

Annual bands in vertebrae validated by bomb radiocarbon assays provide estimates of age and growth of whale sharks

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The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest

Author contribution statement

MM and SC conceived of the idea, HH and PF provided the vertebral samples. JO did the sample preparation and analyses for vertebrae aging. SC contributed bomb radiocarbon results and verified aging results. JO wrote the manuscript, with critical feedback and help from SC, MM, PF and HH.

Keywords

Whale shark, vertebrae, age determination, Validation, radiocarbon dating, Longevity, Growth

Abstract

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Conservation and management strategies for endangered and threatened species require accurate estimates of demographic parameters such as age and growth. The whale shark, Rhincodon typus, is the largest fish in the world and is highly valued in the eco-tourism sector. Despite conservation concerns and advances in our understanding of their life history, basic demographic parameters for growth, longevity and mortality are of questionable accuracy; previous growth studies could not agree whether the vertebral growth bands were formed annually or biannually. Here, we provide the first validation of the annual formation of growth bands within the vertebrae of the whale shark using bomb radiocarbon assays. Ages of up to 50 years were estimated from sectioned vertebrae of sharks collected in Taiwan and Pakistan. There was no cessation of the formation of growth bands in the vertebrae of older sharks and our study provides the oldest observed longevity for this species. Initial estimates of growth (k = 0.01–0.12) and natural mortality rates (M = 0.09) are consistent with those expected of long-lived sharks, which highlights their sensitivity to fishing pressure and conservation concerns.

Contribution to the field

Despite huge conservation interest in whale sharks and considerable advances in the understanding of movement, behavior, connectivity and distribution of this iconic species over the last ten years, limited demographic data, such as age, growth and mortality estimates exist. This is in part because of the lack of availability of whale shark vertebrae, especially old and large specimens. Few studies have attempted to age whale shark vertebrae and discrepancies exists within these studies, such as the annual or biannual formation of growth bands. This manuscript provides the first age validation using bomb radiocarbon assays for the vertebrae of whale sharks. We confirm that growth bands are formed annually in sectioned vertebrae, and that there is no cessation of growth bands in this species, up to at least 50 years old. This study also records the oldest observed longevity of 50 years for whale sharks. Additionally, we provide initial estimates of longevity, growth and natural mortality to improve the accuracy of future population models. We strongly believe that our findings contribute significantly to the conservation efforts of whale sharks at a global scale.

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3

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18 Abstract

- 19 Conservation and management strategies for endangered and threatened species require accurate
- estimates of demographic parameters such as age and growth. The whale shark, Rhincodon 20
- 21 *typus*, is the largest fish in the world and is highly valued in the eco-tourism sector. Despite
- conservation concerns and advances in our understanding of their life history, basic demographic 22
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- 29 provides the oldest observed longevity for this species. Initial estimates of growth (k = 0.01-30 (0.12) and natural mortality rates (M = 0.09) are consistent with those expected of long-lived
- sharks, which highlights their sensitivity to fishing pressure and conservation concerns. 31

32 **Keywords**

33 Whale shark, vertebrae, age determination, radiocarbon, longevity, growth bands

34 Introduction

35 Accurate and reliable estimates of the age and growth of individuals in a population are central to

36 effective strategies for the management and conservation of any species. For teleost marine

37 fishes, estimates of age are usually obtained from counts of the annual growth bands formed

38 within otoliths, which are calcified structures within the skull case (Campana, 2001). For

39 elasmobranchs such as sharks, skates and rays, which lack otoliths, age estimates have been

40 calculated from growth bands formed in the vertebrae (Cailliet, 1990).

41

42 It is critical that age estimates provided by otoliths and vertebrae are accurate, since uncertainty

43 or underestimates surrounding these ages can lead to stock collapses of exploited species (e.g.,

- 44 orange roughy *Haplostethus atlanticus*; Smith et al., 1995), or compromise the effectiveness of
- 45 recovery programs for species that are threatened or endangered. For this reason, many studies
- 46 have sought to validate the timing of the production of growth bands (Campana, 2001). A
- 47 common approach is to tag individuals with a chemical marker such as oxytetracycline (OTC)
- 48 that is laid down within an otolith or vertebrae. Individuals are released and when recaptured at
- 49 some time in the future, the tag acts as a time stamp that allows the rate of deposition of
- 50 subsequent growth bands to be determined. For large fishes and sharks that are relatively long-
- 51 lived and difficult to tag and recapture, validation of annual banding patterns can also be
- 52 obtained through an analysis of bomb radiocarbon in vertebrae. Above-ground testing of
- thermonuclear weapons in the 1950s and 60s increased the ratio of carbon 14 isotopes in the
- 54 atmosphere that were then mixed into the ocean, passed up food webs and incorporated into
- 55 marine organisms. As a result, the timing of the deposition of bands can be validated by
- 56 comparing carbon isotope values within vertebrae, with an isotope baseline chronology of known

age (Campana, 2001; Campana et al., 2002; Goldman et al., 2012).

58

59 The whale shark, *Rhincodon typus*, is a huge (up to 18 m length; McClain et al., 2015), highly

60 migratory, filter-feeding shark found in all tropical and warm temperate seas (Compagno, 2001;

61 Chen et al., 2002; Stevens, 2007). It forms aggregations in productive coastal areas and is a

62 highly valued target for marine eco-tourism (e.g., Huveneers et al., 2017). However, the whale

63 shark has recently been classified as Endangered (IUCN Red List; Pierce and Norman, 2016) and

64 there is now an urgent need for reliable and accurate information on age and growth of the

65 species in order to develop effective conservation and management strategies. At present, there is

- 66 relatively little demographic data available, especially for large or mature individuals. Using X-
- 67 radiography, Wintner (2000) analysed the growth bands in whole vertebrae of juveniles that had
- 68 stranded on the coast of South Africa to develop an initial growth curve for the species. More
- 69 recently, Hsu et al. (2014) provided growth and age estimates for individuals collected from a
- 70 fishery in Taiwan and used marginal increment ratios and centrum edge analysis to conclude that
- 71 growth bands were deposited biannually in both whole and sectioned vertebrae. The reliability of
- the age estimates of these studies remains unknown and is of concern, because other studies

- show that whole vertebrae are known to provide underestimates of age and longevity, and thus
- overestimates of growth rate in slow-growing sharks (Cailliet and Goldman, 2004; Harry, 2018;
- 75 Natanson et al., 2018). To our knowledge, only one study has attempted to validate an ageing
- 76 method for whale sharks, which involved a captive immature shark reared in an aquarium after
- being fed OTC. When the animal died two years later, two growth bands were observed
- 78 following the OTC mark (Wintner, 2000).
- 79
- 80 Here, we provide the first age validation of whale sharks using bomb radiocarbon assays. We
- 81 then used sectioned vertebrae from a small sample of sharks to provide initial estimates of
- 82 growth, longevity and mortality data that can be used in support of current conservation and
- 83 management efforts.

84 Methods

85 <u>Sample collection</u>

- A subset of vertebral samples were taken from 92 vertebral samples that were previously
- 87 published in Hsu et al. (2014). These were dead individuals that had been landed by the
- 88 Taiwanese fishery, before the whale shark fishery was closed in November 2007 (Hsu et al.,
- 89 2012). The vertebral sample from Pakistan was obtained from a dead stranded whale shark.

90 Sample preparation and age interpretation

- 91 The vertebral samples from Hsu et al. (2014) were sectioned with a single cut using paired
- 92 blades separated by a spacer on an Isomet low-speed diamond-bladed saw. Sections were
- 93 digitally photographed at 2048 x 1536 resolution using a digital color Leica camera DFC295
- 94 mounted on a stereo microscope Leica M205C (Leica Microsystems, Germany), while immersed
- 95 in ethanol. Age interpretation was based on images enhanced for contrast using Adobe
- 96 Photoshop CS6, following the interpretation criteria of Natanson et al. (2002). The precision of
- 97 the age determinations was quantified with both average percent error (APE) and coefficient of
- 98 variation (CV) (Campana, 2001).

99 <u>Bomb radiocarbon analyses</u>

- 100 Vertebrae used for bomb radiocarbon age validation were taken from two specimens that had
- 101 died after becoming entangled in fishing gear. A 10 m total length (TL) female with an estimated
- 102 weight of 7000 kg was landed in Karachi, Pakistan in Feb 2012. One of the cervical vertebrae
- 103 was cleaned of tissue and then stored frozen. A second individual, a mature male weighing 8500
- 104 kg with TL of 9.9 m was landed in Taiwan in April 2005. A cervical vertebra over the gills was
- 105 extracted and stored in ethanol until assay. Vertebral growth bands from both sharks were
- 106 isolated from 1 mm thick longitudinal sections of the vertebrae. All sections were prepared
- 107 using the same procedure outlined above. Sections were digitally photographed at 2048 x 2048

108 resolution under a binocular microscope at 16-40X magnification using reflected light while

- 109 immersed in ethanol.
- 110

111 Multiple samples from each of the vertebral sections (N = 11 samples; 5-13 mg each) were 112 extracted from growth bands visible in the corpus calcareum region while working at 16X 113 magnification under a binocular microscope. For the shark landed in Taiwan, the first three 114 growth bands were extracted as a single sample from the vertebral section. For the shark landed 115 in Pakistan, the first-formed growth band (distal to the birth band) was extracted, as were 116 individual growth bands corresponding to later growth. Extracted samples were isolated as solid 117 pieces using a Gesswein high-speed hand tool fitted with steel bits < 1 mm in diameter. The 118 presumed date of sample formation was calculated as the year of shark collection minus the 119 annulus count from the birth band to the mid-point of the sample. After sonification in Super Q 120 water and drying, the sample was weighed to the nearest 0.1 mg in preparation for ¹⁴C assay with accelerator mass spectrometry (AMS). AMS assays also provided δ^{13} C (‰) values, which were 121 122 used to correct for isotopic fractionation effects. Radiocarbon values were subsequently reported as Δ^{14} C, which is the per mil (‰) deviation of the sample from the radiocarbon concentration of 123 124 19th-century wood, corrected for sample decay prior to 1950 according to methods outlined by 125 Stuiver and Polach (1977). The mean standard deviation of the individual radiocarbon assays 126 was about 4‰.

127

128 To assign dates of formation to an unknown sample, it is necessary that the Δ^{14} C of the unknown

129 sample be compared with a Δ^{14} C chronology based on known-age material (a reference

130 chronology). Since whale sharks are surface planktivores, we assumed that a reference

131 chronology for dissolved inorganic carbon (DIC) in surface waters was most appropriate for our

analysis. Therefore, we used a reference chronology developed from young known-age otoliths

- 133 (calcium carbonate) in the northwest Atlantic (Campana et al., 2008), which has a period of
- increasing bomb radiocarbon values nearly identical to that of surface waters off of both Pakistan
- and Taiwan (Andrews et al., 2011a). We also included another reference chronology based on

136 corals from the Mentawai Islands in Sumatra, Indonesia (Grumet et al., 2004).

137 <u>Growth models</u>

138 Preliminary growth estimates were obtained from length-at-age data using two types of growth

139 model. The first was a conventional 3-parameter von Bertanlanffy growth function (von

140 Bertalanffy, 1938) and the second was a logistic growth function (Smart et al., 2013) with

- 141 length-at-birth fixed at 60cm (Chang et al., 1997).
- 142

143 3-parameter von Bertanlanffy growth function:

144
$$L_t = L_0 + (L_\infty - L_0)(1 - e^{-kt})$$

145

146 Logistic growth function with fixed length-at-birth:

147
$$L_t = \frac{L_{\infty}L_0 e^{kt}}{L_{\infty} + L_0 (e^{kt} - 1)}$$

148

149 where L_t is length-at-age t, L_0 is length-at-age 0, L_{∞} is asymptotic length and k is the growth 150 coefficient.

151

Longevity estimates generally require either a precisely defined growth model or an estimate of
mortality rate, neither of which were available here. Therefore, only the observed maximum age
is reported here. Natural mortality was estimated from two equations. The first was based on the
linear regression equation of observed maximum age (Hoenig, 1983):

- 156
- 157 158

 $\ln(M) = 1.44 - 0.982 \times \ln(t_{max})$

The second natural mortality estimate was based on the non-linear least squares equation of observed maximum age, with a prediction error of 0.32 (Then et al., 2015):

161

163

 $M = 4.899 \times t_{max}^{-0.916}$

164 where M is the estimated instantaneous rate of natural mortality and t_{max} is the observed 165 maximum age.

166 **Results**

167 <u>Counts of growth bands in vertebrae samples</u>

168 All vertebrae exhibited distinct growth band (annulus) patterns (Fig. 1). The birth mark was

169 identified as the most pronounced first band. Subsequent annuli consisted of a pair of alternating

170 opaque and translucent bands that crossed the entire centrum, except in the oldest sharks. Band

width decreased with age, narrowing substantially in the oldest individuals (Fig. 1). Counts of

growth bands in 20 sharks ranged from 15 to 50 (Table 1). Ageing precision was acceptable

across both readers, with an average percent error (APE) of 5.5% and coefficient of variation

174 (CV) of 8.2%.

175 <u>Bomb radiocarbon assays and age validation</u>

176 The date of formation of the vertebral samples was estimated in two ways: (1) through age

177 determination of the shark based on growth band (annulus) counts; and (2) through comparison

178 of annulus Δ^{14} C values with the values known to be present in surface marine waters at the time

179 (the NWA reference chronology). Agreement between the annulus- and Δ^{14} C -based dates would

180 confirm that the annuli were interpreted correctly for age estimation, at least on average. Under-

181 or over-ageing of annuli would be apparent as a left or right phase-shifting of the reference curve

182 relative to the assay values.

- 183
- 184 Eleven samples from two whale sharks, aged 35 and 50 years based on growth band counts, were
- analyzed for Δ^{14} C (Table 2). Assay values ranged between 15.1 70.0. Two of the samples,
- 186 including one with the earliest date of formation (1962.5), were too depleted in Δ^{14} C (15.1 and
- 187 20.6) to have formed post-bomb (Fig. 2), but no pre-bomb samples were identified. The
- 188 remaining Δ^{14} C values all ranged between 40 and 70, which is consistent with a post-bomb year
- 189 of formation. All samples were characterized by δ^{13} C values consistent with typical shark
- 190 vertebrae of metabolic origin (mean = -13.6; SE = 0.4; Table 2).
- 191
- 192 All of the assay values aligned well with the reference chronologies (Fig. 2a), with no obvious
- 193 bias to one side or the other. Since errors in growth band counts would result in misalignment of
- 194 the reference and assay values, the assay results indicate that the two sharks must have been aged
- 195 correctly, at least on average. The 35-year old shark from Taiwan was least informative in this
- 196 respect, since its post-bomb assay value indicated only that the shark could not have been over-
- aged by more than 10 years. On the other hand, ageing error of more than about 5 years would
- 198 have been apparent as an obvious misalignment in the 50-year old Pakistan shark.
- 199 Preliminary growth, longevity and mortality estimates
- 200 Both sexes were combined for estimation of growth (Fig. 2b). The von Bertanlanffy growth
- function produced an asymptotic length $L_{\infty} = 2189$ cm and a growth coefficient k = 0.014 year⁻¹.
- 202 The logistic growth function with a fixed length-at-birth $L_0 = 60$ cm produced estimates of $L_{\infty} =$
- 203 1071 cm and k = 0.122 year⁻¹. We caution, however, that the estimates of asymptotic length and
- 204 growth coefficients are uncertain because of low sample size. The maximum observed age was
- 205 50 years based on vertebral ageing and bomb radiocarbon assays. The Hoenig (1983) estimated
- rate of instantaneous natural mortality was 0.09 year⁻¹, while the estimate from Then et al. (2015)
- 207 was 0.14 year^{-1} .

Table 1. Summary details for vertebral samples. TL = total length (cm). RT19 and RT20 were

samples used in the bomb radiocarbon analyses. All samples were collected in Taiwan except forRT20, which was collected in Pakistan.

ID	Date of collection	Sex	TL (cm)	Weight (kg)	Growth bands
RT01	18 Mar 2001	F	425	760	23
RT02	26 May 2005	F	345	400	18
RT03	NA	М	596	2000	24
RT04	NA	NA	NA	NA	18
RT05	NA	М	423	750	18
RT06	NA	М	391	600	21
RT07	18 May 2005	М	421	700	25
RT08	30 Sep 2005	М	372	350	20
RT09	26 Apr 2005	М	358	360	16
RT10	3 July 2005	Μ	494	1100	16
RT11	6 Oct 2005	F	NA	NA	15
RT12	2 Jul 2005	М	503	905	18
RT13	13 Sep 2005	Μ	300	200	18
RT14	10 Jul 2005	Μ	430	450	19
RT15	18 Jun 2005	Μ	386	450	17
RT16	NA	NA	NA	NA	19
RT17	10 Oct 2005	М	526	NA	19
RT18	3 May 2005	Μ	268	123	17
RT19	Apr 2005	Μ	990	8500	35
RT20	Feb 2012	F	1000	7000	50

211

Growth bands sampled 1-3	Date of formation 1972.0	δ ¹³ C (‰)	$\Delta^{14}C$ (‰)	-
1-3	1972.0	-15.1		
		1011	81.3	
0-1	1962.5	-13.3	15.1	
1	1962.5	-13.3	15.1	
2	1963.5	-13.9	59.4	
3	1964.5	-13.1	70.0	
4	1965.5	-12.9	70.0	
5	1966.5	-15.5	40.0	
5	1966.5	-15.6	40.0	
6	1967.5	-12.8	20.6	
10	1971.5	-12.1	63.4	
15	1976.5	-11.9	45.0	_

212 Table 2. Details for bomb radiocarbon assays. RT19 was collected in Taiwan and RT20 was

- Figure 1. Images of sectioned whale shark vertebrae with annotations of growth bands. (A)
- 216 Vertebra from Taiwan (RT04) showing 18 growth bands. (B) Vertebra from Pakistan (RT20)
- used for bomb radiocarbon assay showing 50 growth bands. Scale bars -1 cm.





- Figure 2. Results of bomb radiocarbon assays and growth models. (A) Bomb radiocarbon (Δ^{14} C)
- 221 results of whale shark vertebrae from two locations (Pakistan red crosses; Taiwan blue
- 222 diamond) compared to two reference chronologies (carbonate surface water reference from north
- 223 west Atlantic solid line; coral reference from Sumatra dashed line). (B) Length-at-age data
- fitted with logistic (solid purple) and von Bertanlanffy (dashed red) growth models. Data pooled
 - between sexes for both models. (A) 100 50 Δ¹⁴C (‰) 0 NWA reference Sumatra Coral Pakistan Taiwan -50 1940 1960 1980 2000 Year of sample formation (B) 1000 Logisti Von Bertanlanffy 800 Total Length (cm) 600 Sex F 400 M 40 50 20 30 Age (years)

226

225

228 Discussion

229 Our study used bomb radiocarbon assays to provide the first validated age estimates for whale

sharks. We showed that growth bands in sectioned vertebrae can provide accurate estimates of

sharks aged up to 50 years old. These results confirm the use of sectioned vertebrae as age

232 indicators for these sharks, as is also the case for other large species, such as white (Hamady et

al., 2014), shortfin mako (Natanson et al., 2006), sandbar (Andrews et al., 2011b), and porbeagle

- (Natanson et al., 2002) sharks. We found no evidence that vertebral counts underestimated the
 age of older individuals, as can be the case for porbeagle and white sharks (Francis et al., 2007;
 - Hamady et al., 2014), presumably because the much larger asymptotic body size means that
 - there is no cessation of vertebral growth in the older sharks we sampled in our study.
 - 238

239 Although our understanding of the movements, behavior, connectivity and distribution of whale 240 sharks have improved dramatically over the last ten years (Schmidt et al., 2009; Sequeira et al., 241 2012; Sequeira et al., 2013), basic life history traits such as age, longevity and mortality remain 242 unknown and are frequently inferred (e.g., Bradshaw et al., 2007). This lack of basic demographic information has been consistently highlighted in multiple reviews of the biology 243 244 and ecology of whale sharks (Colman, 1997; Stevens, 2007; Rowat and Brooks, 2012). Few studies have directly estimated age, growth and longevity from vertebral samples of wild 245 populations, due to the lack of samples. To our knowledge, only two studies (Wintner, 2000; Hsu 246 et al., 2014) have analyzed vertebral growth bands to provide age estimates. In the first of these, 247 248 Wintner (2000) used x-radiography to count bands within the vertebral centra of 15 whale sharks from South Africa and assumed that these were formed annually. The oldest specimen was a 249 250 male with 31 growth bands (770 cm precaudal length), but a von Bertanlanffy growth model could not be fitted to the data. A second, more recent study by Hsu et al. (2014) analyzed the 251 252 vertebrae of 92 whale sharks collected by a fishery off the coast of Taiwan. Age validation was 253 based on two forms of marginal increment analysis, which gave inconsistent results. This 254 approach has been criticized as a problematic form of age validation, but is often the only technique available to researchers when mark-recapture studies are not feasible (Campana, 2001; 255 256 Cailliet and Goldman, 2004). Based on this validation, Hsu et al. (2014) assumed that two 257 growth bands were formed each year. In their study, the oldest specimen (a male, 988 cm total 258 length) had 42 growth bands and was thus assumed to be 21 years old. Perhaps more 259 importantly, counts of growth bands by Hsu et al. (2014) were made in the intermedialia region, 260 which contrasts to most other studies that use the corpus calcareum region of shark vertebrae for 261 age interpretation (e.g., Campana et al., 2002; Christiansen et al., 2016). Our results, based on 262 growth bands visible in the corpus calcareum region of sectioned vertebrae and validated with 263 bomb radiocarbon assays, confirmed that growth bands must have formed annually, suggesting 264 that the study of Hsu et al. (2014) overestimated growth rates of the species. 265

Our estimate of k = 0.014 year⁻¹ for whale sharks from the von Bertanlanffy growth model was 266 267 lower than the estimates provided by both Wintner (2000) and Hsu et al. (2014). The study by 268 Wintner (2000) reported linear growth for 15 individuals, all of which were less than 8 m in 269 length and under 30 years old. To constrain the growth curve, Wintner (2000) added two 270 theoretical data points (60 and 100 years with 14 m TL) to obtain k = 0.032 or 0.021 year⁻¹ 271 respectively with L_{∞} of 13.7 m TL. The more recent study by Hsu et al. (2014) included the 272 lengths of 3 full-term embryos and used a modified 2-parameter von Bertanlanffy growth model 273 to obtain two growth curves that were based on either biannual or annual deposition of growth 274 bands. For annual growth bands, they reported estimates of k = 0.021 year⁻¹ with L_∞ of 15.3 m 275 TL. In our study, the predicted L_{∞} (21.9 m TL) was close to the largest maximum length ever 276 recorded in the wild, estimated at 20 m from Taiwan in March 1987 (Chen et al., 2002) and close 277 to maximum sizes recorded in other locations (McClain et al., 2015). This suggests that the 278 growth models of both Wintner (2000) and Hsu et al., 2014 underestimated maximum sizes of whale sharks. We did, however, find a large difference between the growth coefficients of the 279 280 von Bertanlanffy and the logistic growth models, with the latter having higher growth coefficients but seeming to underestimate L_{∞} . In this context, it is important to note that our 281 dataset represents a small sample of individuals and only included two mature individuals, hence 282 283 it is likely that the asymptotic length estimated in the von Bertanlanffy growth model was poorly 284 constrained and thus unrealistic. Actual growth parameters are probably bracketed by the results 285 of the two growth models. Given the closure of the fishery in Taiwan and the protection of whale 286 sharks in the waters of many of the countries where they occur (Rowat and Brooks, 2012), 287 increased sample sizes are likely to rely on unfortunate but opportunistic events such as stranding 288 (Wintner, 2000; Speed et al., 2009) to provide new vertebrae for analysis. Alternatively, photo-289 identification and imagery techniques may now offer a means to estimate *in-situ* growth rates for 290 whale sharks, for at least the individuals and size classes participating in nearshore aggregations 291 (e.g., Perry et al., 2018).

292

293 Our estimates of natural mortality for whale sharks, ranging from 0.09 - 0.14 year⁻¹ was close to those of other large species of sharks, such as the filter-feeding basking shark (0.07 year⁻¹; Pauly, 294 2002; Campana et al., 2008), white (0.08 year⁻¹; Mollet and Cailliet, 2002) and scalloped 295 hammerhead (0.10 year⁻¹; Cortés and Brooks, 2018) sharks. These estimates are generally 296 297 considered low, however, for smaller whale sharks (< 3 m TL), mortality rates may be higher, since the early juvenile stage is likely to be the most vulnerable to predators (Rowat and Brooks, 298 2012). Information on this life history stage is difficult to gather, because neonatal and very 299 300 young whale sharks are only rarely encountered and are assumed to reside in the open ocean 301 away from coasts (Rowat et al., 2008).

302

303 Our estimates of slower growth and greater observed longevity have important implications for 304 conservation of whale sharks. Underestimation of longevity and overestimation of growth is a 305 serious concern for management strategies for fisheries, because it has led to population crashes

- due to overharvesting (e.g., orange roughy; Smith et al., 1995). The case for whale sharks is
- 307 somewhat different from other species that are targeted in fisheries, in part because they are
- 308 protected across most of their distribution (Bradshaw et al., 2008; Hsu et al., 2012). This status
- 309 reflects the continuing rise and value of eco-tourism in sites where they aggregate, such as
- 310 Ningaloo Reef in Western Australia (Meekan et al., 2006). Although the harvesting of whale
- 311 sharks has been reduced for over a decade, the sizes and abundances of populations have
- declined in multiple regions (Theberge and Dearden, 2006; Bradshaw et al., 2008), which is
- reflected in the recent upgrade of the species from Threatened to Endangered by the IUCN RedList (Pierce and Norman, 2016). Given the slow growth rates, extended longevity, late maturity
- and global connectivity of this species (Bradshaw et al., 2007; Graham and Roberts, 2007;
- 316 Sequeira et al., 2013), this species is likely to be highly susceptible to sources of anthropogenic
- mortality such as ship-strike (Bradshaw et al., 2007; Speed et al., 2008). We are hopeful that the
- 318 demographic data we have provided in this study will help to improve the accuracy of population
- 319 models (e.g., persistence, survival) and hence, better inform management and conservation
- 320 efforts for this iconic species.

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326 Author Contributions

327 MM and SC conceived of the idea, HH and PF provided the vertebral samples. JO did the sample

- 328 preparation and analyses for vertebrae aging. SC contributed bomb radiocarbon results and
- verified aging results. JO wrote the manuscript, with critical feedback and help from SC, MM,
- **330** PF and HH.

331 Conflict of Interest

332 The authors declare that there is no conflict of interests.

333 Data Availability

All relevant data is contained within the manuscript.

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