

Using bomb radiocarbon to estimate age and growth of the white shark, *Carcharodon carcharias*, from the southwestern Indian Ocean

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Abstract Knowledge of age and growth parameters is vital to the conservation and management of white sharks (*Carcharodon carcharias*), but ages have not been validated for all populations and growth rates can vary regionally. Bomb radiocarbon (¹⁴C) analyses conducted on four individual white sharks [329, 414, 487, and 537 cm fork length (FL)] from the southwest Indian Ocean (SWI) were proximally aligned with $\Delta^{14}\text{C}$ reference chronologies accepting established error, providing evidence to support annual band pair formation to 30–38 years for the SWI population. To enable comparison with previous studies on

bomb radiocarbon in white sharks, a subset of specimens from the northwest Atlantic Ocean (NWA; 223.5, 441, and 493 cm FL) and northeast Pacific Ocean (NEP; 214, 365, and 429 cm FL) were also analyzed for ¹⁴C, revealing samples from the SWI were more enriched in ¹⁴C than samples from the NWA or NEP. Vertebral band pair counts were then determined for a larger set of white sharks from the SWI (140–422 cm FL, $n = 51$) resulting in age ranges of 1–38 years. The Gompertz growth model best described the SWI data, with an asymptotic size (L_{∞}) of 496.77 cm FL and length at birth (L_0) of 134.08 cm FL. The results of this study indicate white sharks in the SWI are longer-lived and grow more slowly compared to past estimates, but these data are more similar to recent age and growth estimates from other geographically distinct populations. This has important implications for the management of this species in the waters off southern Africa.

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Introduction

Conservation of threatened species is complicated by data deficiencies such as accurate age estimates. Age estimates are central to the determination of a species' growth rate, longevity, and age at sexual maturity, parameters that enable more effective management planning (Campana 2001; Cailliet and Goldman 2004; Cailliet and Andrews 2008). In the past, the inclusion of inaccurate age estimates in stock assessments of several commercially important marine species has led to overexploitation of stocks (Lai and Gundersen 1987; Campana 2001; Cailliet and Andrews 2008).

For elasmobranchs, the majority of age and growth studies have relied on calcified structures, usually the vertebral centra, to estimate the age of an individual (Ridewood 1921; Cailliet et al. 2006; Goldman et al. 2012). This aging

technique is based on the assumption that band deposition occurs with a fixed periodicity, typically on an annual basis, and that band pairs (one opaque and one translucent band that together represent one year) are counted to obtain an age estimate for each individual (Cailliet and Goldman 2004). However, the interpretation of annual band pairs can be complicated by the presence of non-annual growth marks and other factors such as somatic growth that have been found to influence band deposition, e.g., Pacific angel shark (*Squatina californica*; Natanson and Cailliet 1990), basking shark (*Cetorhinus maximus*; Natanson et al. 2008), and wobbegong sharks (*Orectolobidae ornatus*, *O. maculatus*, and *O. halei*; Huvneers et al. 2013). Annual periodicity of band pairs must consequently be validated for each species and across the size range of animals for a species (Beamish and McFarlane 1983; Cailliet et al. 2006).

Bomb radiocarbon (^{14}C) dating has become a valuable tool to validate annual band pair formation in elasmobranchs (Goldman et al. 2012). This method capitalizes on the rapid increase in radiocarbon in the world's oceans as a result of atmospheric testing of thermonuclear devices in the 1950 s and 1960 s (Druffel and Linick 1978; Broecker and Peng 1982). The synchronous uptake of radiocarbon acts as a time stamp for year of formation in accretionary structures, e.g., otoliths (Kalish 1993; Campana 1999), mollusks (Weidman and Jones 1993), and elasmobranch vertebrae (Campana et al. 2002). As a result, the $\Delta^{14}\text{C}$ value of consecutive samples from such tissues can be compared to a reference chronology to determine the year of formation for each band in the tissue sampled. Following this approach, bomb radiocarbon analysis has confirmed annual band pair formation in the vertebrae of several shark species including juvenile to adult animals (Campana et al. 2002; Ardizzone et al. 2006; Kneebone et al. 2008; Passerotti et al. 2010). It has also revealed, however, that vertebral growth bands may not accurately reflect the correct number of years after a certain stage/time in an individual's lifetime. This phenomenon has been reported in sandbar (*Carcharhinus plumbeus*; Andrews et al. 2011), sand tiger (*Carcharias taurus*; Passerotti et al. 2014), and white (*Carcharodon carcharias*; Hamady et al. 2014; Andrews and Kerr 2015) sharks and is commonly referred to as "missing time" (Passerotti et al. 2014). Moreover, bomb radiocarbon analysis has also found that annual band pair formation can vary between populations of the same species; for example, annual band pair formation was validated to 26 years for porbeagle sharks (*Lamna nasus*) in the northwest Atlantic Ocean (NWA; Campana et al. 2002), while in New Zealand annual band pair deposition was confirmed to approximately 20 years, but ages had been underestimated by up to 20 years in individuals older than 20 (Francis et al. 2007). This indicated vertebral growth had slowed or ceased in the slower-growing New Zealand population (Francis et al.

2007). Presumably, the same phenomenon is responsible for the missing band pairs in the other shark studies (Natanson et al. 2014; 2015).

The white shark is a globally distributed, large marine predator that is listed as vulnerable on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species and protected throughout its range by inclusion on Appendices I and II of the Convention on Migratory Species (CMS). International trade of white sharks is further regulated by listing on Appendix II of the Convention on International Trade of Endangered Species of Flora and Fauna (CITES). Age-reading studies of white sharks in the northeast Pacific Ocean (NEP; Cailliet et al. 1985), the southwest Indian Ocean (SWI; Wintner and Cliff 1999), and off the coast of Japan (Tanaka et al. 2011) suggested a maximum age of 12–15 years. These estimates were obtained by analyzing X-radiographs (X-rays) of vertebral centra and assumed annual deposition of band pairs. Initial attempts to validate annual periodicity of band pair counts in white sharks through the use of oxytetracycline in the SWI (Wintner and Cliff 1999) and bomb radiocarbon analysis for the NEP (Kerr et al. 2006) were inconclusive. Recently, Hamady et al. (2014) confirmed annual band pair formation for the NWA population up to 44 years with a suggested longevity of ~73 years, when accounting for a slowing or cessation of band pair deposition in the outer portion of the vertebral centra. Following this study, Natanson and Skomal (2015) determined age and growth parameters for a larger number of individuals in the NWA, finding that white sharks can live to a minimum of 44 years and mature much later than previously estimated (26 and 33 years for males and females, respectively). Following the reanalysis of bomb radiocarbon data for white sharks in the NEP and accounting for slowing or ceased growth in the vertebral centrum, Andrews and Kerr (2015) suggested that the white sharks in their study lived for >30 years.

The objective of the current study was to validate annual band pair deposition in the vertebrae of white sharks from the SWI using bomb radiocarbon dating and to estimate standard growth parameters from band pair counts for a larger number of individuals. In addition, a subset of specimens from the NWA and NEP were also processed following our methods to allow a comparison of bomb radiocarbon data among regions and to illustrate methodological differences.

Methods

A total of 55 white shark vertebrae were obtained from the KwaZulu-Natal Sharks Board (KZNSB), KwaZulu-Natal, South Africa. The KZNSB maintains a series of bather protection nets and drumlines along the coastline

of KwaZulu-Natal on the east coast of South Africa (Cliff and Dudley 2011). Captured live specimens are tagged and released according to the KZNSB protocols, while deceased individuals in good condition are transported to the laboratory for biological sampling. Fifty-three individual white sharks were sampled from 1991 to 2009, comprising 28 females [140–422 cm fork length (FL)] and 25 males (151–414 cm FL). Additional vertebral centra were obtained from an individual captured off Gansbaai on South Africa's Western Cape coast in 1987 (female, 537 cm FL) and from an individual captured off the coast of Malindi, Kenya, in 1996 (female, 487 cm FL). For all sharks included in this study, sex, maturity, and precaudal length (PCL) were recorded. PCL was measured as the straight-line distance from the tip of the snout to the precaudal notch as defined by Dudley et al. (2005). All lengths were converted to straight fork length using the following equation: $FL = 1.100 PCL + 3.554$ ($n = 142$; Cliff et al. 1996a).

For both bomb radiocarbon analysis and band pair counts, vertebral centra were excised anterior to the first dorsal fin and stored frozen. Prior to analysis, vertebrae were cleansed of excess tissue and oven-dried for 48 h at 40 °C. A single vertebral section from each individual was prepared by a single cut using paired blades separated by a spacer on an IsoMet® low-speed diamond saw (Buehler-Whitby, ON, Canada) to produce a bow-tie section of 1 mm thick.

For age-reading (band pair counts), sections were digitally photographed (Spot Insight camera, Sterling Heights, MI, USA) at 2048 × 2048 resolution under a binocular microscope (Wild M5, Leica Microsystems, ON, Canada) at 16–40× magnification using reflected light while immersed in ethanol. Age interpretation was based on images enhanced for clarity and contrast using Adobe Photoshop CS2 using image enhancement methods described by Campana (2014) and using the band interpretation criteria of Natanson et al. (2002). Three non-consecutive counts of translucent bands visible in the corpus calcareum (Fig. 1) were made by a single reader (SE Campana) without knowledge of shark length or any previous age estimate.

Samples for bomb radiocarbon assays were extracted from growth bands visible in the corpus calcareum from each of four selected SWI white sharks (Table 1), while working at 16× magnification under a binocular microscope. Extracted samples were isolated as solid pieces using a Gesswein high-speed hand tool fitted with steel bits <1 mm in diameter. Each of two sharks had one sample extracted from an area near the birth band of the vertebra (Table 2), while each of two sharks had three samples extracted from various positions along the growth sequence of the corpus calcareum (Table 2; $n = 8$ extracted samples

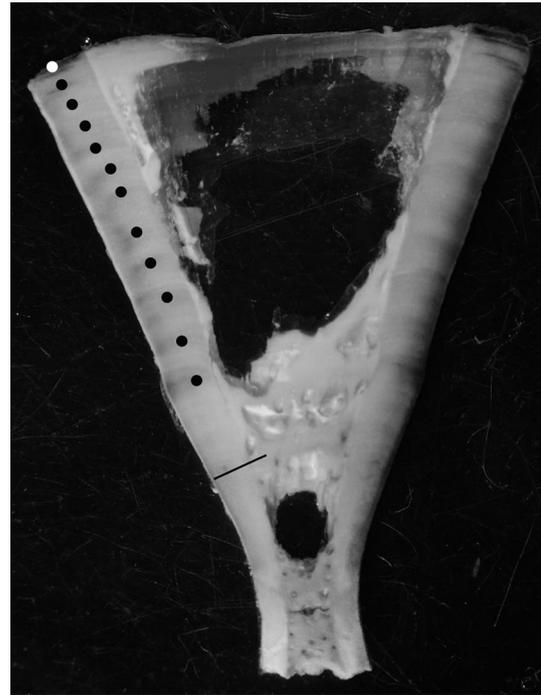


Fig. 1 Vertebral section from a 292 cm FL male white shark (*Carcharodon carcharias*) aged 12 years from band pair counts. Circles indicate translucent bands. Black line indicates birth mark

total). The presumed date of band formation was back-calculated from the band pair age and year of shark collection. After sonification in Super Q water and drying, extracted samples were weighed to the nearest 0.1 mg in preparation for ^{14}C assay with accelerator mass spectrometry (AMS). AMS assays also provided $\delta^{13}\text{C}$ (‰) values, which were used to correct for isotopic fractionation effects. Radiocarbon values were subsequently reported as $\Delta^{14}\text{C}$, which is the per-mille (‰) deviation of the sample from the radiocarbon concentration of nineteenth-century wood, corrected for sample decay prior to 1950 according to the methods outlined by Stuiver and Polach (1977). The mean standard deviation of the individual radiocarbon assays was ~5 ‰.

To enable a comparison among samples from this study and recently published $\Delta^{14}\text{C}$ values for white sharks in other regions, a subsample of white sharks from the NEP ($n = 3$; Kerr et al. 2006) and the NWA ($n = 3$; Hamady et al. 2014) were re-assayed. The analytical protocol for the preparation, extraction, and ^{14}C analysis of these samples was identical to that described above for the SWI animals, i.e., demineralization was not undertaken and all samples were taken from the corpus calcareum (Table 1). Independent of previously published age estimates for these sharks, ages were determined by counting band pairs as detailed above. Samples for bomb radiocarbon analysis were

Table 1 Summary of white shark (*Carcharodon carcharias*) vertebral samples for $\Delta^{14}\text{C}$ analysis

Shark ID	Region	Sex	Fork length (cm)	Year collected	Estimated age (years)	Birth year	Bands sampled
Gansbaai	SWI	F	537	1987	31	1956	3
Kenya96	SWI	F	487	1996	30	1966	1
IFA91016	SWI	M	329	1991	18	1973	3
TRA92004	SWI	M	414	1992	38	1954	1
WH 1	NEP	M	365	1978	21	1957	1
WH 3	NEP	M	214	1968	6	1962	1
WH 17	NEP	M	429	1982	46	1936	3
WS 57	NWA	M	441	1981	31	1950	2
WS 100	NWA	M	223.5	1968	8	1960	1
WS 105	NWA	M	493	1986	66	1920	2

Ages were estimated from band pair counting. Birth year was determined as year collected minus estimated age. Bands sampled are the number of bands extracted and analyzed for $\Delta^{14}\text{C}$

SWI southwest Indian Ocean ($n = 4$), NEP northeastern Pacific Ocean ($n = 3$), NWA northwestern Atlantic Ocean ($n = 3$)

Table 2 Results of bomb radiocarbon dating for white sharks (*Carcharodon carcharias*)

Shark ID	Fork length (cm)	Estimated age (years)	Band sampled	Year of formation	$\delta^{13}\text{C}$	$\Delta^{14}\text{C}$	CV of assigned band pair formation ^a
<i>Southwest Indian Ocean</i>							
Gansbaai	537	31	1.5	1957.5	-16.6	-8	5.1
			3	1959	-11.3	12.3	4.9
			9.5	1965.5	-11.2	23.7	3.7
IFA91016	329	18	1	1974	-12.2	26.3	3.0
			6	1979	-11.4	78.7	2.1
			15	1988	-12.7	74.7	0.6
Kenya96	487	30	2	1968	-10.1	41.4	4.9
TRA92004	414	38	1.5	1955.5	-9	-0.6	6.4
<i>Northeast Pacific Ocean</i>							
WH 1	365	21	0-1	1957.5	-12.3	-43.29	
WH 3	214	6	1	1963	-17.9	-181.16	
WH17	429	46	1-2	1937.5	-13.5	-148.94	
			21-25	1959	-29.8	-181.16	
			36-40	1974	-13.1	-3.67	
<i>Northwest Atlantic Ocean</i>							
WS 57	441	31	7-9	1958	-13.4	-68.2	
			17-19	1968	-14	4	
WS 100	223.5	8	0-1	1960.5	-13.6	-22.7	
WS 105	493	66	37-40	1958.5	-12.7	-77.1	
			48-55	1971.5	-13.2	10.9	

Estimated age and band sampled were based on band pair counting. Year of formation was calculated as the year of birth plus the estimated age of the band sampled

^a CV = 17.4 %

extracted from the first growth band pair after the birth mark for all three white sharks from the NEP (Table 2). For one individual (WH 17), an additional two assay samples were extracted along the corpus calcareum closer to the

outer edge from approximately the same locations as the original study (Kerr et al. 2006). Assay samples from the NWA sharks were removed from the first formed band pair after the birth mark for one individual (WS 100). For WS

57 and WS 105, two samples each were extracted along the corpus calcareum (Table 2).

To assign a date of formation to each bomb radiocarbon assay sample, it is necessary to compare the $\Delta^{14}\text{C}$ value of the unknown sample to the $\Delta^{14}\text{C}$ value of an environmentally similar reference chronology. In the absence of a local $\Delta^{14}\text{C}$ reference chronology, two substitute reference chronologies were used for all three white shark populations. First, we compared white shark $\Delta^{14}\text{C}$ values with a previously validated chronology from a hermatypic coral (*Porites lutea*) from Watamu Reef, Kenya (Grumet et al. 2002; Passerotti et al. 2014). It was assumed that the Watamu Reef coral $\Delta^{14}\text{C}$ chronology would be similar to the SWI region because both regions have a common source of oceanic water (South Equatorial Current of the Indian Ocean; Gordon 1986; Passerotti et al. 2014). Due to the documented phase lag of $\Delta^{14}\text{C}$ values in shark species, the white shark $\Delta^{14}\text{C}$ values were also compared with a validated chronology for the porbeagle shark from the NWA (Campana et al. 2002), which has been used as an indicator of how ^{14}C -depleted carbon sources may be reflected in shark species. When plotting white shark $\Delta^{14}\text{C}$ values against the reference chronologies, annual band pair deposition was assumed and $\Delta^{14}\text{C}$ values were plotted at year of band formation for each assay sample. To provide an estimate of age range for each individual assay sample from the SWI, i.e., a measure of potential age error, the difference between collection year and year of band pair formation was multiplied by the coefficient of variation (CV; Campana 2001; Ardizzone et al. 2006), which was calculated for the combined set (bomb radiocarbon and age estimation) of white shark ages from the SWI ($n = 55$). If the assigned year of formation was to the left of the reference chronology, it is possible the age was overestimated, while a shift to the right of the reference chronology indicates possible age underestimation. To estimate the potential range in ages for each individual for the SWI samples, the year of formation for the earliest sample assayed was shifted to align with the Watamu reef coral chronology (maximum) or the porbeagle reference chronology (minimum).

To determine ages for the larger sample size of sharks from the SWI ($n = 51$, excluding individuals analyzed for bomb radiocarbon), band pairs were counted as described above. To examine the variation in within reader counts, the coefficient of variation (Campana 2001) was calculated. The first clear growth band following the birth mark was presumed to represent the first year of growth (Casey et al. 1985). An angle change in the corpus calcareum was also used to confirm the identity of the birth mark, if present. To confirm the location of the birth mark, measurements from the midpoint of the isthmus to the birth mark were taken, the relationship between vertebral radius (VR) and FL was

calculated, and size at birth was back-calculated using a modified Dahl-Lea method (Cailliet and Goldman 2004).

To estimate growth parameters for white sharks from the SWI, the Schnute (1981) growth model was fit to length-at-age estimates based on observed band pair counts for the 55 individuals. Due to low sample sizes, sexes were combined for all analyses. The Schnute general model is as follows:

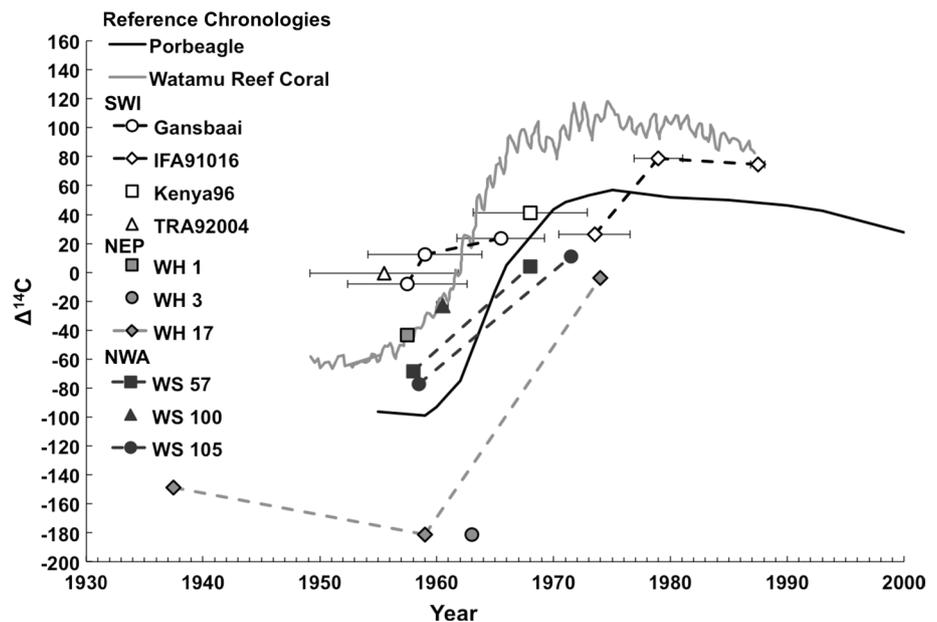
$$L_t = \left[L_1^b + \left(L_2^b - L_1^b \right) \frac{1 - e^{-a(t-t_1)}}{1 - e^{-a(t_2-t_1)}} \right]^{\frac{1}{b}},$$

where L_t is the length at time t (in years), L_1 is the length at age t_1 , L_2 is the length at age t_2 , t_1 is set to the lowest observed age ($t_1 = 1$), t_2 is set to the highest observed age ($t_2 = 38$), a is a constant (time^{-1}) describing the constant relative rate of the relative growth rate, b is a dimensionless constant describing the incremental relative rate of the relative growth rate, where $a \neq 0$ and $b \neq 0$. To fit several of the more commonly used growth models, the values of parameters a and b were adjusted; for the von Bertalanffy model, $a > 0$ and $b = 1$, and for the logistic growth model, $a > 0$ and $b = -1$ (Schnute 1981). The Gompertz function was described by the following (where $a > 0$ and $b = 0$; Schnute 1981):

$$L_t = L_1 e^{\ln\left(\frac{L_2}{L_1}\right) \frac{1 - e^{-a(t-t_1)}}{1 - e^{-a(t_2-t_1)}}}$$

Estimates for each parameter (a , b , L_1 , L_2) were determined using nonlinear least-squares regression methods in R (R Core Team 2014). Common parameter estimates (e.g., asymptotic size, L_∞ , and theoretical size at birth, t_0) were calculated following Schnute (1981). Length at birth (L_0) was estimated from the resulting equation for each growth model. Using the “nlstools” package in R, 95 % confidence intervals (CI) were constructed for parameter estimates via bootstrap methods (Baty and Delignette-Muller 2011). Final model selection was determined by lowest AIC_c value (Akaike 1973; Burnham and Anderson 2002) and concordance with known biological parameters. The AIC_c difference (Δ_i) in each model was calculated based on the lowest observed AIC_c value ($\text{AIC}_{c,\text{min}}$) as $\Delta_i = \text{AIC}_{c,i} - \text{AIC}_{c,\text{min}}$ to provide an estimate of the magnitude of difference between each model and the best model in the set. The model with the lowest AIC_c value was considered to have strong support, and models with values of $\Delta_i < 2$ were considered indistinguishable in terms of fit (Burnham and Anderson 2002). In the case of models having values of $\Delta_i < 2$, known biological parameters were used to determine the best fit model. To approximate model likelihood, the Akaike weight (w_i) of each model was also calculated (Burnham and Anderson 2002). The growth model analyses were then repeated using ages adjusted to align with the reference chronologies (Watamu Reef coral and porbeagle,

Fig. 2 $\Delta^{14}\text{C}$ values of white sharks from the southwest Indian Ocean (SWI), north-east Pacific Ocean (NEP), and northwest Atlantic Ocean (NWA) compared to two $\Delta^{14}\text{C}$ reference chronologies: the porbeagle shark from the NWA (Campana et al. 2002) and a hermatypic coral from Watamu Reef off the coast of Kenya (Grumet et al. 2002). Horizontal error bars represent uncertainty associated with age estimation from growth bands (CV = 17.4 %)



separately) for the four specimens that underwent bomb radiocarbon analysis.

Results

Bomb radiocarbon analysis

Eight samples from four SWI sharks were analyzed for $\Delta^{14}\text{C}$ (Table 2); ages based on band pair counts were estimated as 18–38 years. Assay samples with the earliest date of formation for the SWI sharks, 1955.5 and 1957.5, were relatively enriched in ^{14}C (-0.6‰ TRA92004 and -8.0‰ Gansbaai, respectively; Fig. 2), and no samples were available to measure pre-rise $\Delta^{14}\text{C}$ values for white sharks from this region. The $\Delta^{14}\text{C}$ values of samples from TRA92004 and the first two assay samples from Gansbaai were to the left of the coral chronology. When accounting for analytical error and aging error (CV), these values overlapped with the coral chronology and values for the remaining two sharks (Kenya96 and IFA91016) aligned with the porbeagle chronology (Fig. 2). The error associated with assigned year of band pair formation for each sample (CV) ranged between 0.6 and 6.4 years (Table 2). Accepting the above errors, the observed sample proximity to the reference chronologies provides support for annual band pair formation for white sharks in the SWI to 30–38 years. Shifting the year of sample formation to align with the coral reference chronology altered ages by -5.5 to 11 years, while aligning assay samples with the porbeagle reference chronology altered ages by -10.5 to 4 years (Table S1).

The range of values for the NWA (-77.1 to 10.9‰) and the NEP (-181.2 to -3.7‰) sharks captured pre-bomb

values and the rapid increase in $\Delta^{14}\text{C}$ (Table 2). The $\Delta^{14}\text{C}$ values for the NWA specimens were within the range of values reported by Hamady et al. (2014; Table 3), while samples from the NEP specimens had more depleted $\Delta^{14}\text{C}$ values than those reported by Kerr et al. (2006; Table 3). Samples from two specimens (WH 1 and WS 100) aligned with the coral reference chronology (Fig. 2). For three specimens (WH 17, WS 57, and WS 105), the timing of rapid increase in $\Delta^{14}\text{C}$ aligned with the porbeagle reference chronology (Fig. 2). For one specimen (WH 3), the single assay sample was more depleted than both reference chronologies; therefore, we were unable to determine whether it aligned with a reference chronology (Fig. 2).

Age determination

The FL-VR relationship was best described by a linear equation (Fig. 3). The mean birth mark (\pm standard deviation) measurement was 8.6 ± 0.16 mm ($n = 36$) from the isthmus of the vertebrae. The modified Dahl-Lea back-calculated size at birth was 127 ± 2.0 cm FL. This back-calculated birth size agrees with the previous values of 100 cm PCL (back-calculated) and 135 cm PCL (predicted value) for white sharks from South Africa (Wintner and Cliff 1999) and is within the range of size at birth reported for other white shark populations (120–150 cm total length; Francis 1996; Uchida et al. 1996; Natanson and Skomal 2015), indicating the birth mark was correctly identified.

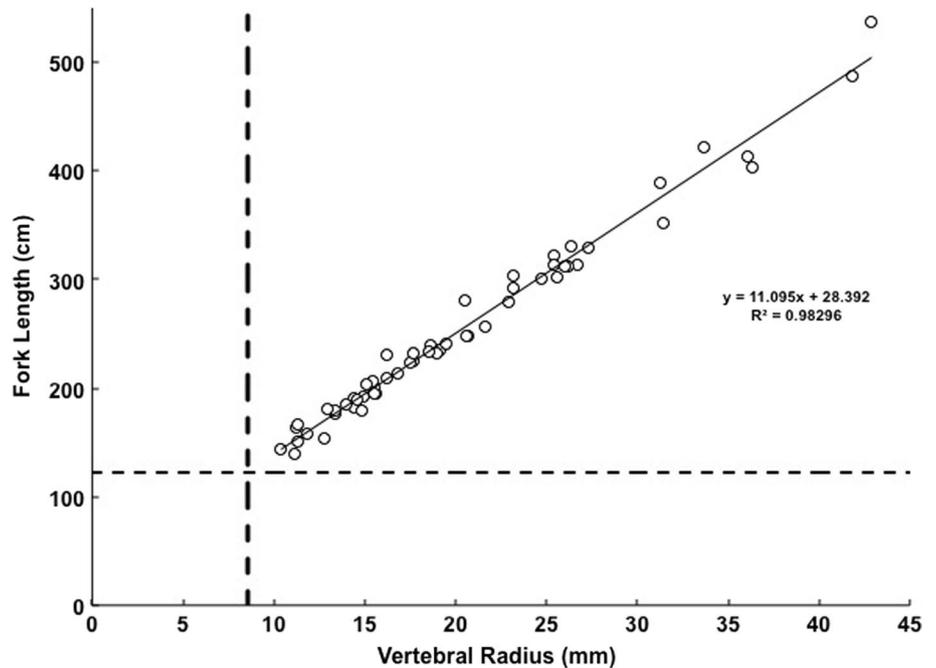
The youngest ages determined by band pair counts for the SWI were one (140 cm FL female) and four years old (151 cm FL male). The oldest estimated age for both sexes was 38 years (403 cm FL and 414 cm FL, female and male, respectively; Fig. 4). The CV for three replicate counts was

Table 3 Summary of bomb radiocarbon dating results for white sharks (*Carcharodon carcharias*) using untreated vertebral samples from this study compared to demineralized samples from previous studies [northeast Pacific Ocean (NEP; Kerr et al. 2006); northwest Atlantic Ocean (NWA; Hamady et al. 2014)]

Shark ID	Current study			Original study		
	Estimated age (years)	Band sampled	$\Delta^{14}\text{C}$ (untreated)	Estimated bomb $\Delta^{14}\text{C}$ age (adjusted age)	Band sampled	$\Delta^{14}\text{C}$ (demineralized)
<i>Northeast Pacific Ocean</i>						
WH 1	21	0.5	-43.29	7 (>22)	1	-59.7
WH 3	6	1	-181.16	3 (12)	1	-72.2
WH 17	46	1.5	-148.94	18 (30, 37+)	2	-74.1
		23	-181.16		7	-65.6
		38	-3.67		12	-29.2
					17	34.7
<i>Northwest Atlantic Ocean</i>						
WS 57	31	8	-68.2	44	1	-54.97
		18	4		17	-62.25
WS 100	8	0.5	-22.7	9	1.5	1.83
WS 105	66	38.5	-77.1	73	1	-60.34
		52	10.9		42	-57.07

Estimated age is that based on band pair counting from the current study. Estimated bomb $\Delta^{14}\text{C}$ age determined in the NEP and the NWA by bomb radiocarbon analysis presented in the original studies (Kerr et al. 2006; Hamady et al. 2014); adjusted age for the NEP sharks accounts for missing annuli according to Andrews and Kerr (2015)

Fig. 3 Relationship between vertebral radius and fork length for white sharks (*Carcharodon carcharias*) in the southwest Indian Ocean. The horizontal line represents the size at birth calculated in this study (129 cm), and the vertical line represents the mean radius of the birth mark (8.6 mm, $n = 36$)



17.4 %. Two mature females included in this study were aged 30 (487 cm FL) and 31 (537 cm FL) years; however, one 38-year-old female (403 cm FL) was immature. The three mature males were aged 16 (312 cm FL), 18 (352 cm FL), and 38 (414 cm FL) years.

Growth analysis

Growth curves were generated using band pair counts from the 55 vertebral samples including the four unadjusted ages from bomb carbon sampled animals (Fig. 4). The

Fig. 4 Gompertz growth curve based on vertebral band pair counts for white sharks (*Carcharodon carcharias*) from the southwest Indian Ocean (SWI). Individuals aged by bomb radiocarbon analysis and using unadjusted ages are indicated by squares (open, females $n = 2$; closed, male $n = 2$). Open circles (females, $n = 28$) and black circles (males, $n = 23$) indicate length at age data for each individual. The solid black line is the Gompertz growth model with 95 % confidence intervals (dashed lines)

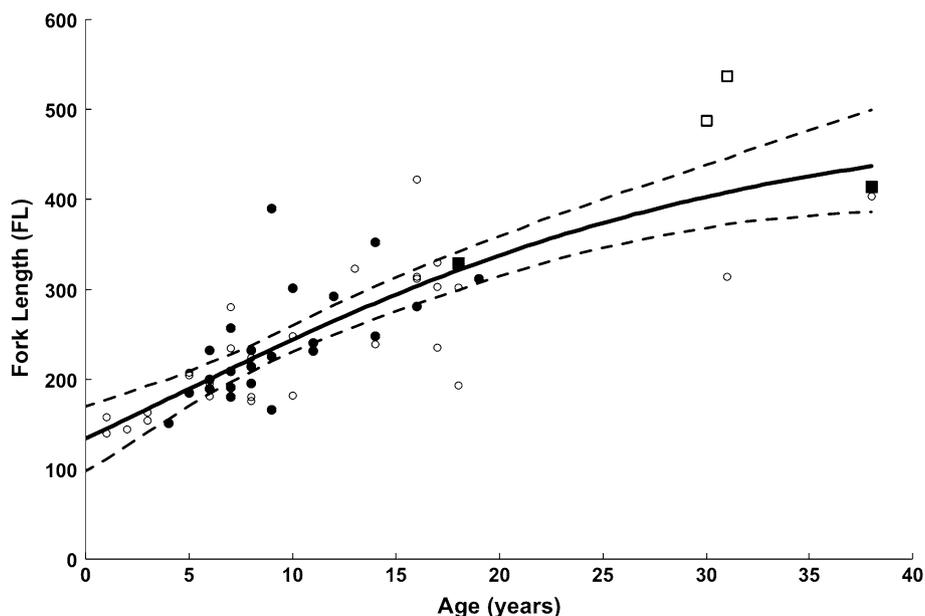


Table 4 Relative goodness of fit for each candidate growth model for white sharks (*Carcharodon carcharias*) from the southwestern Indian Ocean based on 55 sharks (including the four bomb carbon specimen with unadjusted ages)

Model	k	AIC _c	Δ_i	w_i	LL
Gompertz	4	595.20	0	0.31	-293.20
Logistic	4	595.23	0.03	0.31	-293.22
von Bertalanffy	4	595.31	0.11	0.29	-293.26
Schnute general model	5	597.62	2.42	0.09	-293.20

Models are ranked from best to worst fit

k = total number of regression parameters, including the error term; AIC_c = second-order Akaike information criterion; Δ_i = Akaike difference; w_i = Akaike weight; and LL = log-likelihood

Gompertz, logistic, and von Bertalanffy growth models all had $\Delta_i < 2$, indicating they were statistically indistinguishable (Table 4). The Gompertz growth curve had the lowest AIC value and estimated parameters that were the most biologically realistic; therefore, it was chosen as the most appropriate model (Fig. 4; Table 5). Using adjusted ages for the four bomb radiocarbon specimens to the porbeagle reference chronology along with the 51 ages estimated from band counts, the Schnute general model would not converge; however, the other three models were statistically indistinguishable (Table S2). When the age for the four bomb radiocarbon specimens was adjusted to the coral reference chronology, the Gompertz, logistic, and von Bertalanffy growth models all had $\Delta_i < 2$, indicating they

Table 5 Growth model parameters for white sharks (*Carcharodon carcharias*) from the southwest Indian Ocean based on vertebral age estimates and including the four bomb carbon specimen with unadjusted ages

Model	a	b	L_1	L_2	L_∞	L_0	t_0
Gompertz	0.061 (0.02–0.10)	0	144.90 (113.18–176.03)	436.80 (388.80–502.89)	496.77 (404.37–947.57)	134.08 (98.85–168.03)	–
Logistic	0.091 (0.050–0.14)	-1	150.41 (121.32–179.90)	434.77 (384.83–501.17)	466.03 (392.62–692.53)	141.28 (110.00–173.10)	–
von Bertalanffy	0.03 (0.00–0.07)	1	138.47 (99.28–176.67)	439.96 (390.92–501.43)	583.53 (-440.06 to 2018)	124.65 (77.88–168.54)	-7.86 (-23.02 to -2.98)
Schnute general model	0.07 (-0.12 to 0.32)	-0.18 (-7.06 to 6.30)	145.97 (86.59–175.14)	436.36 (384.50–498.95)	489.15 (385.39–1006.79)	135.53 (63.18–168.60)	–

The bootstrap 95 % confidence intervals for each parameter are indicated in parentheses below the number

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 = estimated length at age 1; L_2 = estimated length at age 38; L_∞ = asymptotic fork length; L_0 = length at birth; t_0 = theoretical age at zero length. All lengths presented are given in fork length (cm)

were statistically indistinguishable. For all 7 models using adjusted age data, the AIC values were higher than when the original bomb radiocarbon ages were used. In addition, the confidence intervals for estimated parameters were greater for models that included adjusted ages (Table S3). Ages that were not adjusted to reference chronologies were consequently used as the best estimate for growth parameters of white sharks in the SWI (Fig. 4; Table 5).

Discussion

The current study provides evidence to support annual band deposition for white sharks from the SWI to 30–38 years of age, accounting for error associated with the year of band formation. Bomb radiocarbon assay samples of SWI white sharks were not adjusted to account for a cessation of band pair growth because individual error associated with the assigned year of formation (CV) overlapped with the $\Delta^{14}\text{C}$ reference chronologies. While the current precedent in the literature is to adjust ages to a reference chronology, there is no standard agreement on the most appropriate reference chronology to use (i.e., coral reference chronology vs. porbeagle reference chronology; see Hamady et al. (2014); Andrews and Kerr (2015)). Additionally, the directional shift in year of band formation was not uniform (i.e., individual $\Delta^{14}\text{C}$ values were both to the left and right of the reference chronologies). It is possible that the oldest sharks from the SWI in this study were over aged; however, when $\Delta^{14}\text{C}$ data from this study were shifted to align with either reference chronology, growth model fit was worse and confidence intervals for model parameters were greater than for models with unadjusted data. Therefore, using the unadjusted ages was deemed to provide the best estimate of age and growth for white sharks in the SWI.

Recent studies using bomb radiocarbon to validate the age of white sharks in the NEP and NWA described years of life that were not recorded in the band pairs of the vertebrae, requiring the $\Delta^{14}\text{C}$ chronologies to be shifted to align with the reference chronology. Hamady et al. (2014) found that one individual estimated to have 44 band pairs corresponded with the bomb radiocarbon reference chronology; however, two individuals with 33 and 35 band pairs required age estimates to be corrected (+7 and -3, respectively) to align with the bomb radiocarbon reference chronology. In contrast, in the reanalysis of the Kerr et al. (2006) data, individuals previously aged as young as three years old required a correction for band pairs that were not continuously formed to align with the reference chronology (Andrews and Kerr 2015). This correction increased the age estimate of three individuals by 9–15 years. The maximum age of these white sharks was limited by the coral reference chronology; however, details on the early part of growth

were not available for WH 17 and therefore the maximum age may have been higher (Andrews and Kerr 2015). The variability in occurrence of missing annuli among the three white shark studies indicates that the age at which growth ceases or slows is not consistent. Additional samples from pre-bomb years and during the rapid increase in $\Delta^{14}\text{C}$ would be required to fully determine whether band pair deposition ceases in the vertebrae of the SWI population.

Diet is the main source of carbon in the vertebral collagen of sharks (Fry 1988; Campana et al. 2002), and the transfer of carbon from prey is considered to be slower than the direct uptake of dissolved inorganic carbon DIC (i.e., the carbon source for corals and fish otoliths). This delay can cause a phase shift in the $\Delta^{14}\text{C}$ values of vertebrae toward more recent years. Furthermore, this effect increases with trophic level and, for species that are known to feed on carbon-depleted sources (i.e., deepwater prey), the effect is more evident (Campana et al. 2002; Kerr et al. 2006). White sharks off southern Africa use offshore (deepwater) resources (Hussey et al. 2012; Smale and Cliff 2012) that incorporate a more depleted $\Delta^{14}\text{C}$ value (Broecker and Peng 1982; Campana 1999). Thus, the slight lag of white shark $\Delta^{14}\text{C}$ values for two of the white sharks (IFA91016 and Kenya96) compared to the Watamu Reef coral reference chronology is expected and has been observed in several species including the porbeagle (Campana et al. 2002) and shortfin mako (*Isurus oxyrinchus*; Ardizzone et al. 2006) sharks. Accepting age and analytical error, the Gansbaai assay samples approximately aligned with the Watamu Reef coral chronology and then shifted to approximately align with the porbeagle reference chronology potentially reflecting a diet shift, which is known to occur in white sharks (Tricas and McCosker 1984; Estrada et al. 2006; Hussey et al. 2012). Diet shifts over ontogeny have also been observed in the $\Delta^{14}\text{C}$ chronologies of tiger (*Galeocerdo cuvier*) sharks, where assay samples from the juvenile portion of the vertebrae aligned with the coral reference chronologies, while that of adults were phase lagged and were more closely aligned with the porbeagle chronology (Kneebone et al. 2008).

The percentage of organic and inorganic material can vary along the vertebrae, leading to unequal contributions from different carbon sources (Hamady et al. 2014), and therefore, it has been suggested that collagen (the organic portion) should be isolated to obtain an unbiased (by DIC) $\Delta^{14}\text{C}$ value (Kerr et al. 2006; Hamady et al. 2014). Kerr et al. (2006) conducted a preliminary study using replicate samples from three individuals to compare the effects of demineralization and determined that untreated samples were enriched in ^{14}C relative to the demineralized samples. The opposite effect was observed in the current study, whereby the untreated samples were more depleted in ^{14}C than the demineralized samples from the original study

(Kerr et al. 2006). The degree of mineralization within shark vertebrae varies by species (Porter et al. 2006), indicating that species-specific studies are required to examine the effect of demineralization on $\Delta^{14}\text{C}$ values in elasmobranch vertebrae. Currently, there is no consensus on the requirement for demineralization, and bomb radiocarbon analysis has been successfully tested on multiple species both with (Ardizzone et al. 2006; Kerr et al. 2006; Andrews et al. 2011; Hamady et al. 2014) and without (Campana et al. 2002; Francis et al. 2007; Passerotti et al. 2014) performing demineralization prior to analyzing the vertebrae for $\Delta^{14}\text{C}$. As there are likely differences in age and growth parameters among populations of a species, a systematic study examining the effects of demineralization on the $\Delta^{14}\text{C}$ value of vertebral tissue in sharks is required. A standard sample preparation protocol would benefit cross-study comparisons.

The $\Delta^{14}\text{C}$ values for the SWI white sharks were relatively enriched compared to $\Delta^{14}\text{C}$ values for white sharks from the NWA and NEP in both the current and original studies (Kerr et al. 2006; Hamady et al. 2014; Andrews and Kerr 2015), confirming that differences in $\Delta^{14}\text{C}$ values among the three populations were not due to the methodological differences. Direct comparison between $\Delta^{14}\text{C}$ values for the individual sharks from the NWA in this study and the original study (Hamady et al. 2014) could not be made, as samples were not taken from the exact same locations in the vertebrae. The $\Delta^{14}\text{C}$ values from the current study were within the range of $\Delta^{14}\text{C}$ values reported by Hamady et al. (2014), however, suggesting that there is little to no effect of demineralization on $\Delta^{14}\text{C}$ values in white shark vertebrae. The difference in $\Delta^{14}\text{C}$ values for NEP white sharks between the current study and the original study may be a result of samples being extracted from a slightly different location on the vertebrae for this study compared to Kerr et al. (2006).

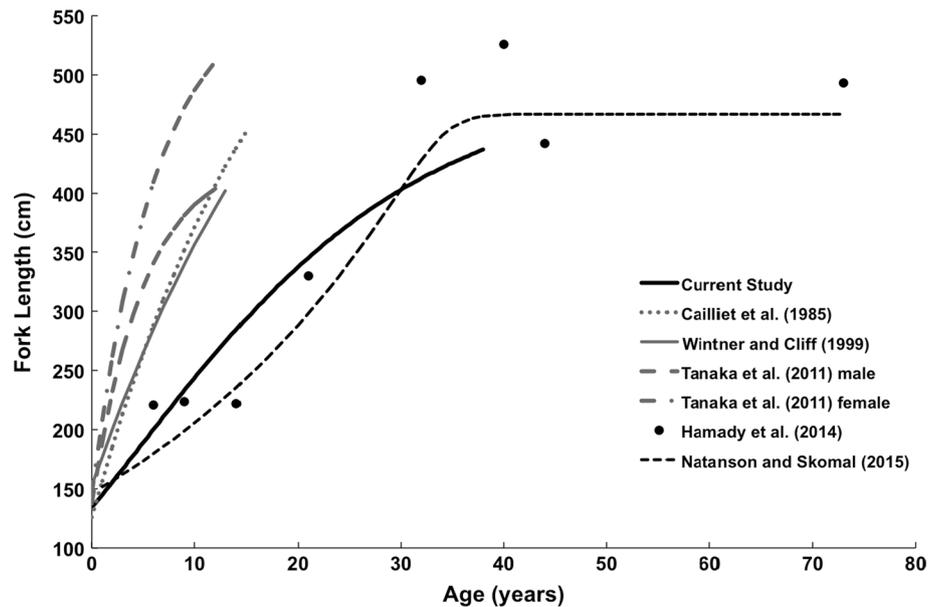
The amplitude of the $\Delta^{14}\text{C}$ values in the coral from Watamu Reef is greater, and the timing of the rapid increase in ^{14}C slightly lags that of coral reef chronologies in the Atlantic and Pacific Oceans (Druffel and Linick 1978; Druffel 1989; Druffel et al. 2001; Roark et al. 2006). However, two individuals (one each from NEP and NWA) had good alignment with the Watamu Reef coral reference chronology (WH 1, WS 100). The earliest band formed in specimens WS 57 and WS 105 was not sampled, but the two assayed samples from each specimen (ages 31 and 66, respectively) were phased lagged and more in line with the porbeagle reference chronology, possibly indicating that these two individuals underwent a diet shift. The highly depleted $\Delta^{14}\text{C}$ values for WH 3 and WH 17 were not expected, but highly depleted $\Delta^{14}\text{C}$ values were also reported for a white shark (WH 6) in the NEP (Kerr et al. 2006). While we could not align WH 17 with either

reference chronology, the timing of its increase in $\Delta^{14}\text{C}$ aligns with the rapid increase in $\Delta^{14}\text{C}$ observed in the reference chronologies. White sharks have been documented using deepwater carbon sources in the NEP which is likely influencing the $\Delta^{14}\text{C}$ values in this region and further complicating the interpretation of these specimens (Kerr et al. 2006; Andrews and Kerr 2015). The absolute differences in $\Delta^{14}\text{C}$ values among populations are likely due to depth and water mixing rates of the different ocean basins (Weidman and Jones 1993; Kalish 1995; Campana 1999), which is supported by the $\delta^{13}\text{C}$ variability observed in the sampled white sharks (Table 2). Individual migration patterns and changes in migration/residency throughout ontogeny could also contribute to the recorded variation in $\delta^{13}\text{C}$ values. The highly depleted $\delta^{13}\text{C}$ value for WH 17 (-29.8‰) was unexpected given the range of $\delta^{13}\text{C}$ values measured in this specimen, and this value is likely an anomaly (due to measurement error). Further investigation is required to determine whether the highly depleted $\Delta^{14}\text{C}$ values in the NEP are a common occurrence.

Age estimates for white sharks from the SWI in this study indicate the maximum age (30–38 years) is older than previously estimated (13 years, 373 cm PCL) by Wintner and Cliff (1999). The Wintner and Cliff (1999) study, however, did not include larger sharks such as those used in the current study. This new maximum age range for SWI sharks that accounts for error in age estimates and difference between sexes agrees with that observed in the NEP (~ 30 ; Andrews and Kerr 2015), but is younger than that determined for the NWA ($\sim 73, 44$; Hamady et al. 2014; Natanson and Skomal 2015). The differences in the maximum age among populations are likely due to the specimens available (i.e., Fig. 5, the number of large animals and the largest sharks included) and not due to absolute differences in the maximum age among populations, although this needs to be confirmed. Additionally, it has been suggested that males are older than females at similar body sizes (Hamady et al. 2014); therefore, the lack of large males in this study could have contributed to the lower maximum age.

Dudley and Simpfendorfer (2006) determined that the size at 50 % maturity for male white sharks captured in the KZN beach protection program was 344 cm FL; using the growth curve from the current study, the age at 50 % maturity for males is 20 years old, whereas using the previous growth curve (Wintner and Cliff 1999) the age at 50 % maturity would be 12 years old. The minimum age of mature individuals in this study (16 (312 cm FL) and 30 (487 cm FL) years for males and females, respectively) was greater than previous estimates of 8–10 years (325–352 cm FL; males) and 12–13 years (390 cm FL females; Wintner and Cliff 1999). However, the age of the smallest mature white shark in this study is slightly lower than the age of

Fig. 5 Comparative white shark (*Carcharodon carcharias*) growth curves. Gompertz growth curve from this study. Also included are the Schnute general model growth curve from Natanson and Skomal (2015) and von Bertalanffy growth curves from Cailliet et al. (1985), Wintner and Cliff (1999), and Tanaka et al. (2011). Bomb radiocarbon estimated ages from Hamady et al. (2014) are indicated by black circles



maturity for white sharks in the NWA (26 (352 cm FL) and 33 (417 cm FL) years for males and females, respectively; Natanson and Skomal 2015). Due to the range in size, 271–365 cm FL (males) and 390–464 cm FL (females), at maturity reported for white sharks globally (Cailliet et al. 1985; Francis 1996; Pratt 1996; Wintner and Cliff 1999; Tanaka et al. 2011) and the relatively small sample size, it is likely that there is an overlap in the age at maturity between the two populations.

Accepting that the largest individuals included in previous studies that used X-ray analysis were smaller than those included in the current study, growth curve parameters estimated that white sharks in the SWI are slower-growing than previously suggested by Cailliet et al. (1985), Wintner and Cliff (1999), and Tanaka et al. (2011; Fig. 5). The growth curve parameters from the current study were similar to those recently estimated for white sharks in the NWA using validated band pair counts (Hamady et al. 2014; Natanson and Skomal 2015; Fig. 5), providing additional support for these values. The estimation of L_{∞} was limited by the small number of large individuals included in this study, which led to wider confidence intervals. Including additional large individuals would be required to provide greater confidence in the L_{∞} estimate.

A recent population estimate (Towner et al. 2013) determined that while the population of white sharks in Gansbaai, South Africa, is larger than at other aggregation sites, there has not been a marked increase in population size since a previous population estimate undertaken 16 years prior (Cliff et al. 1996b). Given the evidence for a low rebound potential for white sharks (Smith et al. 1998), the higher ages at maturity found in this study could provide a plausible explanation for why this population has not

recovered. Regional management plans for this species should account for slower growth, later age at maturity, and longer life spans.

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