa

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Abstract.–Age and growth of the blacktip shark, *Carcharhinus limbatus*, from the east coast of South Africa were investigated by counting growth rings in vertebral centra. The vertebrae of 41 females (41–181 cm precaudal length [PCL]) and 51 males (42–182 cm PCL) were examined. Three methods successfully enhanced the visibility of growth rings: crystal violet staining of the centrum face, microscopic examination of the whole vertebra, with transmitted light and dark field, and "bow tie" sectioning of the vertebra. The results of the three methods were compared by using the average percentage error index and statistical means. Age and growth estimates were obtained from microscopic examination of the whole vertebra, the method which provided the most accurate ring counts and gave the second highest reproducibility.

The data for males and females were combined and the von Bertalanffy parameters obtained were L_∞= 193.6 cm PCL, K = 0.21 yr^{-1} and t_0 = –1.2 yr. Age at maturity was 7 years (156 cm PCL) for females and 6 years (150 cm PCL) for males. The oldest aged female was 11 years (179 cm PCL), the oldest aged male was 10 years (179 cm PCL) old. Mean calculated growth rates were 24 cm/yr for the first three years, 11–13 cm/yr through adolescence, and 5–6 cm/yr after maturity.

Back-calculated lengths were lower than observed lengths and Lee's phenomenon was apparent. In 83% of the vertebrae the band immediately after the change in angle was translucent. Opaque band deposition is assumed to occur in summer.

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The Natal Sharks Board (NSB) operates a shark fishery on the east coast of South Africa that is aimed at protecting beach users against shark attack (Cliff et al., 1988a). The sharks are caught in large-mesh gill nets, which fish throughout the year off the more popular recreational beaches of KwaZulu-Natal. Concern has arisen over the possible impact of over 30 years of gillnetting on shark populations off this coast (Dudley and Cliff, 1993a). One of the 14 species contributing to the annual catch of about 1,440 sharks is the blacktip shark, *Carcharhinus limbatus*. Between 1978 and 1994 an annual average of 121 *C. limbatus* were caught in the nets. Information about the distribution, fecundity, size at maturity, diet, and movements of *C. limbatus* is given by Bass et al. (1973) and Dudley and Cliff (1993b).

Research on ageing is an integral part of life history studies of exploited species. This study estimates age and growth of *C. limbatus* from vertebral ring counts. Comparable information exists for this species from the Gulf of Mexico (Branstetter and McEachran, 1986; Branstetter, 1987a; Killam and Parsons, 1989).

Materials and methods

Sampling

Sharks were sampled in the NSB nets from 1985 to 1991. Each net was 214 m long, 6 m deep, had a 50-cm stretched mesh, and was set in water 10–14 m deep, parallel to and 300–400 m from the shore. For details of the netting operation see Cliff et al. (1988a).

Precaudal length (PCL) was measured in a straight line from the snout tip to the precaudal notch and was used throughout this study. For comparison with literature which reported total length (TL), as defined by Branstetter (1987b), the following equation was generated by Dudley and Cliff (1993b):

$$TL = 1.334 \times PCL + 4.27 \quad [n=94, r=0.999; \text{ range } 40.5\text{–}190.0 \text{ cm}]$$

Maturity was assessed on the basis of the criteria of Bass et al. (1973). Males were considered mature only if the claspers were fully calcified. Sperm is produced before claspers are fully calcified and was therefore not regarded as a criterion of maturity. Females were considered mature by the presence of a ruptured hymen and large eggs (>15 mm diameter) in the ovary. In addition, a uterus width of more than 5 cm indicated maturity (Dudley and Cliff, 1993b).

Vertebral samples were taken anterior to the origin of the first dorsal fin from 41 females (41–181 cm) and 51 males (42–182 cm). The vertebrae were stored in various ways: dry (71%); in 70% isopropyl alcohol after fixing in 10% formalin for two weeks (15%); frozen (12%); or processed fresh (2%). Individual centra were soaked in a 5.25% solution of sodium hypochlorate for 10–40 minutes and the connective tissue was then removed with forceps.

Ring-enhancing methods

Five methods to enhance visibility of growth rings were tested. X-radiography[1] and silver nitrate staining[2] failed to clarify the rings and were discarded. The crystal violet staining technique (CV method) of Schwartz (1983) was modified in that the corpus calcareum was stained with a 0.01% solution of crystal violet for 2–10 minutes and then destained with 50% isopropyl alcohol until the desired color intensity was obtained. In the second (UT) method the entire cleaned, unstained vertebra was viewed through a dissecting microscope with transmitted light and a dark field. In the "bow tie" (BT) method, as described by Branstetter and McEachran (1986), a sagittal section was cut from the centrum and successively polished with 200-, 400-, and 600-grit sandpaper to a thickness of 0.5 cm. The section was mounted on a glass microscope slide with clear epoxy resin for viewing.

Ring counts

A growth ring was defined as a band pair, composed of one calcified, opaque band and of one less-calcified, translucent band. A change in angle on the centrum face, a result of the difference between fast intra-uterine and slower post-natal growth (Walter and Ebert, 1991), was regarded as the birth mark. Birth was defined as age zero and two embryos which were close to term, a 42 cm male and a 41 cm female, were included in establishing the von Bertalanffy growth curves (VBGC).

Three nonconsecutive ring counts for each method were made without knowledge of the animal's length and previous counts. Count reproducibility was determined by using the average percentage error (APE) and the APE index as described by Beamish and Fournier (1981). An upper limit in the APE was arbitrarily set at 20% for each vertebra. Samples were discarded if, after a single recount, they were still above this limit. For each method, a mean of the three counts was used as an age estimate. In the fourth (ALL) method, a mode of all nine readings was taken as an age estimate. This method was chosen to compensate for possible over- or under-counting tendencies of the different methods.

The von Bertalanffy growth parameters (VBGP) were computed with Marquardt's algorithm (Draper and Smith, 1981). The von Bertalanffy growth equation was fitted by using the nonlinear regression procedure of STATGRAPHICS®. The equation is

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

where L_t = length at age t in years, L_∞= maximum theoretical length, K = the rate at which L_∞ is reached, and t_0 = the theoretical age at length zero.

The VBGC were then examined for their goodness of fit. A poor goodness of fit in all four methods may be due to a wide variation in the growth of individuals, whereas a poor fit in a single method would suggest inaccurate age estimates.

Centrum analyses

Confirmation of the annual periodicity of growth rings (Cailliet et al., 1983, a and b) was attempted with centrum analyses. The band immediately after the change in angle and the outermost band were classified as translucent or opaque. The nature of the last deposited band was related to the month of capture, and the observed and expected ratios of translucent to opaque last bands were compared.

Distance from the focus to the outer edge of the opaque band of each growth ring, marginal increments, dorsal diameter, and dorsal "birth diameter" were measured in a transverse plane along a straight line through the focus. A relationship between centrum diameter and animal length was investigated and the Dahl-Lea method of back calculation (Carlander, 1969) was used, in which

$$PCL_t = CD_t \times PCL_c/CD_c,$$

where PCL_t = length at age t, CD_t = centrum diameter at age t, PCL_c = length at capture, and CD_c = centrum diameter at capture.

Results

The APE indices were 8.1% for the CV method (n=87), 8.9% for the UT method (n=86), and 9.4% for the BT method (n=87). These results indicated that all three methods were of similar reproducibility. The APE index for the ALL method was 13.0% (n=80).

[1] Standard x-radiography, mammography, and a technique producing zerograms.

[2] A modification of the method of Stevens (1975).

The clarity of the growth rings seemed to be affected by storage method. The rings in fresh, frozen, or alcohol-stored vertebrae were clearer (especially with the UT method) than those stored dry. Fixation in formalin, despite its decalcifying properties, did not appear to affect band clarity adversely.

The growth curves obtained for males and females from each of the four methods were visually very similar; those obtained with the UT method are given in Figure 1. The VBGP for each sex are given in Table 1. Because no significant difference between the sexes was found with the UT, BT, CV, or ALL methods (ANCOVA, $P>0.52$, $P>0.95$, $P>0.43$, $P>0.91$, respectively), the data were combined. The growth curves for the four different methods were also visually very similar (Fig. 2). The BT method had the worst good-

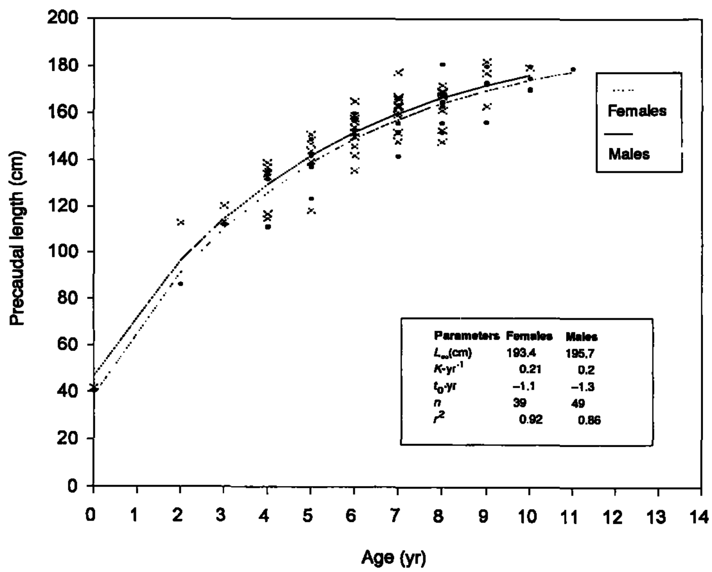

Figure 1

Von Bertalanffy growth curves for male (×) and female (·) blacktip shark, *C. limbatus*. Age estimates were obtained by examination of unstained vertebrae with transmitted light (UT method).

Table 1

Comparison of von Bertalanffy growth parameters for male and female *C. limbatus* and for sexes combined. Age estimates were obtained with four ageing methods. UT = unstained-vertebra technique; BT = "bow tie" technique; CV = crystal-violet–staining technique; and ALL = nine-readings technique.

	Method											
	UT			BT			CV			ALL		
	Male	Female	**Both**	Male	Female	**Both**	Male	Female	**Both**	Male	Female	**Both**
L_∞ (cm)	195.7	193.4	**193.6**	184.2	174.3	**177.7**	191.0	194.0	**192.2**	191.8	190.4	**190.7**
SE	10.9	7.8	**6.3**	9.1	4.9	**4.4**	10.9	8.7	**6.8**	10.0	9.4	**6.6**
K (yr^{-1})	0.20	0.21	**0.21**	0.21	0.28	**0.25**	0.19	0.18	**0.19**	0.21	0.21	**0.21**
SE	0.04	0.03	**0.02**	0.04	0.04	**0.03**	0.04	0.03	**0.02**	0.04	0.04	0.03
t_0 (yr)	–1.3	–1.1	**–1.2**	–1.6	–0.9	**–1.2**	–1.3	–1.2	**–1.3**	–1.2	–1.1	**–1.1**
SE	0.4	0.3	**0.3**	0.5	0.3	**0.3**	0.5	0.4	**0.3**	0.4	0.4	**0.3**
n	49	39	**88**	49	39	**88**	49	40	**89**	45	35	**80**
r	0.86	0.92	**0.89**	0.81	0.97	**0.84**	0.83	0.92	**0.87**	0.85	0.89	**0.87**

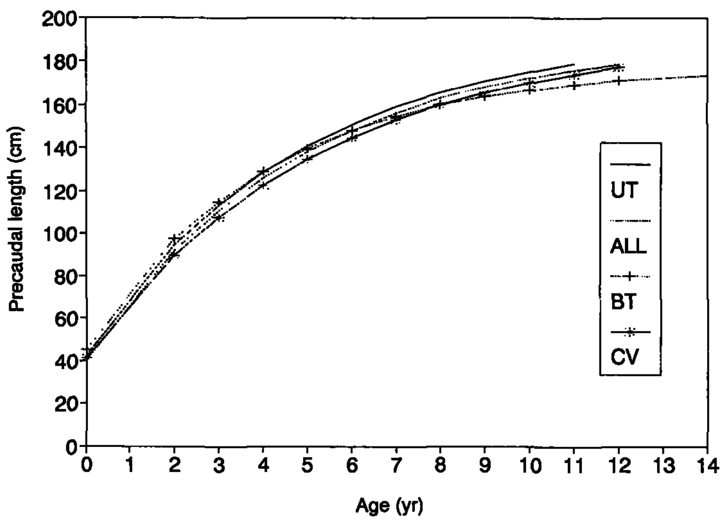

Figure 2

Von Bertalanffy growth curves for the blacktip shark, *C. limbatus*. Age estimates were obtained with four different methods: UT = unstained-vertebra technique; BT = "bow tie" technique; CV = crystal-violet-staining technique; and ALL = nine-readings technique.

ness of fit and the greatest difference between the L_∞ value and the observed maximum length. The best goodness of fit was found for the UT method, which was therefore used to obtain age estimates.

Centrum analyses

A distinct prebirth mark, a translucent band appearing before the birth mark, was found in 20% of the vertebrae but in none of the embryonic vertebrae. In 83% of the vertebrae, the first band immediately after the change in angle was a narrow translucent one.

The first three growth rings were all clearly visible in each of the three ring-enhancing methods. Difficulty was experienced in resolving bands at the centrum edge in older specimens; therefore, accurate marginal increment measurements could be obtained only for the five specimens younger than four years, and the marginal increment analysis was omitted. The observed ratio of translucent to opaque last bands differed significantly from the expected ratio (χ^2 test, $P<0.001$, $n=89$); consequently, annual periodicity of the growth rings could not be confirmed.

A linear relationship was found between centrum diameter and PCL (Fig. 3). As there was no significant difference between the sexes (Student's t-test, $P>0.2$), the data were combined. The intercept of the linear regression was very close to zero (–0.039 cm), and we felt that any correction, such as the Fraser-Lee method (Branstetter, 1987a; Carlander, 1969), was unnecessary.

Mean back-calculated lengths were lower than observed values, except at age zero, where back-calculated birth size was 42 cm and the observed value was 41 cm (Table 2). Lee's phenomenon, a tendency for back-calculated lengths of older fish in the earlier years of life to be systematically lower than those of younger fish at the same age (Carlander, 1969; Smith, 1983), was apparent (Fig. 4). For example, in a shark aged 10 years, there was a 33.6 cm difference between observed and back-calculated length at age four; whereas an animal aged five had only a 21.6 cm difference at age four.

Age and growth estimates

The smallest female (86 cm) was two years, the largest (181 cm) was eight years old (Fig. 5). The two smallest mature females, one of which was pregnant, measured 156 cm and were both seven years old. The smallest (113 cm) and largest (182 cm) males were two and nine years old, respectively. The smallest mature male (150 cm) was six years old. The oldest female (179 cm) was 11 years and the oldest male (179 cm) was 10 years old. Size at birth was calculated to be 43 cm.

Growth rates calculated from mean observed lengths were lower, especially for immature sharks,

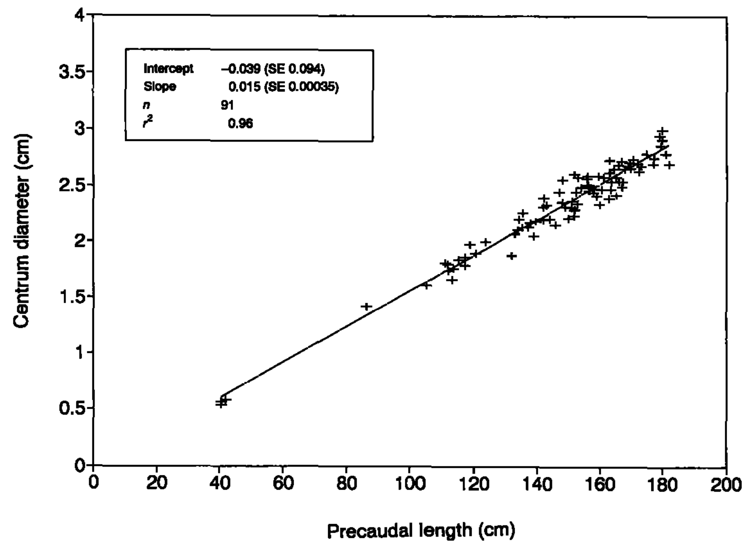

Figure 3

Relationship of length to centrum diameter for combined sexes of the blacktip shark, *C. limbatus*.

Table 2

Observed and back-calculated lengths at age for *C. limbatus*. Age estimates were obtained by examination of the unstained vertebrae with transmitted light.

	Observed PCL (cm)				Back-calculated PCL (cm)			
Age	Min	Max	Mean	*n*	Min	Max	Mean	*n*
0	41	42	41	3	36	55	42	89
1	—	—	—	0	44	81	62	89
2	86	113	100	2	60	103	79	89
3	105	121	113	4	72	132	94	86
4	111	152	128	13	84	158	109	81
5	119	151	139	11	96	159	122	69
6	136	165	153	15	106	162	135	55
7	142	177	160	17	118	177	144	41
8	148	181	164	14	130	182	154	24
9	156	182	172	7	137	193	160	10
10	170	180	175	5	150	185	162	7
11	—	—	179	1	—	—	—	0

than those calculated from mean predicted lengths (Fig. 6). The mean growth rate for predicted lengths over the first three years was 24 cm/yr. Adolescent sharks, until age six or seven, grew an average of 11–13 cm/yr. After maturity the growth rate dropped to 5–6 cm/yr.

Discussion

The APE index for each of the three different ring-enhancing methods (8.1–9.4%) was higher than that of Brown and Gruber (1988), who used alizarin-red-S–stained and unstained "bow tie" sections of

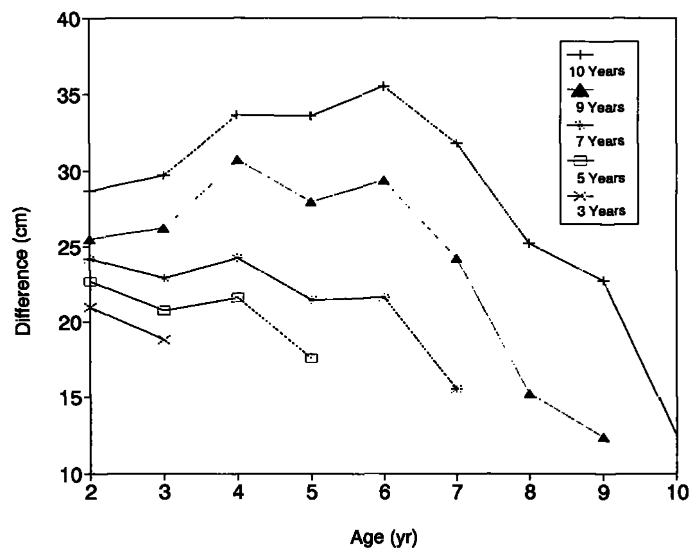

Figure 4

Differences between mean observed and mean back calculated lengths at age for the blacktip shark, *C. limbatus*, aged 3,5,7,9, and 10 years.

indicated whether the prebirth marks were present in all vertebrae examined.

In 83% of the vertebrae, the band immediately after the change in angle was a narrow, translucent one. Bass et al. (1973) and Dudley and Cliff (1993b) sampled pregnant females with well-developed embryos between September and February, suggesting that birth takes place in summer. If the assumption made earlier, that the change in angle is formed at birth is correct, then the translucent band is associated with summer growth. This is contrary to most other ageing studies using vertebral growth rings. Branstetter (1987a) noted that in *C. limbatus*, band calcification occurred in the northern hemisphere summer. He also found that "the first growth band, bordered by the birth annulus and the first postnatal annulus, represented approximately 6 months growth." Killam and Parsons (1989) found that translucent ring deposition occurred during December and January but referred to a translucent "birth" ring, although the sharks are born in May and June, the northern hemisphere summer. In the only other study of this nature in southern Africa, Walter and Ebert (1991) found that in *C. brachyurus* opaque bands are deposited in spring or summer.

Brown and Gruber (1988) found that the change in angle in *Negaprion brevirostris* was not laid down

Negaprion brevirostris and had an APE index of 3.4% (n=55). Their high level of reproducibility is probably a result of counting monthly circuli, where the higher frequency and number of these rings inherently results in a low APE. The statistical differences among our three ring-enhancing methods, assessed by comparing APE indices and goodness of fit of the growth curves, were small, and it is was difficult to decide which of the three produced both the most accurate and the most reproducible results. The UT method, although having the second best reproducibility, was chosen because of its best goodness of fit.

Centrum analyses

A prebirth mark, a translucent band, was found in only 20% of the vertebrae. Branstetter (1987a) found that at least one growth ring formed in *C. limbatus* during embryonic development, but Killam and Parsons (1989) found none. Prebirth marks have also been found in *Carcharhinus plumbeus* (Casey et al., 1985), *C. leucas* (Branstetter and Stiles, 1987), *C. brevipinna* (Branstetter, 1987a), and *C. brachyurus* (Walter and Ebert, 1991). None of these authors, however,

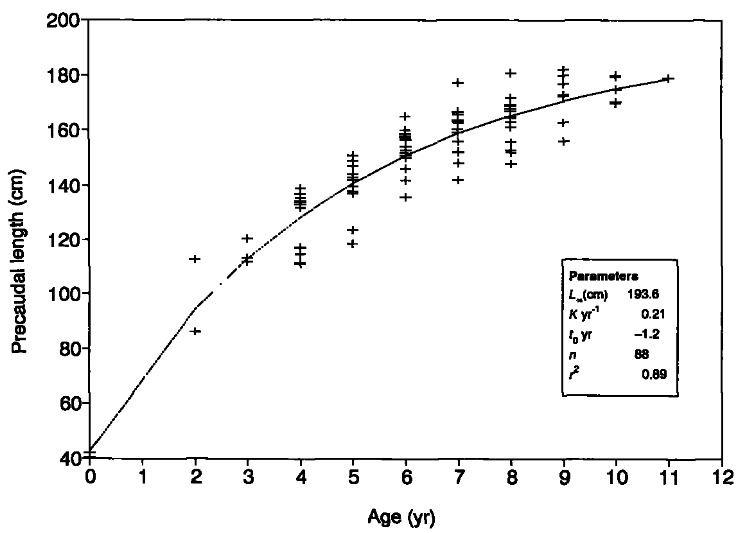

Figure 5

Von Bertalanffy growth curve for the blacktip shark, *C. limbatus*, sexes combined. Age estimates were obtained by examination of the unstained vertebrae with transmitted light.

at birth, but during the first summer growth. This provides a more plausible explanation for the nature of initial band deposition found in *C. limbatus* from southern Africa. The narrow, translucent band found immediately after the change in angle is deposited during the first winter growth, and subsequent opaque bands are the result of summer growth. Clearly, the relationship between change in angle and birth requires investigation.

Centrum edge analysis (where the ratio of translucent to opaque last bands differed significantly from the expected ratio) and the inability to perform marginal increment analysis did not shed light on the periodicity of band deposition. The inability to perform the latter on sharks older than four years is not unique to the present study. Killam and Parsons (1989) used only sharks with two or three growth rings for this analysis. In our study, the shark nets tended to select for large sharks; consequently few small *C. limbatus* were sampled and only five animals younger than four years were available.

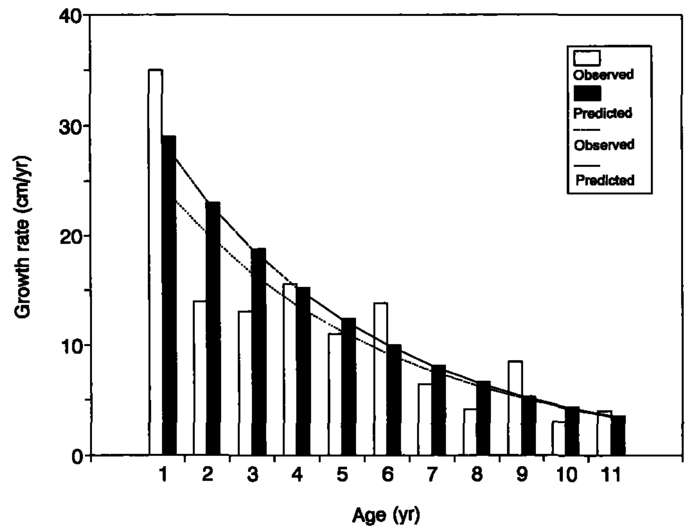

Figure 6

Observed and predicted annual growth of the blacktip shark, *C. limbatus*, in each age class.

All age estimates from vertebral growth rings are based on the assumption of an annual growth-ring deposition. According to Cailliet (1990), the annual periodicity of calcified growth zones has been proven for only five species and partly confirmed for 25 species, including *C. limbatus* (Branstetter, 1987, a and c; Killam and Parsons, 1989). A project was initiated recently in which all shark species, including *C. limbatus*, found alive in NSB nets were injected with oxytetracycline. In this study, growth ring periodicity for *C. limbatus* from southern Africa could not be confirmed, owing to a lack of holding facilities for large sharks and to the absence of any recaptured sharks injected with oxytetracycline.

A linear relationship between vertebral diameter and animal length was also found in *C. limbatus* by Branstetter (1987a) and Killam and Parsons (1989) and has been found in several other shark species (Cailliet et al., 1983b; Schwartz, 1984; Branstetter, 1987b). The existence of this relationship in the present study justified the use of the Dahl-Lea method of back calculations. These back calculations were not used to confirm growth-ring periodicity, because this method is based on several assumptions and has inherent problems (Smith, 1983) but was used to test for Lee's phenomenon and to derive a comparison with observed values. Unfortunately, the use of mean age estimates in this study created discrepancies in back calculations. The number of observed lengths per age class, plus the number of back-calculated lengths in the next age class, does not always add up to the total number of observed lengths. This phenomenon is evident in Table 2.

Mean back-calculated lengths were lower than observed values, as was found by Killam and Parsons (1989). Branstetter (1987a) found that observed lengths were slightly greater than back-calculated values. Lee's phenomenon was encountered in the present study. Even the exclusion of slow-growing individuals in age classes with few individuals did not affect the phenomenon. Killam and Parsons (1989) noted that it appeared to occur at some ages, but no consistent trend was identified. Branstetter (1987a) found no evidence of Lee's phenomenon in *C. limbatus*.

Age and growth estimates

The mean back-calculated birth size was slightly lower than the size of the neonates, as found by Branstetter (1987a) and Killam and Parsons (1989) (Table 3). On the basis of neonate sizes, *C. limbatus* from KwaZulu-Natal is born at a slightly larger size than are those from the Gulf of Mexico. Branstetter (1987a) remarked that in general *C. limbatus* is smallest in the northwestern Atlantic and largest in the Indian Ocean. This is not only evident in birth sizes but also in sizes at maturity and maximum sizes (Table 3).

On the KwaZulu-Natal coast, *C. limbatus* of both sexes mature at similar ages, males at six years and females at seven years. They mature at similar

Table 3

Comparison of life history and von Bertalanffy growth parameters for *C. limbatus* from different regions.

Parameters	Northwestern Gulf of Mexico, Branstetter (1987a)	Tampa Bay, Florida, Killam and Parsons (1989)	KwaZulu-Natal, east coast of South Africa
L_∞ (cm)	128.7	121.6 ♂ 142.9 ♀	193.6
K (yr^{-1})	0.274	0.276 ♂, 0.197 ♀	0.21
t_0 (yr)	–1.2	–0.88 ♂ –1.15 ♀	–1.2
Age at maturity (yr)	4–5 ♂ 7–8 ♀	4–5 ♂ 6–7 ♀	6 ♂ 7 ♀
Length at maturity (cm)	94 ♂ 109–113 ♀	97–99 ♂ 115–118 ♀	150 ♂ 156 ♀
Oldest animal (yr)	5.8 ♂ [1] 9.3 ♀	9 ♂ 10 ♀	10 ♂ 11 ♀
Length of oldest animal (cm)	108 ♂ 125 ♀	117 ♂ 131/132 ♀	179 ♂ 179 ♀
Observed maximum length (cm)	108 ♂ 125 ♀	117 ♂ 134 ♀	182 ♂ 181 ♀
Mean back-calculated birth length (cm)	39	37 ♂ 36 ♀	42
Mean neonate length (cm)	43 (n=33)	42 (n=1)	47[2] (n=3)
n	13 ♂, 34 ♀, 7 unknown	54 ♂, 86 ♀	51 ♂, 41 ♀

[1] This value does not reflect the attainable age (Branstetter, 1987a).
[2] Converted from Bass et al. (1973).

lengths (males: 146–150 cm, n=728; females: 151–155 cm, n=615) and attain the same maximum size of 190 cm (Dudley and Cliff, 1993b). The calculated L_∞ of 193.6 cm is close to these observed maximum lengths which were far greater than those reported by Killam and Parsons (1983) and Branstetter (1987a), in which males mature at less than 100 cm and females at 110–120 cm, with females attaining a greater maximum length than did males (Table 3).

Immature *C. limbatus* from KwaZulu-Natal grew more rapidly than those from other areas. Juveniles grew an average of 24 cm/yr and adolescents 11–13 cm/yr. Appropriate conversion of the growth rates obtained by Killam and Parsons (1989) reveals adolescent growth of 7–8 cm/yr. Branstetter (1987a) found that juveniles grew 15 cm/yr, which slowed down to 8 cm/yr through adolescence. While individuals from the two blacktip shark populations mature at similar ages, especially females, their corresponding lengths are markedly different (Table 3). After maturity, the difference in growth rates were less marked: 5–6 cm/yr in our study, 4–5 cm/yr (Branstetter, 1987a), 2–3 cm/yr (Killam and Parsons, 1989), but maximum lengths showed a marked difference at similar ages (Table 3).

The differences in growth rates between the populations appear to be large. It is tempting to attribute the differences to factors such as sample size and sampling bias, preparation techniques, and reader accuracy and precision (Cailliet et al., 1990). A comparison of two ring-enhancing methods revealed that with the BT ageing method, the growth rate for juvenile sharks from KwaZulu-Natal was about 23 cm/yr and for adolescents 10–11 cm/yr. These values are similar to those obtained with the UT method and higher than those from the Gulf of Mexico. With the BT method, mature sharks grew at a rate of 3 cm/yr, which is slower than the 5–6 cm/yr of the UT method, but similar to the values obtained by Killam and Parsons (1989).

It is therefore possible that the UT method, by overestimating the growth of mature animals, may underestimate the age of these sharks. Nevertheless, given the large differences in size at birth and maturity and in maximum size between sharks of the two populations (Table 3), there is no apparent reason to question the large differences in growth rates between immature sharks of the two populations.

Dudley and Cliff (1993b) found that 66% of *C. limbatus* caught in NSB nets were mature. If age at maturity of females is taken at seven years, maximum age at 11 years, the gestation period as 14 months, and the median litter size as six (Dudley and Cliff, 1993b), the maximum fecundity of a female is about 24 pups. Most carcharhinids have a two-year reproductive cycle (Branstetter, 1981), but there is evidence for a three-year reproductive cycle in *C. limbatus* from South Africa (Dudley and Cliff, 1993b). Catch rates for this species since 1978, the earliest period for which accurate catch data are available, have shown no trend (Dudley and Cliff, 1993b) and can be interpreted as reflecting a relatively constant annual harvesting of immigrants (Wallet, 1973; Cliff et al., 1988b). Despite its low fecundity, catches are sustained by the wide distribution of *C. limbatus* in the western Indian Ocean, in which the small netted region falls largely outside the nursery grounds of this species (Dudley and Cliff, 1993a).

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