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Age and growth of the white shark, *Carcharodon carcharias*, in the western North Atlantic Ocean

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Abstract. Age and growth estimates for the white shark (*Carcharodon carcharias*) in the western North Atlantic Ocean (WNA) were derived from band pair counts on the vertebral centra of 81 specimens collected between 1963 and 2010. We used two previously published criteria to interpret band pairs and assessed the validity of each method using Δ^{14}C levels from a recent bomb radiocarbon validation study and existing Δ^{14}C reference chronologies in the WNA. Although both criteria produced age estimates consistent, to varying degrees, with different reference chronologies, only one was considered valid when life history information was used to select the appropriate reference chronology and minimum/maximum ages based on bomb carbon values were taken into consideration. These age estimates, validated up to 44 years, were used to develop a growth curve for the species, which was best described using the Schnute general model (sexes combined). These results indicate that white sharks grow more slowly and live longer than previously thought.

Additional keywords: carbon-14, lamnid, vertebral column.

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Introduction

The white shark, *Carcharodon carcharias*, is well documented in the western North Atlantic (WNA) from Newfoundland to the Gulf of Mexico, including the Bahamas and parts of the Caribbean (Bigelow and Schroeder 1948; Templeman 1963; Casey and Pratt 1985; Compagno 2001). However, the species is relatively elusive in the WNA and efforts to study its life history and ecology have been hampered by the inability of researchers to predictably encounter these sharks. Much of what is known of the species in this region is limited to the analysis of distribution records (Templeman 1963; Casey and Pratt 1985; Curtis *et al.* 2014), a few behavioural observations (Carey *et al.* 1982; Pratt *et al.* 1982), and the opportunistic examination of dead specimens (Pratt 1996). Recent increases in local abundance off Cape Cod, MA (Skomal *et al.* 2012) have provided satellite tagging opportunities, which are producing new information on fine- and broad-scale movements in the WNA (G. Skomal, Massachusetts Division of Marine Fisheries, unpubl. data). However, in addition to other important biological information (e.g. reproductive biology, feeding ecology), age and growth estimates are lacking for this species in the WNA.

Throughout their global range, white sharks, *C. carcharias*, like many shark species, are subjected to varying degrees of commercial and recreational fisheries exploitation (Stevens *et al.* 2000). Although retention has been prohibited off the east coast of the USA since 1998 (NMFS 1999), there is still by-catch mortality (Curtis *et al.* 2014) and the extent to which this species has been affected is unknown. Efforts to effectively manage white shark populations require basic life history information, including valid age and growth estimates.

Age and growth parameters have been estimated for the white shark in several regions of the world, including the eastern North Pacific Ocean off California (Cailliet *et al.* 1985), the western Indian Ocean off South Africa (Wintner and Cliff 1999), and the western North Pacific Ocean off Japan (Tanaka *et al.* 2011). In all these studies, white sharks were aged from banding patterns interpreted from x-radiographs of whole vertebrae. However, age estimates derived in these studies were not validated, though Wintner and Cliff (1999) attempted to validate (with oxytetracycline injection) and verify (with marginal increment analysis) the periodicity of band pair deposition; however, neither method was conclusive. In addition, Kerr *et al.* (2006) attempted to validate ages derived from vertebrae for the eastern North Pacific Ocean population of white sharks using bomb radiocarbon analysis. They concluded that dietary and migratory issues combined to eliminate the possibility of validation from their data. Nonetheless, age estimates from these previous studies were similar, indicating that growth is relatively rapid and the white shark is not long lived relative to other elasmobranch species. Indeed, maximum sample ages (i.e. band pairs) ranged from 12–15 years for sharks ranging from 411.6- to 473.8-cm fork length (FL) (calculated using

Kohler *et al.* 1996; also see Cailliet *et al.* 1985; Wintner and Cliff 1999; Tanaka *et al.* 2011).

Recently, longevity estimates for the white shark in the WNA were derived from vertebral banding patterns using bomb radiocarbon analysis (Hamady *et al.* 2014). Researchers used eight sharks of varying sizes and validated annual periodicity up to 44 years – concluding that white sharks in the WNA can reach an estimated 73 years of age. In the current study, we applied two band pair counting criteria, including that used by Hamady *et al.* (2014), to interpret band pairs in the vertebrae of the white shark and derive age estimates. We assessed the validity of each set of age estimates using the vertebral Δ^{14}C samples reported in Hamady *et al.* (2014) and existing bomb carbon reference chronologies to examine the effect of criteria choice on the bomb radiocarbon results and, ultimately, calculate the most viable growth curve for this species.

Materials and methods

Vertebrae were obtained from white sharks caught on research cruises, taken by commercial and recreational fishing vessels, and landed at recreational fishing tournaments from 1963 to 2010. Sampling took place between Prince Edward Island, Canada, and New Jersey, USA. When possible, vertebrae between the number 15 and 20 were excised from each specimen. The vertebrae were trimmed of excess tissue and stored either frozen or preserved in 10% buffered formalin or 70% ethanol (ETOH). To determine if the number of growth band pairs differed along the vertebral column, whole columns were removed when possible.

For age analysis, only vertebral samples from white sharks that had been measured in 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 downward from the tip of the upper caudal lobe to form a right angle – OTB), or total weight (WT) were used. All lengths reported are in centimetres unless otherwise noted. Conversions used in this study were:

$$\mathrm{FL} = 0.94 \times \mathrm{TL} - 5.74$$

$$\mathrm{WT} = (7.58 \times 10^{-6}) \times \mathrm{FL}^{3.08}$$

in which for FL $R^2 = 0.998$ and $n = 112$ (Kohler *et al.* 1996) and for WT $R^2 = 0.980$ and $n = 125$ (Kohler *et al.* 1996) weights (kg) and lengths (cm) are expressed in metric units.

Sample processing

One vertebra from each sample and every fifth vertebra from the whole columns were removed for processing. Each centrum was sectioned through the middle along the sagittal plane using a Raytech gem saw[A] (Middletown, CT, USA) to ~0.6 mm. Larger vertebrae were sectioned with a trim saw with a diamond blade (Model TC-6, Diamond Pacific Tool Corp., Barstow, CA, USA). Sections were stored in 70% ETOH. Each section was digitally photographed (resolution 640 × 480) while submerged in water on a black background with a video camera (model CCD 72, Dage-MTI, Michigan City, IN, USA) attached to a stereomicroscope (Model SZX9, Olympus Corporation, Shinjuku-ku, Tokyo, Japan) using reflected light. Band pairs (consisting of one opaque and one translucent band; see below for specific criteria) were counted and measured from the images using Image Pro 4 software (Media Cybernetics, Rockville, MD, USA). In some cases, brightness and/or contrast was adjusted to better examine the band pairs. Measurements were made from the midpoint of the notochordal remnant (focus) of the full section to the opaque growth bands at points along the internal corpus calcareum. The radius of each centrum (VR) was measured from the midpoint of the notochordal remnant to the distal margin of the intermedialia along the same diagonal as the band pair measurements.

The relationship between FL and VR was used to assess the allometric relationship between vertebral and body growth and, thus, the utility of the former as an ageing structure. Regressions were fit to the male and female data and an ANCOVA was used to test for statistically significant differences between the sexes.

Vertebral band interpretation

Two methods of band pair interpretation were used for comparison. In Criterion A, all band pairs passing from the corpus calcareum across the intermedialia to the other side of the corpus were counted. This was the band interpretation ultimately used to produce the age estimates for Hamady *et al.* (2014), which strictly followed the criteria set forth by Casey *et al.* (1985) for the sandbar shark (*Carcharhinus plumbeus*). Criterion B followed the band pair definition used in validated age studies of the porbeagle and the shortfin mako, which are closely related phylogenetically to the white shark (Compagno 2001) and defined as 'broad opaque and translucent bands each of which was composed of distinct thinner rings' (Campana *et al.* 2002; Natanson *et al.* 2002, 2006; Ardizzone *et al.* 2006). The primary difference between these techniques is that Criterion B counts 'broad' bands, whereas Criterion A includes all bands that pass through the corpus calcareum including many of the 'distinct thinner rings' defined within the broad bands and not counted by Criterion B.

For both criteria, the first opaque band distal to the focus (centre of the centra) was defined as the birth band (BB). A slight angle change in the corpus calcareum coincided with this band. The identity of the BB was confirmed with back-calculation and comparison with the VR or BB from young of the year (YOY) samples.

Entire vertebral columns were collected from sharks of various lengths to examine band pair counts along the column (Natanson and Cailliet 1990). Band pair counts, using both criteria, were plotted against location along the vertebral column of every fifth vertebra to determine if band counts varied along the vertebral column. Presuming the counts remained the same, any vertebrae obtained could be used for ageing.

Band counts and precision

To standardise counting procedures and ensure that the readers were consistent between counts, 23 (12 males and 11 females

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[A] Reference to Trade Names does not imply endorsement by NMFS.

over a size range representative of the entire sample 122–459 cm; Criterion A) and 28 samples (15 males and 13 females over a size range representative of the entire sample 111.5–493 cm; Criterion B) were prepared as reference sets. Using the two criteria for band interpretation, readers came to a consensus count for these samples. To ensure readers were consistently using the correct criteria, quality control was maintained with periodic examination of the reference set.

Age estimates were determined using three rounds of independent estimates by three readers. Count one was considered a trial to familiarise each reader with the species' vertebral banding patterns; counts two and three were used for age estimation. The primary reader counted using both criteria with two different secondary readers (GBS Criterion A; Kelsey James, Criterion B). Pair-wise estimates of ageing bias and precision between each reader's third count were examined using bias graphs, contingency tables and Chi-Square tests of symmetry and average percent error (APE) (McNemar 1947; Bowker 1948; Beamish and Fournier 1981; Campana *et al.* 1995; Hoenig *et al.* 1995; Evans and Hoenig 1998). Contingency tables and Chi-Square tests of symmetry were calculated between readers and within both counts of each reader for Criterion A and between the third counts of each reader for Criterion B. APE was calculated between readers and within both counts of each reader for both criteria. Only samples with band counts beyond the BB were used in the APE and Chi-Square analyses.

Once it was determined that there was no bias and precision estimates were acceptable, a consensus was reached by reading the centra together on samples with counts disagreeing by two or greater. The final assigned ages were derived from the third counts of both readers with the following exceptions. When the counts differed by one, the count of the primary reader was used. On those samples that differed by two or more bands, the third count (of either reader) was accepted if it agreed with a count of that specimen by the primary reader. If count agreement could not be reached, the vertebrae were read together to reach a consensus (34.6 and 13.5% of all samples, Criteria A and B respectively). Quality control was maintained by periodically recounting the reference set and cross-checking the readings.

Bomb radiocarbon analysis

Eight samples from the current study were analysed for bomb carbon age validation by Hamady *et al.* (2014) using Criterion A. To validate Criterion B, we used bomb carbon data from four of these specimens (W28, W100, W57, W105) that were alive during the period of rapid increase of ^{14}C in the world's oceans. We chose not to use data from those fish (W117, W134, W143 from Hamady *et al.* 2014) that did not have Δ^{14}C values in the rise portion of the reference chronologies, as these had limited value. Additionally, we did not utilise band pair counts from one vertebral sample from the head (W81) because we found lower band pair counts in the anterior region of the vertebral column (see Results). For each of the four specimens examined, we used the sampling locations along each vertebra, as marked in photographs and obtained in the supplementary materials (Hamady 2014; Hamady *et al.* 2014), to align the Criterion B band pairs with the locations of the Δ^{14}C samples. These were then plotted against reference chronologies under the assumption of annual band pair deposition (following the technique of Hamady *et al.* 2014; using Criterion A). Shifts in the curves were made using the techniques in Hamady *et al.* (2014) to optimise alignment to the Δ^{14}C rise of the references. Additionally, we fit a linear trend to the rise portion (1959–1975) of the porbeagle chronology for comparison (Campana *et al.* 2002).

Bomb radiocarbon data were used to obtain minimum or maximum ages for the four sampled specimens and sample W81. Minimum age estimates for the three specimens with pre-bomb Δ^{14}C levels (W57, W81, W105) were calculated as the length of time between the initial rise of Δ^{14}C in the reference chronologies (1959 for the WNA otolith chronology, 1958.5 for Florida coral, and ~1960 for the porbeagle chronology) and the date of capture. For the two specimens with Δ^{14}C levels that fell on the rising curve (W28, W100), the maximum age of the shark was determined by matching the pre-birth Δ^{14}C value to the corresponding year on the reference chronologies, which was then subtracted from the capture date. Both the initial rise and the reference chronologies can be considered dated references (Francis *et al.* 2007).

Growth curve estimation

White shark growth was modelled from the length-at-age estimates derived from band pair counts using the Schnute (1981) growth model, which includes several of the most commonly used growth models as per Natanson *et al.* (2014). This method allows for a more direct comparison of parameter estimates between models. The general model requires the specification of two reference ages, t_1 and t_2, which were set near the lower and upper end of the range observed (Criterion A: $t_1 = 1$ year, $t_2 = 50$ years; Criterion B: $t_1 = 1$ year; $t_2 = 25$ years). The general model also has the four following parameters: L_1, length at age $t_{1;}$ L_2, length at age t_2; a, a constant (time^{-1}) describing the constant relative rate of the relative growth rate; and b, a dimensionless constant describing the incremental relative growth rate of the relative growth rate. As per Natanson *et al.* (2014), we used the general model and three special cases, which correspond to the specialised von Bertalanffy (VBGF; von Bertalanffy 1938), Gompertz (Ricker 1975), and logistic growth models (Ricker 1979) most frequently described in elasmobranch age and growth studies (Goldman *et al.* 2012). Owing to the lack of large individuals, particularly females, we chose not to model the sexes separately.

Final model selection was based on statistical fit, which was evaluated by the small-sample, bias-corrected form of the Akaike Information Criterion (AIC$_c$; Akaike 1973; Burnham and Anderson 2002). The smallest AIC$_c$ value was considered the 'best' fit of the models considered. The AIC$_c$ difference (Δ_i) of each model was calculated based on the lowest observed AIC$_c$ value (AIC$_{c,min}$) as $\Delta_i = \text{AIC}_{c,i} - \text{AIC}_{c,min}$ to provide an estimate of the magnitude of difference between each model and the best model in the set. Models with values of Δ_i <2 were considered to have strong support; those with Δ_i >10 had essentially no support and were removed from consideration. Models that differed by <2 were considered indistinguishable in terms of fit (Burnham and Anderson 2002). The Akaike weight (w_i) of each model was also calculated to approximate model likelihood (Burnham and Anderson 2002).

Confidence intervals (95%) were constructed for parameter estimates by bootstrap methods using the 'nlstools' package in R (R Development Core Team 2010) (Baty and Delignette-Muller 2011; see Natanson *et al.* 2014 for details). Parameter estimates typically reported (e.g. asymptotic size, L_∞; theoretical size at birth, t_0) were calculated following Schnute (1981) for comparison with other studies. Length-at-birth (L_0) was estimated from the resulting equation for each growth model.

Growth curves were generated from age estimates derived from the band interpretation criterion that was deemed more appropriate after examination of Criterion B relative to the bomb carbon data and examination of minimum and maximum age calculations for both criteria. Validated ages and band pair counts were used in these models. All samples over the highest age for which annual band pair deposition was validated (44 years for Criterion A; see results) were removed from the dataset. Bomb radiocarbon age estimates were used in place of counts when applicable.

Results

Vertebral samples from a total of 77 white sharks (112–526 cm; 41 male, 36 female) were processed for this age analysis. Two samples were taken from the extreme head or tail: one of these was not included in the growth curve analysis though it is plotted on the graphs; the other was validated using bomb radiocarbon (W81; Hamady *et al.* 2014) and is included in all calculations for Criterion A, but eliminated for Criterion B. Five males were not used in the growth curve because they were older than the validated ages and the band pair counts could not be considered annual. The FL–VR relationship was best described by a linear equation (Fig. 1). There were no significant differences between the sexes for intercept ($P = 0.65$) or slope ($P = 0.77$). Therefore, we calculated the regression for sexes combined:

$$\mathrm{FL} = 10.8 \times \mathrm{VR} + 35.6$$

$$(R^2 = 0.98,\ n = 75)$$

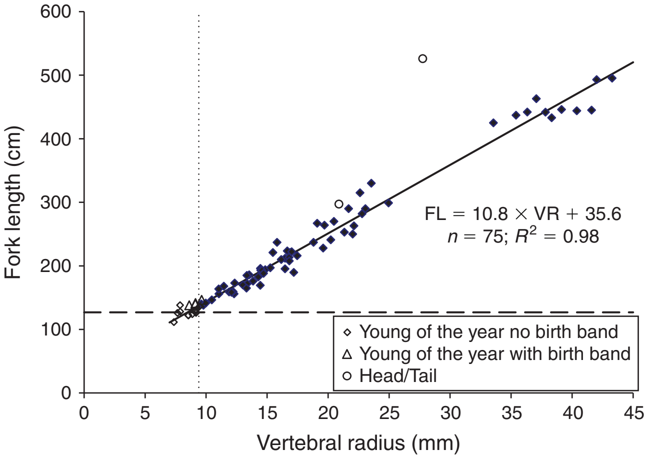

Fig. 1. Relationship between vertebral radius and fork length for white sharks, *Carcharodon carcharias*, in the western North Atlantic Ocean sexes combined. The horizontal line represents the size at birth (122-cm fork length, FL; Francis 1996; Uchida *et al.* 1996) and the vertical line represents the mean radius of the birth mark (9.4 mm; $n = 64$).

The examination of every fifth vertebra from five whole vertebral columns (142–222 cm) and the first 35 vertebrae from a 463-cm specimen, using both criteria, suggested that band counts varied along the vertebral column (Fig. S1). In general, vertebrae collected from the torso had higher counts than those at the head or tail. However, we found white shark vertebral sections difficult to read, particularly using Criterion B where our variance and reader bias were high, which may account for some of the variability. Additionally, changes in the shape of vertebral centra along the column, including the lack of an angle change at birth, affected the ability to maintain consistent band interpretation, particularly for Criterion B. Although we cannot positively conclude that band pair counts change along the column, the higher counts in the samples from the abdominal region suggest that variation along the column may not be solely due to counting variability or morphology. The majority of our samples were removed from under the gills and, to minimise variability, we attempted to use only centra from this area. Given that the abdominal vertebrae, in general, had higher counts, our band pair counts may be biased low and, thus, considered minimum estimates. As it was possible to distinguish approximately where each vertebra originates on the column based on the vertebral processes (Fig. S2), we chose not to use counts or measurements from vertebrae known to come from the head or tail areas as they were likely to be undercounted using either method.

The BB was clearly defined as a distinct and consistent opaque band that coincided with a slight change in the angle of the corpus calcareum (Fig. 2). The BB and VR were the same using both criteria. The mean BB measurement from the total sample (mean BB ± 95% CI = 9.4 mm ± 0.2 mm, $n = 60$) was similar to the mean BB measurement from four YOY white sharks (138.0–146.5 cm; mean VR ± 95% CI = 9.1 mm ± 0.7 mm) and slightly higher than the mean VR of 11 YOY white sharks that had not yet formed a BB (111.5–138.2 cm; mean VR ± 95%

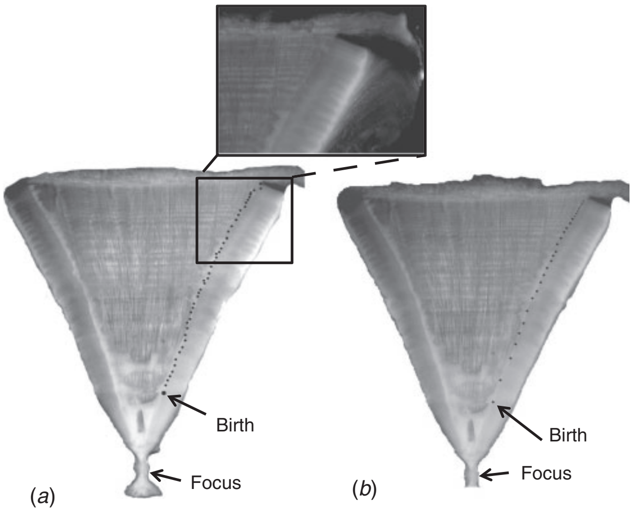

Fig. 2. Photograph of a vertebral section (W57; 442-cm fork length, FL) from a validated male white shark, *Carcharodon carcharias*, estimated to be 44 years old using: (*a*) Criterion A and 27 years old using (*b*) Criterion B. Inset shows the vertebral edge enlarged. Band pairs, birth band and focus are indicated.

CI = 8.5 mm ± 0.5 mm) (Fig. 1). The smaller size of the VR at birth in these latter fish indicates growth for a period before depositing the BB. Using the mean radius of the BB and the modified Dahl-Lea method of back calculation (because the regression did not pass through the origin; Cailliet and Goldman 2004), size at birth was calculated at 122.6 cm. This value agrees with previous estimates (122 cm FL; Francis 1996; Uchida *et al.* 1996; both report size at birth 120–150 cm TL, mean = 135 cm TL, converted FL = 122 cm) indicating that we correctly identified the BB.

Band counts – Criterion A

No bias was found between the third counts of the entire sample, using Criterion A, by both readers. There were no significant differences between the third counts of both readers using the Bowker, NcNemars or Evans–Hoenig tests of precision $\chi^2_{42} = 46.3$, $P > 0.05$; $\chi^2_{7} = 7.1$, $P > 0.05$; $\chi^2_{1} = 1.7$, $P > 0.05$ respectively. Additionally, the value for APE was 8.8% ($n = 64$), which was considered acceptable, particularly because of the difficulty in reading the vertebrae of this species. Owing to the lack of bias, the non-significant outcome of the Chi-Square tests, and the high overall band pair counts in this species, this level of precision was considered acceptable for replicating the counts of the primary reader.

No bias was observed and there were no significant differences between counts two and three of the primary reader using the Bowker or NcNemars tests of precision $\chi^2_{27} = 26.0$, $P > 0.05$; $\chi^2_{3} = 5.4$, $P > 0.05$ respectively, though there was a significant difference using the Evans–Hoenig test $\chi^2_{1} = 4.8$, $P < 0.05$. The APE value of 4.0% ($n = 66$) was considered acceptable for this species.

Band counts – Criterion B

The bias graphs of the third counts of both readers indicated that the secondary reader (KJ) slightly undercounted the primary reader (LJN) on samples with band pair counts of 8–23, 27, and 28 (Fig. 3). There were no significant differences in the third counts of both readers using the Bowker or NcNemars tests of precision $\chi^2_{29} = 30.3$, $P = 0.40$; $\chi^2_{1} = 2.6$, $P = 0.10$ respectively; however, there was a significant difference using Evans–Hoenig ($\chi^2_{5} = 12.1$, $P = 0.03$). The value for APE was 11.4% ($n = 54$), which was considered acceptable given the difficulty in reading this species using Criterion B and the relative agreement of the Chi-Square tests. Additionally, the lack of specimens at some of these ages contributed to variability in the counts. The within-reader comparison of counts two and three produced an APE value of 9.1% for the sample.

Bomb radiocarbon analysis – Criterion A

Using Criterion A and a combination of the Florida coral (primarily for young fish) and WNA otolith chronologies (W81 and W105) and porbeagle chronologies, Hamady *et al.* (2014) partially validated the periodicity of band pair formation using bomb radiocarbon. They found annual band deposition in five

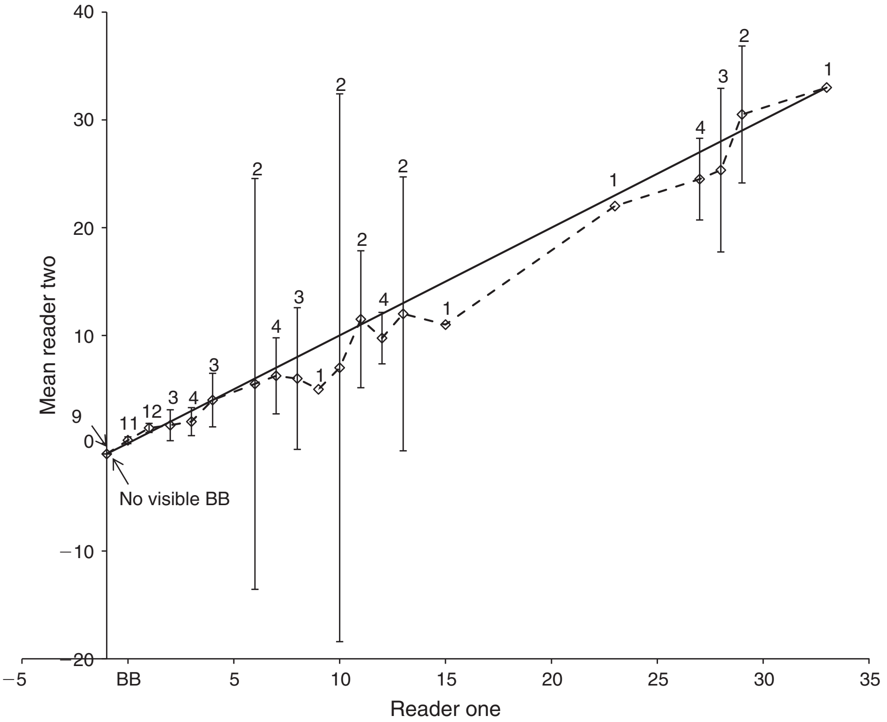

Fig. 3. Age bias graph for pair-wise comparison of 74 white shark, *Carcharodon carcharias*, vertebral counts from the third independent age readings by each reader using Criterion B. Each error bar represents the 95% confidence interval for the mean age assigned by Reader 2 to all fish assigned a given age by Reader 1. The one to one equivalence line is also presented. BB, birth band. N values are presented for each band pair count.

specimens up to 44 and 35 years of age for males and females respectively (Table 1). However, this was not the case for three samples. The age of one male was underestimated by 21 years using vertebrae; this (W105; 493 cm FL) specimen had 52 vertebral band pairs, yet was aged at 73 based on bomb carbon. In contrast, the head and tail vertebrae of our largest sample, a (W81) 526-cm female, were aged at 44 and 33 respectively, but 39 years using bomb carbon. Given the band pair count variation along the column noted above, the band count from an abdominal vertebra would have been higher, thereby overestimating age in this female. The age of another large female (W134; 495.3 cm) was overestimated by 4 years using vertebral band pairs (35 years) when compared with 31 years using bomb carbon. Given the confidence intervals around the bomb carbon estimates and the more recent (1996) sampling of this fish (the bomb carbon curve could be slightly shifted), we believe this sample is essentially validated at ~31–35 years (Hamady *et al.* 2014). Collectively, these results suggest that Criterion A growth curves are accurate up to at least 44 years for males and between 31 and 35 years for females. However, beyond these ages, our vertebral banding data may significantly underestimate male and overestimate female white shark age. The bomb radiocarbon age estimates for the largest white sharks in our sample were 39 years (W81; 526 cm) for females and 73 years (W105; 493 cm) for males.

Table 1. Band pair counts from the vertebrae of four white sharks used for bomb radiocarbon analysis

Counts for Criterion A are from Hamady *et al.* (2014)

Sample ID	Count criterion A	Count criterion B	Fork length (cm)	Date captured
W28	6	2+	220.9	23-Aug-67
W57	44	26	442	5-Oct-81
W100	9	4	223.5	17-Aug-68
W105	52	27	493	6-Aug-86

Bomb radiocarbon analysis – Criterion B

In the current study, four of the eight specimens used in Hamady *et al.* (2014) were counted using Criterion B (Table 1). Agreement between the band pair counts and the reference chronologies was evident in three of these sharks (W28, W100 and W57) with estimated ages of 2+, 4 and 26 respectively (Fig. 4*a–c*). Ages derived using Criterion B more closely aligned with the porbeagle reference chronology than did the counts using

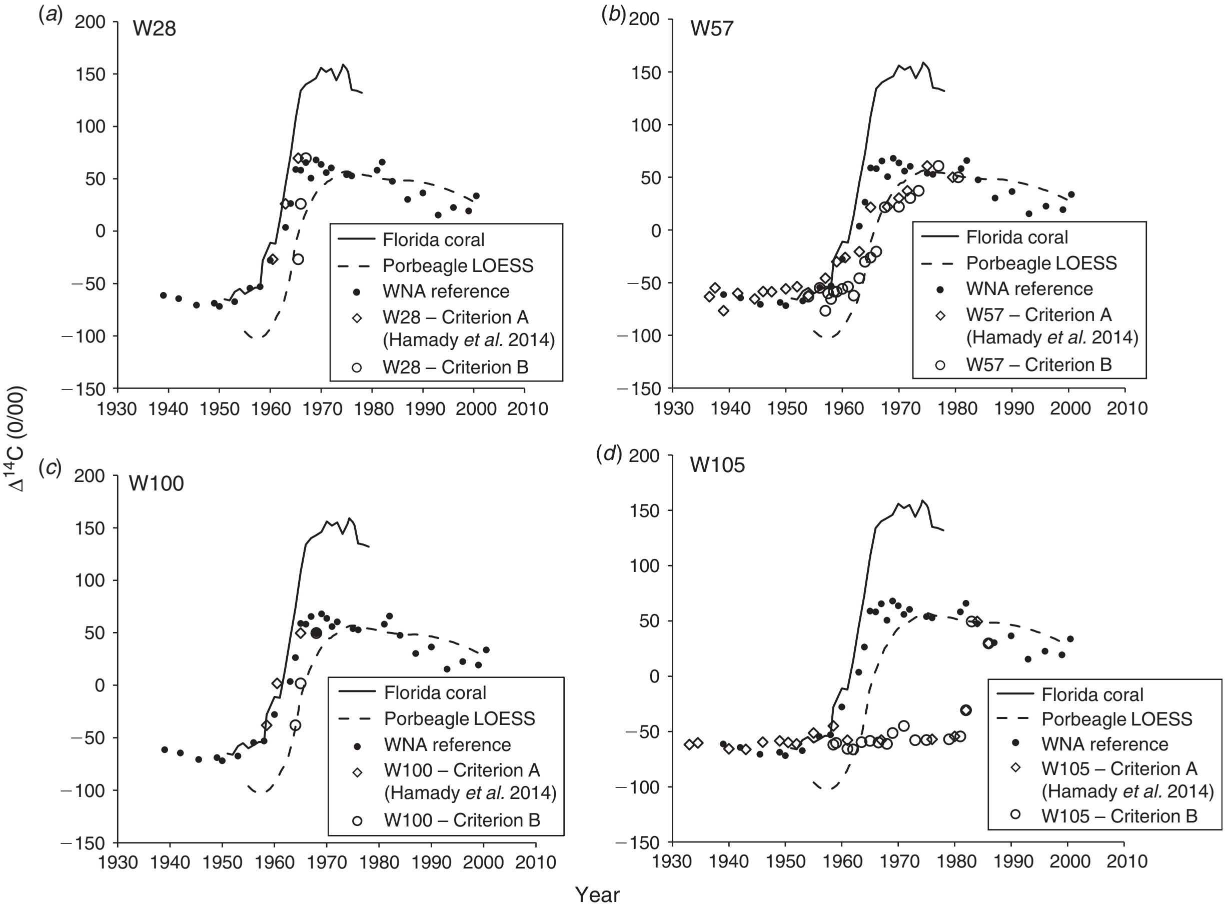

Fig. 4. White shark $\Delta^{14}C$ results compared with three reference chronologies. Results are presented for each specimen analysed using Criterion B and are compared with those derived using Criterion A (Hamady *et al.* 2014).

Criterion A (Hamady *et al.* 2014), although in the case of the youngest two samples (W28, W100) the first two sampling points aligned with the porbeagle whereas the third aligned more closely with the WNA reference (Fig. 4*a*, *b*). These data suggest that vertebral band pairs derived using Criterion B can be considered annual up to 26 years. The fourth individual (W105) was estimated at 27 years using Criterion B, but did not align with any of the reference chronologies and had an offset Δ^{14}C value similar to that observed using Criterion A (Fig. 4*d*). Based on the WNA otolith reference and the porbeagle chronology, the age of this shark would have to be shifted 23 and 15 years respectively, to align with these chronologies (Fig. 5). This would increase the estimated age of this specimen to 50 or 42 years using the WNA or porbeagle chronologies respectively.

Minimum and maximum age estimates for the five specimens used for bomb radiocarbon analysis were dependent on the chronology used (Table 2). However, the overall minimum ages of samples W57, W81 and W105 were 21.8, 23.7 and 26.7 years and the maximum ages of samples W28 and W100 were 8.7 and 10.7 years respectively (Table 2).

Growth curves – Criterion A

Based on the maximum and minimum ages calculated from the bomb radiocarbon data (see above), it was evident that the band pair counts using Criterion B underestimated age (see Discussion), therefore we did not calculate growth curves based on Criterion B band pair counts. Hamady *et al.* (2014) validated minimum age using band pair counts with Criterion A.

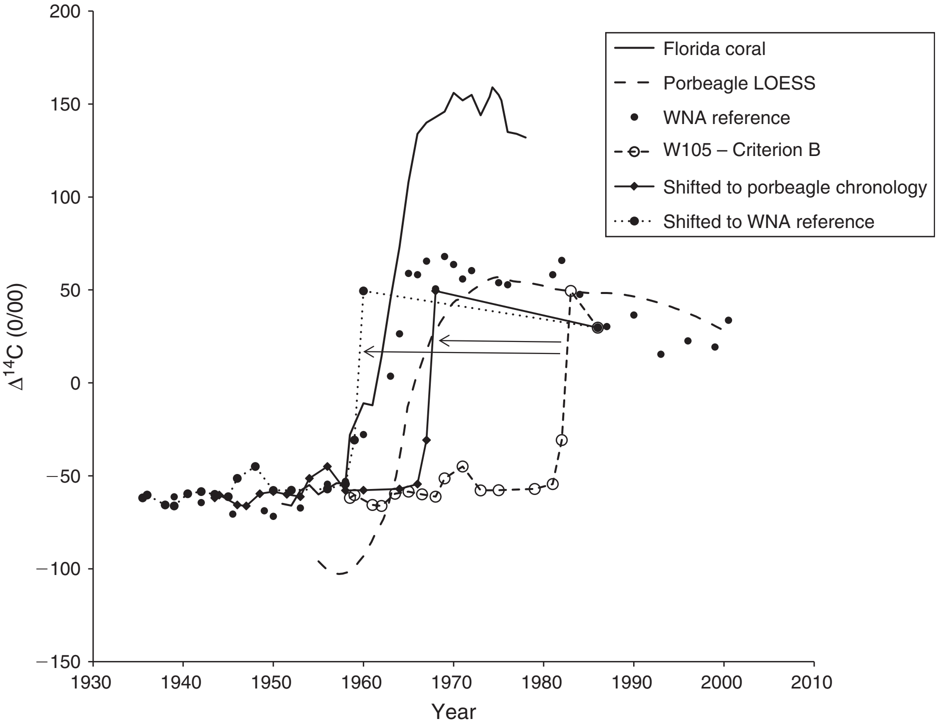

Fig. 5. White Shark W105 Δ^{14}C levels using Criterion B compared with three reference chronologies and shifted to align with the references.

Table 2. Minimum (a) and maximum (b) age estimates based on pre-bomb Δ^{14}C levels (see text for details)

The dates under each chronology correspond to the location on the reference of the pre-bomb Δ^{14}C values. Minimum and maximum ages are listed by chronology. Age estimates from centra are presented for comparison. FC, Florida coral; WNA, western North Atlantic Ocean; PL, Porbeagle LOESS

Sample	Year captured	Chronology			Minimum age			Age estimate from centra	
		WNA	PL	FC	WNA	PL	FC	Criterion A	Criterion B
W57	1981	1959	1960	1958.5	22.8	21.8	23.3	44	26
W81	1983	1959	1960	1958.5	24.7	23.7	25.2	33	18
W105	1986	1959	1960	1958.5	27.7	26.7	28.2	52	27
					Maximum age				
W28	1967	1959	1964.5	1959	8.7	3.2	8.7	9	4
W100	1968	1960	1964	1958	8.7	4.7	10.7	6	2

Therefore, we consider this technique validated up to age 44 and use bomb radiocarbon age estimates from Hamady *et al.* (2014) for those specimens older than 44 and included in the growth curve calculation. Growth curves were generated using the band pair counts (sexes combined) from a total of 70 (34 male, 36 female) vertebral samples using Criterion A. Five males were not included in the growth curve estimation because they were older than the validated ages and the band pair counts could not be considered annual; however, these specimens were plotted for comparison. The Schnute general model provided the best statistical fit (Tables 3, 4; Fig. 6). Of the multiple models applied, only the Schnute general model fit the length at age data well (Table 3).

Table 3. Relative goodness-of-fit for each growth model for *Carcharodon carcharias* in the western North Atlantic using Criterion A

Models are ranked from best to worst fitting. AIC$_c$, the small-sample, bias corrected form of the Akaike information criterion, Δ_i, Akaike difference; k, total number of regression parameters; LL, log-likelihood; w_i, Akaike weight

Model	k	LL	AIC$_c$	Δ_i	w_i
Schnute 1	5	−324.19	659.31	0.00	0.99
Logistic	4	−330.14	668.89	9.58	0.01
Gompertz	4	−332.82	674.26	14.95	0.00
VBGF	4	−336.43	681.48	22.17	0.00

Discussion

In this study, we used vertebral banding patterns to age white sharks in the NWA and produced dramatically different results highly dependent on the criteria chosen for band interpretation as well as the Δ^{14}C reference chronology used for validation. Criterion A, used by Hamady *et al.* (2014), produced validated ages up to 44 years based largely on the Florida coral and WNA otolith Δ^{14}C reference chronologies. However, vertebral band pair counts using Criterion B on the same specimens produced much lower age estimates (to age 26), which aligned predominantly on

Table 4. Schnute General Model growth model parameters for *Carcharodon carcharias* from the western North Atlantic based on age estimates from vertebral sections using Criterion A

a, a constant (time^{-1}) describing the constant relative rate of the relative growth rate; b, a dimensionless constant describing the incremental relative rate of the relative growth rate; L_1, length at age t_1; L_2, length at age t_2; and t_1 and t_2 are two reference ages (see text for values). Traditional growth parameter estimates of L_∞, asymptotic fork length, and L_0, length at birth are provided for comparison. All lengths presented are given in fork length (cm). The 95% bootstrap confidence intervals for each parameter are indicated in parentheses below when relevant

a	b	l_1	l_2	L_∞	L_0
0.65 (0.25–0.70)	−19.23 (−20.24–−7.73)	151.80 (145.18–159.28)	466.82 (444.85–488.73)	466.82 (444.93–489.16)	146.73 (139.87–154.51)

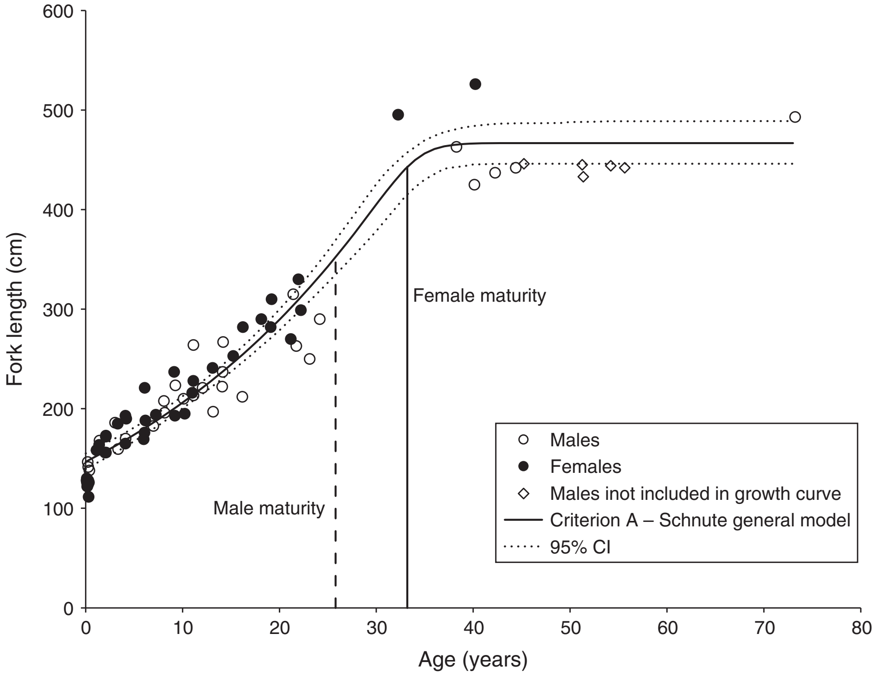

Fig. 6. White shark, *Carcharodon carcharias*, growth based on vertebral band counts derived using Criterion A with Schnute general model growth curves and 95% confidence intervals.

the porbeagle reference chronology. Using either criterion, an age shift was required in the largest male to account for missing time in the vertebral centra of this specimen. Clearly, both criteria cannot be considered valid (i.e. they are mutually exclusive), thus the use of vertebral centra and/or the validation technique as indicators of age in this species must be examined carefully.

The use of band pair counts in the vertebral centra of elasmobranchs has been considered the foremost ageing technique for decades (Cailliet 1990). In fact, band pair interpretation criteria are highly subjective (Cailliet 1990; Campana *et al.* 2002). Visually, the band pairs on the vertebral centra of the white shark differ substantially from the porbeagle and shortfin mako in having more, finer band pairs that cross from the corpus through the intermedialia to the opposite side. For small individuals, it was difficult to distinguish the broad banding using the porbeagle criteria (Criterion B) in many samples, thereby leading to inconsistent counting. As the centra grow, it appears that some of these finer band pairs group together to form the broader band pairs observed on the lower portions of the centra of the larger specimens (Fig. 7). However, this can be indistinguishable in young sharks and, therefore, lead to over-counting these specimens using Criterion A and possibly even Criterion B as the broad band pairs are difficult to distinguish. Ridewood (1921) noted that the white shark has more numerous radiating lamellae than the porbeagle and shortfin mako sharks, and we hypothesise that this difference in vertebral structure leads to increased banding on the face of the centrum. The difference between the porbeagle and white shark band pair patterns supports the use of Criterion A, which adjusts for differences in the structure of the centra.

The decision of which criterion produced 'valid' age estimates using bomb radiocarbon is tightly linked to the Δ^{14}C reference chronology chosen. As a lamnid shark, the white shark could be expected to follow the porbeagle Δ^{14}C chronology; however, its habitat and diet, which differ markedly from the porbeagle, are influential factors. Δ^{14}C values from the smaller samples (W28, 100) aligned more closely to the WNA and Florida coral chronologies (Hamady *et al.* 2014). Using Criterion B, these same samples aligned at younger ages with the porbeagle chronology, but ultimately aligned with the WNA otolith chronology at older ages (Fig. 4). The ages estimated for sample W57 (44 and 26 years; criterion A and B respectively), a 442-cm white shark, were also highly dependent on the reference curve accepted. The Δ^{14}C values in the white sharks sampled were not as low as those from the porbeagle or shortfin mako sharks, thereby suggesting that they eat less ^{14}C-depleted prey than those species and providing further support for the use of the WNA and Florida coral reference chronologies. The lack of a dietary shift to ^{14}C-depleted prey (Campana *et al.* 2002) is not unprecedented in large sharks and has been documented in tiger (*Galeocerdo cuvier*) and sand tiger sharks, (*Carcharias taurus*; Kneebone *et al.* 2008; Passerotti *et al.* 2014). Additionally, white shark sightings data in the WNA clearly indicate that this species occupies coastal habitat (Curtis *et al.* 2014) and does not appear to consume heavily depleted prey like that of the porbeagle (Campana *et al.* 2002). Although there are indications from recent WNA satellite tagging data that white sharks do move into depleted areas, this movement is limited to a few large individuals (G. Skomal, unpubl. data) and does not appear to be reflected in the Δ^{14}C signal.

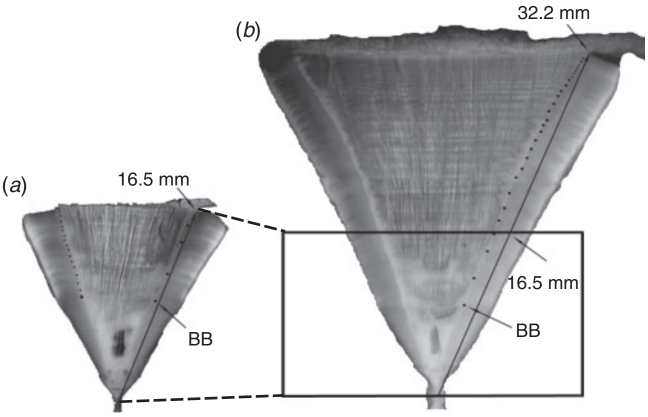

Fig. 7. Example of the number of band pairs on: (*a*) a small (212-cm fork length, FL) male White Shark with a 16.5-mm vertebral radius. Counts using Criteria A and B are on the left and right respectively, and (*b*) a large (442 cm FL; 36.2-mm radius of each centrum, VR) specimen showing counts using Criterion B. The area of the large sample where the smaller sample would fit is marked as are the vertebral radius measurements. BB, birth band.

Minimum and maximum ages derived from the reference curves and the Δ^{14}C data indicate that Criterion B underestimated the ages of the larger specimens. Although the minimum ages estimated for W81 and W105 are similar to the band pair counts using Criterion B, this does not account for growth before the rise in Δ^{14}C. Although the band pair count for W57 is higher than the minimum estimated age, it is not high enough to account for the pre-rise samples. The extent to which ages are underestimated by Criterion B in the smaller specimens is not quite as clear and highly dependent on reference chronology. For example, the band pair count of W28 is only slightly higher than the maximum age based on the porbeagle Δ^{14}C reference curve (4 *v.* 3), but well below the maximum ages derived using Criterion A, which align well with the other reference curves. Moreover, age estimates for W100 also support the use of Criterion A and the WNA and FL coral reference chronologies.

Of particular interest are the results derived from specimen W105, which, regardless of band interpretation criteria, did not align with any of the Δ^{14}C reference chronologies (Fig. 4). Despite the dramatic difference in age estimate derived from the two criteria, a shift of 15–23 years was needed to align with either the porbeagle or WNA reference chronologies respectively (Fig. 5). This clearly demonstrates that time is not being recorded in older white sharks. Hamady *et al.* (2014) suggested that the largest individuals may experience a change in the rate of deposition of vertebral material at some point after maturity, or that the band pairs become so thin as to be unreadable. This is not unique to white sharks as band pair counts appear to also underestimate age in older individuals in other shark species (Kalish and Johnston 2001; Francis *et al.* 2007; Andrews *et al.* 2011; Natanson *et al.* 2014). Additionally, Kerr *et al.* (2006) attributed their inconsistent bomb carbon results to depleted prey and offshore migration; however, this was before the concept of missing time (Francis *et al.* 2007; Passerotti *et al.* 2014). It is possible that age underestimation and missing time would also explain their results. This observation provides additional evidence that Criterion A provides more accurate estimates of age because those derived using Criterion B underestimated age.

Given the evidence noted, we believe that the WNA reference chronology and the use of Criterion A provide the more realistic, and parsimonious, estimates of age for this species up to age 44. As previously discussed, both sets of criteria fit the white shark and, in fact, both sets can be consistently followed in counting all sections, although Criterion A produces closer precision both within and between readers. The bomb radiocarbon results and life history information on the white shark indicate that Criterion B underestimates age. However, it does not fully support the use of Criterion A because of the pre-bomb segment and the missing time; thus, validation up to age 44 is consistent with the data. These data suggest that care must be taken when choosing a reference chronology and criteria for band pair validation using bomb radiocarbon. As we observed in the present study, other species may also be 'validated' with different criteria depending on the reference chronology. Thus, we feel it is essential that other aspects of the life history (such as habitat and diet) be explored when choosing a chronology before deciding on the accuracy of ages. The variability we observed using both criteria when coupled with the failure of the vertebrae to record time, reduce the viability of our age estimates.

By coupling our growth band interpretation using Criterion A with concurrent bomb radiocarbon validation, we were able to produce a growth curve for the white shark in the WNA. The lack of data on large white sharks precluded our ability to model the sexes separately; however, it is clear from the graph that male and female growth rates appear to diverge before the size of male maturity (Fig. 6). The decreased growth of males after maturity observed in this study is common for elasmobranch species (Bishop *et al.* 2006; Natanson *et al.* 2002, 2006). However, this is the first instance where bomb carbon ageing has shown that band pair counts overestimate the age of an elasmobranch species and, therefore, male and female band pair deposition appears substantially different.

Bomb radiocarbon age validation has been used to validate the annual periodicity of vertebral band deposition in two lamnid species in the western North Atlantic, the shortfin mako and the porbeagle (Campana *et al.* 2002; Ardizzone *et al.* 2006). However, these species did not exhibit variability in band pair counts along the vertebral column, regardless of the size of the specimen (Natanson *et al.* 2002, 2006; Bishop *et al.* 2006). The fact that the number of band pairs is not consistent along the white shark vertebral column is unusual for a lamnid, but has been previously found in angel, *Squatina californica*, and basking, *Cetorhinus maximus*, sharks (Natanson and Cailliet 1990; Natanson *et al.* 2002, 2006, 2008; Bishop *et al.* 2006). The greater number of band pairs in the abdominal region of the white shark is possibly related to structural support required for growth in girth, particularly in a large mature female. As has been described in the angel shark (Natanson and Cailliet 1990), it is possible that growth in abdominal girth for this species requires structural deposition at a rate that exceeds the growth in girth for the head and tail. This would not necessarily be required by male white sharks, which are not likely to attain the same girth as pregnant females. Hence, vertebral band deposition would continue at a different rate. The increase in girth for the female and need for structural support may explain why the band pair count in the large female was higher than the bomb radiocarbon estimated age. Further study of band pair deposition as it relates to girth in these sharks is warranted to resolve this issue.

The estimated ages for both sexes in this study and Hamady *et al.* (2014) greatly exceed the previously published maximum age estimates for this species of 15 years from the eastern North Pacific Ocean (473.8 cm, Cailliet *et al.* 1985), 13 years from the western Indian Ocean off South Africa (415 cm; Wintner and Cliff 1999), 12 years from the western North Pacific Ocean (411.6 cm, Tanaka *et al.* 2011), and 22 band pairs in a large pregnant female (~500 cm) taken off New Zealand (Francis 1996). The current results also indicate a much slower growth rate (Fig. 8). It is difficult to determine if these differences in growth are related to methodology, inter-oceanic differences in life history or genetics, or a combination of these factors. White sharks from all previous studies were aged using x-radiographs of whole vertebrae as opposed to sectioned vertebrae in the current study. We found that white shark vertebrae were very difficult to 'read' because the bands are diffuse and very tightly spaced. This is particularly true for larger (and older) fish, in which vertebral bands are compacted at the centrum edge (Fig. 2). The interpretation of ageing criteria becomes very difficult in sectioned vertebrae and is likely to be virtually impossible in whole vertebrae. Whole vertebrae simply do not allow for high band resolution in older, slower growing fish (Skomal and Natanson 2003; Goldman *et al.* 2012). Moreover, x-radiographs tend to obscure the finer detail in the centra that, along with the overlap of the front and back of the centra in the x-radiograph, would lead to undercounting and make the band pair counts more difficult and less reliable (Goldman *et al.* 2012). Therefore, counts from whole vertebrae generally underestimate ages in larger individuals; Kerr *et al.* (2006) found sections to have generally higher band counts than whole centra in white sharks. Additionally, recent evidence indicates that the white shark in the western North Atlantic is genetically different from those in other oceans (D. Chapman,

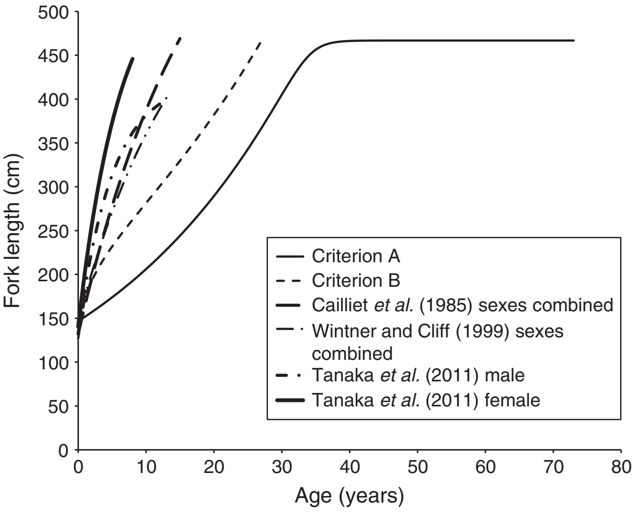

Fig. 8. Schnute general model growth curve generated from vertebral data using Criterion A for white sharks, *Carcharodon carcharias*, in the western North Atlantic, included for comparison are the von Bertalanffy growth curves of other studies.

pers. comm., 2012) and, therefore, this difference in growth could be an effect of this variation. Although it is possible that white sharks exhibit population-level differences in growth, the disparities between the validated age estimates derived in the current study and the unvalidated estimates from previous studies are unrealistically large (>30 years). Instead, it is more likely that the use of whole vertebrae is responsible for much of these differences and, therefore, growth of the white shark in other regions is equally as slow.

Estimates of size and age at maturity for the white shark are broad and variable depending on the study. Pratt (1996) studied male white sharks in the WNA and suggested that the smallest mature male in his sample (352 cm FL) should be considered size at maturity. Francis (1996) suggested that female size at maturity occurred over a broad size range (female 450–500 cm TL, 417–464 cm FL). Based on the current study and these minimum size estimates, age at maturity is 26 and 33 years for male and female white sharks respectively. These ages at maturity significantly differ from previous estimates for this species, which ranged from 4 to 10 years and 7–13 years for males and females respectively (Cailliet *et al.* 1985; Wintner and Cliff 1999; Tanaka *et al.* 2011).

These new age estimates, which result in much later ages at maturity, change our current understanding of white shark demographics and will likely result in reduced population replacement rates (Mollet and Cailliet 2002). Although this species has been prohibited from retention in the WNA (NMFS 1999), it is still subjected to an unquantified level of by-catch mortality. Given the lack of white shark population estimates in this region, it is difficult to predict what effects this mortality has had or will have on this species.

Supplementary material

The Supplementary material is available from the journal online (see http://www.publish.csiro.au/?act=view_file&file_id=MF14127_AC.pdf).

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