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Preliminary study of vertebral growth rings in the whale shark, *Rhincodon typus*, from the east coast of South Africa

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Synopsis

Growth rings (GR) in vertebral centra of 15 whale sharks, *Rhincodon typus*, four female (418–750 cm precaudal length), 10 male (422–770 cm), and one of unknown sex (688 cm), were examined using x-radiography. GR counts were made from scanned images and count precision was determined using the average percentage error index (4.19%) and the index of precision D (3.31%). In females, counts ranged from 19 GR (418 cm) to 27 GR (750 cm); in males from 20 GR (670 cm) to 31 GR (770 cm). Three mature males had 20 GR (670 cm), 24 GR (744 cm) and 27 GR (755 cm). A female with 22 GR (445 cm) was adolescent. There was a linear relationship between centrum dorsal diameter and body length, and back-calculated body lengths at number of GR are presented. A linear relationship between body length and number of GR prevented the calculation of von Bertalanffy parameters from either observed or back-calculated values.

Introduction

The whale shark, *Rhincodon typus*, has a circum-global distribution in tropical and warm temperate seas, occurring both in oceanic and coastal waters (Compagno 1984). The species has become increasingly popular with marine tourism operations in locations where its occurrence appears to be predictable (Coleman 1997). There has been, however, evidence of a decline in whale shark sightings in one such location, i.e. Ningaloo Reef in western Australia (Taylor 1996). In addition, traditional and commercial fisheries exist and it may be that this conflict of interests led the Maldives, for example, to introduce a ban on whale shark fishing in 1993 (Hanfee[1]). The small traditional fishery in the Philippines reported declining catches (Anon. 1996, Trono[2]), which presumably led to the closure of this fishery in 1998 (Yaptinchay[3]). In contrast, a significant fishery targeting this species has developed in India, at least partly as a result of an increasing demand for whale shark meat in Southeast Asia (Hanfee[1]).

The IUCN Red List of Threatened Species lists *R. typus* as data deficient (Fowler[4], WCMC[5]). Coleman (1997) summarises the limited knowledge about the biology and ecology of the species, which is based mainly on occasional strandings, incidental and commercial captures, and sightings. It was established only recently that the whale shark is obligate lecithotrophic livebearer, based on a captured female of 10.6 m total length which contained 300 embryos (Joung et al. 1996). This discovery highlights the fact that there

[1] Hanfee, F. 1998. Whale shark fishery in India. Shark News 12: 11.
[2] Trono, R. 1996. Philippine whale shark and manta ray fisheries. Shark News 7: 13.
[3] Yaptinchay, A.A. 1998. Closure of Philippines whale shark fishery. Shark News 11: 11.
[4] Fowler, S. 1996. Red list assessments for sharks and rays. Shark News 8: 4-5.
[5] WCMC. Species under threat. WWW Site, Cambridge, UK, cited 13 April 1999, <URL:http://www.wcmc.org.uk/species/data/species_sheets/whalesha.html>.

is no information about age at maturity or maximum age for this species.

Whale sharks were held captive in the Okinawa Expo Aquarium in the 1980s (Cailliet et al.[6]). These authors examined a vertebra of a whale shark kept for 630 days while being fed with food containing oxytetracycline (OTC) and established that in this particular specimen a pair of translucent and opaque marks was deposited annually. Additional two specimens have been held in the Osaka Aquarium since 1990 and 1995, respectively (Kitafuji & Yamamoto 1998, Wilson Australian Institute of Marine Science personal communication 1999). These captive animals have hitherto provided the only age and growth information for this species.

Ages of sharks are commonly determined by investigating growth rings in their vertebrae (Cailliet et al. 1983a, 1986). Access to whale shark vertebrae, however, is very limited, especially those combined with accurate length measurements of the animal. In South Africa, 36 whale shark strandings were reported in the period 1984–1995 (Beckley et al. 1997), with an additional seven strandings in KwaZulu-Natal (KZN) in 1997 (Natal Sharks Board (NSB) 1999 unpublished data). The NSB, an organisation which operates a shark control program to protect beach users in KZN against shark attack (Cliff et al. 1988), has been collecting vertebra samples from stranded animals where possible. This study is a preliminary investigation of vertebra growth rings in *R. typus*, limited by the small number of available samples.

Materials and methods

Between 1991 and 1998, vertebra samples and morphometric information were collected partly by NSB staff or by volunteers from 15 whale sharks stranded on the KZN coast. Precaudal length (PCL), total length (TL) and/or fork length (FL), as depicted in Figure 1a, were measured as accurately as conditions allowed. To facilitate comparison of length measurements, data compiled by Beckley et al. (1997) were combined with data from this study and the following equations were calculated for converting body lengths:

$$\mathrm{TL} = 1.252\ \mathrm{PCL} + 20.308\ (n = 21,\ \text{range 254–780 cm PCL, 95\% confidence limits on slope: 1.18 and 1.325},\ r^2 = 0.986),$$

$$\mathrm{FL} = 1.106\ \mathrm{PCL} + 7.919\ (n = 7,\ \text{range 422–770 PCL, 95\% confidence limits on slope: 1.028 and 1.184},\ r^2 = 0.996),$$

$$\mathrm{TL} = 1.063\ \mathrm{FL} + 26.491\ (n = 8,\ \text{range 473–850 FL, 95\% confidence limits on slope: 0.893 and 1.234},\ r^2 = 0.975).$$

Embryos have a higher ratio of tail length to body length than adults (Garrick 1964), so a separate equation was computed for embryos and neonates. Using the equation of Bass et al. (1975), where TL = PCL + 0.8 UCL (upper caudal length), and measurements provided by Wolfson (1983) and Chang et al. (1997), the equation is

$$\mathrm{TL} = 1.306\ \mathrm{PCL} + 1.226\ (n = 9,\ \text{range 26–48 cm PCL, 95\% confidence limits on slope: 1.182 and 1.430},\ r^2 = 0.989).$$

PCL is used throughout the study unless indicated otherwise. Where possible, NSB staff assessed maturity based on the criteria of Bass et al. (1975). Males were considered mature only if the claspers were fully calcified and their outer clasper length was noticeable longer than the pelvic fin length. In females, the condition of the ovary and the width of the uteri were used as indicators of maturity. The absence of an investigated mature female, however, limited the ability to assess maturity.

Vertebral samples were removed from four females (418–750 cm), 10 males (422–770 cm), and one specimen of unknown sex (688 cm). Nine samples were removed from the region anterior to the first dorsal fin, two from over the pectoral fins, and one at the precaudal notch; in three specimens the region sampled was not recorded (Table 1). Individual centra were cleaned by removing the connective tissue with a scalpel and forceps and were stored frozen.

[6] Cailliet, G.M., S. Uchida, W. Laurendine & J. Brennan. 1986. Structure and growth zone formation of vertebral centra from captive Okinawan whale sharks (*Rhincodon typus*). Abstract presented at the ASIH/AES meeting 1986.

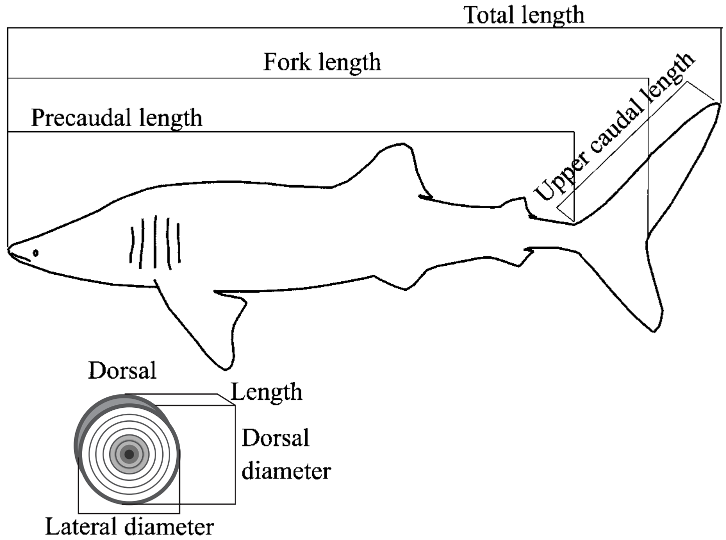

Figure 1. Schematic drawings depicting, a – body measurements (after Compagno 1984) and b – vertebral measurements used in this study.

Table 1. Details of sample animals. A dash indicates data not recorded. Bold values were calculated. Immature animals are labelled with i, mature with m. First dorsal fin is abbreviated with 1 D. Locality details for the first five animals are recorded by Beckley et al. (1997).

No.	Stranding locality	Stranding date	Lengths of animal (cm)			Sex	Maturity	Vertebral sample
			PCL	FL	TL			
1	Umdoni	11.3.1995	705	—	**903**	M	i	at precaudal notch
2	Warner Beach	12.12.1991	670	—	903	M	m	anterior to 1 D
3	Nhlabane	17.1.1995	694	—	910	M	i	—
4	Umzumbe	1.4.1992	654	—	866	M	i	—
5	Red sands	20.12.1995	445	497	**577**	F	i	over pectoral fins
6	Nhlabane	3.12.1996	422	473	560	M	i	anterior to 1 D
7	Scottburgh	12.12.1996	755	843	945	M	m	—
8	Cape Vidal	23.8.1997	**418**	523	544	F	—	anterior to 1 D
9	Cape Vidal	5.9.1997	**711**	820	910	M	—	anterior to 1 D
10	Cape Vidal	9.9.1997	770	850	890	M	—	anterior to 1 D
11	Cape Vidal	22.9.1997	750	827	904	F	—	anterior to 1 D
12	Cape Vidal	25.9.1997	688	789	875	U	—	over pectoral fins
13	Cape Vidal	7.11.1997	610	—	760	M	—	anterior to 1 D
14	Cape Vidal	9.11.1997	744	835	922	M	m	anterior to 1 D
15	Cape Vidal	18.11.1998	605	—	**778**	F	—	anterior to 1 D

X-radiography was then used to enhance the visibility of the growth rings. X-radiographs of whole centra (previously thawed for approximately 24 hours) were prepared on a Phillips Optimus 50 generator with a Phillips Bucky Diagnost tube using Kodak Lanex Fine (Extremity) film and were processed using a Kodak x-omat 3000 RA processor. All centra were x-rayed with the corpus calcareum facing the tube at a set distance of 100 cm, using direct exposure, and settings ranged from 40–44 kV and 16–50 mAs. The x-radiographs were then scanned using an Agfa DuoScan scanner and Adobe© Photoshop. Ulead

ImagePals GO!© and CorelDRAW!® were used to enhance and work with the images.

A growth ring (GR) was defined as a band pair, comprising one calcified (opaque) and one less-calcified (translucent) band. One reader, without knowledge of the shark's length or previous counts, made three non-consecutive GR counts from the scanned images. Count reproducibility was determined using the average percentage error (APE) as described by Beamish & Fournier (1981). An upper limit for 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 calculated. In addition, the index of precision *D* (Chang 1982) and the within-reader bias (Officer et al. 1996) were determined.

Length and dorsal and lateral diameter of each centrum (Figure 1b) were measured in a straight line using a vernier calliper. The angle change on the centrum face was regarded as the birth mark (Walter & Ebert 1991, Wintner & Cliff 1998). The 'birth diameter' was then marked on the scanned images and the distance from the focus to the outer edge of each GR was measured using CorelDRAW!®.

The relationships between different centrum dimensions and body length were examined. Sexes could not be compared, as there were only four females. Statistical outliers were determined using Statgraphics® and were, when evident, eliminated. As there was a linear relationship between centrum dorsal diameter and body length, 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 dorsal diameter at GR t, PCL_c = length at capture, and CD_c = centrum dorsal diameter at capture. A von Bertalanffy growth function (von Bertalanffy 1938) was then fitted to both observed and back-calculated data using the nonlinear regression procedure of STATGRAPHICS®.

Results

Details of each fish, including length(s), sex, maturity and date of sampling are shown in Table 1. Due to the large size of these fish, accurate measurements and consistency in the vertebral region sampled were often hampered by the orientation of each animal and the locality in which it was stranded. X-radiography settings for individual vertebrae are shown in Table 2. In all examined vertebrae large areas of basidorsal and basiventral cartilage alternated with areas of calcification (Ridewood 1921) (Figure 2). The exception was vertebra no. 1 which was taken at the precaudal notch and showed a 'snowflake-like' calcification pattern (Figure 3). For this reason this vertebra was not included in further analyses.

Bands were visible both in the cartilage and the calcified parts. In addition, all vertebrae, with the exception of no. 3 and no. 11 showed a circle of 'heavy calcification', i.e. broad calcified bands were visible in the cartilage and the calcified parts (Figure 2, Table 2). In most vertebrae the lateral diameter was larger than the dorsal diameter. The ratio of lateral to dorsal diameter ranged from 0.92 to 1.12 (mean 1.02, $n = 14$). It was very difficult to discern an angle change as the centrum face had a generally very steep slope. Therefore the 'birth diameter' was also determined on the x-radiographs as the diameter where a first circular pattern was evident. The mean measured 'birth diameter' was 1.05 on the centrum face and 0.76 on the x-radiographs.

The relationship between centrum dorsal diameter and PCL showed a linear trend with an original intercept of −4.226 cm. Two additional data points from smaller animals (one vertebra was taken from anterior to the first dorsal fin, the region sampled in the other animal is unknown) were provided by Cailliet and Uchida (Moss Landings Marine Laboratories and Okinawa Expo Aquarium, respectively). Their inclusion in the regression changed the intercept only a little (−3.079) and the Fraser-Lee method (Carlander 1969) was used to correct the intercept to zero (Figure 4). A third data point from Cailliet and Uchida (personal communication), a vertebra sampled at the precaudal notch, is shown in Figure 4, but was not included in the regression. There was a linear relationship between centrum length and PCL (Figure 5) and no centrum length data were available from Cailliet and Uchida (personal communication).

Using a birth size range of 41–48 cm PCL (Wolfson 1983, Chang et al. 1997), the calculated centrum diameter at birth is between 0.74 and 0.86 cm . As this was close to the values obtained from the x-radiographs (mean = 0.76 cm, range 0.5–1.16, $n = 14$) they were used as 'birth diameters' and not the angle change observed on the centrum face. Therefore, prebirth marks that were evident when using the latter method, were now regarded as GR.

GR were clearly visible in all vertebrae (e.g. Figure 2) with the exception of vertebra no. 1 (Figure 3). GR

Table 2. Details of vertebral dimensions and x-radiography settings.

No.	Vertebral dimensions (cm)			X-radiography		'Birth diameter' (cm)		Circle of 'heavy calcification' (cm)
	Dorsal diameter	Lateral diameter	Length	kV	mAs	X-radiograph	Centrum face	
1	6.5	6.9	4.17	40	16	N/A	N/A	N/A
2	10.21	11.65	7.80	40	32	0.66	1.20	4.60
3	13.67	13.55	8.64	40	40	0.73	0.94	N/A
4	12.00	12.20	7.70	40	40	0.66	1.01	6.20
5	6.53	6.65	4.90	40	16	0.62	0.94	5.14
6	6.18	6.47	5.13	40	16	0.50	1.12	5.46
7	15.11	15.00	9.74	44	40	0.94	1.00	7.53
8	7.16	6.96	5.96	40	16	0.73	1.06	6.30
9	13.85	13.62	8.64	42	50	0.65	1.14	6.92
10	15.90	14.63	9.17	40	32	0.94	0.90	6.89
11	12.67	13.48	8.96	40	40	0.85	1.00	N/A
12	12.70	13.09	9.45	40	40	0.71	1.10	6.68
13	8.00	8.25	6.64	40	25	0.64	1.28	5.15
14	13.94	14.05	9.50	44	40	1.16	1.12	6.33
15	10.60	11.92	7.70	40	32	0.82	0.93	6.49

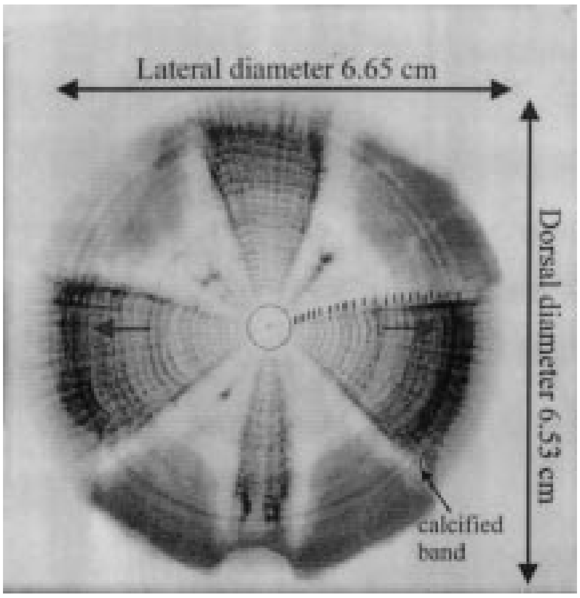

Figure 2. X-radiograph (inverted image) of a vertebra from a female whale shark, 445 cm PCL. Sample taken from over the pectoral fins. The circle indicates the 'birth diameter'. Grey arrows indicate the circle of 'heavy calcification'.

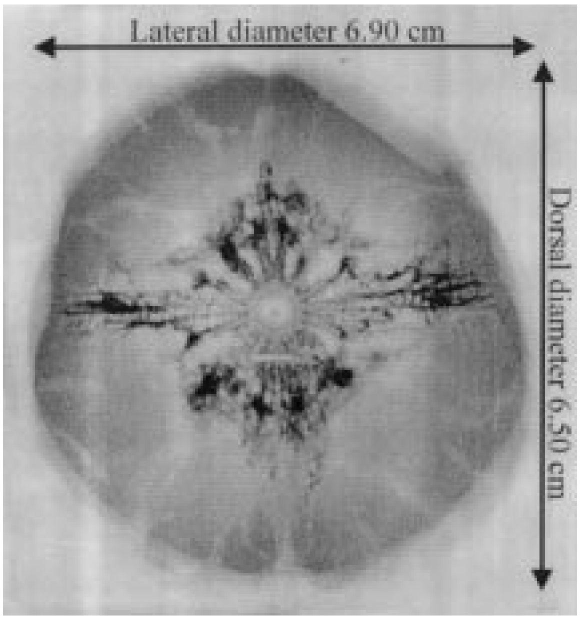

Figure 3. X-radiograph (inverted image) of a vertebra from a male whale shark, 705 cm PCL. Sample taken at the precaudal notch.

counts from the three rounds and their APE and *D* indices are shown in Table 3. The values for the APE index and *D* for the whole sample were 4.19% and 3.31%, respectively. Some within-reader bias was evident in that there was a significant difference between round 1 vs. 2 (pairwise *t* tests, $p = 0.018$), indicating a higher bias of counts in round 2. There was no significant difference, however, between round 1 vs. 3 and round 2 vs. 3 ($p = 0.10$, $p = 0.094$, respectively). In most of the samples (71.4%), the difference between the three counts was only one or two GR and for this reason a mean of the three counts was taken.

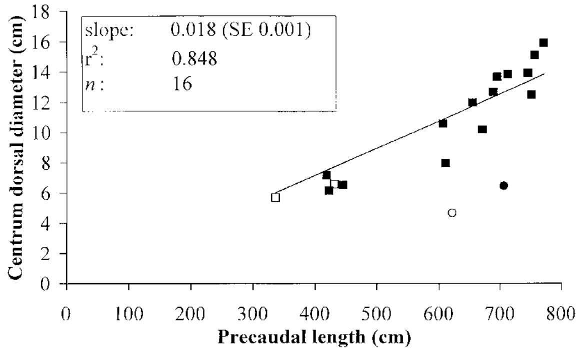

Figure 4. Relationship between centrum dorsal diameter and PCL. The circles indicate vertebrae taken at the precaudal notch and were not included in the regression. Open markers indicate data provided by Cailliet and Uchida.

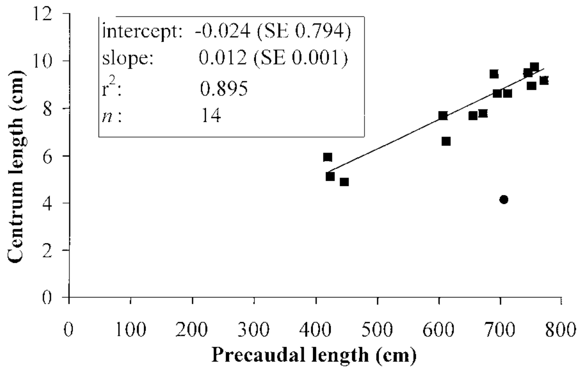

Figure 5. Relationship between centrum length and PCL. The circle indicates vertebra no. 1, taken at the precaudal notch, and was not included in the regression.

In females, counts ranged from 19 GR (418 cm) to 27 GR (750 cm), and in males from 20 GR (670 cm) to 31 GR (770 cm). Maturity was assessed in eight animals only and three mature males had 20 GR (670 cm), 24 GR (744 cm) and 27 GR (755 cm). A female with 22 GR (445 cm) was adolescent (Tables 1, 3).

The relationship between PCL and observed number of GR can be seen in Figure 6 that includes eight data points from other studies. Five of these were assumed to correspond to 0 GR: two small free-swimming specimens of 41 and 42 cm (Wolfson 1983), the maximum and mean sizes of embryos from a litter of 300 full term pups (48 and 39 cm, respectively) and the PCL (45 cm) of one surviving individual from this litter (Chang et al. 1997). The other three data points were provided by Cailliet et al.[6]. Mean back-calculated lengths were lower than observed values (Table 4). The calculated

Table 3. Growth ring counts from the three rounds and their APE values and indices of precision *D*.

No.	Counts			Mean	SE	APE (%)	*D* (%)
	1st	2nd	3rd				
2	18	20	21	20	0.88	5.65	4.48
3	24	26	26	25	0.67	3.51	2.63
4	18	25	22	22	2.03	11.28	9.36
5	22	22	21	22	0.33	2.05	1.54
6	20	22	19	20	0.88	5.46	4.34
7	26	27	28	27	0.58	2.47	2.14
8	19	20	19	19	0.33	2.30	1.72
9	26	25	26	26	0.33	1.73	1.30
10	30	32	31	31	0.58	2.15	1.86
11	26	30	26	27	1.33	6.50	4.88
12	26	24	24	25	0.67	3.60	2.70
13	21	21	20	21	0.33	2.15	1.61
14	23	24	25	24	0.58	2.78	2.41
15	20	24	23	22	1.20	6.97	5.38

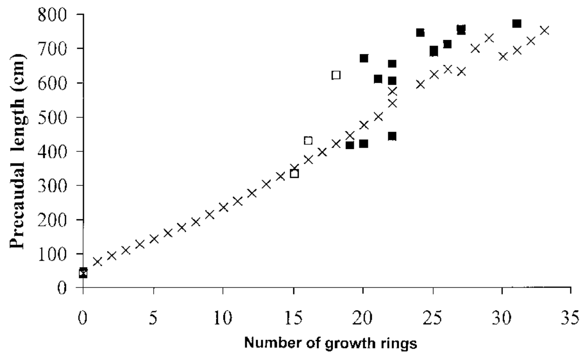

Figure 6. Relationship between PCL and observed number of growth rings (solid squares). Open squares at 0 GR indicate data taken from Wolfson (1983) and Chang et al. (1997). The other three are from Cailliet et al.[6] Crosses indicate mean back-calculated length at GR.

data mimicked the linear trend shown by the observed data, and in neither case could a von Bertalanffy growth curve be fitted.

Discussion

X-radiography to enhance the visibility of GR in elasmobranch vertebrae has been used successfully in studies of several species (Cailliet et al. 1983a,b, Yudin & Cailliet 1990, Ferreira & Vooren 1991, Yamaguchi et al. 1996, Wintner & Cliff 1998) and the technique produced good results in *R. typus*. The vertebral structure of adult *R. typus*, however, with its large areas

Table 4. Observed and back-calculated body lengths (cm) at number of growth rings (GR).

No. of GR	Back-calculated values (cm)					Observed values (cm)				
	Min	Max	Mean	SD	n	Min	Max	Mean	SD	n
0	29	61	42	8	14					
1	37	105	77	22	14					
2	45	137	95	28	14					
3	56	160	111	31	14					
4	65	182	128	35	14					
5	77	195	145	35	14					
6	91	217	161	37	14					
7	106	237	178	38	14					
8	112	254	194	42	14					
9	136	283	215	43	14					
10	152	314	237	48	14					
11	165	341	254	51	14					
12	184	376	278	54	14					
13	202	413	304	58	14					
14	217	442	327	62	14					
15	228	465	351	64	14					
16	249	484	376	65	14					
17	263	512	399	68	14					
18	282	538	423	71	14					
19	303	563	447	72	14	420	420	420	—	1
20	313	610	477	83	13	422	670	546	175	2
21	329	640	502	80	13	610	610	610	—	1
22	346	670	540	88	12	445	654	568	109	3
23	357	676	575	81	11					
24	374	694	595	91	9	744	744	744	—	1
25	397	717	624	94	9	688	694	691	4	2
26	417	744	639	108	7	710	710	710	—	1
27	445	713	632	109	5	755	750	753	4	2
28	648	734	698	47	3					
29	662	770	729	59	3					
30	675	675	675	—	1					
31	693	693	693	—	1	770	770	770	—	1
32	720	720	720	—	1					
33	750	750	750	—	1					

of basidorsal and basiventral cartilage and areas of calcification with radiating lamellae, did not resemble any of the vertebral patterns described by Ridewood (1921). Even the vertebrae of adult basking sharks, *Cetorhinus maximus*, showed a very different pattern from that observed in the whale shark. Although this is not unexpected as both species belong to different orders (Orectolobiformes, family Rhincodontidae and Lamniformes, family Cetorhinidae), some resemblance could be anticipated as both species exhibit similar size, life style and feeding behaviour. The only similarity in the vertebral structure of the adult animals is the presence of 'radiating lamellae' (Ridewood 1921).

The variation in the ratio of centrum dorsal and lateral diameter was independent of overall size of the vertebrae. This is probably a result of differences in the sampling region (Table 1). That there may be significant differences in the vertebral calcification patterns according to location on the vertebral column is supported by the extreme difference shown in the sample taken at the precaudal notch. It might be imperative in the future to obtain samples at exactly the same location, e.g. always one meter anterior to the first dorsal fin, or even to take a longer sample of the vertebral column.

A linear relationship between centrum diameter and body length has been found in several shark species

(Cailliet et al. 1983b, Schwartz 1983, Branstetter & McEachran 1986, Wintner & Cliff 1996, 1998, Yamaguchi et al. 1996, Seki et al. 1998) and was also found in the present study (Figure 4). It is tempting to exclude the two apparent visual outliers in Figure 4, but both vertebrae (no. 2 and 13) were sampled anterior to the first dorsal fin, in common with most of the samples. As mentioned above, vertebra dimensions vary according to sampling region but this is unlikely to account for the outliers – particularly given that vertebrae taken from other locations (no. 5 and 12) did not deviate as much. The use of the centrum lateral diameter, rather than the dorsal diameter, had little effect on the intercept (−3.612). It is interesting to note that vertebral length, however, which also showed a linear relationship to body length, had an intercept close to zero. It is possible that centrum length is more important in supporting the animal than centrum diameter, particularly in view of the size and weight of this species.

The APE index of 4.19% was considered acceptable as it was lower than that of Cailliet et al. (1990) for *Mustelus manazo* (6.9–12.7%, n = 80–87) and Wintner & Cliff (1998) for *Carcharodon carcharias* (5.3–6.1%, n = 108–112). The *D* value of 3.31% was also considered acceptable as it was similar to that of Natanson & Kohler (1996) for *Carcharhinus obscurus* (3.3%, n = 42) and lower than that of Cailliet et al. (1990) (6.8–12.7%, n = 27–30) and Wintner & Cliff (1998) (3.9–4.1%). Despite this comparatively good reproducibility and precision, GR counts varied greatly with body length and it seems that in some specimens they may have been underestimated (Figure 6). This is probably due to the structure of the vertebrae, which have a wide margin where no GR are clearly visible (Figure 2). All vertebrae, however, should thus have been equally underestimated and it is more likely that GR counts were overestimated in the three animals in the 400 cm range, especially when compared with the data from Cailliet et al.[6] (Figure 6).

Mean back-calculated body lengths at number of GR were generally lower than observed values. Back-calculated birth size (42 cm) was close to observed birth size (41–48 cm) (Wolfson 1983, Chang et al. 1997). As both observed and back-calculated data showed a linear trend, no von Bertalanffy growth curve could be fitted.

Length measurements of a female and male captive whale shark held in the Osaka aquarium (Kitafuji & Yamamoto 1998, Wilson personal communication) also showed a linear trend (Figure 7). Measurements were taken on 10 July each year, with the exception of

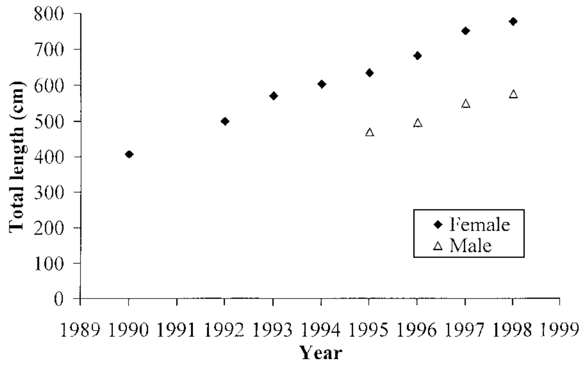

Figure 7. Growth shown by a female and male captive whale shark held in the Osaka aquarium.

1990 and 1995 (11 July) and 1992 and 1993 (7 June). There were no data for the female in 1991. Using the first and last reported measurements, the animals could be assigned 13 and 24 GR (female) and 15 and 19 GR (male) (Table 4) and thus the total time interval 11 and four years, respectively. This is close to the observed eight and three years. Alternatively, predicted total growth for the female is 291 cm, whereas observed growth was 369 cm. For the male, the values are 96 cm and 106 cm, respectively. Therefore the female grew 1.3 times faster and the male 1.1 times faster than predicted from back-calculated values.

Assuming that this slightly faster growth is a result of captivity, the predictions from the present study are comparable with the observed growth if approximately one GR is deposited per year. This corresponds with the finding of Cailliet et al.[6] who examined the vertebra of a whale shark kept in the Okinawa Expo Aquarium for 630 days while being fed with food containing OTC. These authors established that in this particular specimen a pair of translucent and opaque marks was deposited annually. In addition, their observed GR numbers for specimens of 335, 431 and 621 cm were similar to the results of this study (Figure 6).

Although the findings of the aquarium work are in agreement with the linear growth observed in this study it is unlikely that whale sharks near maximum size continue with this type of growth. The evident growth pattern is probably due to the fact that no animals over 800 cm were available in this study. Specimens of larger size have been reported (Compagno 1984, Karbhari & Josekutty 1986, Joung et al. 1996) and the inclusion of such larger animals could change the linear growth pattern. To investigate this, an additional

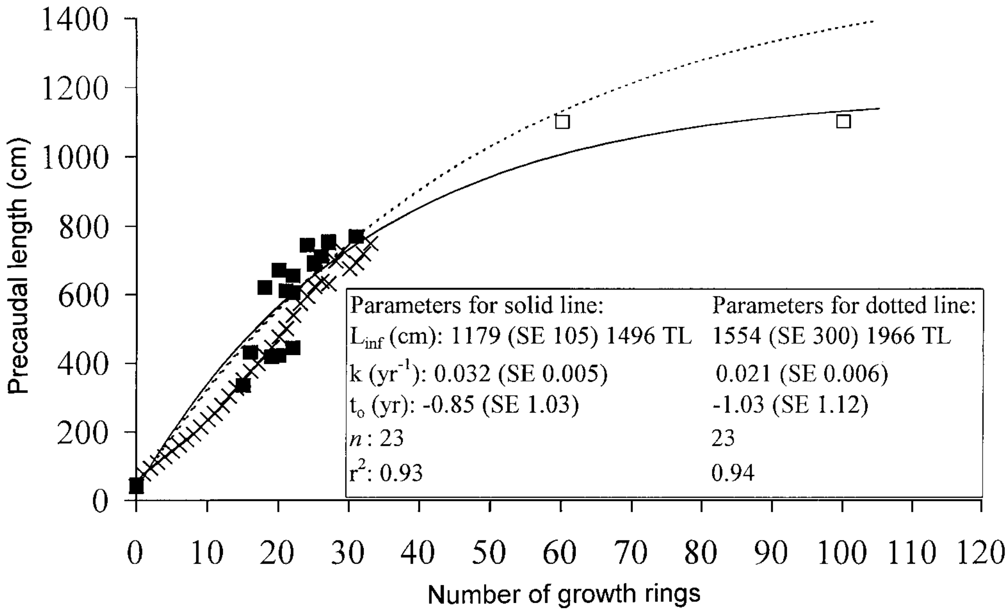

Figure 8. Von Bertalanffy growth curves fitted to observed data (solid squares) and theoretical data taken from Pauly (2000) (open squares). Crosses indicate mean back-calculated length at GR.

two 'data points' were included. Pauly (2000) used two approaches to estimate the von Bertalanffy parameter k for the whale shark. Both assumed a L_∞ of 11.02 m (14 m TL). In addition, the first approach was based on the assumption that the length-weight relationship of *R. typus* was similar to that of the basking shark *C. maximus*, the second on the assumption that both species have similar gill areas at similar sizes. The two estimates of k were 0.062 yr^{-1} and 0.051 yr^{-1} which would imply an age of 100 or 60 years, respectively at 11.02 m (Pauly 2000). Pauly (2000) suggested that the 60-year estimate seemed more sensible, but stressed the tentative nature of both. Nevertheless, these two theoretical data points were separately added to the observed data and two tentative von Bertalanffy growth curves could be fitted (Figure 8).

It is interesting to note that when using an age of 100 years at 11.02 m, the von Bertalanffy parameter estimates had lower standard errors and L_∞ was close to the reported maximum length of 10.8 m (13.7 m TL) (Compagno 1984) and the assumed L_∞ of 11.02 m (14 m TL) of Pauly (2000). Which of the two curves, if either, describes growth in the whale shark accurately will be solved only by inclusion of vertebrae from larger animals which again emphasises the preliminary nature of this study.

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