Age and growth estimates for the Zambezi shark, *Carcharhinus leucas*, from the east coast of South Africa

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Abstract. Growth rings (GR) were counted in vertebrae of 69 female (56–221 cm precaudal length; 3–238 kg) and 54 male (57–216 cm; 3–180 kg) *C. leucas*. Annual GR deposition could not be confirmed by centrum edge analyses but was assumed on the basis of 'mark–recapture' analysis of 10 sharks held captive for between 2.2 and 20 years in an aquarium. GR counts indicated that the largest female and male were 32 years (221 cm) and 29 years (216 cm), respectively and the smallest mature female and male were 14 years (197 cm) and 25 years (196 cm). Length at 50% maturity was 193 cm (21 years) and 190 cm (20 years) for females and males, respectively. Maximum age is >50 years, and the two specimens (216, 217 cm) that have been held in the aquarium for 20 years are both estimated to be >29 years. Von Bertalanffy parameters for the combined sexes were $L_\infty = 230$ cm, $k = 0.071$ year^{-1}, $t_0 = -5.12$ years, and Gompertz parameters were $w_0 = 24$ kg, $G = 2.86$, $g = 0.046$ year^{-1}.

Introduction

The Zambezi shark, *Carcharhinus leucas*, has been implicated in more shark attacks than any other carcharhinid in KwaZulu-Natal (KZN) and is one of the main species responsible for incidents on this coast (Cliff 1991). Past attacks resulted in the installation of protective measures at various beaches along the coast and ultimately in the creation of the Natal Sharks Board (NSB). Initially, Zambezi shark catches (then combined with *C. amboinensis*) decreased from 194 animals in 1966 to 30 in 1977 (Cliff and Dudley 1991). After 1978, when separate data became available for the two species, there was no significant trend in CPUE for *C. leucas* (Cliff and Dudley 1991). Dudley (2000) subsequently found that this species not only exhibited a significant decline in catch rates between 1978 and 1999, but also a decrease in size over time. Cliff and Dudley (1991) suggested that *C. leucas* is not highly migratory and that the nets may therefore have a large but localized impact.

Information such as length at maturity, maximum lengths and fecundity of this species on the KZN coast is contained in Bass *et al.* (1973) and Cliff and Dudley (1991). For an improved understanding of population dynamics it is necessary to know the ages corresponding to the above lengths. The only available information is that of Branstetter and Stiles (1987), who used 59 vertebrae from the northern Gulf of Mexico, and Thorson and Lacy (1982), who used 15 vertebrae and eight recaptures from Lake Nicaragua. In this study ages were estimated using vertebral ring counts from 123 Zambezi sharks captured by the NSB.

Materials and methods

Sampling

The majority of sharks were sampled in the NSB nets between 1984 and 1995. For details of the netting operation see Cliff *et al.* (1988). The remainder (6.5%) was caught in experimental nets or drumlines (Dudley 1995; Dudley *et al.* 1998). Precaudal length (PCL) was measured in a straight line from the snout tip to the precaudal notch and is used throughout this study, unless indicated otherwise. To compare findings with those reported in total length (TL) or fork length (FL), the following equations were used to convert lengths:

$$[PCL] = 0.81\,[TL] - 9.16 \qquad \text{(Cliff and Dudley 1991)}$$
$$[PCL] = ([FL] - 2.779)/1.08 \qquad \text{(Cliff and Dudley 1991)}$$

Mass was determined by weighing each shark and subtracting the mass of gut contents where they exceeded 1 kg. Two animals were not weighed and their mass was estimated from the length–weight equation of Cliff and Dudley (1991). Maturity was assessed on the basis of the criteria of Bass *et al.* (1973) and Cliff *et al.* (1988). Length at 50% maturity was determined by applying a logistic function, in combination with maximum-likelihood estimation, to data from sharks caught between 1978 and 1999. Vertebral samples were taken anterior to the origin of the first dorsal fin from 69 females (56–221 cm; 3–238 kg) and 54 males (57–216 cm; 3–180 kg). The 56 and 57 cm specimens were full-term embryos. Vertebrae were stored either frozen (64%), dried (24%), or in 70% isopropyl alcohol (12%).

Ring counts

Vertebral sections were prepared following Branstetter and McEachran (1986) where a sagittal section was cut from the centrum and mounted on a glass microscope slide. Sections, ~1 mm thick, were then viewed through a stereo microscope with transmitted light and a dark field. A growth ring (GR) was defined as a band pair, composed of one calcified

(opaque) and one less-calcified (translucent) band. The angle change 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 and assigned as [GR] = 0.

Two readers made three non-consecutive GR counts (three rounds) and count reproducibility was determined by use of the average percentage error (APE) index (Beamish and Fournier 1981) and the index of precision *D* (Chang 1982). An upper APE limit was arbitrarily set at 20% for each vertebra and samples above this limit were discarded. The two embryos with 0 GR were not included in these analyses because they can distort the APE index (Officer *et al.* 1996). In addition, the percentage agreement among the three counts for each reader and in paired GR counts between the readers was investigated. Within-reader and between-reader bias was determined according to Officer *et al.* (1996) and Campana *et al.* (1995).

Centrum analyses

Dorsal centrum diameter was measured in a transverse plane along a straight line through the focus of each vertebra with a calliper (Wintner and Cliff 1998). Distance from the focus to the outer edge of each GR was measured along the internal corpus calcareum with an ocular micrometer. The relationships of centrum diameter with shark length and with mass were examined. Sexes were compared by use of Student's *t*-tests on slopes and elevations (Zar 1974). Statistical outliers were determined with Statgraphics® and eliminated.

The Dahl–Lea method of back-calculation (Carlander 1969) was used to determine length at previous GR and the Monastyrsky method of back-calculation (Francis 1990 citing Bagenal and Tesch 1978) was used to calculate mass at GR

$$M_t = ([CD]_t/[CD]_c)^b M_c$$

where M_t is mass at GR_t, M_c is mass at capture, CD_t is centrum diameter at GR_t, CD_c is centrum diameter at capture and b is the constant derived from the multiplicative regression of *M* on CD.

Confirmation of the annual periodicity of GR (Cailliet *et al.* 1983; Cailliet 1990) was attempted by two methods of centrum analysis. First, the last deposited band was classified as translucent or opaque and related to the month of capture (Kusher *et al.* 1992), and observed and expected ratios of translucent to opaque last bands were compared with χ^2 tests. Second, the marginal increment ratio (MIR) (Hayashi 1976; Skomal 1990) was calculated and plotted against month.

Age and growth

The program PC-YIELD II (Punt and Hughes 1989) was used to determine which of 10 different growth models provided the best fit to the data sets. The von Bertalanffy parameters (VBP) were computed according to the equation of von Bertalanffy (1938). The Gompertz growth parameters were also calculated, from the equation

$$w_t = w_0 e^{G(1-e^{-g \cdot t})}$$

where w_t is mass at GR_t, *G* is initial exponential growth, and *g* is exponential rate of decline (Silliman 1967; Ricker 1975).

Between 1964 and 2000, 10 *C. leucas* specimens were in held an aquarium at Sea World, Durban, with time in captivity ranging from 2.2 to 20 years. The aquarium is 13.8 m long, 9.1 m wide and 3.2 m deep. All sharks were measured upon capture ('marking') and eight again upon death or release ('recapture'). In addition, four of the animals were measured at irregular intervals using a photographic method described by Govender *et al.* (1991). The lengths of the two animals currently in the aquarium were also determined by this method. Both animals were caught in 1980, but the exact capture date was not known and for the purpose of calculations was assumed to have been 16

November 1980. The measurements were treated as mark–recapture data and the von Bertalanffy equation was fitted according to Fabens (1965) and Francis (1988). In both methods t_0 was calculated from a birth size of 56 cm (Cliff and Dudley 1991) and all growth equations were fitted by the nonlinear-regression procedure of SPSS©. Tests were conducted with a significance level of $\alpha = 0.05$.

Results

Of the 123 processed vertebrae, six were unreadable (Reader 1) and were discarded. Vertebrae stored in alcohol were generally more difficult to read, because there was less contrast between the bands. The APE index and *D* values for Reader 1 were 5.1% and 4.0%, respectively (Table 1). No individual sample had an APE of >20%; 98 samples had an APE of <10% and the highest was 17.9%. Reader 2 found all samples readable and the APE index and *D* values were 7.7% and 5.8%, respectively, after discarding six samples with an APE of >20% (Table 1). Here, 75 samples had an APE of <10% and the highest was 18.8%. The three counts differed by two GR or less in 73% of the readings of Reader 1 and 50.5% of the readings of Reader 2 (Table 1). For this reason, a mean of the three counts was taken as a GR estimate. The two readers agreed or differed by one GR in 61.4% of the sample (Table 1).

Within-reader bias of Reader 1 showed lower counts in round 3 than in round 2, whereas Reader 2 counted rounds 2 and 3 higher than round 1 (Table 1). Between-reader bias

Table 1. Comparison of count reproducibility, agreement in counts and bias; vertebral rings of *C. leucas*

APE, average percentage error; CV, coefficient of variation; *D*, index of precision; GR, growth ring; ns, not significant; s, significant

	Reader 1	Reader 2	Between 1 and 2
No. vertebrae			
unreadable	6	0	
APE >20%	0	6	
APE	5.1%	7.7%	
CV	7.0%	10.0%	
D	4.0%	5.8%	
Difference in GR			
0	11.3%	4.4%	22.0%
1	35.6%	23.5%	39.4%
2	26.1%	22.6%	24.8%
3	16.5%	16.5%	6.4%
>3	10.5%	33.0%	7.4%
Bias			
Round 1–2	ns, $P = 0.415$	s, $P = 0.035$ (2 higher)	
Round 2–3	s, $P = 0.014$ (3 lower)	ns, $P = 0.053$	
Round 1–3	ns, $P = 0.139$	s, $P = 0.000$ (3 higher)	
Between mean GR			s, $P = 0.026$ (2 higher)
n (excl. 2 embryos)	115	115	109

was also evident, with Reader 2 counting higher than Reader 1 (Table 1). An age bias plot (Campana *et al.* 1995) showed a linear bias until 16 GR and then non-linear GR estimation bias. The counts of Reader 1 were used for the rest of the analyses because they showed higher precision, higher percentage agreement between rounds and less within-reader bias.

Centrum analyses

A statistically significant linear relationship was found between centrum diameter and PCL (Fig. 1). As there was no significant difference between the sexes in the slopes and elevation, data were combined. The intercept was close to zero, so no Fraser–Lee correction (Carlander 1969; Branstetter *et al.* 1987) was used. Mean back-calculated lengths were higher than observed values (Table 2) and Lee's phenomenon (Carlander 1969; Smith 1983) was evident, but not consistently. The relationship between mass and centrum diameter also showed no significant difference between the
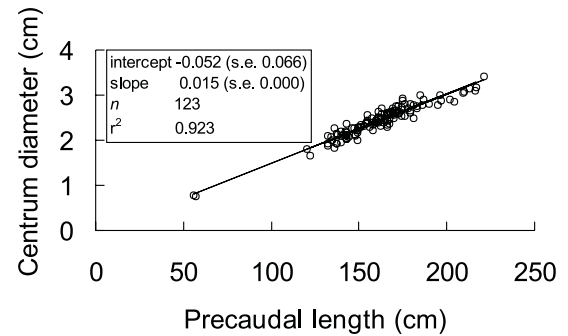

Fig. 1. Relationship between centrum diameter and length for *C. leucas*.

sexes in the slopes and elevation (Fig. 2). Again, back-calculated mass was higher than observed values (Table 3) and Lee's phenomenon was evident, but not consistently.

In 57.4% of the sample the first band after the angle change was translucent. The observed ratio of translucent to opaque

Table 2. Observed and back-calculated precaudal length (PCL) at growth ring (GR) for *C. leucas*

No. of GR	Observed PCL (cm)					No. of GR	Back–calculated PCL (cm)				
	Min.	Max.	Mean	s.d.	*n*		Min.	Max.	Mean	s.d.	*n*
0	56	57	57	1	2	0	50	77	63	5	115
1	–	–	–	–	–	1	57	115	81	10	115
2	–	–	–	–	–	2	67	123	96	11	115
3	–	–	–	–	–	3	75	135	107	12	115
4	–	–	–	–	–	4	85	149	116	13	115
5	120	149	135	21	2	5	91	153	124	13	113
6	122	132	127	7	2	6	96	161	131	12	111
7	136	136	136	–	1	7	100	167	138	13	107
8	132	164	145	10	10	8	118	173	145	12	101
9	140	168	151	8	14	9	122	179	151	12	85
10	135	171	148	13	10	10	127	188	155	12	71
11	137	163	152	11	6	11	131	197	162	13	56
12	138	176	160	11	17	12	137	199	167	13	45
13	143	186	166	11	16	13	143	207	170	14	30
14	143	197	168	13	13	14	150	213	173	15	19
15	166	190	178	13	4	15	167	204	179	10	16
16	174	183	179	5	4	16	175	200	185	8	10
17	173	213	185	19	4	17	185	210	197	8	7
18	169	172	171	2	2	18	195	209	200	6	4
19	181	181	181	–	1	19	198	201	200	1	3
20	204	204	204	–	1	20	201	206	204	2	3
21	185	209	197	17	2	21	204	209	207	3	3
22	202	202	202	–	1	22	207	214	211	4	3
23	–	–	–	–	–	23	210	221	216	6	3
24	210	210	210	–	1	24	213	213	213	–	1
25	196	196	196	–	1	25	216	216	216	–	1
26	–	–	–	–	–	26	217	217	217	–	1
27	217	217	217	–	1	27	–	–	–	–	–
28	–	–	–	–	–	28	–	–	–	–	–
29	216	216	216	–	1	29	–	–	–	–	–
30	–	–	–	–	–	30	–	–	–	–	–
31	–	–	–	–	–	31	–	–	–	–	–
32	221	221	221	–	1	32	–	–	–	–	–

$y = ax^b$; slope=b, intercept=loga
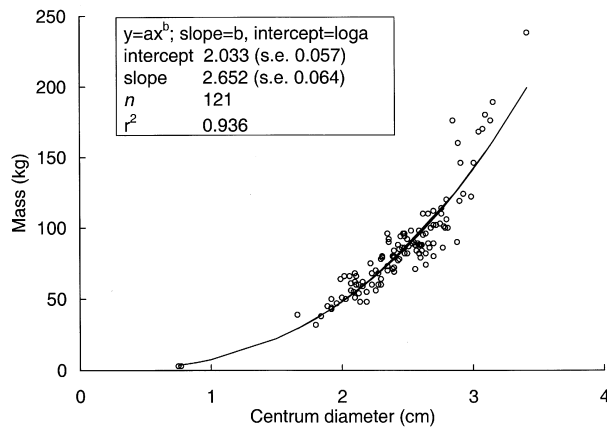intercept 2.033 (s.e. 0.057)
slope 2.652 (s.e. 0.064)
n 121
r^2 0.936

Fig. 2. Relationship between mass and centrum diameter for *C. leucas*.

last bands did not differ significantly from the expected ratio (χ^2 test, $n = 66$), irrespective of whether opaque band deposition was assumed to occur in spring/summer or in autumn/winter. For these analyses only vertebrae were used for which the nature of the investigated band was the same in all three counts. Investigating only summer months (22 December – 20 March) and winter months (21 June – 22 September), did not alter the result ($n = 31$). Also, the observed ratio of translucent to opaque last bands did not differ significantly from the expected ratio ($n = 66$) when assuming a deposition of two GR per year, again irrespective of whether opaque band deposition was assumed to occur in summer and winter or in spring and autumn. Analysis of the percentage occurrence of opaque and translucent bands per season (Fig. 3) could indicate that GR formation starts with the occurrence of opaque bands in autumn and finishes with a translucent band in summer. MIR analysis (Fig. 4), however, also failed to show a clear trend of GR formation.

Table 3. Observed and back-calculated mass at growth ring (GR) for *C. leucas*

| No. of GR	Observed mass (kg)					No. of GR	Back–calculated mass (kg)				
	Min.	Max.	Mean	s.d.	n		Min.	Max.	Mean	s.d.	n
0	3	3	3	0	2	0	4	14	7	2	115
1	–	–	–	–	–	1	5	36	13	5	115
2	–	–	–	–	–	2	8	53	21	7	115
3	–	–	–	–	–	3	11	65	28	10	115
4	–	–	–	–	–	4	15	75	35	12	115
5	32	64	48	23	2	5	17	81	42	12	113
6	39	45	42	4	2	6	19	97	48	14	111
7	38	38	38	–	1	7	22	105	55	15	107
8	44	80	61	11	10	8	33	114	62	15	101
9	47	90	69	12	14	9	35	125	69	17	85
10	48	103	67	18	10	10	39	142	76	19	71
11	50	82	68	13	6	11	43	160	83	20	56
12	55	96	81	13	17	12	48	147	89	20	45
13	64	135	90	17	16	13	54	163	95	22	30
14	54	160	91	24	13	14	75	176	102	26	19
15	88	120	105	17	4	15	89	176	111	22	16
16	100	114	107	7	4	16	105	149	122	13	10
17	90	176	118	40	4	17	122	170	148	18	7
18	89	98	94	6	2	18	141	176	157	18	4
19	101	101	101	–	1	19	148	184	160	20	3
20	176	176	176	–	1	20	154	194	169	22	3
21	122	168	145	33	2	21	160	206	177	25	3
22	146	146	146	–	1	22	166	218	185	28	3
23	–	–	–	–	–	23	173	238	197	36	3
24	170	170	170	–	1	24	179	179	179	–	1
25	146	146	146	–	1	25	186	186	186	–	1
26	–	–	–	–	–	26	189	189	189	–	1
27	189	189	189	–	1	27	–	–	–	–	–
28	–	–	–	–	–	28	–	–	–	–	–
29	180	180	180	–	1	29	–	–	–	–	–
30	–	–	–	–	–	30	–	–	–	–	–
31	–	–	–	–	–	31	–	–	–	–	–
32	238	238	238	–	1	32	–	–	–	–	–
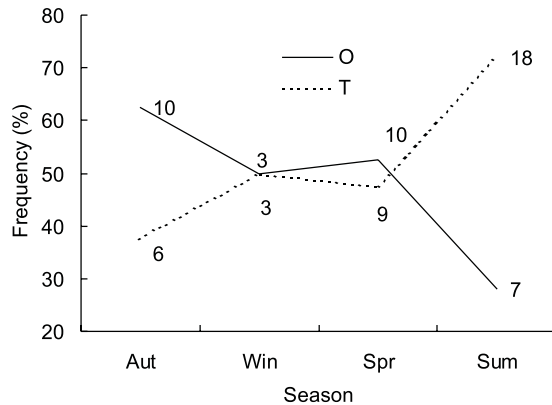
Fig. 3. Percentage occurrence of opaque (O) and translucent (T) bands per season. Numbers indicate sample size.
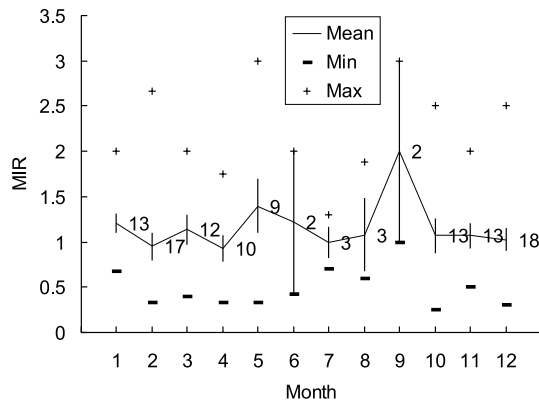

Fig. 4. Mean, minimum and maximum marginal increment ratio (MIR) per month. Numbers indicate sample size. Vertical bars, s.e.
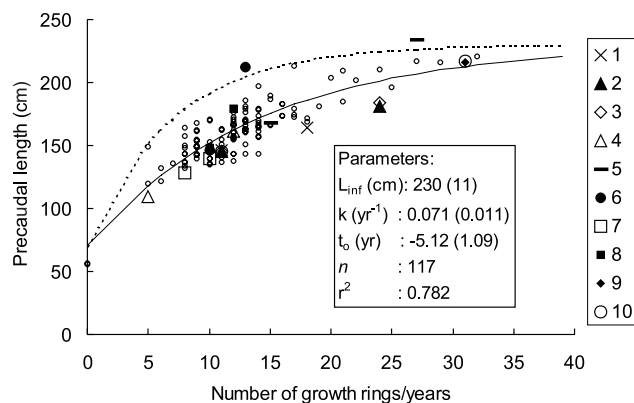

Fig. 5. Von Bertalanffy growth curve for *C. leucas* fitted to observed data (○). Dashed line indicates curve assuming 2 growth rings per year, numbers 1–10 indicate captive animals for which ages were determined by Fabens' 'mark–recapture' method. In parenthesis, s.e.

Table 4. Details of 10 *C. leucas* held captive at Sea World, Durban
Bold, measured. Italics, assumed to be 16 November 1980

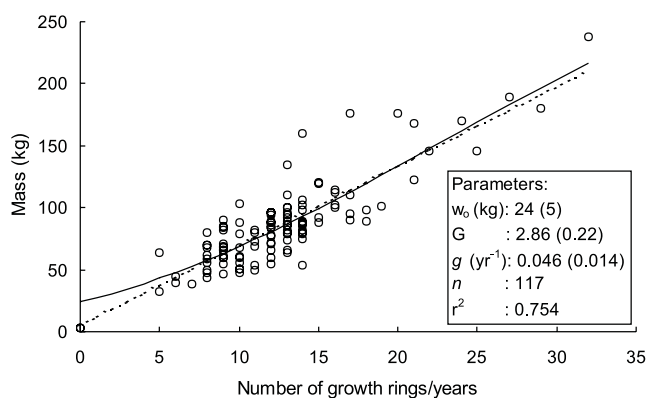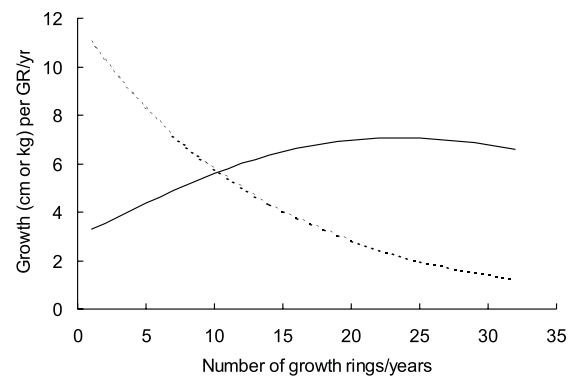| Animal	Date	Length (cm)		Growth (cm)	
		Total	Precaudal	Observed	Calculated
1	20/v/64	191.2	146		
male	30/xi/71	213.2	164	22	35.2
2	20/v/66	190	145		
female	30/xi/71	213.2	164	23.2	27.9
	07/i/80	235	181	21.8	25.4
3	20/v/66	190	145		
unknown	22/ii/80	238.9	184	48.9	53.5
4	12/xii/79	145.4	109		
female	04/ix/80	156	117	10.6	6.2
	17/vii/81	165	124	9	6.9
	21/x/81	169.1	128	4.1	2.0
	19/iv/82	174.1	132	5	3.7
	08/x/82	179.3	136	5.2	3.4
	30/iii/83	188.6	144	9.3	3.3
	01/viii/83	190	145	1.4	2.3
	31/iii/86	210	161	20	16.2
5	18/xii/80	218.5	168		
unknown	17/vii/81	226.3	174	7.8	2.5
	21/x/81	228.2	176	1.9	1.1
	19/iv/82	235.2	181	7	2.0
	08/x/82	236.2	182	1	1.9
	30/iii/83	241.3	186	5.1	1.8
	01/viii/83	253.7	196	12.4	1.3
	31/iii/86	258.4	200	4.7	9.0
	30/xi/92	300	234	41.6	16.3
6	18/i/83	185.4	141		
female	30/iii/83	200	153	14.6	1.2
	01/viii/83	220.5	169	20.5	2.1
	31/iii/86	272.6	212	52.1	14.9
7	06/xii/83	169	128		
unknown	31/iii/86	192	146	23	15.6
8	15/i/84	183.8	140		
male	31/iii/86	232	179	48.2	13.2
9	*16/xi/80*	190	145		
female	16/xi/00	269	**216**	79	65.1
10	*16/xi/80*	190	145		
male	16/xi/00	271.8	**217**	81.8	64.9

Age and growth

The von Bertalanffy growth function was the most appropriate model for the data sets of each sex. The growth function was linearized and there was no difference between males and females (ANCOVA). The VBP for the combined

Table 5. Von Bertalanffy parameters for *C. leucas* obtained by different methods and studies

	Mark–recapture This study		Vertebral growth rings	
			This study	Branstetter and Stiles (1987)
	Fabens (1965)	Francis (1988)		
L_∞ (cm) (s.e.)	234 (31)	207 (NA)	230 (11)	222 (?)
k (year^{-1}) (s.e.)	0.066 (0.04)	0.076 (NA)	0.071 (0.011)	0.076 (?)
t_0 (year) (s.e.)	–4.12 (NA)	–4.16 (NA)	–5.12 (1.09)	–3.0 (?)
n	27	27	117	59
r^2	0.858	NA	0.782	?

Fig. 7. Predicted growth in mass (solid line) and length (dotted line) for *C. leucas*.

sexes were: L_∞ = 230 cm, k = 0.071 year^{-1}, t_o = –5.12 year (Fig. 5). Table 4 shows the details of the 10 captive animals. All PCL were calculated from TL with the exception of animals 9 and 10. With the Fabens method, the calculated L_∞ was unrealistically high as a result of the low sample size. It was therefore constrained to the largest observed animal in the aquarium (234 cm), only slightly smaller than the largest recorded in South Africa (240 cm) (Smale personal communication in Cliff and Dudley (1991). Ages at capture/'marking' were calculated from the VBP obtained from 'mark–recapture' analysis (Table 5) and the observed interval in captivity was added (Fig. 5). Despite the slight difference in VBP between the two methods (Table 5), calculated capture/'marking' ages differed by only one year in all but one animal, and calculated growth using the two methods also differed by only 0.4–0.7 cm. Therefore only ages calculated with the Fabens method are shown in Fig. 5.

On the basis of the similarity of ages obtained with vertebral GR counts and 'mark–recapture' analysis, annual GR deposition was assumed, and the largest female and male were 32 year (221 cm) and 29 year (216 cm), respectively.

Fig. 6. Gompertz growth curve for *C. leucas* fitted to observed data (○). Dashed line indicates a linear fit. In parenthesis, s.e.

The smallest mature female and male were 14 years (197 cm) and 25 years (196 cm), respectively. Length at 50% maturity was 193 cm (21 years) and 190 cm (20 years) for females and males, respectively. Maximum age, defined as the age where the animal is within <1% of its asymptotic size (Fabens 1965) was calculated at 49 years, and the two specimens (216, 217 cm) currently held in the aquarium for over 20 years are both estimated to be over 29 years old. Observed growth of the captive sharks varied about that predicted from vertebral GR counts (Table 4).

A Gompertz growth curve was fitted to the mass–GR data and the heaviest female and male were 32 years (238 kg) and 29 years (180 kg), respectively (Fig. 6). Calculated growth was 11 cm (3 kg) for the first year, 3 cm (7 kg) at age at 50% maturity (20–21 years) and 1 cm (7 kg) at 32 years (Fig. 7). The upper asymptote of the Gompertz growth curve, i.e. the maximum attainable weight, was calculated as 419 kg.

Discussion

The APE index and index of precision D can be used to indicate the reproducibility of age estimations (Beamish and Fournier 1981; Chang 1982) and in this study the APE indices of 5.1–7.7% were lower than the 9.2–9.7% of the same readers for *Galeocerdo cuvier* (Wintner and Dudley 2000) and similar to the 5.3–6.1% of Wintner and Cliff (1998) for *Carcharodon carcharias*. D values (4.0–5.8%) were also lower than the 7.1–7.4% of Wintner and Dudley (2000) and similar to those of Wintner and Cliff (1998) (3.9–4.1%), thus indicating similar reproducibility. Despite this reproducibility, some bias was evident, in that Reader 2 counted higher in round 2 and 3 than in round 1 and was also consistently higher than Reader 1. Similar bias between rounds has also been found by Officer *et al.* (1996), who attributed this to the reader's being less experienced. Branstetter and Stiles (1987) also found that one reader read *C. leucas* vertebrae consistently higher, and their percentage agreement between readers was similar to ours with >50% differing by 0–1 GR.

The relationship between centrum diameter and length for *C. leucas* was linear, as was found also by Branstetter and Stiles (1987) and Thorson and Lacy (1982). The relationship between mass and centrum diameter was multiplicative and, as with the centrum diameter and length relationship, there was no difference between the sexes, although Cliff and Dudley (1991) found a difference in mass–length relationships between the sexes. Back-calculated lengths at age varied widely, as was experienced also by Branstetter and Stiles (1987), and mean values were slightly higher than observed values. Lee's phenomenon was evident, although not consistently, and was reported also by Branstetter and Stiles (1987) for this species. Back-calculated mass at age mimicked the trends of back-calculated lengths.

Centrum edge analyses are commonly used to investigate GR periodicity in shark vertebrae (Cailliet 1990; Simpfendorfer 1993; Branstetter and Musick 1994; Natanson *et al.* 1995). In this study, the observed frequencies of translucent and opaque bands did not differ significantly from the expected values irrespective of assuming opaque band deposition either in summer or in winter or in both summer and winter (two GR per year). Fig. 3 could indicate that GR formation starts with the occurrence of opaque bands in autumn and finishes with a translucent band in summer, but MIR analysis failed to show a clear trend of GR formation. This is probably due to the small sample sizes in the winter months.

In an attempt to resolve the question of periodicity, 'mark–recapture' data from 10 animals held in captivity were used. Recapture data can be used to verify the periodicity of growth zones (Cailliet 1990) and is one of the most successful age validation methods (Cailliet and Tanaka 1990). In addition, it can be used to supplement information derived from vertebral GR counts (Casey *et al.* 1985; Natanson *et al.* 1999; Natanson *et al.* in press). Various growth functions can be fitted to mark–recapture data (Gulland and Holt 1959; Fabens 1965; Francis 1988; Hearn and Leigh 1994). In the Fabens method, the predicted 'recapture' length depends only on length at 'marking', time elapsed and L_∞ and k. Despite the low sample size and the small time intervals used, capture/'marking' ages calculated for the captive animals fitted well with the observed number of GR in animals of similar size, as do the ages at 'recapture' derived from adding the observed years in captivity. This is not the case when assuming a deposition of two GR per year (Fig. 5), where the captive animals are all much smaller at the same GR ages. That this is not a result of slow captive growth is supported by the observation that the majority of the captive animals exhibited faster growth than predicted from vertebral growth (Table 4).

Francis (1988) pointed out that L_∞, k and growth calculated from mark–recapture data can not be compared with those estimated from age–length data, and so we have used 'mark–recapture' only to investigate GR periodicity. On the basis of the above findings, we are assuming annual GR periodicity for *C. leucas* in this study. Branstetter and Stiles (1987) also found, on the basis of MIR analysis, that the first growth band in *C. leucas* represented six months' growth and subsequent bands were annual growth increments.

Age and growth

Back-calculated size at birth (63 cm) was slightly higher than the 55 cm reported by Cliff and Dudley (1991) and slightly higher than the 56–57 cm of the two full-term embryos in the present study. Birth size calculated from the VBP was 70 cm. This large size is probably due to the lack of small animals in the sample causing an underestimation of early growth, a problem Branstetter and Stiles (1987) also faced in their sample. Birth sizes reported from other areas (Clark and Von Schmidt 1965; Sadowsky 1971; Jensen 1976; Branstetter 1981; Thorson and Lacy 1982; Snelson *et al.* 1984; Branstetter and Stiles 1987) were generally smaller, with similar sizes seeming to be exceptionally large embryos or neonates.

There was considerable, sex-independent, variation in age at length, which was also found by Branstetter and Stiles (1987). In the present study, for example, two females aged 8 and 12 years were both 143 cm and two males aged 8 and 12 years were 143 cm. Our smallest mature male, at 25 years (196 cm) was much older than the 16.2-year-old (176 cm) male reported by Branstetter and Stiles (1987). Our smallest mature female (14 years, 197 cm) was very likely being underestimated, with a calculated age of 22 years. With an age of 22 years, the animal would also have been much older than the 18.2-year-old (174 cm) female of Branstetter and Stiles (1987). These differences are a result of our length at 50% maturity being larger (190–193 cm, 20–21 years) than the 161–169 cm maturity range (14–15 years) for males and the >173 cm (18 years) for females given by Branstetter and Stiles (1987). Our largest and oldest *C. leucas* were a 32-year (221 cm) female and 29-year (216 cm) male, again older and larger than those of Branstetter and Stiles (1987), who reported a 21.3-year, 189 cm female and 24.2-year, 208 cm male. Sosa-Nishizaki *et al.* (1998), using soft X-rays, reported a single 167 cm specimen as having 14 GR. The largest specimen in the ageing study of Thorson and Lacy (1982) was a 194 cm female estimated at 15.7 years; they suggested ages at maximum sizes at 16 years (194 cm) and 12 years (164 cm) for females and males, respectively. This would indicate a much more rapid growth for older animals than in either the present study or that of Branstetter and Stiles (1987), and the latter attributed this to Thorson and Lacy (1982)'s extrapolation of the last known growth rate to the largest known size for their population.

Our L_∞ (230 cm) was slightly greater than the two largest animals in the sample but close to the largest *C. leucas* recorded in South Africa (240 cm) (Smale personal communication in Cliff and Dudley (1991)), the largest in captivity (234 cm) and the two largest measured by Bass *et al.*

(1973) (233 and 234 cm). It was also slightly larger than the 222 cm recorded by Branstetter and Stiles (1987) (Table 5). It seems that *C. leucas* in South African is not only born slightly larger but also grows larger and matures at a larger size than it does in other areas (Clark and von Schmidt 1965; Jensen 1976; Branstetter 1981; Thorson and Lacy 1982; Snelson *et al.* 1984; Branstetter and Stiles 1987). A similar phenomenon was found by Wintner and Cliff (1996) for South African *C. limbatus*; size at maturity and maximum size were larger than those reported from the Gulf of Mexico. South African *Galeocerdo cuvier* also matures at a larger size than those from the Gulf of Mexico and the north-western Atlantic (Wintner and Dudley 2000). Natanson and Kohler (1996) found that *C. obscurus* from South Africa grew slightly larger than those from the western North Atlantic but that the two populations had overlapping sizes at maturity. Differences in age at maturity and/or maximum age between populations of the above three species, however, are less clear.

Growth of *C. leucas* was variable but the 8–4 cm year^{-1} for 5–16 years and <4 cm year^{-1} thereafter were similar to the 10–5 cm year^{-1} and 4–5 cm year^{-1} of Branstetter and Stiles (1987) for the same periods. Owing to the lack of small specimens, however, our growth rate of 11–8 cm year^{-1} for the first five years is an underestimate, a point also noted by Branstetter and Stiles (1987). Instead of the 15–10 cm year^{-1} for the first five years, they suggested 20–15 cm year^{-1}, which is close to the growth rates observed by Thorson and Lacy (1982) (18–12 cm year^{-1}). Schmid *et al.* (1990) and Schmid and Murru (1994) reported growth rates for five neonatal *C. leucas* captured and held in an aquarium as about 26–28 cm year^{-1} for the first 2.8–3.0 years. Growth rate was 14 cm year^{-1} in years 4–5 and 8 cm year^{-1} during years 6–7. Another neonate grew 42 cm in its first year and 15 cm year^{-1} over the following 16 months (Schmid *et al.* 1990). Our only two comparable captive animals (Animal 4 and Animal 7), calculated (from vertebral GR) to be four and six years old at time of capture, grew ~12 cm year^{-1} in the first 2.9 years and in the next three years ~10 cm year^{-1} (Animal 4) and 10 cm year^{-1} in a period of 2.4 years (Animal 7), which is similar to the findings of Schmid *et al.* (1990) and Schmid and Murru (1994). This captive growth was faster than predicted from GR and Schmid and Murru (1994) stated that captive growth for *C. leucas* is faster than observed in the wild.

Little growth information is available from tagging *C. leucas* in this area. Bass (1977) reported two specimens growing 9 cm in 1.5 years (tagged at 93 cm) and 11 cm in 7.7 years (tagged at 169 cm). Growth rates for another four animals were 1.3, 7.5, 8.8 and 16.1 cm year^{-1} for specimens tagged between 132 and 153 cm (Bullen and Mann 2000). Of these six, four grew faster and two slower than predicted from GR counts. Although the variable growth rate of this species and our underestimation of early growth hamper comparisons, it seems that the aquarium growth is faster and tagging growth similar to the predicted growth.

Observed growth in mass was also variable and smaller than the captive growth reported by Schmid and Murru (1994) and Schmid *et al.* 1990). They observed an average weight increase of 10.8 kg year^{-1} in the fourth year, increasing further to 14.4 kg year^{-1} in the fifth year and then decreasing to 6 kg year^{-1} in the sixth year and subsequently decreasing further to 2.4 kg year^{-1}. Our Gompertz growth curve again underestimated early growth because birth weights are exceptionally high (14–24 kg). A linear relationship between mass and age for the first five years seems to describe growth more accurately (yielding, for example, a birth weight of 5 kg); thereafter, growth calculated from Gompertz parameters is similar to linear growth (Fig. 6).

Age at mass also varied considerably. For example, three 89 kg females were 13, 14, 18 years and two 80 kg males were 8 and 14 years old. That is not surprising, because mass at length can vary greatly for both sexes (Cliff and Dudley 1991; this study). For example, four 166 cm females differed by 32 kg. Our 221 cm female weighed 238 kg, whereas Compagno and Smale (1986) reported a 227 cm female weighing only 196 kg. Two males at 161 cm differed by 15 kg and two males at 202 and 210 cm weighed 146 and 170 kg. Calculated maximum weight is 419 kg, higher than the observed 315.4 kg reported by Smale (personal communication in Cliff and Dudley (1991)). The inflection point of the Gompertz curve (Ricker 1975) of 154 kg (Fig. 6), corresponding to ~23 years, is also visible in Fig. 7 where growth decreases again. This point corresponds approximately with age at 50% maturity.

Maximum age is 49 years for a length of 230 cm, which would indicate that this species matures at 41–43% of its life span and 83–84% of its 'asymptotic' length. With a birth size of ~23% of L_∞ and k <0.1, *C. leucas* falls within Branstetter's (1990) category of shark species with small neonates and slow growth. With reference to Cortés' (2000) results of a principal component analysis of life-history traits, the species is characterized as being large with large offspring, slow growth, generally high longevity and reduced litter size. Cliff and Dudley (1991) reported an average litter size of 8.7 (range 6–12, $n = 7$) and a very low percentage pregnancy, and they suggested a possibly low fecundity for *C. leucas*. These characteristics are consistent with the observed significant decline in catch rates between 1978 and 1998 and the decrease in size over time (Dudley 2000).

An apparent reduction in nearshore abundance of *C. leucas* in the vicinity of netted beaches is one of the major contributing factors in the reduction of shark attacks (Wallett 1983). Cliff and Dudley (1991) suggested, on the basis of tagging data, that *C. leucas* may be relatively sedentary in KZN waters and that the netting programme may have had a large but localized impact on the species. They described an instance where an isolated group of large *C. leucas* survived at a particular beach despite more than two decades of netting both north and south of this installation. Bullen and Mann (2000), also using tagging data, speculated that this species

may remain in specific 'home ranges' along the coast and that the population is small or that individuals are prone to recapture. The decline in catch rates and mean size (Dudley 2000), however, could also indicate a less localized stock depletion, given the other fisheries that affect this species both within and to the north of the netted region. Sousa *et al.* (1997) reported not only shark by-catch of the artisanal and industrial prawn fishery in Mozambique, but also directed semi-industrial and industrial fisheries that catch *C. leucas*. Recreational anglers also catch this species in Mozambique (Sousa *et al.* 1997) and in South Africa. Although both the increase in *C. leucas* CPUE and contribution to the total shark catch in fishing competition data between 1979 and 1999 are non-significant (using data from Pradervand 2000), these trends may indicate increased recreational fishing pressure. The slow growth and late age at maturity of *C. leucas* when compared with other species caught in the protective nets (Wintner and Cliff 1996, 1998; Wintner and Dudley 2000), coupled with observed catch trends, lend support to the effort-reduction programme of the NSB, which started with a 25% net reduction in September 1999.

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