

# Using bomb radiocarbon analyses to validate age and growth estimates for the tiger shark, *Galeocerdo cuvier*, in the western North Atlantic

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**Abstract** Refined and validated age and growth determinations are necessary for a proper understanding of tiger shark (*Galeocerdo cuvier*) life history characteristics in the western North Atlantic (WNA). Age and growth estimates were derived from band counts of 238-sectioned vertebral centra. Bomb radiocarbon analysis of ten band pairs extracted from four vertebral sections suggested that band pairs are deposited annually up to age 20. Males and females were aged to 20 and 22 years, respectively, although longevity estimates predict maximum ages of 27 and 29 years, respectively. Two- and three-parameter von Bertalanffy and Gompertz growth functions fit to length at age data demonstrated that growth rates were similar for males and females up to around 200 cm fork length (FL) after which male growth slowed. Both sexes appear to reach maturity at age 10. The two-parameter von Bertalanffy growth function provided the best biological fit to length at age data generating parameter estimates of:  $L_{\infty} = 330$  cm FL,  $k = 0.131$  for males and  $L_{\infty} = 347$  cm FL,  $k = 0.124$  for females, with  $L_0$  set at 62 cm FL. This study provides a rigorous description of tiger shark age and

growth in the WNA and further demonstrates the utility of bomb radiocarbon as an age validation tool for elasmobranch fish.

## Introduction

The tiger shark, *Galeocerdo cuvier*, is a member of the family Carcharhinidae that occurs worldwide in temperate and tropical waters (Castro 1983). In the western North Atlantic (WNA), it resides year round off the coast of Florida, making migrations as far north as Nova Scotia, Canada, during warm summer months (Kohler et al. 1995). In this region, tiger sharks mature between 258 and 265 cm fork length (FL; Branstetter et al. 1987) and have been reported to attain a maximum size of 550 cm total length (469 cm FL; Castro 1983). The Fisheries Management Plan (FMP) for sharks in the Atlantic Ocean (Anonymous 1993) classifies the tiger shark within the large coastal complex. The US inshore longline fishery does not specifically target tiger sharks; however, small tiger sharks are frequently caught incidentally (Natanson et al. 1999). Furthermore, due to their large size, recreational fishermen often enter these sharks into fishing tournaments (Bigelow and Schroeder 2002). Despite a wide range and occurrence in several fisheries, substantial information on fisheries data, and life history characteristics, is limited for this species in the WNA. A review of the status of several shark species by Castro et al. (1999) demonstrates this lack of data, listing the tiger shark as category 1, or an “exploited species that cannot be placed on any of the subsequent categories, because of lack of data.” Other studies have suggested 80 (Musick et al. 1993) and 65% (Baum et al. 2003) declines in tiger shark catch rates in the WNA over the last 30 years. Worldwide, the tiger shark

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is listed as a lower risk/near threatened species by the IUCN red list (<http://www.redlist.org>).

Four studies have described age and growth estimates for the tiger shark within the last 25 years. DeCrosta et al. (1984) published the first age estimates for the tiger shark using vertebral band counts from 28 specimens captured off the coast of Hawaii. Branstetter et al. (1987) produced age and growth estimates for the tiger shark in the Gulf of Mexico and WNA based on vertebral band counts from 25 and 44 sharks, respectively. A subsequent study of the WNA population by Natanson et al. (1999), using tag and recapture data from 42 tiger sharks at liberty for > 0.9 years, did not corroborate age estimates of Branstetter et al. (1987), although a direct comparison of these studies could not be made due to the techniques used to generate their respective growth models. Most recently, Wintner and Dudley (2000) utilized band pair counts from 90 tiger sharks captured in the southwest Indian Ocean to generate age estimates for the species, and validate age up to 5 years using vertebrae from oxytetracycline (OTC)-injected tagged and recaptured individuals. Despite the existing age and growth data for the species worldwide, no comprehensive, validated data exists for the tiger shark population in the WNA.

A new method of age validation that has proved effective for some elasmobranchs is the use of bomb radiocarbon ( $^{14}\text{C}$ ). In the 1950s and 1960s, atmospheric testing of atomic bombs resulted in the rapid and well-documented increase in radiocarbon in the world's oceans (Druffel and Linick 1978). This rather discrete rise in radiocarbon was almost synchronous in marine carbonates such as corals, bivalves and fish otoliths around the world (Campana 1997) and can be used as a time-specific marker for age validation in many species (Druffel 1989; Kalish et al. 1997; Kerr et al. 2005). Specifically, it is the agreement of a bomb  $^{14}\text{C}$  record from a species with age in question, with a known bomb  $^{14}\text{C}$  reference time-series that can be used as a tool for age validation. Within fish, skeletal structures containing growth bands such as otoliths or vertebrae have been documented to have recorded and preserved those ambient  $^{14}\text{C}$  levels (Kalish 1993). Campana et al. (2002) demonstrated that a bomb radiocarbon pulse was both recorded and preserved within the vertebrae of porbeagle shark, *Lamna nasus*, and were able to validate vertebral band pair counts as accurate indicators of age in *L. nasus* up to 26 years. More recently, Ardizzone et al. (2006) used similar techniques to validate annual vertebral band pair periodicity in the shortfin mako (*Isurus oxyrinchus*) from the WNA.

Despite the presence of published age and growth data for the tiger shark in the WNA, the lack of validation and inconsistency between studies limits the utility of these data for management purposes. Thus, in light of recent successes, the current study sought to employ bomb

radiocarbon techniques, as outlined in Campana et al. (2002) and Ardizzone et al. (2006), to validate age and growth estimates for the tiger shark in the WNA. Furthermore, this study updated the work of Natanson et al. (1999) with additional tag-recapture data.

## Materials and methods

### Vertebrae collection

Between 1962 and 2005, the National Marine Fisheries Service (NMFS) Apex Predators Investigations (API) collected vertebrae from 238 tiger sharks captured on research cruises, commercial and recreational fishing vessels, and at sportfishing tournaments in the WNA. When possible, the 15th–20th vertebrae were excised; otherwise a section of the vertebral column was removed from above the branchial region near the 5th gill arch. After dissection, vertebrae were labeled with morphological measurements, sex, date and source before being stored frozen, in 70% ethanol, or in 10% buffered formalin, at the NMFS laboratory in Narragansett, RI, USA. Only vertebrae samples that had either a measured fork length [FL—tip of the snout to the fork in the tail, over the body (OTB)], total length (TL—tip of the snout to a point on the horizontal axis intersecting a perpendicular line extending down from the tip of the upper caudal lobe to form a right angle, OTB; Kohler et al. 1995), or weight (WT, kg) were utilized for this study. For consistency, all measurements were converted to OTB FL using the regression equations (Kohler et al. 1995):

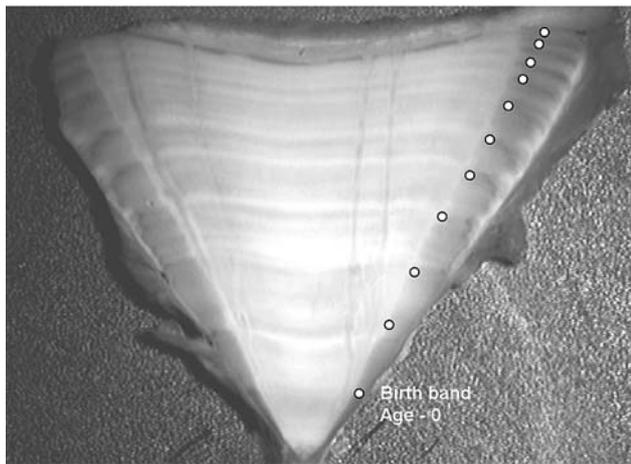
$$\text{FL} = 0.8761 (\text{TL}) - 13.3535 \quad (N = 44, R^2 = 0.9887)$$

$$\text{WT} = 2.5281 \times 10^{-6} (\text{FL})^{3.2603} \\ (N = 187, R^2 = 0.9550)$$

All length measurements are in centimeters (cm), and all length measurements reported in this study will be in OTB FL unless otherwise noted.

### Age and growth analysis

One vertebra from each sample was removed for aging. Prior to processing, individual centra were thawed and cleaned of excess tissue. Centra were cut in the middle along the sagittal plane using a Raytech Gem Saw<sup>TM</sup> fitted with two diamond blades separated by a 0.6-mm spacer to create a “bow-tie” section. Individual “bow-tie” sections were placed in small tissue capsules, labeled and stored in 70% ethanol. Each section was digitally photographed using a MTI CCD 72 video camera attached to a SZX9 Olympus stereo microscope using reflected light. Sections were photographed at various magnifications depending on



**Fig. 1** Vertebral section from a 267-cm FL female tiger shark aged 10 years. Circles denote individual band pairs

vertebral size. Band pairs (consisting of one opaque and one translucent band) were counted and measured using Image Pro 4™ software to estimate individual fish age (Fig. 1). Measurements were made from the focus of the bow-tie to the top of each opaque growth band visible within the corpus calcareum. The birth band (age zero) was identified as the first opaque band distal to the focus coinciding with an angle change in the corpus calcareum (Fig. 1; Casey et al. 1985). The location of this band was confirmed through comparison of the birth band radius (BR) measurement to the vertebral radius (VR) of late term embryos and young of the year (YOY) fish. Vertebral radius was measured from the focus to the distal margin of the intermedialia along the inner corpus calcareum.

A plot of FL versus VR was created to aid in the confirmation of the birth band and to determine if vertebrae grew proportionally with fish length. Regressions were plotted for both male and female data and compared statistically using an analysis of covariance (ANCOVA). Since vertebrae vary in size throughout the vertebral column, for consistency, only vertebrae obtained from above the branchial region were included in this analysis.

Two, non-consecutive band counts were made for each vertebrae by the senior author without knowledge of fish length or any previous age estimate. A second ager, working independently of the first, examined a sub-sample of 59 vertebrae of varying sizes and sex to ensure proper interpretation of vertebral bands.

#### Data analysis

All age estimates generated from vertebral counts were adjusted based on date of capture relative to a theoretical birth date. This method provides a more precise estimation of fish age through a comparison between birth date and

capture date. Tiger sharks are reported to pup from April to June in the WNA (Clark and von Schmidt 1965; Branstetter 1981; Castro 1983); however, based on an abundance of YOY sharks in late April and early May (NMFS unpublished data) a theoretical birth date of May 15 was utilized for all fractional age calculations. To calculate fractional age, date of capture was converted into a Julian day, and subtracted from 136 (May 15). This difference, or the number of days of growth completed after a theoretical May 15th birthday, was divided by 365.25 days to obtain a decimal (fractional age). The decimal was then added to the total band count to obtain a more precise estimation of actual fish age. Fractional age was used in all growth models.

Precision was examined through estimation of coefficient of variation (CV) and average percent error (APE). Bias was assessed through the use of contingency tables using Bowker's, McNemar's, and Evans-Hoenig tests (Hoenig et al. 1995; Evans and Hoenig 1998) and age bias plots (Campana et al. 1995).

von Bertalanffy growth functions (VBGF) were fit to length-at-age data for both males and females using the following equation (von Bertalanffy 1938):

$$L(t) = L_{\infty} \left( 1 - e^{-k(t-t_0)} \right)$$

where

- $l_t$  total length at time  $t$  (age in years)
- $L_{\infty}$  asymptotic length
- $k$  Brody growth constant
- $t_0$  theoretical age at zero length

A two-parameter version of the VBGF was also fit to observed length at age data for comparison. This model incorporates an estimate of size at birth ( $L_0$ ) in place of  $t_0$ , subsequently creating a steeper initial slope as the function is forced through  $L_0$ . The equation is

$$L(t) = L_{\infty} - (L_{\infty} - L_0)e^{-kt}$$

Size at birth varies greatly for the tiger shark; however, in order to enhance comparison to other published age and growth studies for this species (Branstetter et al. 1987; Natanson et al. 1999), a birth size of 62 cm was chosen for use in the two-parameter model and throughout the study.

A Gompertz growth model (Ricker 1975) was also fit to length at age data for both sexes:

$$L(t) = L_0 e^{G(1-e^{-kt})}$$

where

- $L_{\infty}$   $L_0 e^G$  is the mean maximum FL ( $t = \infty$ );
- $k$  (=g in Ricker 1975) is a rate constant (per year), and
- $L_0$  fork length at birth.

All growth models were calculated using a nonlinear regression function in Statgraphics™ (Manugistics, Inc., Rockville, MD, USA).

Several criteria were utilized to evaluate the growth curve that best described tiger shark growth. All curves were compared statistically using Akaike's (1973) Information Criterion (AIC), and standard error (SE) of parameter estimates. Lastly, the degree by which parameter estimates (particularly  $L_0$  and  $L_\infty$ ) of each model corroborated with known size at birth and maximum total length were evaluated.

#### Tagging data

Between 1962 and 2004, tiger sharks have been actively tagged as part of the NMFS Cooperative Shark Tagging Program. All sharks were tagged and/or recaptured by biologists, as well as sport and commercial fishermen. Of the thousands of tagged and recaptured tiger sharks, 217 were deemed to have been reliably measured at the time of tagging and recapture. Reliability was assessed based on prior knowledge of the individual's expertise or on detailed questioning of those individuals as to the method used for measurement. All measurements from these fish were converted to FL using the equations published by Kohler et al. (1995).

The Gulland and Holt (1959) and Francis (1988a) models were employed to estimate VBGF parameters from the tag-recapture data. The Gulland and Holt (1959) method uses a graphical interpretation of the recapture data to produce estimates of  $L_\infty$  and  $k$ . Annual growth rate (cm/year) was plotted against average FL between tagging and recapture to calculate linear regression coefficients. The slope of the line is equal to  $-k$  and the  $y$ -intercept is equal to  $L_\infty$ . Due to constraints of the model, only fish at liberty for  $\geq 0.9$  years depicting positive growth were included in this analysis.

The Francis (1988a) method (GROTAG) was utilized to analyze all 217 fishes measured at tagging and recapture. This model uses maximum likelihood techniques to estimate growth parameters and variability from tagging data. Specifically, coefficient of variation ( $v$ ), measurement errors ( $m$  and  $s$ ) and outlier contamination ( $p$ ) are estimated, as well as growth rates between two specified lengths ( $\alpha$  and  $\beta$ ). These specified lengths were chosen to lie within the range of the majority of the tagged individuals, or 90 and 124 cm ( $g_\alpha$  and  $g_\beta$ , respectively).

To elucidate the most accurate VBGF parameters  $L_\infty$  and  $k$  from the data, initially a simple model constrained by only  $\alpha$  and  $\beta$  was utilized, followed by the successive addition of the aforementioned parameters ( $v$ ,  $m$ ,  $s$ ,  $p$ ). The extent to which these additions improved the model was

determined using log-likelihood ratio tests (Francis 1988a). All GROTAG models were generated using a Solver-based spreadsheet in Microsoft Excel (Simpfendorfer<sup>1</sup>). Due to limitations of the model, the VBGF parameter  $t_0$  cannot be estimated from the tag-recapture data alone; instead, it requires an estimate of absolute size at age such as  $L_0$ . As such,  $t_0$  was solved for using the VBGF:

$$t_0 = t + (1/k)[\ln\{(L_\infty - L_t)/L_\infty\}]$$

where

$L_t$  known length at age (size at birth).

#### Longevity

The oldest fish aged from the vertebral samples provides a rough estimate of longevity. However, this age could be an underestimation within a fished population.

Ricker (1979) calculated time of 95% of  $L_\infty$  using the equation:

$$95\% L_\infty = 5 \left( \frac{\ln 2}{k} \right)$$

where

$k$  growth constant from the VBGF.

#### Bomb carbon analysis and validation

Dried vertebral samples from four sharks known to be alive during the 1960s were sectioned and utilized for radiocarbon analysis. Single samples, taken 1 year (one band pair) from the edge were extracted from vertebral sections obtained from three fish ranging in size from 160 to 178 cm FL. These samples were "time constrained", given that their year of formation is less questionable. Seven samples comprising a series of band pairs, between and including the most recently formed band and the birth band, were extracted from a single centrum of a 325-cm FL female shark caught in 1979. Samples were prepared and assayed for radiocarbon  $^{14}\text{C}$  using Accelerator Mass Spectrometry (AMS) as described in Ardizzone et al. (2006) and Kerr et al. (2006).  $\delta^{13}\text{C}$  (‰) values were assumed at  $-15\text{‰}$  based on a dietary (metabolic) uptake of carbon and levels previously documented in several elasmobranch species (Stuiver and Polach 1977; Fry 1988; Campana et al. 2002, 2006; Ardizzone et al. 2006).

To assign dates to an unknown sample, it is imperative that the  $\Delta^{14}\text{C}$  of the unknown sample be compared with a  $\Delta^{14}\text{C}$  time-series of known age material (Kalish 1993).

<sup>1</sup> Simpfendorfer C, unpublished data (2000). Mote Marine Laboratory, 1600 City Island Park, Sarasota, FL 33577, USA.

Established  $\Delta^{14}\text{C}$  time-series from the northwest Atlantic generated from the porbeagle shark (Campana et al. 2002) and southeastern Florida coral (Druffel 1989) were utilized for comparison with data generated by this study. These time-series were selected based on *G. cuvier*'s habitat, migration and specific capture locations of assayed samples. Once appropriate reference time-series were selected, individual vertebral band pairs were isolated from a vertebral section, and the date of formation of each sampled band pair was estimated. Using the known date of capture, a year of formation can be assigned by back-counting each band pair in the section from the vertebral edge, assuming each successive band pair corresponds to one previous year. Individual band pair samples were then extracted, assayed for  $\Delta^{14}\text{C}$  and plotted against reference time-series based on their estimated year of formation. Congruence between the date estimated from the  $\Delta^{14}\text{C}$  reference time-series and the band count can be used as an indication of valid age estimates, because incorrectly interpreted annuli would result in an anomalous projected birth date distribution relative to the reference time-series (Campana et al. 2002).

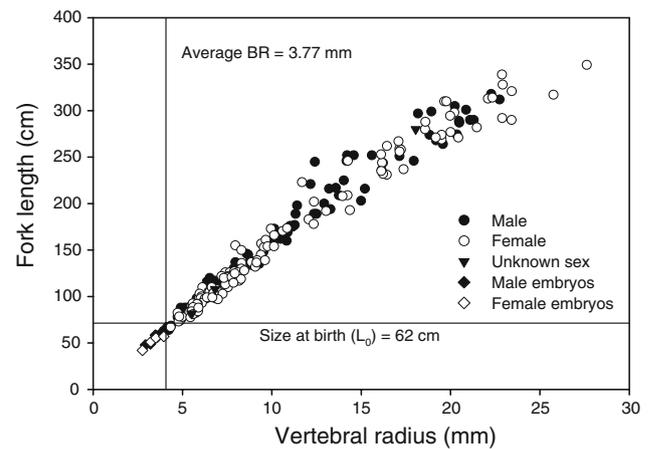
## Results

### Vertebral aging

A total of 238 tiger sharks (109 males, 126 females and 3 of unknown sex) ranging in size from 59.5 to 349.5 cm FL were utilized in this study. Band pairs consisting of one opaque and one translucent band were distinctly visible within each section (Fig. 1). Though bands were visible throughout the corpus calcareum and intermedialia in most sections, band counts were performed using only the corpus calcareum.

The location of the BR was verified through comparison of the VR from YOY and full-term embryos. The BR measured from 237 samples ranged between 2.82 and 4.96 mm, and averaged 3.78 mm (STDEV =  $\pm 0.37$ ). The VR of embryonic tiger sharks (42–58.5 cm FL;  $n = 8$ ) ranged from 2.76 to 3.95 mm, and averaged 3.33 mm ( $\pm 0.38$ ) (Fig. 2). Early YOY tiger sharks (59.5–90 cm FL;  $n = 41$ ) had VR measurements ranging from 3.95 to 5.89 mm ( $\pm 0.54$ ), and an average of 5.14 mm (Fig. 2). Since the mean BR fell between the average VR of the embryonic and YOY tiger sharks, the birth band was identified correctly (Fig. 2).

The relationship between FL and VR was best described by a curvilinear regression ( $R^2 = 0.979$ ), although it provided only a slightly better fit than the linear relationship ( $R^2 = 0.969$ ). Results of an ANCOVA revealed no difference between males and females ( $P > 0.05$ ), thus, the



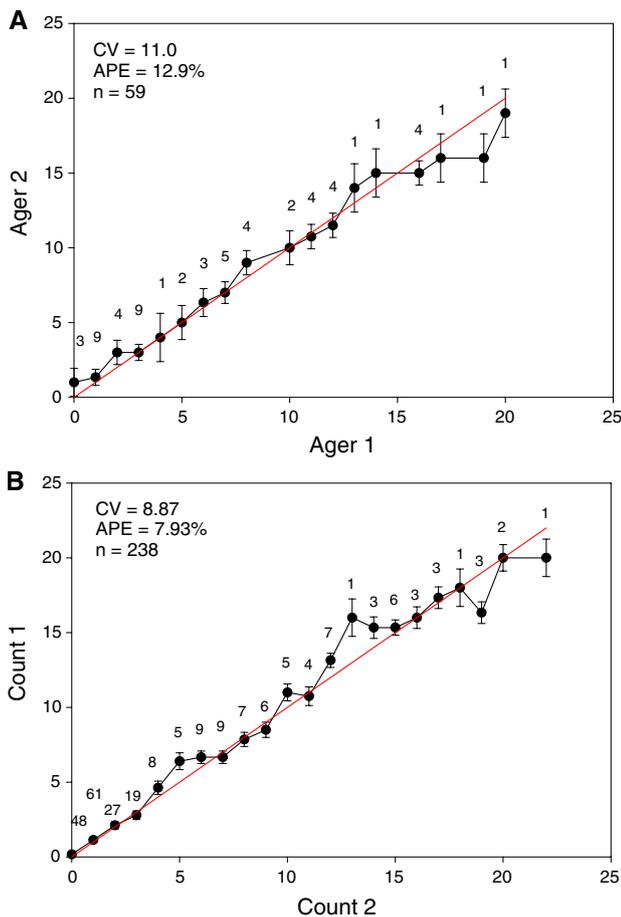
**Fig. 2** Fork length versus vertebral radius graph depicting the mean radius of the birthmark and size at birth. Data for males, females and embryos are reported

data were combined for these analyses. The positive relationship that exists between these parameters suggests that vertebrae are suitable structures for aging this species.

A high degree of precision was observed with respect to both inter and intra reader aging comparisons. The inter-calibration between agers 1 and 2 indicated that 94.9% of all counts differed by two or fewer bands, and 84.7% by one or none. Two counts of the entire sample completed by ager 1 demonstrated 96.6% of all counts within two bands, and 88.7% within one. Coefficient of variation and APE estimates were 11.0 and 12.9%, and 8.87 and 7.93% for inter and intra ager count comparisons, respectively.

Age bias plots generated for both inter and intra ager counts suggested no appreciable bias (Fig. 3). Counts made by both agers were similar with the exception of three large fish (Fig. 3a) differing by one, one and three bands. Such a difference was both expected and considered acceptable given the difficulty that accompanies interpreting closely spaced bands near the centrum edge in large fish and low sample size. Furthermore, the Bowker, McNamara, and Evans-Hoenig Chi-square tests of symmetry gave no indication that differences between and within readers were systematic rather than due to random error ( $\chi^2$  test,  $P > 0.05$ ). Intra ager bias was also considered negligible as band counts correlated highly with one another, again with the exception of the largest fish (Fig. 3b). Given the high degree of precision and the general absence of appreciable bias between both agers and the counts made by ager 1, all analyses were conducted using ager 1's estimates.

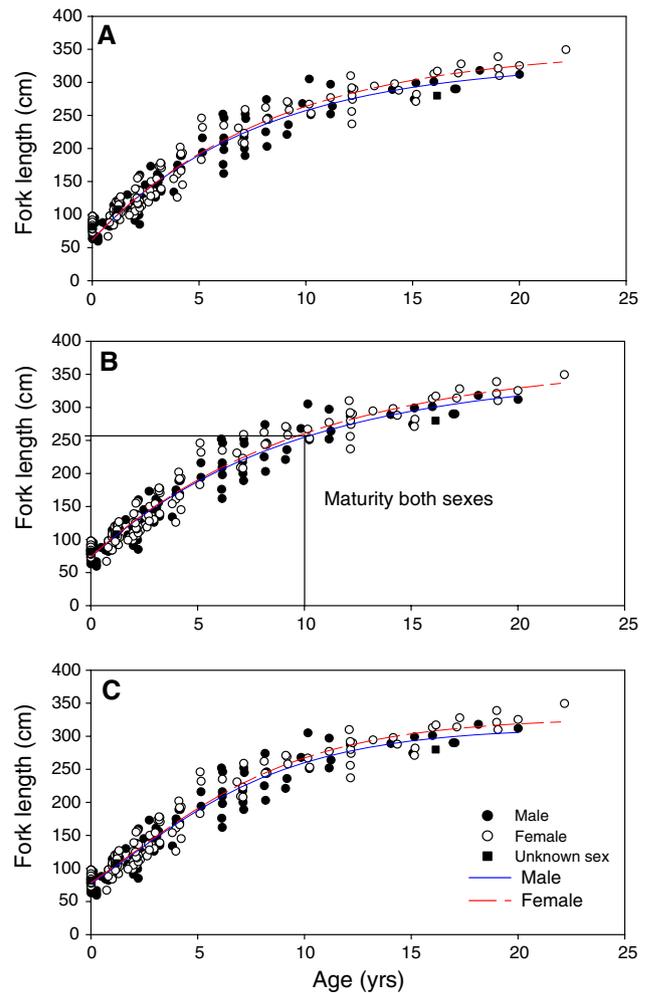
Both the two- and three-parameter von Bertalanffy and Gompertz growth functions fit the vertebral length at age data well for both male and female tiger sharks (Fig. 4). The three-parameter VBGF produced only slightly elevated estimates of  $L_0$ , 73 and 74 cm for males and females, respectively (Table 1), while producing acceptable  $k$  and



**Fig. 3** Age bias plot of the inter (a) and intra (b) reader pairwise age comparisons with 95% confidence intervals around the mean. One to one equivalence line is pictured as well as sample sizes for individual age classes

$L_{\infty}$  estimates. The two-parameter VBGF also produced acceptable estimates for  $k$  and  $L_{\infty}$  with the curve forced through the estimated SAB of 62 cm. The Gompertz growth function generated the largest estimates of  $L_0$ , 77 and 78 cm FL for males and females, respectively, and  $k$ , while slightly underestimating  $L_{\infty}$ . AIC values were very similar for all models with the Gompertz model receiving the lowest overall score. Collectively, examination of statistical comparisons between growth curves, parameter estimates and visual fit suggests that the two-parameter VBGF appears to be the best biological fit to tiger shark vertebral length at age data.

Length at age data suggests that males and females grow at similar rates until around 200–250 cm FL after which male growth slows (Fig. 4). This size range occurs just before the observed length at maturity for both sexes (250 cm FL; Branstetter et al. 1987). The  $k$  estimates generated by the VBGF suggest that females grow at a



**Fig. 4** The two-parameter VBGF (a), three-parameter VBGF (b) and Gompertz growth function (c) plotted through length at age data for males and females. Age at maturity is estimated based on lengths at maturity of Branstetter et al. (1987)

slightly slower rate than males, and ultimately reach a larger maximum size. Considerable overlap existed within the vertebral band pair counts for male and female tiger sharks up to age 20, demonstrating that the overall difference in growth rates was minor (Fig. 4). Data are presented for both sexes when appropriate; however, combined data were used when comparing results of various methods and prior studies.

#### Tag-recapture data

Tag-recapture analyses were performed using data from 217 tiger sharks of both sexes. Size at tagging and time at liberty ranged from 53 to 281 cm FL and 0.005–5.279 years, respectively. Data from all individuals were analyzed with the GROTAG, while only 37 sharks at liberty for greater than 0.9 years were included in the Gulland and Holt (1959) analysis.

**Table 1** Parameter estimates for *Galeocerdo cuvier* generated by the two- and three-parameter VBGF, Gompertz growth function and tag-recapture analyses in this study

Method	Location	Method	Sex	$L_{\infty}$	AIC	SE	$k$	SE	$L_0$	$t_0$	SE	$n$
von Bertalanffy (2 parameters)	WNA, this study	Vertebral counts	M	330	953	11.82	0.131	0.011	<b>62</b>	–	–	109
			F	347	1,087	9.03	0.124	0.007	<b>62</b>	–	–	126
			Combined	340	2,066	7.14	0.126	0.006	<b>62</b>	–	–	238
von Bertalanffy (3 parameters)	This study	Vertebral counts	M	350	943	16.50	0.107	0.012	73	–2.20	0.23	109
			F	369	1,074	13.67	0.100	0.009	74	–2.24	0.21	126
			Combined	361	2,040	10.39	0.102	0.007	74	–2.24	0.15	238
Gompertz	This study	Vertebral counts	M	314	941	–	0.202	0.014	77	–	–	109
			F	328	1071	–	0.194	0.030	78	–	–	126
			Combined	322	2033	–	0.196	0.009	78	–	–	238
Gulland and Holt (1959)	This study	Tag/recapture	Combined	455	–	0.120	–	–	–1.22	–	37	
GROTAG (Francis 1988a)	This study	Tag/recapture	M	211	–	0.464	–	–	–	–0.75	–	101
			F	286	–	0.265	–	–	–	–0.92	–	116
			Combined	274	–	0.283	–	–	–	–0.91	–	217
Branstetter et al. (1987)	WNA	Vertebral counts	Combined	365	–	0.107	–	–	72	–2.35	–	44
	Gulf of Mexico	Vertebral counts	Combined	324	–	0.184	–	–	61	–1.13	–	25
Natanson et al. (1999)	WNA	Tag/recapture	Combined	337	–	0.178	–	–	61	–1.12	–	42
DeCrosta et al. (1984)	Hawaii	Vertebral counts	Combined	362	–	0.155	–	–	35	–0.62	–	28
Wintner and Dudley (2000)	SW Indian Ocean	Vertebral counts	Combined	326	–	0.202	–	–	63	–1.12	–	90

Parameter estimates from previous studies are reported, along with study location and analytical technique. Results for males, females and sexes combined are shown for comparative purposes along with standard error (SE) values for appropriate parameter estimates.

Total length and pre-caudal length measurements from other studies converted to FL using equations presented in the respective text

The bold indicates that 62 cm was a set parameter

Analysis of the data with GROTAG demonstrated the most complex non-linear model (all six parameters included) produced the best fit for these data (Table 2, Model 4). The mean annual growth rates at 90 and 124 cm FL were 45.27 and 36.88 cm/year, respectively (Fig. 5). Growth variability and measurement error were both relatively low. von Bertalanffy growth curves of the sexes combined were similar for the Gulland and Holt (1959) and GROTAG (Francis 1988a) methods for the first 4 years, after which the curves diverged (Fig. 6).

### Longevity

The oldest tiger sharks aged from vertebral samples were a 20-year-old male (312 cm FL) and a 22-year-old female (349.5 cm FL). Longevity estimates based on Ricker (1979) suggest maximum ages of 27 and 29 years for males and females, respectively.

### Validation

Ten samples from four female tiger sharks were analyzed for  $\Delta^{14}\text{C}$  (Table 3).

The radiocarbon time-series obtained from the tiger shark appears to support annual band deposition. However,

appropriate reference time-series appear to vary depending upon the age of the shark during the formation of the sampled growth bands (Fig. 7). For example, bands sampled 1 year from the centrum edge of fish estimated at 3 years of age (2 years old when sampled bands formed) followed the south Florida coral time-series (Druffel 1989) very closely, with up to a 1-year phase lag (Fig. 7). Conversely, samples taken sequentially from the shark estimated to be 20 years at capture (sample T2) were more in phase with the porbeagle reference time-series (Campana et al. 2002; Fig. 7). Overall, the tiger shark samples recorded the rise in radiocarbon beginning in 1958. Radiocarbon levels measured for these replicate samples, taken from the focus of shark T2, were similar ( $-42.5$  and  $-47.6\text{‰}$ ) and comparable in  $\Delta^{14}\text{C}$  level and timing to the Florida coral time-series. No samples could be located to positively measure pre-bomb levels for tiger sharks from this region.

### Discussion

Previous age and growth studies on *G. cuvier* have used various techniques to verify and/or validate band periodicity. DeCrosta et al. (1984) assumed annual periodicity based on close agreement between growth curves

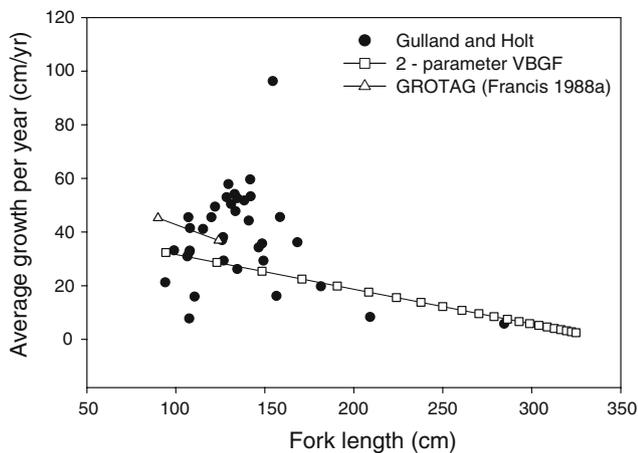
**Table 2** Log-likelihood values and parameter estimates for four growth models fitted to *Galeocerdo cuvier* tagging data using GROTAG (Francis 1988a)

Parameter		Model			
Type	Symbol (unit)	1	2	3	4
<b>Male</b>					
Log likelihood		-386.08	-360.25	-358.64	<b>-357.24</b>
Mean growth rates	$g_{90}$ (cm/year)	40.13	44.85	49.01	49.14
	$g_{124}$ (cm/year)	29.52	32.22	35.27	35.15
Growth variability	$v$	0.73	0.29	0.26	0.28
Measurement error	$s$ (cm)	0 <sup>a</sup>	4.95	4.76	4.93
	$m$ (cm)	0 <sup>a</sup>	0 <sup>a</sup>	-1.86	-1.96
Outliers	$P$	0 <sup>a</sup>	0 <sup>a</sup>	0 <sup>a</sup>	0.037
<b>Female</b>					
Log likelihood		-435.63	-409.46	-409.10	<b>-404.86</b>
Mean growth rates	$g_{90}$ (cm/year)	40.71	42.00	43.49	45.58
	$g_{124}$ (cm/year)	34.18	34.54	35.89	37.68
Growth variability	$v$	0.62	0.29	0.29	0.35
Measurement error	$s$ (cm)	0 <sup>a</sup>	4.49	4.38	4.19
	$M$ (cm)	0 <sup>a</sup>	0 <sup>a</sup>	-0.62	-0.93
Outliers	$P$	0 <sup>a</sup>	0 <sup>a</sup>	0 <sup>a</sup>	0
<b>Sexes combined</b>					
Log likelihood	$l$	-826.68	-774.49	-773.42	<b>-767.77</b>
Mean growth rates	$g_{90}$ (cm/year)	40.02	42.85	44.87	45.27
	$g_{124}$ (cm/year)	33.55	34.79	36.61	36.88
Growth variability	$v$	0.69	0.29	0.28	0.31
Measurement error	$s$ (cm)	0 <sup>a</sup>	4.80	4.67	4.81
	$m$ (cm)	0 <sup>a</sup>	0 <sup>a</sup>	-0.89	-0.96
Outliers	$P$	0 <sup>a</sup>	0 <sup>a</sup>	0 <sup>a</sup>	0.021

Data for males, females and sexes combined are presented, and models with the lowest log-likelihood values indicate the best fit

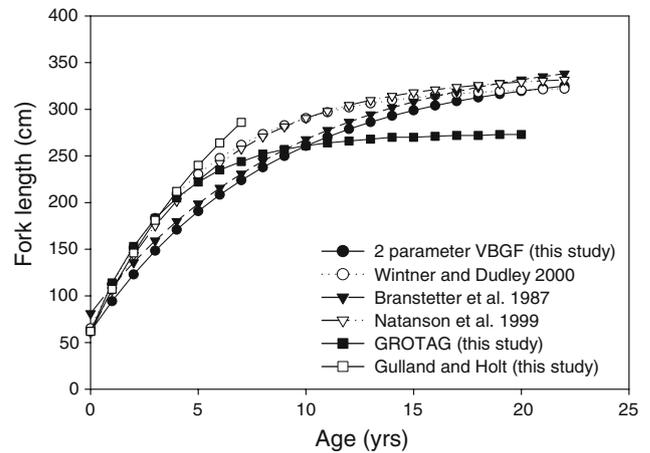
The bold indicates that these were the lowest log likelihood values

<sup>a</sup> Fixed parameters



**Fig. 5** Comparison of the average growth per year of the tiger shark derived from multiple methods

generated from vertebral counts and length frequencies. Branstetter et al. (1987) utilized marginal increment ratio data to demonstrate that one band pair was deposited annually in specimens collected from the Gulf of Mexico and WNA. Wintner and Dudley (2000) utilized vertebrae from three OTC-recaptured tiger sharks to demonstrate



**Fig. 6** Comparison between various growth functions generated for the tiger shark for the sexes combined by several studies and methods

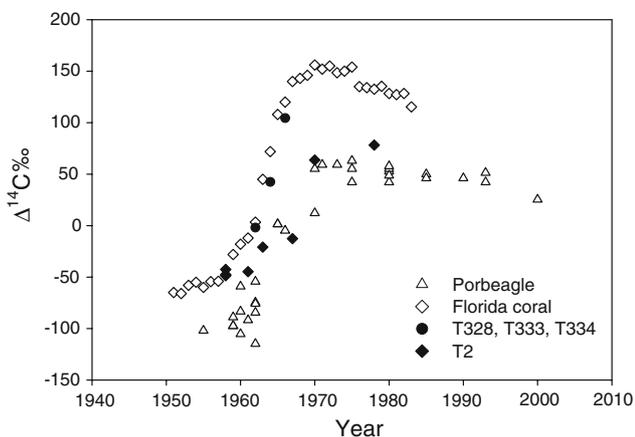
annual band periodicity in tiger sharks representing age classes <5 years in the southwest Indian Ocean. The current study utilized bomb radiocarbon data to validate annual band pair deposition in the tiger shark up to age 20.

All of the growth models provided a good fit to the data as evidenced by the similarities of the AIC values. Based

**Table 3** A summary of samples analyzed for bomb radiocarbon

Sample	FL (cm)	Year of capture	Age at capture	Birth year	Sample year	Age at sampling	$\Delta^{14}\text{C}$	AMS error ( $\pm$ )
T328	160	1963	3	1959	1962	2–3	–1.9	4.5
T333	164.4	1965	3	1961	1964	2–3	42.4	4.1
T334	178	1967	3	1963	1966	2–3	104.4	4.9
T02-1958a	325	1979	20	1958	1958	0	–42.5	3.3
T02-1958b	325	1979	20	1958	1958	0	–47.6	3.7
T02-1961	325	1979	20	1958	1961	2–3	–44.7	3.7
T02-1963	325	1979	20	1958	1963	4	–20.9	4.2
T02-1967	325	1979	20	1958	1967	8	–12.6	4.8
T02-1970	325	1979	20	1958	1970	11	63.7	3.5
T02-1978	325	1979	20	1958	1978	19–20	78.2	4.9

Estimated age and year of formation were obtained through back calculation of band pairs from capture date.  $\delta^{13}\text{C}$  levels are the assumed at  $-15\text{‰}$  according to Stuiver and Polach (Radiocarbon, v 19, p 355, 1977)



**Fig. 7** Bomb radiocarbon ( $\Delta^{14}\text{C}$ ) time-series generated for the tiger shark in comparison with time-series of Florida coral (Druffel 1989) and the porbeagle shark (Campana et al. 2002)

on the AIC comparison, the Gompertz function provided best statistical fit; however, the Gompertz curve did not pass near the known size at birth (62 cm FL) for either sex, and estimated female  $L_{\infty}$  at well below the maximum observed length. In comparison, the two and three-parameter VBGF provided more biologically realistic parameter estimates with only slightly higher AIC values. The two-parameter VBGF best described YOY growth with  $L_0$  set to 62 cm, and was very similar to the three-parameter VB model after age 2. Both models estimated  $L_{\infty}$  within maximum lengths observed for male and female tiger sharks in this study. Thus, despite the slightly better statistical for the Gompertz model, the two-parameter VBGF was the best biological fit to tiger shark vertebral length at age data, given its sound parameter estimates and more realistic depiction of YOY growth. A similar distinction between best biological fit and best statistical fit had to be made by Natanson et al. (2006), who analyzed parameter estimates from the Gompertz and VBGF to determine the

best biological growth curves for *I. oxyrinchus* in the WNA.

Branstetter et al. (1987) obtained age and growth estimates for the sexes combined in the WNA using a three-parameter VBGF. The results from their study are remarkably similar to those of our three-parameter VBGF fit, which is particularly interesting given Branstetter et al.'s (1987) low sample size ( $n = 44$ ) and an absence of individuals from both the lower and upper regions of the growth curve. Similarly,  $k$  and  $L_{\infty}$  estimates generated by the Gompertz growth function are strikingly similar between this study and those obtained by Wintner and Dudley (2000) from the SW Indian Ocean. Collectively, these results suggest that tiger sharks may display similar growth rates worldwide.

Maturity is attained at approximately 10 years for males and females, respectively, utilizing lengths at maturity from Branstetter et al. (1987) of 258 and 265 cm FL and the growth functions provided herein. These estimates are similar to those suggested by Branstetter et al. (1987), but higher than Natanson et al. (1999), who suggested an age at maturity of 7 years based on tag-recapture growth curves. A detailed study of tiger shark reproduction is necessary before any conclusions on age and size at maturity can be drawn for the WNA population of tiger sharks.

Tag and recapture data provided verification of growth curves generated from vertebral band counts through age 2. Inherent differences between growth curves calculated from age-length and length-increment (tagging) data prevent a direct comparison from being made (Francis 1988b). Instead, comparison between growth rates at length is more appropriate. Growth rates were similar for all methods between 90 and 124 cm FL, although tag-recapture analyses predicted noticeably different VBGF parameter estimates overall. The absence of large recaptured sharks likely limited verification from being accomplished after age 2.

The tag/recapture analysis performed in this study served as an update to the work of Natanson et al. (1999). Specifically, the same NMFS API data set analyzed by Natanson et al. (1999) was again analyzed in this study, with the inclusion of all data accrued since 1999. These data were re-analyzed with the Gulland and Holt (1959) method as used by Natanson et al. (1999), as well as by GROTAG (Francis 1988a), a method not included in the previous analysis. The updated Gulland and Holt (1959) analysis produced a lower  $k$  and subsequently higher  $L_{\infty}$  estimates than described by Natanson et al. (1999) for the sexes combined. However, growth rates for each study are very similar up to 200 cm FL. The GROTAG (Francis 1988a) model also described similar growth rates as the Gulland and Holt (1959) analysis of both studies up to 225 cm FL. The largest difference among all three models occurred above 225 cm FL, where each model described different growth rates. These differences were likely due to the inherent differences between the models the inability to analyze identical data sets with both models.

The maximum age estimated in this study was slightly higher than any published estimate for the tiger shark. Previously, the maximum reported age was 20 years (De-Crosta et al. 1984) estimated from a 346-cm FL specimen, while Branstetter et al. (1987) and Wintner and Dudley (2000) aged 315 and 326 cm FL specimens at 16 and 13 years, respectively. The maximum reported length for any tiger shark in the WNA is 391-cm FL (Bigelow and Schroeder 1948); however, the largest fish observed in this study was a 22-year-old, 349.5-cm female. Such a large discrepancy between the maximum reported size and the maximum observed in this study suggests that tiger sharks may live considerably longer than the oldest fish aged in this study (22 years). Published longevity estimates range from 27 to 37 (Branstetter et al. 1987; Natanson et al. 1999) in the WNA, and are consistent with the theoretical longevities estimated by the Ricker (1979) method in this study of 27 and 29 years for males and females, respectively.

Diet is the primary source of carbon used for cartilage growth in elasmobranch fishes (Fry 1988; Campana et al. 2002). As a result, the carbon contained in any one area of the vertebrae is a direct reflection of the carbon contained within the prey items metabolized during the time of growth. With respect to radiocarbon, prey items typically contain carbon that is older than that present in the surrounding water as a result of trophic cascade. Thus, a phase shift toward more recent dates is often evident when measuring radiocarbon in these tissues. This is especially evident in larger animals that typically feed on larger, older, more radiocarbon-depleted prey. In contrast to sharks, most carbon assimilated into calcified structures of teleost fish comes from the surrounding water, allowing for more rapid assimilation of  $^{14}\text{C}$  into calcified tissue.

The close association between the  $\Delta^{14}\text{C}$  time-series obtained from the three young tiger sharks (T328, T333, T334) and the Florida coral (Druffel 1989) may be attributed to the life history of young tiger sharks. Natanson et al. (1999) suggested that a tiger shark nursery exists in coastal waters from Augusta, Georgia to Daytona, Florida, extending from shore to 100 m depth. Within this area, tiger sharks ranging in size from 61 to 120 cm are commonly caught, suggesting tiger sharks remain in this nursery through age 2. Given the relatively shallow depths of this nursery (<100 m) and its close proximity to the Gulf Stream, the area likely remains well mixed throughout the year, and as such allowed for a rapid exchange of radiocarbon between the atmosphere, water and marine carbonates. Since tiger sharks typically prey upon small teleost fish while in the nursery (Kohler<sup>2</sup>), the elevated radiocarbon levels present within their prey would likely cause an elevation in radiocarbon levels within their vertebrae. The assayed samples corresponding with age 2 were formed when these sharks were probably still active within the nursery area, and as such resemble the coral radiocarbon time-series of Druffel (1989) due to their activity within that area.

Ontogenetic dietary changes may be responsible for the phase lag that is evident within the radiocarbon time-series of samples taken from T2. Once tiger sharks move out of the nursery area around age 2 they adopt a more migratory lifestyle. Tiger sharks tagged off the east coast of the United States have been documented to make extensive migrations throughout the North Atlantic, some as far as Africa (Kohler et al. 1995). The adoption of a highly migratory lifestyle coincides with a dietary shift. As tiger sharks move into deeper radiocarbon-depleted waters, they incorporate larger, possibly radiocarbon-depleted prey such as marine mammals, turtles and other sharks into their diet (Kohler<sup>2</sup>). Thus, this dietary shift could be responsible for the depleted radiocarbon levels present in samples taken from T2 after 1961, with samples taken prior to 1961 in accordance with the coral time-series. Furthermore, year-to-year variation in diet and migratory behavior may lead to the deviation of certain samples from reference time-series, as is likely with the 1963 and 1978 samples collected from T2. This kind of phase lag was documented for the white shark (*Carcharodon carcharias*) from the northeastern Pacific Ocean (Kerr et al. 2006).

Underaging is a potential factor in explaining the observed phase lag within the T2 radiocarbon time-series. Band pairs were clearly defined within the section, making it easy to estimate their respective years of formation. If underaging were the source of the phase lag, ages would have been underestimated by 3–6 years, relative to the

<sup>2</sup> Kohler, personal communication (2005). National Marine Fisheries Service. 28 Tarzwell Dr., Narragansett, RI 02882, USA).

Florida coral time-series. However, an underestimation of this degree is unlikely given the caveats associated with the assimilation of dietary derived radiocarbon into the vertebrae.

Collectively, the radiocarbon data generated by this study support annual band periodicity in the tiger shark up to age 20. This conclusion was based on the close agreement between the radiocarbon time-series obtained from the three small tiger sharks and the Florida coral time-series, and between the time-series of the single adult tiger shark and the porbeagle shark. The time-constrained samples taken 1 year from the edge of the small tiger sharks, coupled with the high degree of certainty that accompanies aging young (1- to 2-year-old) sharks, suggest that the close agreement between time-series reflects accurate age determination in tiger sharks to age 3. Likewise, given that the porbeagle radiocarbon time-series was partially based on known-age sharks, the close agreement between the time-series also suggests accurate age determination for *G. cuvier* through age 20. Tag/recapture analyses were consistent with previous work by Natanson et al. (1999) and verified age estimates up to age 2. These findings coupled with strong fits of growth curves to vertebral length at age data provide a rigorous assessment of tiger shark age and growth in the WNA.

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