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A re-examination of the age and growth of sand tiger sharks, *Carcharias taurus*, in the western North Atlantic: the importance of ageing protocols and use of multiple back-calculation techniques

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Abstract Age and growth estimates for sand tiger sharks, *Carcharias taurus*, in the western North Atlantic were derived from 96 vertebral centra collected from sharks ranging from 94 to 277 cm total length (TL), and compared to previously published age and growth data. The oldest female and male sand tiger sharks aged in this study were 17 and 15 years of age, respectively. von Bertalanffy growth parameters derived from vertebral length-at-age data are $L_{\infty} = 295.8$ cm TL, $k = 0.11 \text{ year}^{-1}$, and $t_0 = -4.2$ years for females, and $L_{\infty} = 249.5$ cm TL, $k = 0.16 \text{ year}^{-1}$, and $t_0 = -3.4$ years for males. Sexual maturity is estimated to be 9–10 years for females and 6–7 years for males. Weight-to-length relationships determined for female and male sand tiger sharks in the western North Atlantic are; $W = 1.3 \times 10^{-4} \times L^{2.4}$

($r^2 = 0.84$, $n = 55$) and $W = 9.0 \times 10^{-5} \times L^{2.5}$ ($r^2 = 0.84$, $n = 47$), respectively, and $7.9 \times 10^{-5} \times L^{2.5}$ ($r^2 = 0.84$) for the sexes combined. Our results show sand tigers possess a slower rate of growth than previously thought. This information is crucial for accurately assessing this population's ability to recover, and further justifies the need for this species to be fully protected.

Keywords Elasmobranch · Life history · Growth rate · Back-calculation · Reproduction

Introduction

The sand tiger shark, *Carcharias taurus*, is a large coastal species that inhabits subtropical and temperate waters of the Atlantic, Indian, and western Pacific Oceans, as well as the Mediterranean Sea (Gilmore et al. 1983; Compagno 1984; Pollard et al. 1996). The sand tiger shark is fished or caught as bycatch in all areas it is found, but is of variable importance regionally (Pollard and Smith 2005). In the western North Atlantic Ocean, sand tiger sharks are exposed to several fisheries due to their highly migratory nature (Casey and Kohler 1990; Musick et al. 1993). As a result, the population has been depleted by an estimated 80–90% since the mid 1970s (Musick et al. 1993, 2000). To prevent further decline of sand tiger sharks in the western North Atlantic,

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the sand tiger shark was listed as a prohibited species in the amendment to the National Marine Fisheries Service (NMFS) Fishery Management Plan for Atlantic sharks in 1997 (NMFS 1999). They also have fully protected status in Australian waters and their capture in South African waters is being phased out (Pollard et al. 1996; Anonymous 2002). Although the western North Atlantic population may have stabilized since being listed as prohibited, recovery is not yet apparent (Musick et al. 2000).

There is still some uncertainty in the life-history parameters for sand tiger shark in the western North Atlantic Ocean. Whereas gestation and embryonic growth are well documented in sand tiger sharks, their reproductive periodicity has been a source of some contention. Gilmore (1993) stated that sand tiger sharks reproduce annually in the western North Atlantic Ocean and Gordon (1993) believed they may mate annually in Australian waters. Alternatively, Cliff (1989), and Branstetter and Musick (1994) presented evidence supporting a 2-year reproductive cycle for sand tiger sharks in South African waters and the western North Atlantic, respectively. However, successful captive reproduction over the past 10 years lends strong support to a 2-year reproductive cycle hypothesis (Henningsen et al. 2004). In terms of age and growth, Branstetter and Musick (1994) stated that sand tiger sharks may reach an age of 30–35 years and gave the following von Bertalanffy growth parameters for in the western North Atlantic: $L_{\infty} = 323.0$ cm PCL, $k = 0.14$ year⁻¹, and $t_0 = -2.6$ years for females; $L_{\infty} = 301.0$ cm PCL, $k = 0.17$ year⁻¹, and $t_0 = -2.3$ years for males; and $L_{\infty} = 321.0$ cm PCL, $k = 0.14$ year⁻¹, and $t_0 = -2.6$ for sexes combined. This was based on their estimation that this species forms two pairs of growth bands annually in the vertebral centra. These authors also stated a caveat about their uncertainty of that estimation. A re-calculation of the life-history parameters from Branstetter and Musick's (1994) mean back-calculated lengths-at-age was conducted assuming annual formation of a single pair of growth bands (Goldman 1998), which resulted in the following von Bertalanffy growth parameters: $L_{\infty} = 323.0$ cm PCL, $k = 0.07$ year⁻¹, and $t_0 = -5.1$ for females; and $L_{\infty} = 302.0$ cm PCL, $k = 0.08$ year⁻¹, and $t_0 = -4.5$ for males; and $L_{\infty} = 322.0$ cm

PCL, $k = 0.07$ year⁻¹, and $t_0 = -5.2$ for sexes combined. The difference in these life-history parameter estimations, and their ramifications for management and conservation of this species (Musick et al. 1993, 2000), was the major reason for our re-examination of sand tiger age and growth. Herein, we report our findings, comment on the importance of ageing protocols and use of multiple back-calculation techniques for chondrichthyan fishes, and briefly discuss the reproductive periodicity of this species.

Materials and methods

Sand tiger shark vertebrae ($n = 96$) were obtained by the Virginia Institute of Marine Science (VIMS) ($n = 55$) and from the NMFS Narragansett, RI, laboratory ($n = 41$). (Some samples from each institute were tournament or sport caught.) Twenty-five samples (from the VIMS survey) previously used for analysis by Branstetter and Musick (1994) were re-examined for this study. Vertebral samples and weights of sand tiger sharks used in this study from the VIMS survey were taken between 1980 and 2001; those obtained from NMFS were taken between 1963 and 1991. Vertebral samples were not obtained from all animals that were measured and weighed (over this nearly 40-year period), hence the discrepancy in sample sizes.

Sand tiger sharks taken by VIMS were measured on a straight line from the tip of the snout to the tip of the tail while in a natural position, and precaudal, fork, and total length (TL) (PCL, FL, and TL) were recorded along with sex and weight (when possible). A 20–25 cm section of vertebrae was removed from the area midway between the first dorsal fin and the gills, and stored frozen. Samples provided by NMFS included at least one of the necessary measurements and the date and location of capture. Weights were obtained (by VIMS and NMFS) from 102 sand tiger sharks between 1963 and 1991, including 55 females (95–272 cm TL), and 47 males (100.7–259 cm TL). Data were fitted to the power equation, $W = aL^b$ (using SigmaPlot, SPSS Inc. 2000), where W = weight (kg) and L = length (cm TL). A likelihood ratio test was used to determine whether

differences between female and male weight-length parameters were significant or if a single set of parameters better described the data (Kimura 1980; Cerrato 1990; Quinn and Deriso 1999; Haddon 2001) (SAS Institute Inc. 1999). We use TL measurements throughout this paper in order to make direct comparisons with previously published data on sand tiger shark growth parameters (Branstetter and Musick 1994). Linear regression equations based on measurements taken by VIMS and the NMFS lab, were developed for converting TL to FL and PCL.

Vertebral samples were thawed, cleaned of excess tissue, separated into individual centra, and stored in 70% ethyl alcohol for at least 24 h. Centra were sagittally sectioned immediately adjacent to the focus and then cut again approximately 1.5 mm off-center using an Isomet rotary diamond saw (Buehler, 41, Lake Bluff, IL, USA). The sections were pressed between two pieces of Plexiglas (to prevent warping), air-dried for 24 h under a ventilation hood, and then mounted onto microscope slides. After drying, sections were polished with wet fine grit sand paper (320, 400, and 600) to approximately 0.5 mm and air-dried. Sections were viewed using a binocular dissecting microscope with transmitted light.

Centrum radius (CR) and distance to each ring were measured to the nearest 0.001 mm as a straight line from the central focus to the outer margin of the corpus calcareum (Fig. 1) using a dissecting video microscope with the Optimus image analysis system (Media Cybernetics 1999). TL was plotted against CR to determine the proportional relationship between somatic and vertebral growth.

A banding pattern was readily distinguishable in sectioned centra, with wide translucent bands separated by distinct narrow opaque bands. This pattern occurred on both arms of the corpus calcareum and the band pairs extended across the intermedialia. A notch occurring on the outside edge of the corpus calcareum accompanied the distinct narrow bands (Fig. 1) providing an additional ageing feature, particularly in sections where the cut excluded the radials of the intermedialia. Each pair of wide–narrow bands was considered an annual growth cycle; the narrow bands, hereafter referred to as “rings”, were counted (Fig. 1). An

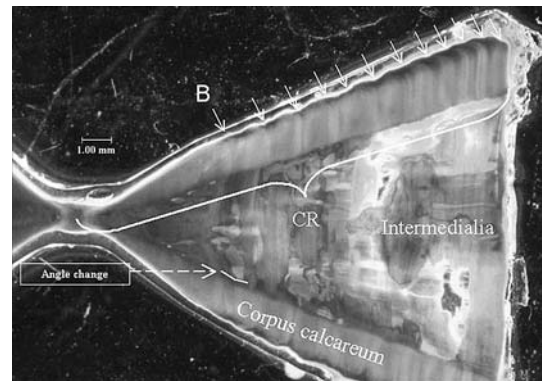


Fig. 1 Sagittal section of an 11-year-old sand tiger shark's vertebral centrum showing typical banding pattern. CR centrum radius. Arrows represent ages

angle change in the intermedialia and a ring on the corpus calcareum were present approximately 6–7 mm from the focus of each centrum and considered to represent a birthmark. The “pre-birth rings” reported by Branstetter and Musick (1994) were present in most specimens, but were not counted nor measured.

Two readers independently aged all centra two times in blind, randomized trials. This allowed the calculation of within-reader precision, and between-reader precision twice. Percent agreement ($PA = [\text{no. agreed}/\text{no. read}]100$), and $PA \pm 1$ year were calculated for 10 cm length groups to test for precision (Cailliet and Goldman 2004; Goldman 2004; Goldman and Musick 2006; Cailliet et al., this issue). We used chi-square tests of symmetry to determine whether difference within and between readers were systematic (biased) or due to random error (Hoenig et al. 1995; Evans and Hoenig 1998; Campana 2001).

A relative marginal increment (RMI) analysis was used to verify the temporal periodicity of ring formation in the vertebrae. This is a standardized marginal increment analysis whereby the margin, or growth area of a centrum from the last narrow growth ring to the centrum edge, is divided by the width of the last fully formed growth increment (Branstetter and Musick 1994; Conrath et al. 2002; Cailliet et al., this issue). Resulting RMI values were compared to the month of capture. Age-zero animals were not included (they have no fully formed increments).

To assist in attempting to validate the periodicity of ring (annulus) formation, two male sand tiger sharks (152.5 and 157 cm TL) captured off of Cape May, NJ, USA, in 1998 for public display, were donated to this study, and injected with oxytetracycline (OTC) at a dose of 25 mg kg⁻¹ body weight (Tanaka 1990; Gelsleichter et al. 1998). One was kept at Ripley's Aquarium, Myrtle Beach, SC, and the other at New England Aquarium, Boston, MA, USA. In 1999, an additional sand tiger (estimated at 164 cm TL) at the New England Aquarium that had a spinal deformity was offered for use in this study and fed OTC (that was injected into its food). Each individual was re-administered (injected or fed) OTC again approximately 1 year later, and two individuals were administered OTC a third time (Table 1). All three sharks were sacrificed using buffered MS222 in either December 2000 or January 2001.

The von Bertalanffy growth function was fit to the vertebral length-at-age data for sand tiger sharks with a nonlinear least squares regression algorithm ("nls" in S-Plus, Mathsoft Inc. 2000) to estimate parameters. The von Bertalanffy growth function is: $L_t = L_\infty \cdot [1 - \exp(-k(t - t_0))]$ where L_t = length at age "t," L_∞ = asymptotic or maximum length, k = the growth coefficient, and t_0 = age or time when length theoretically equals zero. Growth parameters were estimated for the sexes separately and combined. A likelihood ratio test was used to determine whether differences between female and male growth parameters were significant or if a single set of growth parameters better described the data (Kimura

1980; Quinn and Deriso 1999; Haddon 2001) (SAS Institute Inc. 1999).

Back-calculation is a method for describing the growth history of each individual sampled, and numerous variations in methodology exist (see Francis 1990 for a thorough review, and Goldman 2004 for description and application to elasmobranchs). Because our sample size was small and we did not have samples from all 12 months, lengths at previous ages were back-calculated from centra measurements for both sexes and fitted with the von Bertalanffy growth function. von Bertalanffy growth parameter estimates were then obtained from mean back-calculated length-at-age, and from a combination of back-calculated lengths-at-age and our sample data. The relationship between CR and TL for sand tiger sharks was investigated to determine the most appropriate method for back-calculating previous length-at-age. This is critical for obtaining accurate life-history parameter estimates from the von Bertalanffy growth function. To examine the statistical and biological accuracy of back-calculations relative to vertebral sample data (Goldman 2004; Cailliet and Goldman 2004; Goldman and Musick 2006), we compared several proportional back-calculation methods. Three different proportions methods were used and compared with our sample length-at-age data. First, we used the standard Dahl-Lea direct proportions method (Carlander 1969):

$$L_i = \left(\frac{L_c}{CR_c} \right) \cdot CR_i \quad (1)$$

Table 1 Dates, aquarium, sex, lengths, and method of administering oxytetracycline (OTC) to three sand tiger sharks, *Carcharias taurus*

Shark #	Date	Aquarium	Sex	PCL	FL	TL	OTC method
OTC-1	15 October 1998	Ripley's	M	112	127	157	Injected
	15 October 1999			138	157	201	Injected
	18 January 2001			160	181	218.6	Euthanized
OTC-2	15 October 1998	New England	M	110	125	152.5	Injected
	4 November 1999			139	156	188	Injected
	7 October 2000			–	–	–	Fed
	13 December 2000			162	180	219	Euthanized
OTC-3	3 March 1999	New England	M	–	–	164	Fed
	21 November 1999			–	–	201	Fed
	13 October 2000			–	–	–	Fed
	13 December 2000			154	175	210	Euthanized

where L_i = length at ring “ i ”, L_c = length at capture, CR_c = centrum radius at capture, and CR_i = centrum radius at ring “ i ”. Next, we applied a modified version of the Dahl-Lea method that uses parameter estimates from the specific linear fit that described the TL-CR relationship (Francis 1990):

$$L_i = L_c \left[\frac{a + bCR_i}{a + bCR_c} \right] \quad (2)$$

where a and b are the linear fit parameter estimates.

Ricker (1992), Francis (1990), and Campana (1990) suggested that the point of origin of proportional back-calculations should be related to a biologically derived intercept (i.e., length at birth), so we also applied a “size-at-birth-modified” Fraser–Lee equation:

$$L_i = L_c + \left[\frac{(CR_i - CR_c)(L_c - L_{\text{birth}})}{(CR_c - CR_{\text{birth}})} \right] \quad (3)$$

where L_{birth} = length at birth and CR_{birth} = centrum radius at birth. (Based on Gilmore et al. 1983, and Branstetter and Musick 1994, 100 cm TL was used for L_{birth}).

Results

Length equations

Length measurements from 272 sand tiger sharks (137 female, 135 male) were obtained by VIMS and NMFS between 1963 and 2001. Females ranged from 95 to 277 cm TL, and males ranged from 98.4 to 248 cm TL. Fork length and PCL can be derived from TL by:

$$FL = 0.8471 \cdot TL - 0.592 \quad (r^2 = 0.99; n = 138)$$

$$PCL = 0.7736 \cdot TL - 5.05 \quad (r^2 = 0.97; n = 134)$$

Weight-to-length relationships for female and male sand tiger sharks in the western North Atlantic are; $W = 1.3 \times 10^{-4} \times L^{2.4}$ ($r^2 = 0.84$, $n = 55$) and $W = 9.0 \times 10^{-5} \times L^{2.5}$ ($r^2 = 0.84$, $n = 47$), respectively, and $7.9 \times 10^{-5} \times L^{2.5}$

($r^2 = 0.84$) for the sexes combined. A likelihood ratio test showed that a single equation for the sexes combined better describe the data than separate equations for each sex individually ($\chi^2 = 5.3$; $df = 2$; $P = 0.07$).

Vertebral analysis

A linear regression gave a significant fit to the TL-CR data ($TL = 10.753 \times CR + 36.786$; $r^2 = 0.97$; $P < 0.0001$). However, it was important to compare the mean back-calculated results from Eq. 1 through Eq. 3 with our mean sample PCL data to see which method provided better biological accuracy for modeling growth (Goldman 2004; Goldman and Musick 2006).

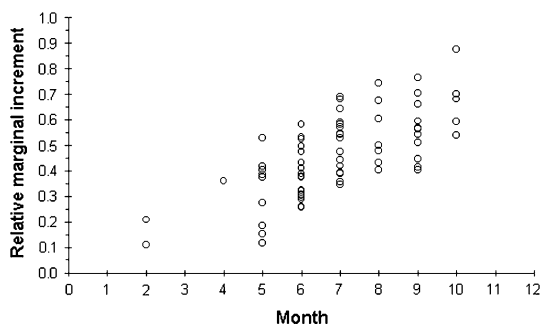
Percent agreement was 68.0% for the first set of blind reads and 75.0% for the second set, and the within-reader PA was 75.0% for reader one (the lead author) and 72.9% for reader two. $PA \pm 1$ -year was $> 92\%$ for all reader comparisons. When grouped by 10 cm length increments, agreement for sharks ≤ 200 cm TL was 100%, except for a single 1 year disagreement in each set of readings, and $100\% \pm 1$ year for sharks ≤ 220 cm TL (Table 2). The chi-square tests of symmetry showed that differences between and within readers were due to random error rather than systematic error (chi-square test, $P > 0.05$ in all cases).

Although we were missing samples from some winter months, RMI analysis indicates that the first postnatal and all subsequent rings form annually between December and February. The smallest relative margins in our sample occurred in February, followed by a consistent increase in RMI with the largest relative margins occurring in October (Fig. 2).

The administration of OTC was successful in marking vertebrae in two of the three sand tiger sharks. The vertebrae from the animal with the spinal deformity did not mark, possibly due to the diseased nature of the spine or due to low weight estimates and subsequently low doses. The two sharks whose vertebrae were successfully marked by the OTC were both aged at 2 years for their date of capture in 1998. One animal had two OTC marks and the other had three (Table 1). The annual

Table 2 Percent agreement (PA) and PA \pm 1 year, for both sets of readings for sand tiger sharks, *Carcharias taurus*, when placed into 10 cm length (TL) groups

Length group (cm)	Read	First set of readings				Second set of readings			
		Agree	Agree \pm 1	PA	PA \pm 1	Agree	Agree \pm 1	PA	PA \pm 1
90.1–100	7	7	7	100	100	7	7	100	100
100.1–110	7	7	7	100	100	7	7	100	100
110.1–120	7	7	7	100	100	7	7	100	100
120.1–130	7	7	7	100	100	7	7	100	100
130.1–140	1	1	1	100	100	1	1	100	100
140.1–150	9	9	9	100	100	9	9	100	100
150.1–160	2	1	2	50	100	2	2	100	100
160.1–170	5	5	5	100	100	4	5	80	100
170.1–180	2	2	2	100	100	2	2	100	100
180.1–190	0	0	0	–	–	0	0	–	–
190.1–200	4	4	4	100	100	4	4	100	100
200.1–210	5	2	5	40.0	100	2	4	40	80
210.1–220	7	3	7	42.9	100	3	7	43	100
220.1–230	7	2	5	28.6	71.4	3	6	43	86
230.1–240	9	2	7	22.2	77.8	4	8	44	89
240.1–250	7	4	7	57.1	100	4	7	57	100
250.1–260	3	0	2	0	66.7	2	3	67	100
260.1–270	4	2	4	50	100	3	3	75	75
270.1–280	3	0	1	0	33.3	1	3	33	100
<i>n</i> =	96	65	89			72	92		
Percent agree				67.7	92.7			75.0	95.8

**Fig. 2** Results of relative marginal increment analysis indicating annual ring formation likely occurs between December and February ($n = 90$)

OTC marks in both specimens were located near points where rings had formed (Fig. 3).

Vertebral length-at-age data from 48 female sand tiger sharks provided von Bertalanffy parameters of $L_{\infty} = 295.8$ cm TL, $k = 0.11$ year $^{-1}$, and $t_0 = -4.2$ years (Fig. 4). von Bertalanffy parameters from the linear-modified Dahl-Lea back-calculations (the most accurate back-calculation method; see below) gave slightly lower k coefficients and slightly higher L_{∞} and t_0 values with or without sample data included (Table 3).

Results from mean back-calculated data had the lowest standard error. Vertebral age data from 48 males provided Bertalanffy parameters of $L_{\infty} = 249.5$ cm TL, $k = 0.16$ year $^{-1}$, and $t_0 = -3.4$ years (Fig. 4). Back-calculated lengths-at-age for male sand tiger sharks (with or without sample data included) again provided slightly lower k coefficients, slightly higher L_{∞} , and t_0 parameters, and mean back-calculated data had the lowest standard error (Table 3). Vertebral age data for the sexes combined ($n = 96$) provided von Bertalanffy parameters of; $L_{\infty} = 280.5$ cm TL, $k = 0.12$ year $^{-1}$, and $t_0 = -4.1$ years. Parameters resulting from back-calculated data for the sexes combined produced results with similar trends as those for females and males (Table 3). A likelihood ratio test showed that separate von Bertalanffy growth models better describe the data for each sex than one model with the sexes combined ($\chi^2 = 22.8$; $df = 3$; $P = 0.000044$).

The linear-modified Dahl-Lea method (Eq. 2) most accurately represented the mean sample length-at-age data. It produced mean back-calculated lengths-at-age within 9.1 cm of mean sample lengths-at-age for female sand tiger sharks, except

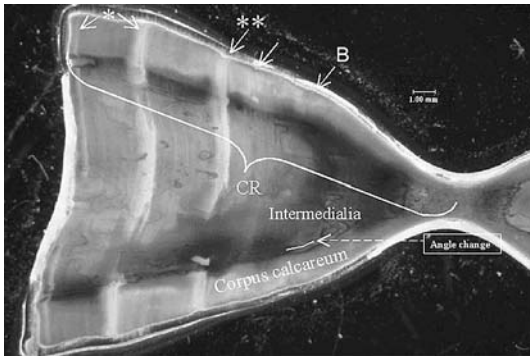


Fig. 3 Sagittally cut vertebral section of OTC sand tiger shark (OTC-2 (from Table 1). Arrows without asterisks represent wild growth. Double asterisks indicates initial OTC mark shortly after capture. Arrows with single asterisks indicate OTC marks and captive growth rings. All three OTC marks can clearly be seen

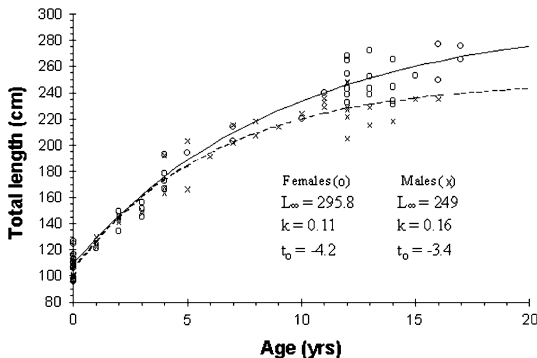


Fig. 4 von Bertalanffy growth curves fitted to female ($n = 48$) and male ($n = 48$) sample data for sand tiger sharks. Estimates for parameters of the von Bertalanffy growth function are summarized

for lengths of approximately 195 and 250 cm TL (Fig. 5a). When applied to males, Eq. 2 produced mean back-calculated lengths-at-age within 9.8 cm of mean sample lengths-at-age for sharks < 195 cm TL. At greater lengths, deviation from mean sample length-at-age ranged from 2.7 to 15.1 cm TL (Fig. 5b). Lee's phenomenon was present with the individual back-calculated data. There was a tendency for some age classes (usually older ones) to underestimate the mean sample length-at-age data after the first few back-calculated ages. This is not too surprising considering the time frame over which samples were obtained, and the potential for sampling variation (i.e., where in the spinal column the vertebrae

were removed). However, Lee's phenomenon was not apparent in the mean back-calculation values, which were, overall, very similar to the mean sample length-at-age data.

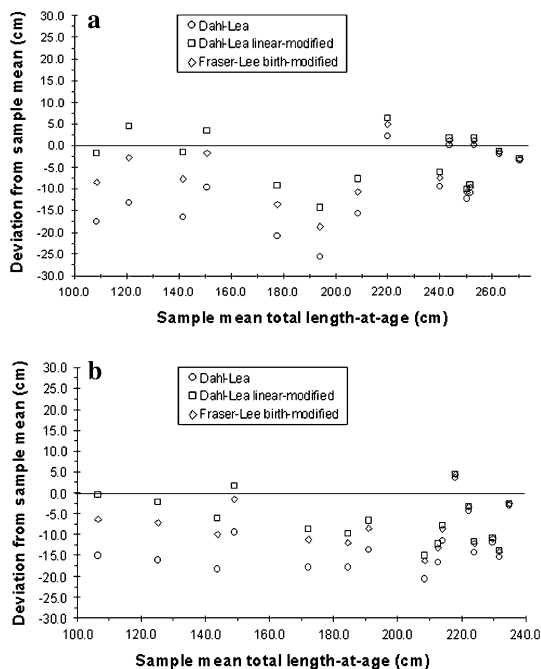
Discussion

Branstetter and Musick (1994) suggested that sand tiger sharks form two rings per year in their vertebral centra whereas our results support a hypothesis that only one ring is formed annually. The difference in ageing protocols and the assumed time of band formation between the two studies is almost certainly the cause of the different results. We feel it is necessary to state the reasons that we did not follow the Branstetter and Musick (1994) ageing protocol in this study, then discuss our results and comment on their ramifications for recovery of the western North Atlantic population.

Branstetter and Musick (1994) “counted and measured rings in the intermedialia”. When the intermedialia was damaged, they counted along the corpus calcareum. We found that using the intermedialia as the primary counting surface for ageing sand tiger sharks could lead to errors. In addition to the distinct banding pattern (i.e., band pairs making up rings) that extended completely across the intermedialia and corpus calcareum, and the presence of notches (at or near the rings) along the outside arm of the corpus calcareum, the intermedialia contained subtle or indistinct bands (similar to the fine feature “rings” discussed in Cailliet et al., this issue). These “indistinct bands” made using the intermedialia as the primary counting (and measuring) surface problematic for the following reasons: (1) they extended completely across the intermedialia, but did not appear on the corpus calcareum (nor were they associated with notches on the corpus calcareum); (2) they did not extend all the way across the intermedialia; (3) part-way across the intermedialia they blended into another indistinct band; (4) part-way across the intermedialia, they blended into a distinct band; (5) the number of indistinct bands (between distinct bands) was inconsistent ranging from 0–5 in number. Additionally, some indistinct bands were seen on the

Table 3 von Bertalanffy growth parameters of female, male, and sexes combined for sand tiger sharks in the western North Atlantic. Numbers in parentheses are standard errors

Females	L_{∞}	k	t_0
Sample data ($n = 48$)	295.8 (14.0)	0.11 (0.02)	-4.2 (0.5)
Back-calculations ($n = 366^a$)	302.4 (7.4)	0.09 (0.006)	-4.6 (0.22)
Mean back-calculation ($n = 18^a$)	308.3 (5.2)	0.09 (0.004)	-4.8 (0.21)
Back-calculations W/sample data ($n = 414^a$)	305.3 (6.9)	0.09 (0.006)	-4.7 (0.20)
Males			
Sample data ($n = 48$)	249.5 (7.2)	0.16 (0.02)	-3.4 (0.4)
Back-calculations ($n = 278^a$)	252.7 (6.1)	0.13 (0.009)	-4.1 (0.2)
Mean back-calculation ($n = 16^a$)	247.5 (3.6)	0.13 (0.009)	-4.2 (0.2)
Back-calculations W/sample data ($n = 326^a$)	256.1 (5.4)	0.12 (0.008)	-4.3 (0.2)
Combined			
Sample data ($n = 96$)	280.5 (9.4)	0.12 (0.01)	-4.1 (0.4)
Back-calculations ($n = 644^a$)	294.7 (6.5)	0.09 (0.005)	-4.8 (0.2)
Mean back-calculation ($n = 34^a$)	293.1 (16.0)	0.09 (0.01)	-5.0 (0.7)
Back-calculations W/sample data ($n = 740^a$)	295.2 (5.7)	0.09 (0.004)	-4.8 (0.2)

^a Not independent**Fig. 5** Mean deviation, from mean sampled total length, of three proportional back-calculation methods for **a** female and for **b** male sand tiger sharks. Data points represent mean back-calculated lengths-at-age. A point on the x-axis would represent zero deviation from the sample mean length-at-age

corpus calcareum, but they did not match up with bands in the intermedialia and did not possess a corresponding notch along the outer arm of the corpus calcareum. These reasons were paramount in our decision to use the corpus calcareum as the

primary counting and measuring surface, with the distinct rings in the intermedialia and notches as “confirmation” of an annulus.

The radials of the intermedialia of carcharhinid sharks are relatively hard, robust, and numerous, making it nearly solid. In contrast, the radials of the intermedialia in lamnoid sharks are less numerous, softer, and quite fragile, and the large amount of interstitial space often prevents its presence in sectioned vertebrae. When present, the outer edge of the intermedialia in lamniform vertebral sections can become warped in a concave manner. When this occurs, the rings near the outer edge of the intermedialia become “bunched up” and indistinguishable. The bands on the corpus calcareum can also become more tightly grouped at the outer edge, particularly in larger/older animals, however the rings have a tendency to remain distinguishable due to the stronger (more stout) nature of the structure. Based on these observations, we suggest that future studies on the age and growth of lamniform sharks use the corpus calcareum as the primary counting and measuring surface.

We found that vertebral growth significantly increased with somatic growth, which along with the reliability of the marginal increment analysis (Fig. 2) demonstrates vertebral growth patterns are a reliable indicator of age in sand tiger sharks. Precision was high between and within readers with limited differences (Table 2) that were attributable to random error. These results

provided a high degree of confidence in the accuracy and precision of our age assessments (from sample data) used in the von Bertalanffy growth model, and hence in the resulting life-history parameter estimates. The similar von Bertalanffy growth parameter estimates generated from our sample data, back-calculated data, and the combination of the two indicate that our sample size was sufficiently large and encompassed the known size range of males, and all but the very upper end of the known size range of females. While these back-calculation results are, of course, dependent on the assumption that growth has not significantly changed over time, and are applicable only to sand tiger sharks, they demonstrate the importance of choosing the appropriate method in order to minimize error (Fig. 5a, b), which results in a greater ability to accurately model growth (Cailliet and Goldman 2004; Goldman 2004).

The RMI conducted by Branstetter and Musick (1994) indicated that specimens from the first part of the year (January–July) had an even number of bands while specimens from the second part of the year (August–December). We found no such relationship—animals from every month of the year from which we had more than a single sample possessed both even and odd numbers of rings. Our RMI analysis indicated that a single ring is formed annually sometime between December and February (Fig. 2). Additionally, the results from the two OTC sharks support the hypothesis that a single ring is formed annually. The annual OTC marks in both specimens were located near points where rings had formed (Fig. 3) even though they were kept under a constant photoperiod and ambient temperature.

Centrum banding patterns may be related to physiological changes induced by changes in environmental parameters such as temperature and photoperiod (Cailliet et al. 1986; Branstetter 1987), however, it has been shown not to be the case for some species such as the little skate, *Raja erinacea* (Natanson 1993), and the Pacific angel shark, *Squatina californica* (Natanson and Cailliet 1990; Cailliet et al. 1992). The north-south migration of sand tiger sharks has been proposed as a possible reason that two rings might be formed in the vertebral centra each

year (Branstetter and Musick 1994) with the primary cue for the migration being either temperature or photoperiod. The primary cue for sand tiger migration has not been demonstrated, but the fact that captive sand tiger sharks appear to form a single ring in their vertebral centra each year makes those possibilities less likely. Vertebral growth is inevitably linked to food intake, and a lack of food for short periods of time can cause subtle bands to appear in vertebral centra of some species (J. Gelsleichter, personal communication). This may explain the “indiscrete bands” we saw in sand tiger vertebrae, and play a role in the annual formation of rings in the centra.

The life-history parameters presented by Goldman (1998) resulted in growth coefficients (k) that were half of those presented by Branstetter and Musick (1994). This is because Goldman (1998) simply doubled the age estimates from Branstetter and Musick (1994) by assuming that one ring was formed annually in the vertebral centra (e.g., a 5-year-old would then be considered to be 10 years of age), and not from the examination of any vertebral samples. In contrast, the estimations of sand tiger life-history parameters presented herein are the combined result of using an independently developed ageing protocol (applied to vertebral samples from 96 sand tiger sharks), a subsequent RMI analysis and the use of a direct validation method (OTC), all of which support a hypothesis that one ring is formed annually in vertebral centra. As such, we believe our results are a much better indicator of sand tiger shark growth parameters than either Branstetter and Musick (1994) or Goldman (1998).

Branstetter and Musick (1994) characterized sand tiger growth based on mean back-calculated lengths-at-age as follows; “growth was 25–30 cm per year for ages 0–1, 20–25 cm per year for ages 2–3, and 15–20 cm per year for ages 4–5. Subadults and adults had a growth rate of 10–15 cm per year for ages 6–7, and growth declined to 5–10 cm per year for ages 8 and greater”. They also characterized growth in females and males to be nearly identical throughout life. Our results indicate that growth is similar up to age 5 at which point-in-time females begin outgrowing males at a significant rate, and that two separate growth

curves should be used to describe the rate at which each sex attains their maximum size (Fig. 4). Mean back-calculated lengths-at-age from this study indicate that growth averaged 14.5–18.5 cm per year for ages 0–1, 13–14.5 cm per year for ages 2–3, and 11 cm per year for age 4. For ages 5 and 6, growth averaged 10–11.2 cm for females and 9.2–9.5 for males; and for age 7 females averaged 9.3 cm per year whereas males averaged 6.8 cm per year. For sand tiger sharks (8 years of age, the growth rates declined to an average of 6.4 cm per year for females and 4.6 cm per year for males.

Female sand tiger sharks become sexually mature at a length of 220–230 cm TL and males mature at 190–195 cm TL (Gilmore et al. 1983). Previous estimates of age at maturity stated that the equivalent ages to those lengths are 6 years for females and about 4 years for males (Branstetter and Musick 1994). Our length-at-age results place age at sexual maturity at 9–10 years for female sand tiger sharks, and at 6–7 years for males. Reproduction in captivity (from copulation to parturition) has been documented in South Africa and Australia. A female sand tiger shark born at Underwater World aquarium, Australia, in 1992 became pregnant in 2000 (resulting in two pre-term stillborn pups ~70–80 cm TL) (Henningsen et al. 2004). Additionally, a male sand tiger born at the New York aquarium in 1994 was exhibiting pre-copulatory behavior in 2001–2002 (H. Walters, personal communication). These data, although captive, provide corroboration to our estimates of age at sexual maturity.

Gilmore (1990) stated that all female sand tiger sharks he examined from Florida to North Carolina between March and January were impregnated and that no resting stage took place in the reproductive cycle of this species. However, Branstetter and Musick (1994) presented strong evidence that a resting stage did occur and that the reproductive cycle was at least 2 years. They presented records from the VIMS longline survey from 29 mature female sand tiger sharks caught off Virginia (during the 1980s and early 1990s) that were all noted as either postpartum or in a resting state with small ovarian egg follicles. Since then, we have records (from the VIMS survey) for an additional 17 mature females that were in the same

postpartum or resting stage condition. The mother of the aforementioned female born at Underwater World, Australia was captured pregnant in 1992, and while in captivity has given birth two more times; in 1997 and 1999 (Henningsen et al. 2004). A gestation period of 9–12 months leaves little to no energetic “turn-around” time for a female to build up her reserves and go through another reproductive cycle, unless there is a resting year. If a female carried pups through a 12-month gestation period, she would immediately have to mate again in order to reproduce the following year. Any time delay in mating would “throw off” her timing for parturition, and at some point-in-time she would require a resting period. The current body of evidence strongly supports a 2-year reproductive cycle for female sand tiger sharks. However, preliminary evidence from captive male sand tiger sharks indicates that they may mate annually (A. Henningsen, personal communication).

Maximum observed age for female and male sand tiger sharks in this study was 17 and 15, respectively. These ages are close to the maximum documented ages of sand tiger sharks in captivity. Govender et al. (1991) reported a male that had been in captivity at an aquarium in Durban, South Africa for 16 years, and there is currently a 20-year-old female (as of 2002) at the National Aquarium in Baltimore, MD, USA (A. Henningsen, personal communication). Branstetter and Musick (1994) estimated longevity at 30–35 years by extrapolating their von Bertalanffy curves generated from back-calculated data. Applying the same technique to our data, longevity may be as high as 40 years for females and 30 years for males. However, estimating longevity using the time required to reach 95% of its asymptotic length (i.e., $5 \times \ln 2/k$, see Fabens 1965; Cailliet et al. 1992) provided longevity estimates of 32–38 for females and 22–27 for males.

Branstetter and Musick (1994) provided a weight–length equation for sand tiger sharks of: $W = 1.62 \times 10^{-6} \times L^{3.15}$. This equation was later found to have an error in it, which has not been published. The corrected weight–length equation is: $W = 1.62 \times 10^{-6} \times L^{3.24}$. Our data for length conversions and maximum size of sand tiger sharks are similar to those from the corrected weight–length equation. The increased sample size

(particularly for smaller individuals) enhances the accuracy and precision of these estimates. More importantly, we were able to determine that a single length–weight curve combined is adequate for describing that relationship for both sexes.

Our estimates of sand tiger shark life-history parameters show that they are much slower growing to adulthood and maximum length than previously assumed. Since our mean back-calculated lengths-at-age gave the smallest standard error in von Bertalanffy estimates (Table 3), they may better represent the life-history parameters of this species and should be considered more valid when used as inputs for determining vital rates. Considering the large population depletion suffered by sand tiger sharks in the western North Atlantic over the past 20 years, this information is crucial for accurately assessing the ability of the population to recover, and further justifies the need for this species to be fully protected. The life-history parameters presented here also allow for a re-adjustment of previously predicted vital rate estimates that can aid managers in taking appropriate steps for sand tiger shark protection and conservation.

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References

- Anonymous (2002) Preliminary draft recovery plan—grey nurse shark. New South Wales Fisheries, Australia
- Branstetter S (1987) Age and growth validation of newborn sharks held in laboratory aquaria, with comments on the life history of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*. Copeia 1987:291–300
- Branstetter S, Musick JA (1994) Age and growth estimates for the sand tiger in the Northwestern Atlantic Ocean. Trans Am Fish Soc 123:242–254
- Cailliet GM, Goldman KJ (2004) Age determination and validation in chondrichthyan fishes. In: Carrier J, Musick JA, Heithaus M (eds) The biology of sharks and their relatives. CRC, Boca Raton, pp. 399–447
- Cailliet GM, Radke RL, Weldon BA (1986) Elasmobranch age determination and verification: a review. In: Uyeno T, Arai R, Taniuchi T, Matsuura K (eds) Indo-Pacific fish biology: Proceedings of the 2nd international conference on Indo-Pacific fishes. Ichthyological Society of Japan, Tokyo, pp. 345–359
- Cailliet GM, Mollet HF, Pittenger GG, Bedford D, Natanson LJ (1992) Growth and demography of the Pacific angel shark (*Squatina californica*), based on tag returns off California. Aust J Mar Freshw Res 43:1313–1330
- Cailliet GM, Smith WD, Mollet HF, Goldman KJ (this issue) Age, growth studies of chondrichthyan fishes: an overview stressing terminology, verification, validation, and growth function fitting. In: Goldman KJ, Carlson JK (eds) Special volume from symposium of the American Elasmobranch Society, July 2005. Environ Biol Fishes, pp. 000–000
- Campana SE (1990) How reliable are growth back-calculations based on otoliths? Can J Fish Aquat Sci 47:2219–2227
- Campana SE (2001) Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J Fish Biol 59:197–242
- Carlander KD (1969) Handbook of freshwater fishery biology, vol. 1. Iowa University Press, Ames
- Casey JG, Kohler NE (1990) Long distance movements of Atlantic sharks from the NMFS cooperative shark tagging program. In: Gruber SH (ed) Discovering sharks. American Littoral Society, Special Publication 14, Highlands, pp. 87–91
- Cerrato RM (1990) Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. Can J Fish Aquat Sci 47:1416–1426
- Cliff G (1989) Breeding migration of the sand tiger shark *Carcharias taurus* in southern African waters. In: Abstracts of the 5th annual meeting of the American Elasmobranch Society, San Francisco, June 1989
- Compagno LJ (1984) FAO species catalogue. Vol. 4. Sharks of the World. An annotated and illustrated catalogue of shark species known to date. Part 1. Hexanchiformes to Lamniformes. FAO Fish Synopsis 125 4(Pt 1):249

- Conrath CL, Gelsleichter J, Musick JA (2002) Age and growth of the smooth dogfish (*Mustelus canis*) in the northwest Atlantic Ocean. *Fish Bull* 100:674–682
- Evans GT, Hoenig JM (1998) Testing and viewing symmetry in contingency tables, with application to readers of fish ages. *Biometrics* 54:620–629
- Fabens AJ (1965) Properties and fitting of the von Bertalanffy growth curve. *Growth* 29:265–289
- Francis RICC (1990) Back-calculation of fish length: a critical review. *J Fish Biol* 36:883–902
- Gelsleichter J, Cortés E, Manire CA, Hueter RE, Musick JA (1998) Evaluation of toxicity of oxytetracycline on growth of captive nurse sharks, *Ginglymostoma cirratum*. *Fish Bull* 96:624–627
- Gilmore RG (1990) The reproductive biology of lamnoid sharks. In: Gruber SH (ed) *Discovering sharks*. American Littoral Society, Special Publication 14, Highlands, pp. 64–67
- Gilmore RG (1993) Reproductive biology of lamnoid sharks. *Environ Biol Fishes* 38:95–114
- Gilmore RG, Dodrill JQ, Linley PA (1983) Reproduction and embryonic development of the sand tiger shark, *Odontaspis taurus* (Rafinesque). *Fish Bull* 81:201–225
- Goldman KJ (1998) Demographic analysis for sand tiger sharks and dusky sharks. Part 3. In: Musick JA, Gelsleichter J, Grubbs RD, Goldman KJ (eds) *VIMS Shark Ecology Program*. Appendix SB-IV-13. National Oceanic and Atmospheric Administration/National Marine Fisheries Service Shark Evaluation Workshop, Panama City, 3 pp., June 1998
- Goldman KJ (2004) Age and growth of elasmobranch fishes. In: Musick JA, Bonfil R (eds) *Elasmobranch Fisheries Management techniques*. Asia Pacific Economic Cooperation, Singapore, pp. 97–132, 370 pp. Electronic version available at <http://www.flmnh.ufl.edu/fish/organizations/ssg/EFMT2004.htm>
- Goldman KJ, Musick JA (2006) Growth and maturity of salmon sharks in the eastern and western North Pacific, and comments on back-calculation methods. *Fish Bull* 104:278–292
- Gordon I (1993) Pre-copulatory behaviour of captive sand tiger sharks, *Carcharias taurus*. *Environ Biol Fishes* 38:159–164
- Govender A, Kistnasamy N, Van Der Elst RP (1991) Growth of spotted ragged-tooth sharks *Carcharias taurus* (Rafinesque) in captivity. *S Afr J Mar Sci* 11:15–19
- Haddon M (2001) Modeling and quantitative methods in fisheries. Chapman & Hall/CRC, Boca Raton
- Henningsen AD, Smale M, Garner R, Gordon I, Marin-Osorno R, Kinnunen N (2004) Captive breeding and sexual conflict. In: *Elasmobranch husbandry manual*. Ohio Biological Survey, Columbus, Ohio, pp. 239–250
- Hoenig JM, Morgan MJ, Brown CA (1995) Analyzing differences between two age determination methods by tests of symmetry. *Can J Fish Aquat Sci* 52:364–368
- Kimura DK (1980) Likelihood methods for the von Bertalanffy growth curve. *Fish Bull* 77:765–773
- Mathsoft Inc (2000) S-Plus 2000 Professional Release 1. Mathsoft Inc., Seattle
- Media Cybernetics (1999) Optimus, version 6.5. Media Cybernetics, Silver Spring
- Musick JA, Branstetter S, Colvocoresses JA (1993) Trends in shark abundance from 1974–1991 for the Chesapeake Bight region of the U.S. mid-Atlantic coast. National Oceanic and Atmospheric Administration, Technical Report. National Marine Fisheries Service 115:1–18
- Musick JA, Harbin MM, Berkeley SA, Burgess GH, Eklund AM, Findley L, Gilmore RG, Golden JT, Ha DS, Huntsman GR, McGovern JC, Parker SJ, Poss SG, Sala E, Schmidt TW, Sedberry GR, Weeks H, Wright SG (2000) Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific salmonids). *Fisheries* 25(11):6–30
- Natanson LJ (1993) Effect of temperature on band deposition in the little skate, *Raja erinacea*. *Copeia* 1993:199–206
- Natanson LJ, Cailliet GM (1990) Vertebral growth zone deposition in angel sharks. *Copeia* 1990:1133–1145
- NMFS (National Marine Fisheries Service) (1999) Final fishery management plan for Atlantic tunas, swordfish and sharks, vols. I–III. U.S. Department of Commerce National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Silver Spring, April 1999
- Pollard DA, Smith AK (2005) IUCN Red List assessment of *Alopias vulpinus*. In: Fowler SL, Cavanagh RD, Camhi M, Burgess GH, Cailliet GM, Fordham SV, Simpfendorfer CA, Musick JA (eds) *Sharks, rays and chimaeras: the status of the chondrichthyan fishes*. IUCN SSC Shark Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK, pp. 250–252
- Pollard DA, Lincoln Smith MP, Smith AK (1996) The biology and conservation status of the grey nurse shark (*Carcharias taurus* Rafinesque 1810) in New South Wales, Australia. *Mar Freshw Ecosyst* 6:1–20
- Quinn TJ, Deriso RB (1999) *Quantitative fish dynamics*. Oxford University Press, New York
- Ricker WE (1992) Back-calculation of fish lengths based on proportionality between scale and length increments. *Can J Fish Aquat Sci* 49:1018–1026
- SAS Institute Inc. (1999) Version 8.0. Statistical Analysis Systems Institute Inc., Cary
- SigmaPlot (2000) Version 6.0. SPSS Inc., Chicago, IL
- Tanaka S (1990) Age and growth studies on the calcified structures of newborn sharks in laboratory aquaria using tetracycline. In: Pratt HL Jr, Gruber SH, Tanuchi T (eds) *Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries*. National Oceanic and Atmospheric Administration, Technical Report, National Marine Fisheries Service 90, pp. 189–202