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Volume 51, 2000

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Academy of Science

Mar. Freshwater Res., 2000, **51**, 43–53

Age and growth estimates for the tiger shark, *Galeocerdo cuvier*, from the east coast of South Africa

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Abstract. Growth rings (GR) in sagitally sectioned vertebral centra of 69 female tiger sharks (102–300 cm precaudal length; 6–412 kg) and 32 males (123–301 cm; 16–396 kg) were counted. In vertebrae from three sharks injected with oxytetracyline (OTC) and recaptured after 18, 389 and 791 days of liberty, respectively, OTC was visible and there was evidence of annual GR deposition. Centrum analyses of the entire vertebral sample failed to confirm this GR periodicity. Assuming annual GR deposition, the youngest female and male aged were 1 year (102 cm) and 2 years (123 cm), and the oldest were 11 years (293 cm) and 8 years (301 cm) respectively. von Bertalanffy parameters for the combined sexes based on back-calculated values were L_∞ 301 cm, k 0.202 year^{-1} and t_0 –1.11 years. Ages calculated for length at 50% maturity were 11 years (274 cm) and 8 years (250 cm) for females and males, respectively. Calculated growth in length decreased from 44 cm (0–1 year) to 4 cm (12–13 years). Gompertz parameters were w_0 14 kg, G 3.73 and g 0.172 year^{-1}. Calculated growth in mass increased from 12 kg (0–1 year) to 38 kg (7–8 years), then decreased to 29 kg (12–13 years). Back-calculated length and mass values were similar to observed values and Lee's phenomenon was not evident in either case.

Introduction

The tiger shark, *Galeocerdo cuvier* (Peron and LeSueur 1822), has a circumglobal distribution in tropical and warm temperate seas (Randall 1992). In the Indo-West Pacific region it occurs from the Red Sea to South Africa (Compagno 1984*a*), and off South Africa it ranges from the Mozambique border to Cape St Francis (Bass *et al.* 1975; Compagno *et al.* 1989). As a common coastal–pelagic species with a wide tolerance of different marine habitats, it can be found from oceanic islands to estuaries (Compagno 1984*a*).

This species has been responsible for shark attacks in South African waters (Cliff 1991) and is one of the 14 common species caught in the gill-nets maintained by the Natal Sharks Board (NSB). The NSB operates a shark fishery in KwaZulu–Natal aimed at protecting beach users against shark attack (Cliff *et al*. 1988). Between 1987 and 1997 an annual average of 55 *G. cuvier* was caught in the nets, with 41% being released alive as part of the NSB's tagging programme and its ongoing efforts to minimize mortalities.

Catch rates of *G. cuvier* have increased since the mid-1970s, a trend which is evident not only in KwaZulu–Natal, but also in the shark control programmes of New South Wales and Queensland, Australia (Paterson 1990; Reid and Krogh 1992; Dudley 1997). This trend, together with the fact that *G. cuvier* is one of the three potentially most dangerous sharks in the nearshore waters of KwaZulu–Natal, has prompted the NSB to investigate age and growth of this species. Knowledge of age at maturity, maximum age, and growth rates is a pre-requisite for age-based methods of stock assessment which in turn can potentially be used for the management of this species.

There have been only two previous attempts at ageing *G. cuvier* based on vertebral growth ring counts. Branstetter *et al.* (1987) used 44 animals from the north-western Atlantic and compared them with 25 animals from the Gulf of Mexico, incorporating the data of Branstetter and McEachran (1986). De Crosta *et al*. (1984) used 28 vertebral samples from Hawaii. The present study provides a growth curve for *G. cuvier* from South Africa based on back-calculated lengths from vertebral growth ring counts from 101 sharks.

Materials and methods

Sharks were sampled throughout the year in the NSB nets from 1987 to 1998. For details of the netting operation see Cliff *et al.* (1988) and Dudley (1997). 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 facilitate comparison of length measurements, the following equations were used:

Total length (TL) as defined by Bass *et al*. (1975):
[TL] = 1.215[PCL] + 16.483 (n = 478; range 90–320 cm PCL; 95% confidence limits on slope: 1.209 and 1.221; r^2 = 0.9971)

TL as defined by Casey and Pratt (1985):
[TL] = 1.259[PCL] + 21.086 (n =151; range 101–301 cm PCL; 95% confidence limits on slope: 1.243 and 1.274; r^2 = 0.9945)

Fork length (FL) as defined by Compagno (1984*b*):
[FL] = 1.074[PCL] + 2.375 (n = 238; range 102–310 cm PCL; 95% confidence limits on slope: 1.069 and 1.08; r^2 = 0.9986)

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Males were considered mature only if the claspers were fully calcified and in females maturity was defined by the presence of distinct ova in the ovary and uteri which had expanded from a thin, tube-like condition to form loose sacs (Bass *et al*. 1975). Length at 50% maturity was determined by use of a maximum-likelihood estimation and data from sharks caught from 1978 to 1998.

Mass was determined by weighing each shark and subtracting the mass of gut contents where they exceeded 1 kg. No embryos were present. One animal was not weighed and mass was calculated from a length–weight curve (NSB, unpublished). Vertebral samples were taken anterior to the first dorsal fin origin from 69 females (102–300 cm; 6–412 kg) and 32 males (123–301 cm; 16–396 kg). Vertebrae were stored either frozen (84%) or dried (16%).

Vertebral centra were prepared by a method similar to that of Branstetter and McEachran (1986) and the resulting sagittal sections were viewed with a stereo microscope and transmitted light and 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 (Casey *et al*. 1985).

Two readers (A, B) made a set of three non-consecutive counts, without knowledge of the shark's length and previous counts. Count reproducibility was determined by four methods as follows. *(1)* The average percentage error (APE) was calculated as described by Beamish and Fournier (1981). An upper limit was arbitrarily set at 20% for each vertebra. Samples were discarded if, after a second set of counts, they were still above this limit, and a final APE index was recalculated. *(2)* The index of precision *D* (Chang 1982) was determined. *(3)* Qualitative assessments were made of the percentage agreement among the three counts for each reader. *(4)* Qualitative assessments were made of the percentage agreement in paired GR counts between the readers.

The relationships of centrum diameter with both shark length and shark mass were investigated. Statgraphics software identified outliers; these were eliminated, and differences between sexes were tested with Student's *t*-test (Zar 1974). The Dahl–Lea method of back-calculation (Carlander 1969) was used in which

$$[\mathrm{PCL}]_t = [\mathrm{CD}]_t\,([\mathrm{PCL}]_c/[\mathrm{CD}]_c)$$

where $[\mathrm{PCL}]_t$ is length at GR t, $[\mathrm{CD}]_t$ is centrum diameter at GR t, $[\mathrm{PCL}]_c$ is length at capture, and $[\mathrm{CD}]_c$ is centrum diameter at capture. The Monastyrsky method of back-calculation (Francis 1990 citing Bagenal and Tesch 1978) was used to estimate mass at age, where

$$M_t = ([\mathrm{CD}]_t/[\mathrm{CD}]_c)^b\, M_c$$

where M_t is mass at GR t, $[\mathrm{CD}]_t$ is centrum diameter at GR t, $[\mathrm{CD}]_c$ is centrum diameter at capture, M_c is mass at capture, and b is the constant derived from the multiplicative regression of M_c on $[\mathrm{CD}]_c$.

Determination of GR periodicity 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). All animals caught in winter were expected to show a translucent last band, animals caught in summer an opaque band (Cailliet *et al*. 1983*a*, 1983*b*, 1986) and expected and observed frequencies were compared by χ^2 test. Second, the marginal increment ratio (MIR) (Hayashi 1976; Skomal 1990) was calculated from the following equation:

$$[\mathrm{MIR}] = ([\mathrm{VR}] - R_n)/(R_n - R_{n-1})$$

where VR is the vertebral radius, R_n is the radius to the last complete GR, and R_{n-1} is the radius to the previously completed GR. Mean MIR, with range and standard error, was then plotted against month.

Additionally, between 1993 and 1997, 93 tiger sharks were injected with oxytetracycline (OTC) solution (Engemycin, Intervet International B.V.), at a dose of 25 mg kg^{-1} body mass (Holden and Vince 1973; McFarlane and Beamish 1987). For details of the injecting and tagging process see Wintner and Cliff (1999).

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 set obtained. The von Bertalanffy growth (VBG) parameters (von Bertalanffy 1938) were computed by use of the nonlinear regression procedure of Statgraphics which uses Marquardt's algorithm (Draper and Smith 1981). In addition, to determine whether GR deposition was related to an increase in mass, the 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 is mass at GR t, w_0 is mass at t = 0, G is initial exponential growth rate, and g is exponential rate of decline in growth rate.

Results

Of the 101 processed vertebrae, one and three samples were considered unreadable by readers A and B, respectively, and discarded. A further seven samples for which both readers had an APE of >20% after the first set of counts were discarded. The final APE index and *D* value of reader A, 9.2% and 7.1%, respectively, were close to those of reader B, indicating similar reproducibility (Table 1). For each reader most counts for each vertebra were the same or differed by only 1 GR (Table 2). For this reason, a mean of the three counts was taken as a GR estimate and used for all further calculations. In 53.4% of the sample the two readers agreed or differed by 1 GR (Table 2).

A linear relationship was found between centrum diameter and length (Fig. 1). As there was no significant difference between the sexes in the slopes (P > 0.5) and elevations (P > 0.2), data were combined and back-calculations were performed on this data set. The intercept was close to zero; therefore no correction, such as that provided by the Fraser–Lee

Table 1. Comparison of average percentage error (APE) precision (*D*) indices
Values are given before and after elimination of vertebrae with an APE >20%

Reader	Preliminary APE index (%)	*D* (%)	*n*	Final APE index (%)	*D* (%)	*n*
A	13.1	9.7	93	9.2	7.1	92
B	14.1	10.9	91	9.7	7.4	90

Table 2. Percentage agreement among the three growth ring (GR) counts for reader A and B and in paired GR counts between readers (A–B)
Numbers in parentheses indicate sample sizes

Difference in GR counts	A	B	A–B
0 GR	16.3 (15)	27.8 (25)	26.1 (23)
1 GR	44.6 (41)	43.3 (39)	27.3 (24)
2 GR	30.4 (28)	25.6 (23)	19.3 (17)
3 GR	8.7 (8)	3.3 (3)	12.5 (11)
4 GR	–	–	5.7 (5)
5 GR	–	–	4.5 (4)
6 GR	–	–	4.5 (4)
n	92	90	88

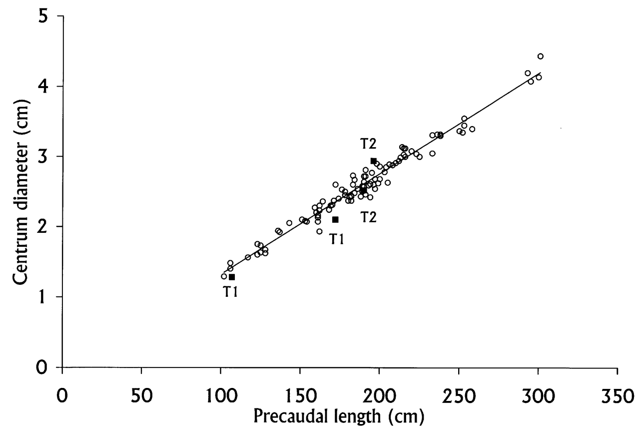

Fig. 1. Relationship between centrum diameter and precaudal length in the tiger shark, *G. cuvier* (sexes combined). ■, values at tagging and recapture for two sharks (T1, T2) injected with OTC. Intercept –0.117 (s.e. 0.053); slope 0.014 (s.e. 0.000); $r^2 = 0.97$; $n = 99$.

Table 3. Observed and back-calculated precaudal length (PCL) at growth ring (GR) for the tiger shark, *G. Cuvier*

No. of GR	Observed PCL (cm) Min.	Max.	Mean	s.d.	*n*	No. of GR	Back-calculated PCL (cm) Min.	Max.	Mean	s.d.	*n*
0	–	–	–	–	–	0	38	103	56	10	90
1	102	106	104	3	2	1	62	170	110	20	90
2	106	182	143	22	19	2	90	206	143	23	87
3	161	204	177	14	16	3	108	217	169	21	72
4	169	223	196	14	18	4	128	236	191	21	54
5	162	238	203	20	18	5	141	253	208	25	38
6	184	253	221	26	9	6	169	277	222	33	13
7	216	258	240	19	4	7	207	284	244	32	4
8	300	300	300		1	8	225	292	258	27	4
9	–	–	–	–	–	9	237	296	269	24	4
10	295	295	295	–	1	10	254	300	281	20	4
11	301	301	301	–	1	11	276	295	288	10	3
12	–	–	–	–	–	12	295	295	295	–	1
13	293	293	293	–	1	13	301	301	301	–	1

method (Carlander 1969; Branstetter 1987), was used. Mean back-calculated lengths ranged from 56 cm (0 GR) to 301 cm (13 GR) and were similar to observed values (Table 3). 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 not evident.

A multiplicative relationship was found between centrum diameter and mass with no significant difference between the sexes in the slopes ($P > 0.2$) and elevations ($P > 0.05$) (Fig. 2). Again, because of the similarity of the regressions for females and males, back-calculations were performed on the combined-sex data. Mean back-calculated masses ranged from 2 kg (0 GR) to 243 kg (13 GR) and were also similar to observed values, except in the larger animals (Table 4). Again, Lee's phenomenon was not evident.

Most vertebrae (66%) had an opaque band immediately after the angle change. Only samples in which the nature of

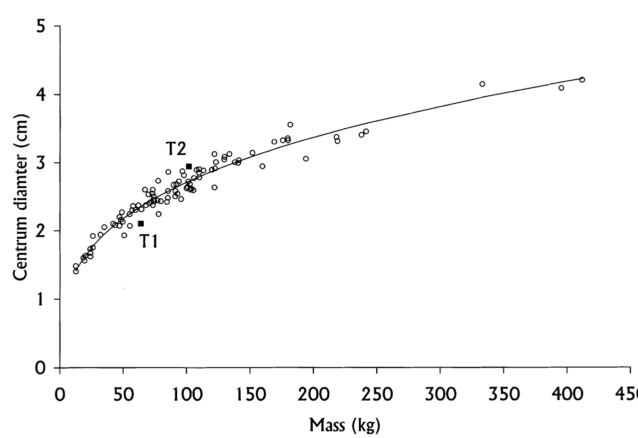

Fig. 2. Relationship between centrum diameter and mass in the tiger shark, *G. cuvier* (sexes combined). ■, values at recapture for two sharks (T1, T2) injected with OTC. $y = ax^b$; $b = 0.314$ (s.e. 0.007); intercept = $\ln(a) = –0.448$ (s.e. 0.03); $r^2 = 0.96$; $n = 97$.

Table 4. Observed and back-calculated mass at growth ring (GR) for the tiger shark, *G. cuvier*

No. of GR	Observed PCL (cm) Min.	Max.	Mean	s.d.	n	No. of GR	Back-calculated PCL (cm) Min.	Max.	Mean	s.d.	n
0	–	–	–	–	–	0	0	13	2	2	90
1	6	13	9	5	2	1	3	71	18	11	90
2	12	78	39	20	18	2	9	129	40	21	87
3	48	110	71	19	17	3	17	150	65	25	72
4	60	130	99	22	17	4	28	189	95	34	54
5	50	219	118	41	18	5	38	241	123	48	38
6	85	241	147	53	10	6	66	261	159	70	13
7	134	238	187	43	4	7	77	284	211	94	4
8	333	333	333	–	1	8	100	308	245	99	4
9	–	–	–	–	–	9	117	341	277	107	4
10	396	396	396	–	1	10	145	380	306	109	4
11	243	243	243	–	1	11	187	412	332	125	3
12	–	–	–	–	–	12	229	229	229	–	1
13	412	412	412	–	1	13	243	243	243	–	1

the first band was the same in all three counts (reader A) were considered. For the purpose of investigating seasonality of band deposition, the last of three counts was used to obtain an adequate sample size. Here, the observed frequencies of translucent and opaque last bands differed significantly from those expected ($P < 0.0001$, $n = 44$).

MIR analysis of the entire sample (Fig. 3) also failed to show a clear trend. The wide MIR range in November could indicate that in some sharks the last GR is fully formed, resulting in a high ratio, whereas in other sharks a new GR was just measurable, resulting in a low ratio.

Three tiger sharks (T1, T2, T3) injected with OTC were recaptured after 791, 389 and 18 days at liberty, respectively. T3 showed faint OTC over the whole centrum face but T1 and T2 had a distinct marker. The shark length and centrum diameters of T1 and T2 are included in Fig. 1. The vertebra of shark T2 showed the OTC in an opaque band (injected 23 May 1995) whereas T1 showed OTC in a translucent band (injected 13 August 1996). The deposition of OTC when injected intramuscularly occurs after a period of weeks (Holden and Vince 1973) or after 21–35 days (Brown and Gruber 1988). The opaque band was therefore deposited in autumn (May/June) and the translucent band in winter (August/September). The last band in the vertebra of T1 was translucent (recapture 4 August 1997), whereas T2 showed an opaque band, with a very thin translucent band at the margin (recapture 12 September 1997).

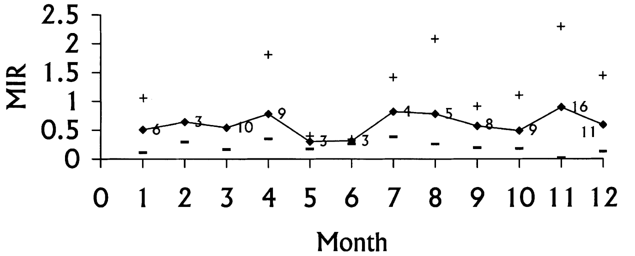

Fig. 3. Marginal increment ratio (MIR: ◆, mean; +, maximum; – minimum) by month (1, January; 12, December) for the tiger shark, *G. cuvier*. Numbers indicate sample size.

Age and growth

A linear growth model provided a better fit than the VBG model for females and males. As this is mainly a result of the lack of vertebrae from animals <100 cm which would adequately flex and anchor the growth curve, a VBG model was fitted to best represent the population as a whole (Fig. 4). In view of the differences in GR counts between the readers (Table 2), the VBG model was also fitted for the other reader and the results were as follows: L_∞ = 517 cm (s.e. 190), k = 0.041 year^{-1} (s.e. 0.025), t_0 = –5.57 years (s.e. 1.54), $r^2 = 0.83$, $n = 92$.

As the VBG parameters of Fig. 4 had lower relative standard errors and a more realistic L_∞, the results of this reader were used for back-calculations, MIR analysis, fitting of the Gompertz growth model, growth calculations, and GR estimates. The VBG model was fitted to the back-calculated data (Fig. 4) and showed a better r^2 value, lower relative standard errors on the parameters, and a more realistic size at birth (60 cm as opposed to 87 cm) than the model calculated from observed values. The VGB model was therefore used in this study.

The shark T1 (Fig. 4) was estimated to have 1 GR at tagging (107 cm) and 3 GR at recapture (172 cm). Using the time at liberty of 791 days, an observed mean annual growth of 30 cm can be calculated. The shark T2 had deposited 4 and 5 GR, respectively, and grew from 190 cm to 196 cm in 389 days. The smallest and largest females had 1 and 13 GR, respectively, and the range in males was 2 and 11 GR (Table 5). The two mature females had 8 and 13 GR, respectively, whereas the four mature males had 6, 6, 10 and 11 GR respectively. Length at 50% maturity was 274 cm for females and 250 cm for males and corresponding number of GR were calculated as 11 and 8, respectively. When relating mass to

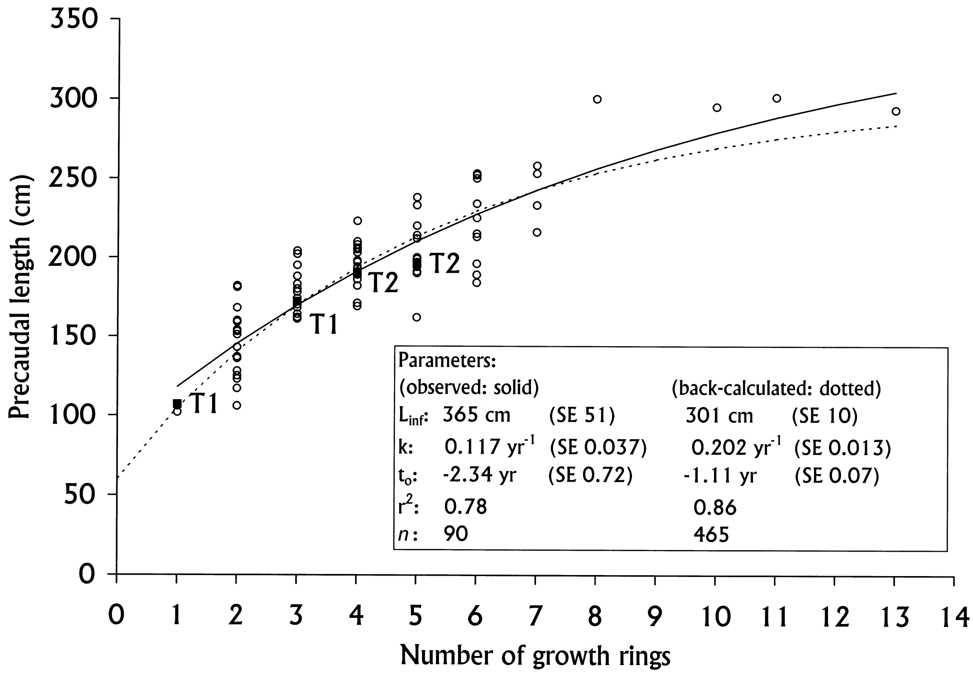

Fig. 4. von Bertalanffy growth curves fitted to observed (○) and back-calculated data, respectively, for the tiger shark, *G. cuvier* (sexes combined). ■, values at tagging and recapture for two sharks (T1, T2) injected with OTC.

Table 5. Growth ring (GR) counts for tiger sharks, *G. cuvier,* of selected precaudal lengths (PCL, cm) or masses (kg)

	Male			Female		
	No. of GR	PCL	mass	No. of GR	PCL	mass
Lowest number of GR	2	123	19	1	102	6
Highest number of GR	11	301	243	13	293	412
Smallest animal	2	123	19	1	102	6
Largest animal	11	301	243	8	300	333
Smallest mature animal	6	250	218	13	293	412
Heaviest animal	10	295	396	13	293	412

number of GR, the heaviest animals had 13 GR (412 kg) and 10 GR (396 kg) (Fig. 5). Calculated mass at birth ranged between 2 kg (Table 4) and 14 kg. Annual growth calculated from predicted lengths decreased from 44 cm for sharks with 1 GR to 4 cm for sharks with 13 GR (Fig. 6), whereas mass increased from 12 kg (1 GR) to 38 kg (8 GR) and then decreased to 29 kg (13 GR) (Fig. 6).

Discussion

The APE indices (9.2–9.7%, $n = 90$–92) were similar to those obtained by Wintner and Cliff (1996) for the blacktip shark, *Carcharhinus limbatus* (9.4%, $n = 87$) and by Cailliet *et al.* (1990) for the star-spotted smoothhound, *Mustelus manazo (*6.9–12.7%, $n = 28$–30); sectioned vertebrae were used in both of those studies. The indices were slightly higher than those for the white shark, *Carcharodon carcharias* (5.3–6.1%, $n = 108$–112), for which vertebral X-radiographs were examined (Wintner and Cliff 1999). In the present study, D values (7.1–7.4%) were higher than those of Natanson and Kohler (1996) for the dusky shark, *Carcharhinus obscurus* (3.3%, $n = 42$, vertebral sections) and those of Wintner and Cliff (1999) at 3.9–4.1% ($n = 108$–112).

The relationship between centrum diameter and shark length in this study was linear, as was the case for several other shark species (Cailliet *et al.* 1983*b*; Schwartz 1983; Branstetter 1987). Branstetter and McEachran (1986) also found a linear relationship for *G. cuvier* from the Gulf of Mexico ($n = 22$). Branstetter *et al.* (1987), however, combining these with data from the north-western Atlantic ($n = 44$), obtained a slightly curvilinear relationship which was more accurately described by separating immature and mature specimens (<232 cm or >232 cm). In the present study the

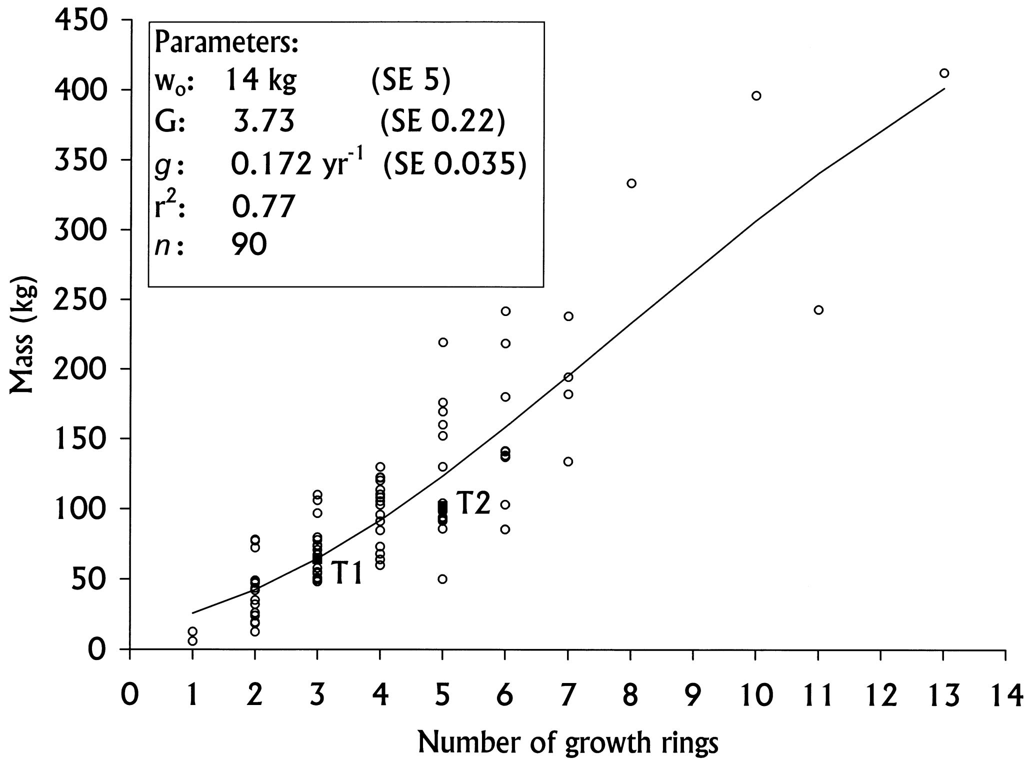

Fig. 5. Gompertz growth curve fitted to observed data for the tiger shark, *G. cuvier* (sexes combined). ■, values at recapture for two sharks (T1, T2) injected with OTC.

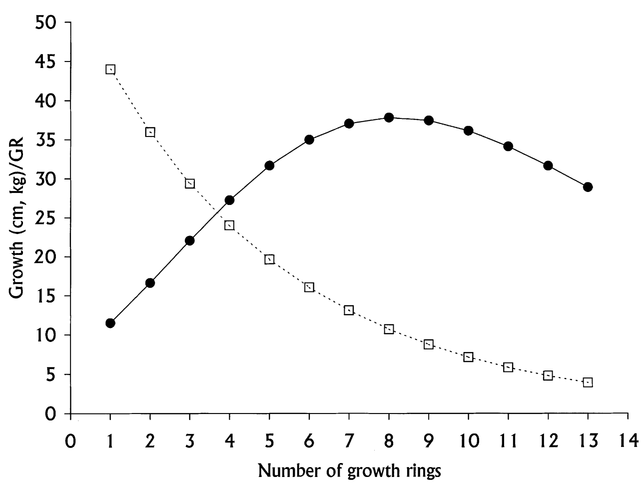

Fig. 6. Predicted growth in mass (solid line) and length (dashed line) per growth ring for the tiger shark, *G. cuvier*.

relationship between centrum diameter and mass was multiplicative and, as with the centrum diameter and length relationship, there was no significant difference between the sexes. Mean back-calculated length and mass values were similar to observed values and Lee's phenomenon was not evident in either case. Branstetter *et al.* (1987) also observed similarity between back-calculated and observed lengths, and they found no indication of Lee's phenomenon in *G. cuvier*.

Typically, opaque band deposition is associated with summer growth (Cailliet *et al.* 1983*b*, 1986; Kusher *et al.* 1992) and, as verification, the nature of the last deposited band can be related to the month of capture. In this study the observed frequencies of translucent and opaque last bands differed significantly from the frequencies expected. The results of the MIR analysis (Fig. 3) also showed no clear trend, even after remeasuring five 'outlier' vertebrae from April, July and August. If, however, the large MIR range in November (spring) represents transition from one GR to the next, and given that *G. cuvier* is born in spring/summer (Clark and von Schmidt 1965; Compagno 1984*a*; Stevens and McLoughlin 1991; Simpfendorfer 1992), this could indicate that a full GR is formed within a year. Additionally, if our interpretation of the vertebral bands in the sharks T1 and T2 is correct, translucent band deposition would occur in winter and spring and opaque band deposition in summer and autumn, which is in keeping with the majority of the vertebrae showing an opaque band immediately after the angle change.

In all three injected tiger sharks (T1, T2, T3) the OTC was visible in the vertebrae. Shark T3 showed faint OTC over the whole centrum face, indicating a faster incorporation time than that reported by Holden and Vince (1973) and Brown and Gruber (1988). Shark T1 showed an observed mean annual growth of 30 cm. With the mean predicted growth/GR in the period from 1–3 GR being 33 cm/GR (Fig. 6) and assuming that one GR is deposited per year, the predicted growth of the shark T1 would be 73 cm in the period of 2.2 years. This is close to the observed value of 65 cm. Shark T2 should have grown 20 cm (Fig. 6). The observed value of 6 cm is probably a result of the length at tagging being estimated and not measured. Assuming that the number of GR represents years, the expected sizes of sharks T1 and T2 at tagging and recapture are in accordance with the observed values of our sample (Fig. 4). The recorded masses at recapture are also in keeping with the observed values of our sample (Fig. 5). The similarity between the observed growth of the injected animals and the predicted growth could suggest that OTC did not affect growth rate adversely, although more recaptured injected animals are necessary for further investigation.

Branstetter *et al*. (1987) and Branstetter and McEachran (1986) demonstrated, using marginal increment analysis, that one growth ring formed annually in the tiger shark from the Gulf of Mexico and north-western Atlantic. De Crosta *et al.* (1984) also concluded that GR are laid down annually for *G. cuvier* from Hawaii, on the basis of the close agreement of growth curves derived from their vertebral counts and from length–frequency data. For this reason, and based on the results from the two recaptured sharks injected with OTC, GR deposition is assumed to be annual. It is noted, however, that the two recaptures represent young age classes (<5 years) only.

Age and growth

There was very little difference in length and mass range between the 69 females and 32 males. The preponderance of females in the sample is a reflection of tiger shark catches in the NSB nets, where the female–male ratio was 2.2 : 1 (1978–97) (NSB, unpublished). A similar preponderance of females was found in other regions (Clark and von Schmidt 1965; Stevens and McLoughlin 1991; Simpfendorfer 1992; Krogh 1994).

Our smallest specimens measured 102 and 106 cm. Branstetter *et al*. (1987) sampled four specimens smaller than 85 cm and De Crosta *et al*. (1984) two smaller than 100 cm. With our largest shark being 301 cm, that of Branstetter *et al*. (1987) 290 cm (n = 68) and that of De Crosta *et al.* (1984) 320 cm (n = 28), our size range is comparable with those of the other two authors. Table 6 shows the VBG parameters for *G. cuvier* from various regions, as obtained by several methods. Comparing the results obtained by using GR counts, our L_∞ is smaller than that of De Crosta *et al*. (1984) and of Branstetter *et al*. (1987). De Crosta *et al.* (1984) verified their results obtained from GR counts using length–frequency analysis as well as with embryonic growth extrapolation. Natanson *et al*. (in press), obtained VBG parameters that were slightly different from those obtained by Branstetter *et al.* (1987) using tag–recapture growth data. Overall, our parameters are closest to those obtained by Natanson *et al.* (in press).

Traditionally, ages of sharks have been related to length (Cailliet *et al*. 1983*b*, 1986). Wintner and Cliff (1999) fitted a Gompertz growth model for *C. carcharias*, as this curve usually describes well the relationship between age and mass (Ricker 1975). The Gompertz growth curve for the tiger shark (Fig. 5) showed a typical asymmetrical sigmoid curve (Gulland 1983; Ricker 1975), with the inflection point at about 215 kg or 8 years. The inflection point is also represented in Fig. 6 where growth rate in mass decreases after 8 years. The presence of this inflection point indicates that we have sampled specimens

Table 6. Comparison of von Bertalanffy growth parameters for the tiger shark, *G. cuvier*, from different regions
GR, vertebral method; F, female; M, male; U, unknown sex

	De Crosta *et al*. (1984)			Branstetter *et al*. (1987)			Natanson *et al.* (in press)	This study
	Central Pacific (Hawaii)			Gulf of Mexico	NW Atlantic	Combined	NW Atlantic	SW Indian
	GR	Length frequency[A]	Holden (1974) method	GR	GR	GR	Tag–recapture growth data	GR
L_∞(cm)	335	337	332	294	336	294	312	301
k (year^{-1})	0.155	0.15	0.149	0.184	0.107	0.158	0.178	0.202
t_0 (year)	–0.619	–1.27	–1	–1.13	–2.35	–1.73	–1.12	–1.11
L range (cm)	40–320	?	–	60–268	85–290	60–290	68–265	102–301
n	28	?	–	25	44	69	42	90
Sexes	?	?	–	7M,10F,8U	19M,25F	26M,35F,8U	17M,25F	26M,64F

[A]Data used by De Crosta *et al* were from Tester (1969) over an adequate range of mass. The biggest shark of the present study weighed 412 kg and the maximum attainable weight was calculated to be 584 kg. The maximum recorded weight for a tiger shark, however, is an all-tackle fishing record of 807 kg from the United States (Anon. 1995).

There is a large, presumably natural, fluctuation in mass at length in this species. In this study, for example, a mature male of 250 cm weighed 218 kg and another of 252 cm, 180 kg. A female of 293 cm weighed 412 kg, whereas another of 300 cm weighed 333 kg. Clark and von Schmidt (1965) found that weights for female *G. cuvier* from Florida within a 15-cm length category differed by as much as 300 kg. This variation in mass explains the discrepancies between observed and back-calculated mass at age (Table 4).

Natanson *et al*. (in press) used length–frequency analysis and found statistically significant differences in annual growth in the first year for tiger sharks obtained from the same locality over a period of five years. They stated that 'it appears that growth of this species is quite variable and probably dependent on environmental conditions'. The differences in the VBG parameters for tiger sharks (Table 6) may be a result of this possible effect of environmental conditions, compounded by the use of different ageing methods and different size ranges.

Our age and growth results obtained from vertebral ring counts compare favourably with a report of observed captive growth. A tiger shark was held in an aquarium at Sea World, Durban, for a period of 316 days (J. Ballard, Sea World and N. Kistnasamy, Oceanographic Research Institute; personal communication). It was 215 cm long when caught in the NSB nets and started eating two hours after being placed in the aquarium. When it died it measured 229 cm and weighed 188 kg. Calculated ages for the above lengths are 7.3 years and 8.2 years (representing a period of 329 days) (Fig. 4) and calculated growth was 11 cm (Fig. 6), all of which are close to the observed values.

The longest tiger shark on record is a 550-cm TL specimen from Cuba (Bigelow and Schroeder 1948, citing Howell-Rivero personal communication). Randall (1992) believes that a length as great as 600 cm TL might eventually be demonstrated. Krogh (1994) reported specimens of over 539 cm TL from New South Wales. Stevens and McLoughlin (1991) recorded a 418 cm TL female from northern Australia and the largest recorded specimen from Townsville was 428 cm TL (Simpfendorfer 1992). Bass *et al*. (1975) reported a female of 410 cm TL and a male of 370 cm TL from the south-west Indian Ocean. Our largest animal measured 385 cm TL and our L_∞ was 400 cm TL, which fall within the above range.

Observed ages of the two mature females were 8 years and 13 years and the four mature males were 6 years, 10 years and 11 years (Table 5), respectively, with an additional animal at 6 years (252 cm, 180 kg). Calculated ages at length at 50% maturity were 11 years (274 cm) and 8 years (250 cm) for females and males, respectively. Bass *et al*. (1975) reported four mature females ranging from 285 (13 years according to this study) to 394 cm and stated that males mature at 225 cm (6 years) or more. Clark and von Schmidt (1965) reported a 219 cm mature female from Florida. The smallest mature animals from the Gulf of Mexico reported by Branstetter *et al*. (1987) for two *G. cuvier* populations were 244 cm (8.8 years) and 232 cm (8.0 years) for females and males, respectively, and 239 cm (9.0 years) and 235 cm (10.1 years) for females and males from the north-western Atlantic, respectively. Natanson *et al*. (in press), however, using the maturity lengths reported by Branstetter *et al*. (1987) and their tag-recapture growth curve, reported age at sexual maturity at 7 years for both sexes. All authors based size at maturity on the smallest recorded specimen in their sample and size at 50% maturity was not reported. The lengths of our smallest mature *G. cuvier* are, nevertheless, greater than those reported from the other three areas.

Size at birth was 56 cm (Table 3) or 60 cm (calculated from growth model) which is close to the sizes reported in the literature. Bass *et al*. (1975) reported a litter of 43 well developed embryos with a mean embryo length of 38 cm from the same study area and the smallest recorded free-swimming *G. cuvier* from the south-west Indian Ocean at 72 cm. Clark and von Schmidt (1965) observed large, near-term embryos of 37–44 cm. Simpfendorfer (1992) reported size at birth at 47–55 cm for *G. cuvier* and the smallest free-swimming specimens reported by Stevens and McLoughlin (1991) were a 45-cm female and a 50-cm male. The smallest specimen reported by De Crosta *et al*. (1984) was about 40 cm and by Branstetter *et al*. (1987) 60 cm (Gulf of Mexico) and 85 cm (north-western Atlantic), with Natanson *et al*. (in press) reporting birth size at 54–58 cm from the latter area.

Assuming a birth size of 56 cm, *G. cuvier* from the south-west Indian Ocean grows 79% of its size at birth in the first year which is lower than the 100% reported by Branstetter *et al*. (1987) and slightly higher than the 66–69% of Natanson *et al*. (in press). It nevertheless places this species in Branstetter's (1990) group of sharks with fast growth (k >0.10; growth in the first year >40% of the birth size). Additionally, *G. cuvier* has a large litter size of 10 to 82 (Randall 1992; Simpfendorfer 1992). The only species listed by Branstetter (1990) as having comparable life history characteristics is the pelagic blue shark, *Prionace glauca*.

The rapid growth and large litter size of *G. cuvier* suggest that mortality rates on the young may be high compared with other shark species (Branstetter 1990). He suggested that young *G. cuvier*, being born in coastal waters where they are subjected to high predation levels, grow rapidly to a refuge size of 200 cm TL. Hoenig and Gruber (1990) suggested that *G. cuvier* grows even faster than an important commercial teleost species, the bluefin tuna, *Thunnus thynnus*. Walker (1998) argued that the conventional view that shark stocks cannot be harvested sustainably was developed from studies of fisheries for species such as the tope shark, *Galeorhinus galeus*. He stated that other species, e.g. the gummy shark, *M. antarcticus*, are far more productive, having a shorter longevity (~16 years *v.* >42 years), breeding more frequently (every 1–2 years *v.* every 3 years), and maturing earlier (3 years *v.* 8–10 years). Both species produce large litters (≤ 38 young *v.* ≤ 43 young). *G. cuvier*, given its rapid early growth, large litter size, and maturation at 10–13 years, may also be a relatively productive species, although its longevity and breeding frequency are unknown.

The NSB nets are probably the main source of fishing mortality for *G. cuvier* in the south-west Indian Ocean, although the species is exploited to a limited extent in other east African countries (Marshall 1997; Sousa *et al.* 1997). The increases in catch or catch rate of *G. cuvier* which have been reported in the KwaZulu–Natal shark control programme as well as in both of those in Australia (Paterson 1990; Reid and Krogh 1992; Dudley 1997) may indicate local increases in abundance. It is unclear whether this is an indirect effect of the programmes themselves but, if so, it is possible that *G. cuvier* enjoys a competitive advantage within a multi-species shark fishery. There may be a response, in terms of increased population growth rate, either to a reduction of the *G. cuvier* population caused by the nets or to a reduction of interspecific competition. In the KwaZulu–Natal programme any advantage may have been enhanced since the late 1980s through the release of all live sharks (Cliff and Dudley 1992). Over the period 1987–97, 41% of the total catch of *G. cuvier* was released, and where possible, tagged. Given that the tiger shark is one of the potentially most dangerous species in KwaZulu–Natal waters, it may be necessary to review this practice.

Acknowledgments

We thank the field staff of the NSB for providing specimens and associated information, Mr. P. Myeza and Mr. P. Zungu for dissecting many sharks and collecting and storing the vertebrae, and Mrs. B. Cunningham for entering the data on computer. Dr. M. O. Bergh of OLRAC (Pty.) Ltd. provided the computer program used to determine the maximum likelihood estimate of size at sexual maturity.

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Manuscript received 24 June 1999; revised and accepted 20 August 1999