Abstract.–Ages of white sharks, *Carcharodon carcharias*, from the east coast of South Africa were estimated by counting growth rings (GRs) in vertebral centra and relating them to length and mass. The vertebrae of 61 females (128–297 cm precaudal length (PCL)) and 53 males (142–373 cm PCL) were examined. Mass range was 42–442 kg for females (n=60) and 46–882 kg for males (n=53). X-radiography was used to enhance the visibility of the GRs in whole centra. Counts were made directly from the x-radiographs by one reader and from scanned x-radiographs by two readers. Count precision for each method and reader was determined by using the average percentage error (APE) index which ranged from 5.3 to 6.1%.

One shark injected with oxytetracycline (OTC) was recaptured after 942 days at liberty. The shark was tagged at 140 cm and 46 kg and grew 69 cm and 104 kg. The OTC was visible in the vertebra and there was evidence of annual growth ring deposition. This could, however, not be confirmed with centrum analyses of the entire sample.

The number of GRs counted varied in the following manner. The female and male with the lowest number of GRs, had 0 GR (131 cm PCL) and 1 GR (142 cm PCL), respectively. The female and male with the highest number of GRs, had 8 GRs (282 cm PCL) and 13 GRs (373 cm PCL), respectively. The smallest mature male had 8 GRs (293 cm PCL); there were no mature females. Von Bertalanffy parameters for the combined sexes were L_∞ = 544 cm PCL, k = 0.065/yr, t_0 = –4.4 yr. Growth calculated from predicted lengths decreased from 26 cm for sharks with 1 GR to 12 cm for sharks with 13 GRs. Gompertz parameters were w_0 = 54 kg, G = 3.94, g = 0.094/yr. Growth calculated from predicted mass increased from 23 kg (1 GR) to 94 kg (13 GRs). Back-calculated lengths and mass were lower than observed values and Lee's phenomenon was evident in both back-calculated lengths and mass but not consistently.

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Age and growth determination of the white shark, *Carcharodon carcharias*, from the east coast of South Africa

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The white shark, *Carcharodon carcharias*, is found worldwide in cold and temperate coastal and shelf waters (Compagno, 1984). As a large, uncommon apex predator, it has received considerable attention from scientists over the past few years. Because of its great resale value, compared with most other sharks, catches of white sharks have increased in various parts of the world, mainly in Australia and South Africa (Compagno, 1990, 1991). Claims of a declining population size in South Australian waters (Compagno, 1991; Bruce, 1992) influenced an initiative to implement protective legislation for this species in South Africa. In 1991 the South African government prohibited the catching or killing of white shark without a permit (Compagno, 1991). This measure was a preemptive protection and is to be reviewed as results of more research into the biology of this species become available (Compagno, 1991). Protection has now also been introduced in California, Florida, and Tasmania (Fergusson et al., in press), as well as in Queensland, New South Wales, South Australia, and Western Australia (Stevens[1])

Legislation in South Africa has prevented this species from being targeted by commercial and recreational anglers. White sharks continue to be caught on the east coast in the nets of the Natal Sharks Board (NSB), which operates a shark control program to protect beach users against shark attack (Cliff et al., 1988). Between 1984 and 1995 an annual average of 40 *C. carcharias* were caught in NSB nets, and 15% were released alive. This activity has formed the basis of a small-scale tagging program that has provided the first estimates of the size of the white shark population (Cliff et al., 1996b). Information about the distribution, diet, movements, and catches of *C. carcharias* in South Africa is available from Bass et al. (1975) and Cliff et al. (1989, 1996a).

Little is known about age and growth of *C. carcharias*, mainly because so few are caught at any one locality, thus hampering collection of vertebral samples for ageing purposes. Knowledge of age at maturity, maximum ages, and growth rates is a prerequisite for age-based methods of stock assessment, which in turn can be used for the management of this species. The only previous attempt at ageing the white shark was that of Cailliet et al. (1985) who had access to only 21 samples, mainly from California. This study attempts to provide age estimates for *C. carcharias* from South Africa from vertebral growth ring counts of 114 sharks.

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[1] Stevens, J. D. 1997. CSIRO Marine Laboratories, Tasmania, Australia. Personal comm

Materials and methods

Sampling

Sharks were sampled in NSB nets from 1984 to 1995. 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 shore. For additional details of the netting operation see Cliff et al. (1988).

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 our findings with those reported in the literature, the following equations were used to convert lengths:

$$Total\ length\ (TL) = 1.251\ PCL + 5.207$$

(n =36; range 131–307 cm PCL; 95% confidence limits on slope: 1.233 and 1.268; r^2=0.9984) (Cliff et al., 1996a); and

$$PCL = 0.8550\ TL - 0.0955$$

(n =58; range 96–447 cm PCL; 95% confidence limits on intercept: –0.130 and –0.061; r^2=0.996) (Mollet and Cailliet, 1996).

Lengths were converted by means of the method considered most appropriate.

Mass was determined by weighing each shark and subtracting the mass of gut contents where they exceeded 1 kg. Maturity was assessed by the criteria of Bass et al. (1973), where males were considered mature only if their claspers were fully calcified. In females, maturity was based on the presence of distinct ova in the ovary and uteri, which had expanded from a thin, tubelike condition to form loose sacs (Bass et al., 1973; Cliff et al., 1988). Vertebral samples were taken anterior to the origin of the first dorsal fin from 61 females (128–297 cm) and 53 males (142–373 cm). Mass range was 42–442 kg for females (n=60) and 46–882 kg for males (n=53). Vertebrae were stored frozen (60%) or in 70% isopropyl alcohol (31%), or dried (9%). Individual centra were cleaned by removing the connective tissue from the corpus calcareum with forceps. Dried samples needed additional soaking in a 5% solution of sodium hypochlorite for 20–40 minutes.

Ring counts

X-radiography was used to enhance the visibility of the growth rings. X-radiographs of whole centra were prepared on an Odel Pollux 700 generator with a Comet tube by using Agfa Ortho (Extremity) film and were processed with an Agfa Curix 160 processor. We x-rayed, using mostly oblique exposure, all centra with the corpus calcareum (Figs. 1A and 2A) facing the tube at a set distance of 100 cm. At 50 mA, exposure times ranged from 0.3 to 0.8 seconds and voltage from 28 to 34 kV. The x-radiographs were then scanned with an Agfa Arcus II scanner and Adobe photoshop software. Ulead ImagePals 2 GO! (Ulead Systems, 1992–94) and CorelDRAW! (Corel Corp., 1993) were used to enhance and work with the images.

A growth ring (GR) was defined as a band pair, composed of one calcified (opaque) and one less-calcified (translucent) band (Fig. 1A). The finer, narrower rings (circuli), also observed by Cailliet et al. (1985), were not used for ageing purposes. The angle change on the centrum face (Fig. 2A), a result of the difference between fast intrauterine and slower postnatal growth (Walter and Ebert, 1991), was regarded as the birth mark.

Counts were made directly from the x-radiographs (XRs) by one reader (A) and from the scanned images (SCs) by two readers (A and B). These three ways of viewing the vertebrae will be called methods XR-A, SC-A, and SC-B, for brevity. Each reader made three nonconsecutive GR counts, without knowledge of the shark's length and previous counts. Count reproducibility was determined by using the following four methods:

1. The average percentage error (APE) as described by Beamish and Fournier (1981) in which an upper limit in the APE was arbitrarily set at 20% for each vertebra (samples were discarded if, after a recount, they were still above this limit) and a final APE index was recalculated and an intrareader comparison (XR-A vs. SC-A) and interreader comparison (SC-A vs. SC-B) of APE values were then conducted;
2. The index of precision D (Chang, 1982);
3. The percentage agreement among the three counts for each method; and
4. The percentage agreement in paired GR counts between the methods.

Centrum analyses

Dorsal centrum diameter and dorsal "birth diameter" were measured in a transverse plane along a straight line through the focus of each vertebra (Fig. 2B). The dorsal "birth diameter" was marked on the x-radiographs and screen images. Distance from the focus to the outer edge of each GR (Fig. 2B) was measured on the scanned images by using CorelDRAW!.

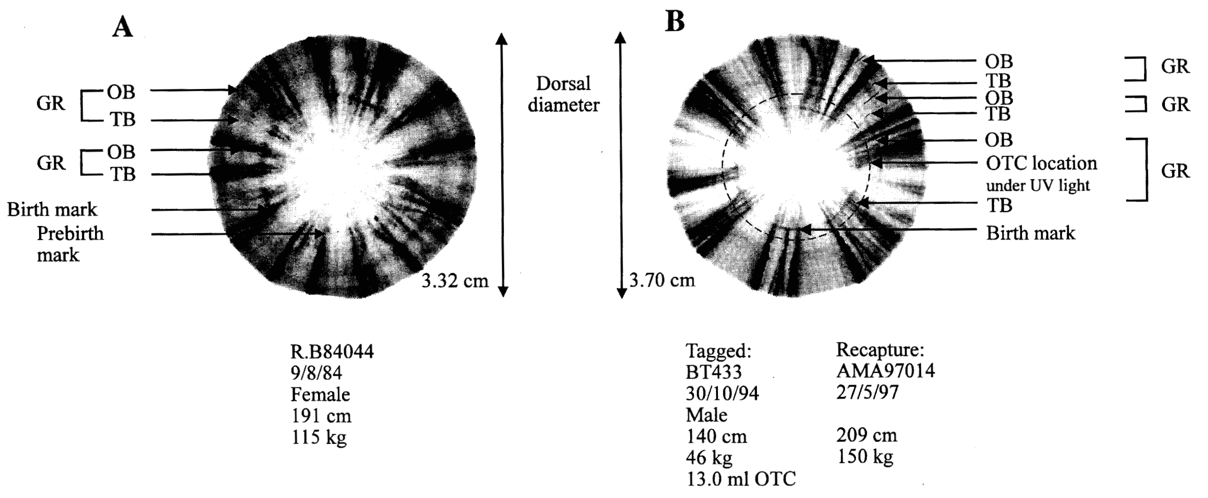

Figure 1

Inverted scanned images of x-radiographs of two white sharks. OB = opaque band, TB = translucent band, GR = growth ring.

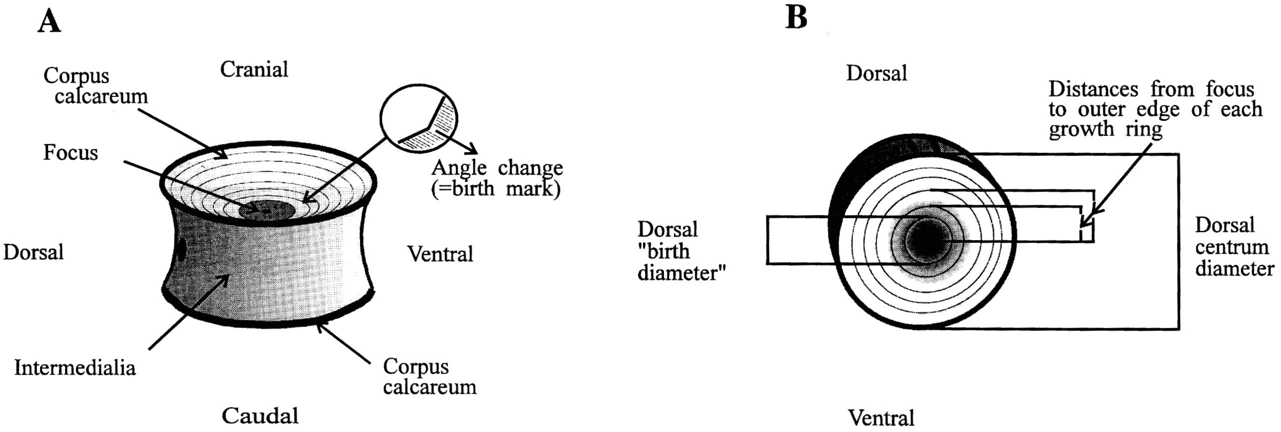

Figure 2

Schematic drawings of a vertebra illustrating terms used in the text.

The relationships between centrum diameter and both shark length and mass were examined by comparing regression lines of both sexes with the procedure of Zar (1974), which compares the slopes and elevations with Student's *t*-tests. Significance levels given in the text are the results of these tests. Outliers were determined by using Statgraphics (STSC, 1991) and eliminated.

The Dahl-Lea method of back-calculation (Carlander, 1969) was used, in which

$$PCL_t = CD_t\,(PCL_c/CD_c),$$

where PCL_t = length at GR t;
CD_t = centrum diameter at GR t;
PCL_c = length at capture; and
CD_c = centrum diameter at capture.

The Monastyrsky method of back-calculation (Bagenal and Tesch, 1978, cited by Francis, 1990) was used to estimate mass at age, in which

$$M_t = (CD_t/CD_c)^b\,M_c,$$

where M_t = mass at GR t;

M_c = mass at capture; and
b = the constant derived from the multiplicative regression of M on CD.

The constant b was derived by using the "body-proportional-hypothesis," where "if a fish at time of capture was 10 per cent smaller than the average fish with the same size of scale, the fish would be 10 per cent smaller than the expected length for the size of that scale throughout life" (Whitney and Carlander, 1956, cited by Francis, 1990).

Confirmation of the annual periodicity of GRs (Cailliet et al., 1983a, 1983b) was attempted with two methods of centrum analyses. First, the last deposited band was classified as translucent or opaque and related to the month of capture (Kusher et al., 1992). The observed and expected ratios of translucent to opaque last bands were then compared. Second, the marginal increment ratio (MIR) (Hayashi, 1976; Skomal, 1990) was calculated with the following equation:

$$MIR = (VR - R_n)/(R_n - R_{n-1}),$$

where VR = vertebral radius;
R_n = radius to the last complete GR; and
R_{n-1} = radius to the previously completed GR.

Mean MIR, with range and standard error, was then plotted against month.

In addition, 16 white sharks (between 1993 and 1995) were injected with oxytetracycline (OTC) solution (Engemycin, Intervet International B.V.), at a dose of 25 mg per kg body mass as recommended by Holden and Vince (1973) and McFarlane and Beamish (1987). Mass was estimated from the mass-length equation of Cliff et al. (1989). The OTC was administered in several places in the muscle around the first dorsal fin with a 15G × 1.5" disposable needle and 20-mL plastic syringe. Each shark was tagged with an orange identification tag (Hallprint PDA large plastic dart tag), labelled "tetracycline" and given a unique "BT" number.

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 obtained by the three methods. Where appropriate, von Bertalanffy growth parameters (VBGP) were computed. The equation (von Bertalanffy, 1938) is

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

where L_t = length at GR t;
L_∞ = maximum theoretical length;
k = the rate at which L_∞ is reached; and
t_0 = the theoretical number of GR at length zero.

To determine whether GR deposition was related to an increase in mass rather than to time of year, Gompertz growth parameters were also calculated. The Gompertz equation (Silliman, 1967; Ricker, 1975) is

$$W_t = w_0 e^{G(1-e^{-gt})},$$

where w_t = mass at GR t;
G = initial exponential growth; and
g = exponential rate of decline.

Both growth equations were fitted by using the nonlinear regression procedure of STATGRAPHICS, which uses Marquardt's algorithm (Draper and Smith, 1981). Because this procedure is highly dependent upon initial estimates for the parameters, a wide range of initial parameters was used to prevent the models converging to a local minimum, i.e. converging to an unwanted stationary point of the sum of squares, rather than to a global minimum (Draper and Smith, 1981).

Table 1

Comparison of average percentage error (APE) indices and index of precision (D) for each method. Values are given before and after elimination of vertebrae with an APE > 0.2.

Methods	Preliminary APE index (%)	D (%)	n	Final APE index (%)	D (%)	n
SC-A	8.9	6.9	114	5.3	4.1	112
SC-B	12.9	9.8	114	5.4	4.1	108
XR-A	9.0	7.0	114	6.1	3.9	110

Results

Of the 114 processed vertebrae, between two and six, depending on the method, had an APE of over 20% after a recount and were discarded (Table 1). The final APE indices and D values showed little differences amongst methods, indicating similar reproducibility (Table 1). The percentage agreement among the three counts was high, e.g. with method SC-A, for 58.0% of the sample the three counts were the same (Table 2). In all three methods the majority of the readings was the same or differed only by one GR. For this reason, a mean of the three counts was

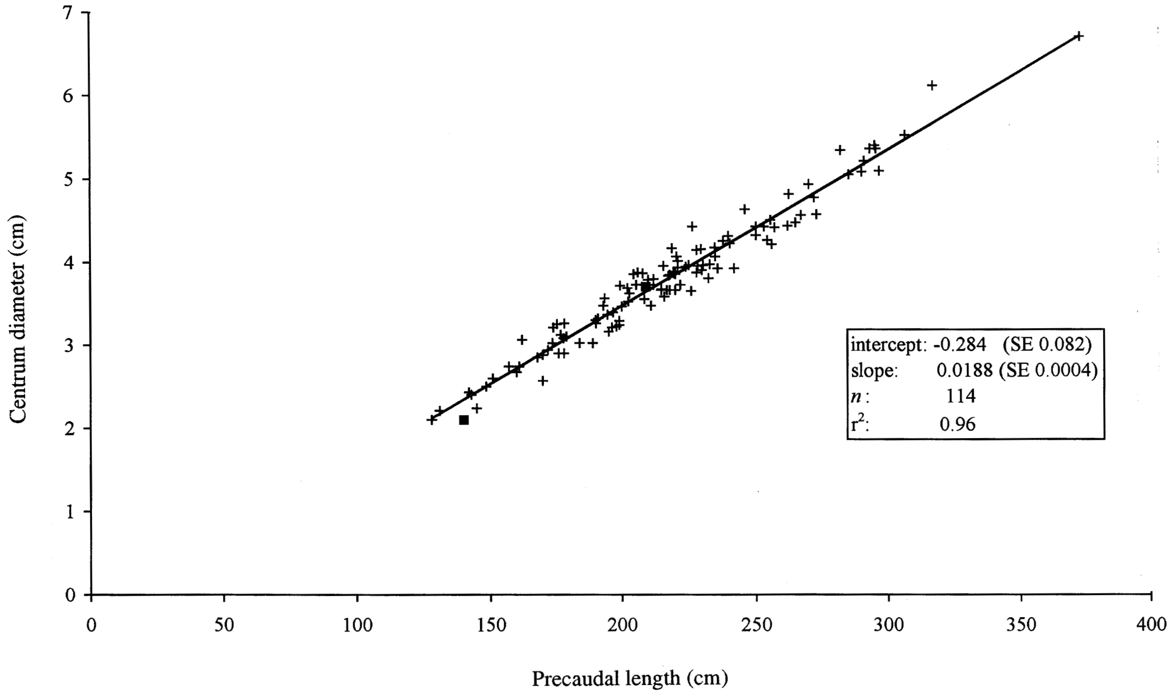

Figure 3

Relationship between centrum diameter and length for combined sexes of the white shark, *C. carcharias.* Squares indicate shark BT433 at tagging and recapture.

Table 2

Percentage agreement among the three counts for each method. Numbers in parentheses indicate sample sizes.

Methods	Difference in GR counts: 0 GR	1 GR	2 GR	3 GR	4 GR	*n*
SC-A	58.0 (65)	33.0 (37)	7.1 (8)	0.9 (1)	0.9 (1)	112
SC-B	61.1 (66)	37.0 (40)	0.9 (1)	0.9 (1)	—	108
XR-A	50.0 (55)	36.4 (40)	11.8 (13)	1.8 (2)	—	110

Table 3

Percentage agreement in paired growth ring (GR) counts between methods. Numbers in parentheses indicate sample sizes.

Methods	Difference between counts: 0 GR	1 GR	2 GR	3 GR	*n*
SC-A - SC-B	42.5 (45)	41.5 (44)	15.1(16)	0.9 (1)	106
SC-A - XR-A	59.6 (65)	34.9 (38)	4.6 (5)	0.9 (1)	109

taken as a GR estimate in all three methods and used for all further calculations. The two readers agreed on the mean GR estimate in 42.5% of the vertebrae; in 59.6% of the vertebrae there was no difference between GR estimates obtained by the same reader using the two methods (Table 3).

Centrum analyses

Prebirth marks were found in all vertebrae with method XR-A and in 33% of the vertebrae with method SC-A (Table 4). Using all three methods, we

Table 4

Percentage of vertebrae where prebirth marks were present and nature of the first band after the angle change.

Method	Prebirth marks %	Prebirth marks *n*	First band after angle change: opaque %	First band after angle change: translucent %	*n*
SC-A	33	114	94	6	62
SC-B	—	—	96	4	97
XR-A	100	114	88	12	81

Table 5

Observed and back-calculated precaudal length (PCL) at number of growth ring for the white shark, *C. carcharias*. Growth ring estimates were obtained with method SC-A.

No. of growth rings	Observed PCL (cm)					Back-calculated PCL (cm)				
	Min	Max	Mean	SD	*n*	Min	Max	Mean	SD	*n*
0	131	131	131	—	1	85	118	100	7	114
1	128	178	156	16	12	96	182	133	17	112
2	161	228	192	19	18	121	221	165	22	99
3	172	236	204	17	25	150	241	191	24	77
4	197	265	225	16	26	169	270	212	25	46
5	215	291	246	22	15	184	261	222	21	22
6	238	297	276	21	7	212	271	240	18	13
7	263	307	287	19	4	233	294	264	19	10
8	282	293	288	8	2	259	301	279	18	5
9	—	—	—	—	—	278	308	289	16	3
10	317	317	317	—	1	300	335	317	24	2
11	—	—	—	—	—	325	325	325	—	1
12	—	—	—	—	—	338	338	338	—	1
13	373	373	373	—	1	350	350	350	—	1
14	—	—	—	—	—	369	369	369	—	1

found that the majority of the vertebrae had an opaque band as the first band after the angle change (Table 4). Only samples where the nature of the first band was the same in all three counts were considered for our analysis.

A statistically significant linear relation was found between centrum diameter and PCL (Fig. 3). There was no significant difference between the sexes in the slopes ($P>0.5$), but a significant difference between the elevations ($P<0.001$). Because the intercepts differed only by 0.02, no visual difference in the predicted values of females and males was perceptible, and the common intercept was used to plot a regression for the combined sexes. The intercept was close to zero; therefore no correction, such as the Fraser-Lee method (Carlander, 1969; Branstetter, 1987), was used.

One of the 16 white sharks injected with OTC (BT433) was recaptured after the completion of the study. The shark was tagged during a fishing competition on 30 October 1994; it measured 140 cm and weighed 46 kg. On recapture 942 days later, on 28 May 1997, it measured 209 cm (150 kg). The squares in Figure 3 indicate the length and centrum diameter of this shark at tagging, i.e. at the OTC marker and at recapture.

Because of the similarity of the above regressions for females and males, back-calculations were performed on combined sex data. Mean back-calculated lengths were lower than observed values (Table 5). 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 evident, but not consistent. In sharks with 7 and 8 GRs, for example, the back-calculated values for each GR class were higher than those for sharks with 6 GRs.

A multiplicative relationship was found between centrum diameter and mass and no significant difference was found between the sexes in the slopes ($P>0.5$), but a significant difference between the elevations ($P<0.001$) (Fig. 4). Again, because of the similarity of the regressions for females and males, back-calculations were performed on combined sex data. Back-calculated mass was lower than observed values (Table 6). Lee's phenomenon was evident, but not consistent, and showed a similar trend to that of back-calculated lengths. Because of the use of mean GRs, the number of observed lengths (or masses) per GR class, plus the number of back-calculated lengths (or masses) in the next GR class, did not always add up to the total number of back-calculated lengths (or masses) of the previous GR class (Tables 5 and 6).

The observed ratio of translucent to opaque last bands differed significantly from the expected ratio (χ^2 test, $P<0.001$, $n=33$), irrespective of whether opaque band deposition was assumed to occur in summer or in winter. For this analysis only vertebrae were used where the nature of the last band was the same in all nine counts (i.e. in all three counts of all three methods). The exclusion of borderline cases, i.e. only summer months (22 Dec–20 Mar) and winter months (21 Jun–22 Sep), did not alter the result

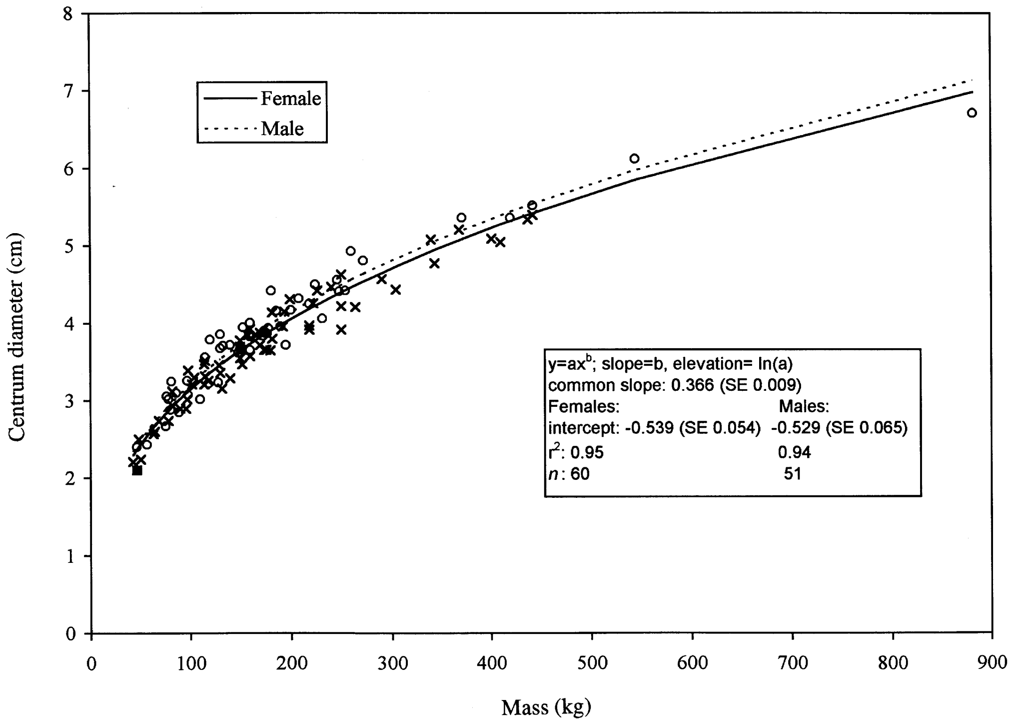

Figure 4

Relationship between centrum diameter and mass for female (x) and male (o) white sharks, *C. carcharias*. Squares indicate shark BT433 at tagging and recapture.

Table 6

Observed and back-calculated mass at number of growth ring for the white shark, *C. carcharias*. Growth ring estimates were obtained with method SC-A.

No. of growth rings	Observed mass (kg)					Back-calculated mass (kg)				
	Min	Max	Mean	SD	*n*	Min	Max	Mean	SD	*n*
0	42	42	42		1	14	36	22	4	112
1	46	97	69	19	11	18	120	48	17	110
2	68	199	120	37	18	33	198	85	31	98
3	81	218	139	35	25	55	256	124	44	76
4	98	250	176	42	26	73	352	164	55	46
5	112	368	234	68	15	90	280	188	48	22
6	218	442	314	84	7	186	313	239	42	13
7	272	442	386	77	4	238	416	310	55	10
8	371	437	404	47	2	351	406	380	23	5
9	—	—	—	—	—	420	504	452	45	3
10	544	544	544	—	1	506	625	565	84	2
11	—	—	—	—	—	618	618	618	—	1
12	—	—	—	—	—	685	685	685	—	1
13	882	882	882	—	1	751	751	751	—	1
14	—	—	—	—	—	859	859	859	—	1

(χ^2 test, $P<0.001$, $n=22$). With method SC-A, and again only with vertebrae where all three counts had the same last band, the observed ratio of translucent to opaque last bands differed significantly from the expected ratio (χ^2 test, $P<0.001$, $n=75$), again irrespective of whether opaque band deposition was

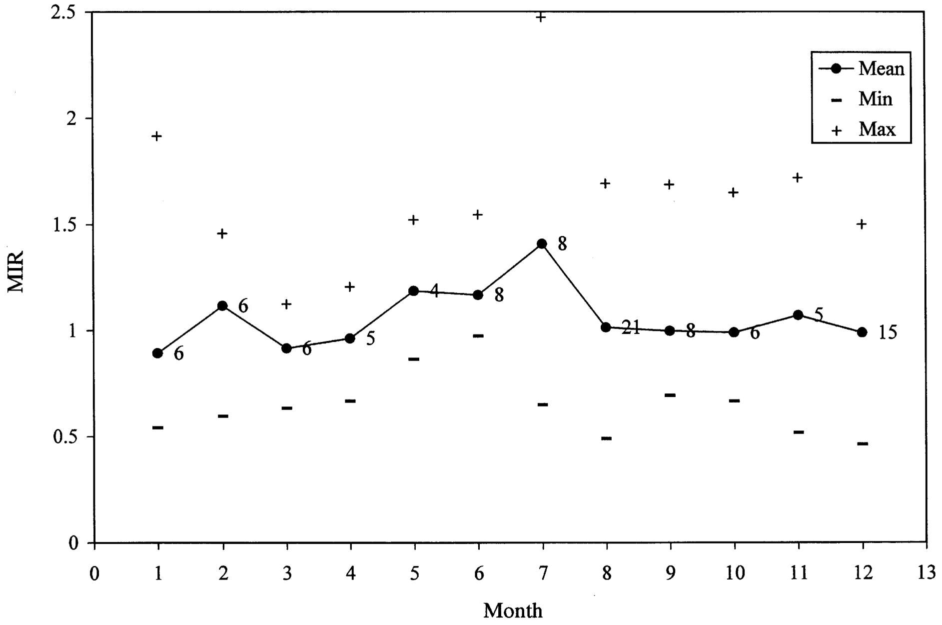

Figure 5

Marginal increment ratio (MIR) by month for the white shark, *C. carcharias*. Numbers indicate sample size, vertical bars indicate the standard error of the mean, and +/– indicates the range. Measurements were obtained by using method SC-A. 1 = January, 12 = December.

assumed to occur in summer or in winter. The exclusion of borderline cases, however, resulted in a significant difference between observed and the expected ratios (χ^2 test, $P<0.001$, $n=39$), assuming opaque band deposition in summer, but no significant difference (χ^2 test, $P>0.05$, $n=39$), assuming a translucent band deposition in summer.

The vertebra of shark BT433 was difficult to read (Fig. 1B), when compared with other sharks of similar length and mass (Fig. 1A). For this reason, we also examined the vertebra with transmitted light (Wintner and Cliff, 1996), and our interpretation of GRs is based mainly on this method. The OTC marker was visible in the opaque band (injected 30 October 1994). The deposition of OTC when injected intramuscularly occurs after a couple of weeks (Holden and Vince, 1973) or 21–35 days (Brown and Gruber, 1988). The opaque band would therefore have been deposited in summer (November or December). The last band in the vertebra was an opaque band. Because the shark was recaptured on 27 May 1997 (the beginning of winter), the translucent band might have been in the process of being formed.

MIR analysis of the entire sample (Fig. 5), however, did not show a distinct time of GR formation because mean and minimum ratios did not get close to zero. The results of a Kruskal-Wallis analysis indicated that there is no relation between MIR and month ($P=0.39$). In view of the results from the above recaptured shark and if the peak in July was regarded as a single peak, we assumed that one GR was formed annually, combined with the minimum MIR trend. With the latter, GR formation may occur during December or January. Because of the ambiguity of the results of the centrum analyses, however, annual periodicity of GR could not be confirmed.

Age and growth

The von Bertalanffy growth function was the most appropriate model for the data sets obtained by both methods SC-A and XR-A. The length-GR data set obtained by method SC-B was not investigated further because two growth models, Putter no. 2 and Gompertz (Punt and Hughes, 1989), provided a better fit than did the von Bertalanffy growth function. In addition, the L_∞ values obtained by the two models were too low to be realistic according to observed sizes of white sharks. Sexes could not be compared because there were no females larger than 300 cm; consequently no meaningful von Bertalanffy growth function could be fitted. Although the VBGP for the two methods SC-A and XR-A differed, there was little difference in the calculated GR over the range of lengths sampled (Fig. 6). Method SC-A had lower relative standard errors and a more realistic L_∞ than

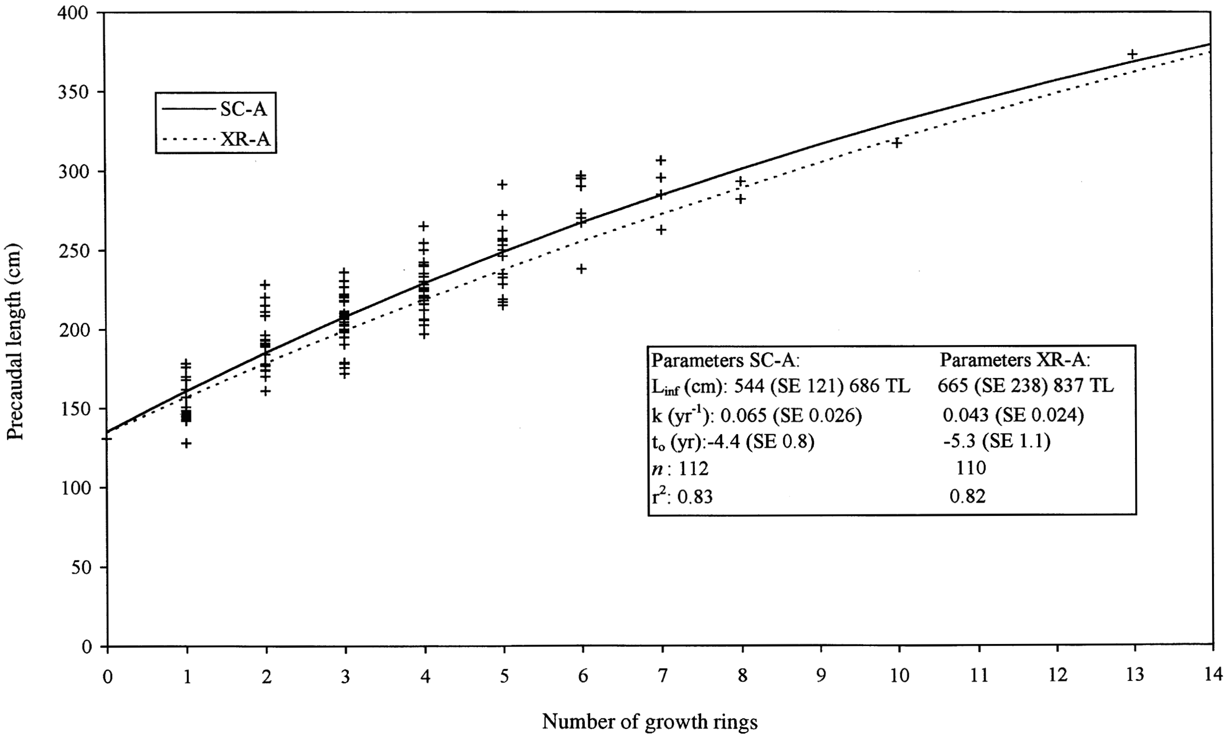

Figure 6

Von Bertalanffy growth curves and parameters for the white shark, *C. carcharias*, sexes combined. Growth ring estimates were obtained by using methods SC-A and XR-A. Observed values (+) are those for the method SC-A. Squares indicate shark BT433 at tagging and recapture.

method XR-A. For these reasons the results of the former method were used for back-calculations, MIR analysis, fitting of the Gompertz growth curve, growth calculations, and GR estimates.

Table 7

Growth ring (GR) counts for animals of certain lengths (PCL, cm) or certain mass (kg).

	Male			Female		
	No. of GRs	PCL	mass	No. of GRs	PCL	mass
Lowest number of GRs	1	142	56	0	131	42
Highest number of GRs	13	373	882	8	282	437
Smallest animal	1	142	46	1	128	42
Largest animal	13	373	882	6	297	442
Smallest mature animal	8	293	371	—	—	—

Table 7 shows the number of GRs counted for various animals. The largest female, an adolescent, (297 cm) had 6 GRs; there were no mature females. Of the three mature males, the smallest had 8 GRs (293 cm), the other two had 10 and 13 GRs (317 and 373 cm), respectively. Size at birth ranged between 100 cm (back-calculated value) and 135 cm (predicted value). Shark BT433 was found to have one GR at tagging (140 cm) and three GRs at recapture (209 cm), after 2.6 yr at liberty (Fig. 1B; Fig. 6).

A Gompertz growth curve was fitted to the mass-GR data (Fig. 7). The female and male with the highest number of GRs, had 8 GRs (437 kg) and 13 GRs (882 kg), respectively (Table 7). Mass at birth ranged between 22 kg (back-calculated value) and 54 kg (predicted value).

Mean growth rates calculated from observed lengths were higher overall than those calculated from predicted lengths (Fig. 8). Mean growth for predicted lengths was 26 cm for the period 0–1 GR, decreasing to 20 cm (4–5 GRs), 16 cm (7–8 GRs), and 12 cm (12–13 GRs). Mean observed growth in mass was also higher than that of predicted values (Fig. 8). Mean growth for predicted mass was 23 kg for 0–

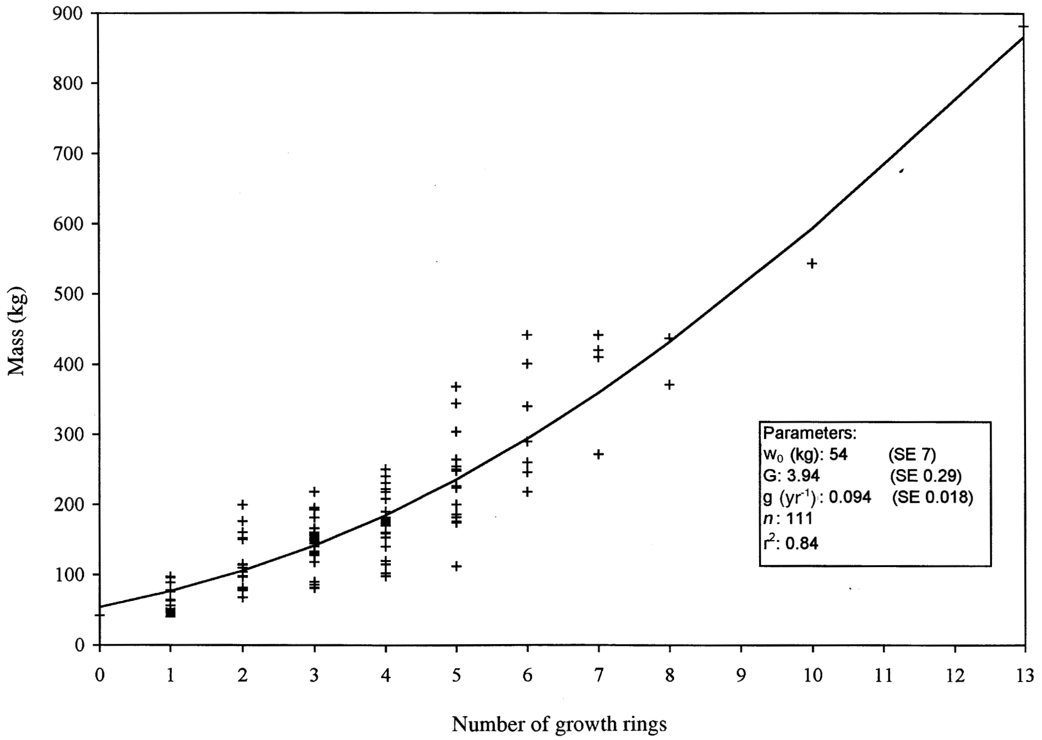

Figure 7

Gompertz growth curve for the white shark, *C. carcharias*, sexes combined. Growth ring estimates were obtained by using method SC-A. Squares indicate shark BT433 at tagging and recapture.

1 GR, increasing to 51 kg (4–5 GRs), 78 kg (7–8 GRs) and 94 kg (12–13 GRs). Shark BT433 grew 69 cm and 104 kg in 2.6 years (Fig. 1B) which represents a mean annual growth of 27 cm and 40 kg.

Discussion

Annual GR periodicity has been partly verified for several species (Cailliet, 1990). For some species of the family Lamnidae, biannual GR periodicity has been reported. Parker and Stott (1965) used the mean length of 17 *Cetorhinus maximus* sampled in winter and 15 sampled in summer and treating them as age classes, derived a tentative growth curve. They stated that their growth curve derived from ring counts of five vertebrae was similar to the first one when a deposition of two GRs per year was assumed. They were, however, careful to note that there was "nothing to indicate beyond doubt that the addition of two rings is the direct result of the passage of an annual seasonal cycle" and said that several findings did not "harmonise with the idea of annual increase of two rings."

Pratt and Casey (1983) determined age and growth of *Isurus oxyrinchus* from the Atlantic by length-month analysis, length-frequency analysis, tag-recapture information, and vertebral ring counts. The results of the first analysis were used to interpret the accuracy of the other methods. Their growth curve for *I. oxyrinchus*, based on back-calculated sizes, agreed closely with those obtained by the other methods if biannual ring deposition was assumed. The vertebrae from four noninjected recaptured *I. oxyrinchus*, however, gave inconclusive results because two supported annual and the other two biannual GR deposition. Pratt and Casey stated that "vertebral rings may thus yield an approximation of age, accurate in the smaller sizes where estimates have been correlated with other methodologies. Adults may not lay down yearly, and it is possible that we have underestimated their age, but we have no data to support this possibility."

Cailliet et al. (1983a) assumed annual GR deposition in *I. oxyrinchus* from California waters. Their growth rate estimates, based on tag-recapture analysis, were therefore half of those of Pratt and Casey (1983) and had a much smaller variation in the estimate. Cailliet et al. (1983a) stated that although "this discrepancy could be related to differences in habitat or environmental conditions or differences in

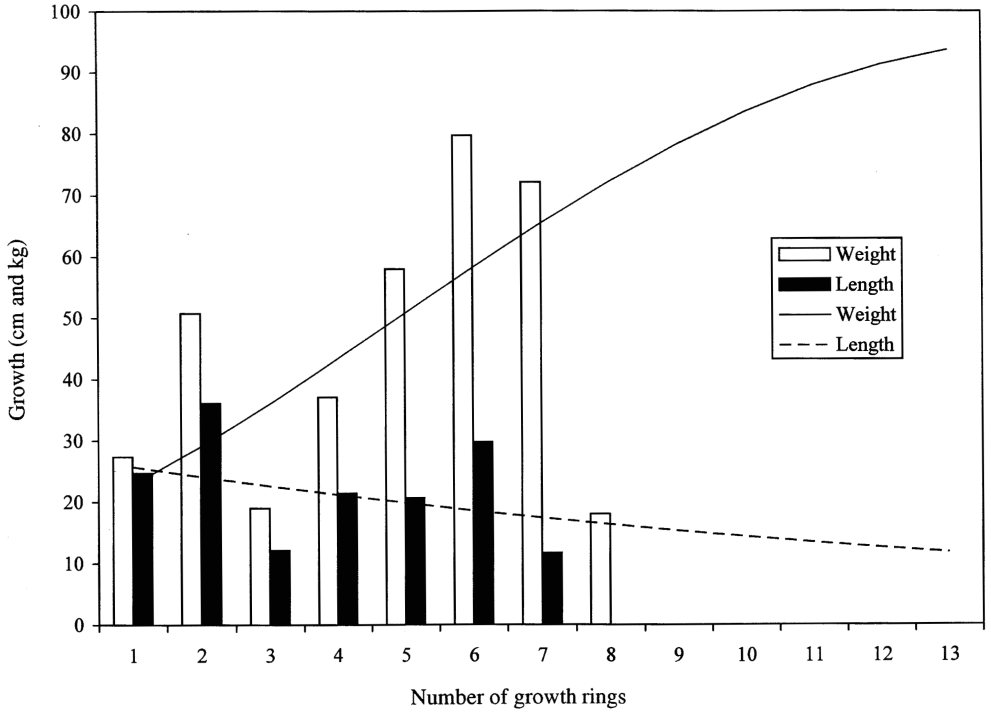

Figure 8

Observed (bar) and predicted (line) growth in mass and length per growth ring for the white shark, *C. carcharias*. Growth ring estimates were obtained by using method SC-A.

sample size or ageing methodology" it was interesting to note "that the growth rate reported by Pratt and Casey (1983) based on their back-calculation from counts of bands on centra, would be similar to ours if each pair of bands from their fish were interpreted as an annual event."

Cailliet et al. (1985) assumed annual GR periodicity in their age and growth study of *C. carcharias*. As with the studies mentioned above, MIR analysis could not be included to validate the temporal periodicity of the GRs. The only lamnoid study to have done so, apart from this one, was that of Branstetter and Musick (1994) on *Carcharias taurus*, which suggested a semiannual periodicity of band and ring formation. However, samples from three winter months were lacking. They also used a "odd-even ring count analysis" to verify this suggestion.

The results of the MIR analysis (Fig. 5) were inconclusive and did not confirm the results from shark BT433. Considerable time was spent on this analysis and great care was taken to discern the last deposited band in order not to overlook a recently formed band. Several vertebrae were remeasured, resulting only in removing the peaks of the curve and not in a reduction of the minimum MIR. Examination of the relative frequency of vertebrae with large MIR to those with low MIR plotted against month (Batista and Silva, 1995) did not shed light on this issue. Annual or biannual GR periodicity for *C. carcharias* could not be confirmed in this study by two centrum edge analyses.

There seems to be some unexplained variation in GR deposition among lamnoids, which is further compounded by our study. Pratt and Casey (1983) stated that in *I. oxyrinchus* instead of the traditional annual ring deposition "a more likely cause for ring formation would be times of stress or deprivation such as migration and mating." Similarly, Branstetter and Musick (1994) suggested that in *C. taurus* the formation of semiannual bands may reflect their north-south seasonal migration pattern, which is prompted in part by changing light and temperature patterns. There is currently not enough evidence to prove a similar migration pattern for *C. carcharias* in South African waters (Cliff et al., 1996a, 1996b).

Traditionally, ages of sharks have been related to length (Cailliet et al., 1983b; Cailliet et al., 1986). Natanson and Cailliet (1990) found that band deposition in *Squatina californica* was not annual but related to somatic growth. We therefore decided to fit a Gompertz growth curve because this curve usually describes the relationship between mass and age well (Ricker, 1975). The curve did not show the typical asymmetrical sigmoid curve but seemed to approach an upper asymptote (Gulland, 1983). It was the method with the lowest relative standard errors for all parameters. Although there is also considerable variation in mass at GR, we felt that the Gompertz growth curve has merit, especially because there is a large change in mass associated with a small increase in length among large sharks. The results of the MIR analysis could be interpreted such that GR formation is not related to time of year but to mass increase (some sharks taking a longer time than others to gain the same amount of mass).

Typically, opaque band deposition is associated with summer growth (Cailliet et al., 1983b, 1986; Kusher et al., 1992), and the nature of the last deposited band can be related to the month of capture to verify this. Using method SC-A and only summer and winter months, we found that the observed ratio of translucent to opaque last bands did not differ significantly from the expected ratio, assuming a translucent band deposition in summer. When we used nine ring counts, however, the analysis did not show any relation between the nature of the last band and season. The analysis could be considered statistically weak owing to the low sample size but was included to emphasize the accuracy of the last band identification. In this study the band immediately after the angle change was opaque in most vertebrae, which is in keeping with Francis (1996) who reported time of parturition of white sharks as spring or summer. In addition, if our interpretation of vertebral bands in shark BT433 is correct, the opaque band would be formed in summer. Because of the inconclusive results of the centrum analyses of the entire sample, however, more recaptures of sharks injected with OTC are needed to confirm this theory.

The relation between centrum diameter and shark length was linear, as was found in *C. carcharias* by Cailliet et al. (1985) and in several other shark species (Cailliet et al., 1983b; Schwartz, 1983; Branstetter, 1987). For another species of the family Lamnidae, *I. oxyrinchus*, Pratt and Casey (1983) found a slightly curvilinear relationship for both females and males. The relation between centrum diameter and mass was multiplicative, which explains the slightly bigger difference in centrum diameter between the sexes than in the relation between centrum diameter and length. The differences between the sexes in both relationships, however, are slight and are probably not of biological significance.

Back-calculated mass and length values were lower than observed values. The differences between mean observed length (or mass) and mean back-calculated length (or mass) at each GR would decrease substantially if the observed GR 0 were treated as GR 1. This could be an indication that the angle change of the corpus calcareum is not formed at birth but in the first summer growth (Brown and Gruber, 1988; Wintner and Cliff, 1996).

X-radiography to enhance the visibility of GRs in elasmobranch vertebrae has been used successfully on several species (Cailliet et al., 1983a, 1983b; Yudin and Cailliet, 1990; Ferreira and Vooren, 1991). This technique was also used in the only other ageing study of *C. carcharias* by Cailliet et al. (1985). They counted GRs directly from x-radiographs and used silver nitrate staining to corroborate counts of larger vertebrae that proved more difficult to read. In our study, scanned images allowed for easy and rapid counts of rings and measurements for back-calculations. In addition, scanned images were easier to interpret because they showed less detail of the narrow circuli and prebirth marks than did the x-radiographs.

Prebirth marks in placental species are normally attributed to the time of placenta formation and attachment (Casey et al., 1985; Branstetter, 1987; Branstetter and Stiles, 1987). In our study, prebirth marks were found in *C. carcharias* vertebrae. No comments on prebirth marks in *C. carcharias*, *I. oxyrinchus*, or *Alopias vulpinus* were made by Cailliet et al. (1985), Pratt and Casey (1983), and Cailliet et al. (1983a), respectively. Branstetter et al. (1987) did not find prebirth marks in *Galeocerdo cuvier*, another aplacental species. Branstetter and Musick (1994), however, found prebirth marks in their *Carcharias taurus* specimens and related the first consistent prebirth ring to the size of the embryo when digestion of the large quantities of eggs begins. We did not relate prebirth marks to embryonic length using back-calculations because they represent growth in utero.

The APE indices for the three methods (5.3–6.1%) were considered acceptable. They were lower than those of the four methods used by Wintner and Cliff (1996) for *Carcharhinus limbatus* (8.1–13.0%, *n*=80–87) and those of Cailliet et al. (1990) who used “bow tie” sections of *Mustelus manazo* (6.9–12.7%, *n*=28–30). *D*-values (3.9–4.1%) were also considered to be acceptable because they were similar to those of Natanson and Kohler (1996) for *C. obscurus* (3,3%, *n*=42) and lower than those of Cailliet et al. (1990) (6.8–12.7%, *n*=27–30).

Age and growth estimates

Only one shark injected with OTC was recaptured (BT433). Although it was at liberty for an adequate time period, an interpretation of the bands on the x-radiograph was difficult, and therefore the results were based mainly on viewing the vertebra with transmitted light. The number of GRs counted, however, were the same with these two methods and for both authors. While at liberty, the shark's mean annual growth increment was 28 cm and 42 kg. Francis (1996) reported size at birth between 92 and 116 cm and weight at birth between 12 and 32 kg and given that this shark was 140 cm and 46 kg at tagging, it is reasonable to assume that its age was in the region of one year. This estimation was confirmed by the OTC marker being visible at the edge of the first GR (Fig. 1B).

Table 8

Comparison of von Bertalanffy growth parameters. The bold values were obtained by refitting the data.

	Our study (SC-A)	Cailliet et.al (1985)	
		Their results	Refitted excluding 3 large animals
Range PCL	128–373	110–434	110–394
Range TL	165–472	129–508	129–461
VBGP			
L_∞	544 (686 TL)	653 (764 TL)	569 (666 TL)
SE	121	**134 (157 TL)**	110 (129 TL)
k	0.065	0.058	0.072
SE	0.026	**0.023**	0.028
t_0	–4.4	–3.5	–3.3
SE	0.8	**0.72**	0.72
n	112	21	18
r^2	0.83	**0.98**	0.97

Because we counted three GRs at recapture, the mean predicted growth/GR in the period from 1 to 3 GRs was 24 cm/GR and 33 kg/GR (Fig. 8). Assuming that one GR is deposited per year, the total growth of shark BT433 would be 62 cm and 86 kg in the period of 2.6 years. If the GR deposition is biannual, which is not impossible given the difficulty in interpreting this vertebra (Fig. 1B), the mean predicted growth would be 18 cm/GR and 32 kg/GR; this would amount to a total growth in a period of 2.6 yr (5.2 GR) of 94 cm and 166 kg. Because BT433 grew 69 cm and 104 kg, the first of these two predictions fits the observed growth better than the second.

Further evidence to support the hypothesis of annual GR deposition can be found in Figures 6 and 7. If the number of GRs represents years, the expected size and mass of shark BT433 at tagging and recapture after 2.6 years is in accordance with the observed values of our sample (Fig. 6). Assuming biannual GR deposition, we believe the shark's size and mass at tagging is still in accordance with the observed values (Fig. 7); however, it would have been in the region of 288 cm and 375 kg at recapture. Because evidence of annual GR deposition in *C. carcharias* is based on the recapture of a single shark injected with OTC and because our centrum analyses neither confirmed nor contradicted annual ring deposition, the discussions below are based on number of GRs rather than years.

Our VBGPs, in the absence of very large sharks, were L_∞ = 544 cm (SE 121), k = 0.065/yr (SE 0.026), and t_0 = –4.4 yr (SE 0.8). We fitted a von Bertalanffy growth curve to the data points presented by Cailliet et al. (1985) in order to compare standard errors (Table 8). The results were very similar, but given the larger sample size in our study, it would appear that there is greater variation in length at number of GRs in *C. carcharias* from South Africa.

Our largest shark (373 cm) measured 452 cm TL. The absence of larger sharks in our study undoubtedly accounts for the lower L_∞ of 544 cm (686 cm TL), as opposed to that of Cailliet et al. (1985) of 654 cm (764 cm TL). This finding was confirmed when the three markedly larger sharks (494–508 cm TL) of their study were omitted and the recalculated L_∞ was 569 cm (666 cm TL) (Table 8). The conversion of the original data of Cailliet et al. (1985) from TL to PCL had no effect on the VBGP and their standard errors. One should keep in mind, however, that comparisons of L_∞ are somewhat hampered by the fact that TL length is measured in two different ways (Mollet et al, 1996) by various authors, although the difference in *C. carcharias* is not as pronounced as, e.g., in members of the family Carcharhinidae.

The maximum size attained by the white shark is the subject of much interest and controversy and, more importantly, uncertainty (Ellis and McCosker, 1991). Randall (1973, 1987) refuted the lengths of 1113, 900, and 640 cm TL attributed to *C. carcharias*. According to him, the largest reliable measured white shark is 513 cm (600 cm TL). Mollet et al. (1996) calculated the size of two large white sharks, using three morphometric measurements, at 453–701 cm (530–820 cm TL) and 393–598 cm (460–700 cm TL), respectively. These results were consistent with the estimated TL of >700 and 700 cm, respectively. They concluded that the most solid TL estimates for these two sharks were those original estimates. Our L_∞ is larger than the shark from Randall and is smaller than the data of Mollet et al. (1996) and Cailliet et al. (1985).

Our growth coefficient is similar to that found by Cailliet et al. (1985), and both are an order of magnitude lower than that of *I. oxyrinchus* at 0.203–0.266 (Pratt and Casey, 1983) and that of *Lamna nasus* at 0.116 (Aasen, 1963). In the first year of growth, *C. carcharias* grows 19–26% of its size at birth which is less than that of other lamnoids (Branstetter, 1990). Our findings place *C. carcharias* in Branstetter's (1990) group of sharks with slow growth (k<0.10; growth in the first year<30% of the birth size).

In our study, back-calculated size at birth was 100 cm and calculated value was 135 cm. The smallest accurately measured free-swimming *C. carcharias* in southern Africa was 108 cm (140 cm TL) (Smith, 1951) and the sizes of the smallest white sharks caught at the NSB are 128–145 cm. "Umbilical scars" (Cliff et al., 1996a) were present in sharks of 138, 143, 144, and 145 cm, including the 131 cm (0 GR) specimen of this study. If the presence of these scars is interpreted as an indication of recent birth, it is tempting to suggest a very wide range in size at birth, between 100 and 145 cm. These scars, however, may persist for some time after birth and given a growth of about 25 cm/yr in newborn sharks, birth size of *C. carchirias* would be more in the region of that reported by Francis (1996), i.e. 92–116 cm (120–150 cm TL). Our range in mass at birth (22–54 kg) is also substantial, which is in keeping with Francis (1996) who stated that the range in mass at birth for *C. carcharias* is quite pronounced.

Our three mature males had 8, 10, and 13 GRs (293, 317, and 373 cm; 371, 544, and 882 kg, respectively). The NSB has caught immature specimens larger and heavier than our smallest mature, e.g. a 295 cm (420 kg) and a 306 cm (442 kg) specimen (Cliff et al., 1996a). Pratt's (1996) smallest mature male was 299 cm (379 cm TL), which is similar to our shark; however, he notes that sizes at sexual maturity for male *C. carcharias* vary widely in the literature. These differences could be due to a variation in length at maturity depending on location, both compounded by the use of different length conversion equations and maturity criteria. If the number of GRs is taken as an age estimate, assuming annual GR deposition, male *C. carcharias* in South Africa would mature between 8–10 years which is similar to the findings of Cailliet et al. (1985) who worked with a size at maturity of 313–365 cm (366–427 cm TL), corresponding to an age of 9–10 years. This age at maturity is higher than that of other lamnids, e.g. that of male *I. oxyrinchus* at 2–3 years (Pratt and Casey, 1983) and male *L. nasus* at about 5 years (Paust and Smith, 1986).

No mature female has ever been examined from NSB nets, and the biggest female in our study was 297 cm (6 GRs). The biggest female on record is an immature 348 cm specimen (Cliff et al., 1989), and Bass et al. (1975) reported a mature female of 352 cm (445 cm TL). Again if GRs are deposited annually, the above specimens would be 11 and 12 years, respectively. Age at maturity for female *C. carcharias* in South Africa would then be at least 12–13 years, slightly higher than that for males. Again, this age at maturity is higher than in other lamnids, e.g. that for female *I. oxyrinchus* at 7 years (Pratt and Casey, 1983) and female *L. nasus* at 9–10 years (Paust and Smith, 1986).

Although this study could not conclusively prove annual or biannual GR periodicity, the recapture of one shark injected with OTC provided some evidence for annual GR deposition. Assuming that only one growth ring is laid down per year, then *C. carcharias* from South Africa is relatively slow growing in comparison with other lamnoids. This observation would support current protective legislation. The NSB nets are now the only directed source of apparent fishing mortality for *C. carcharias* in South Africa. Cliff et al. (1996b) were of the opinion, using their estimates of mortalities, that the current fishing mortality did not represent overfishing of the white shark stock. Examination of interannual catch rates of *C. carcharias* in the NSB nets showed an significant decline immediately following the introduction of netting, but thereafter (1978–93) there was no significant change (Cliff et al., 1996a). Because they are apex predators, *C. carcharias* are likely to have a small population size (Cliff et al., 1996b), and we have no knowledge about the fecundity and nursery grounds of this species in South African waters. Any possible relaxation of the South African current legislation will depend on improved knowledge about population size, immigration and emigration, natural mortality, and fecundity of *C. carcharias* from South Africa.

Any such relaxation, however, is highly unlikely given the increasing protection that has been granted to this species worldwide. It is now also protected in some states of America (Fergusson et al., in press) and Australia (Stevens[1]), where such legislation is based on a more limited knowledge or understanding of the biology and population dynamics of this species.

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