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1 **Age and growth of the bull shark (*Carcharhinus leucas*) around**
2 **Reunion Island, South West Indian Ocean**

3

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14

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19

20

21 **Abstract:**

22 Sharks exhibit varied demographic strategies depending on both the species and the population
23 location, which make them more or less vulnerable to fishing. Accurate evaluation of local age
24 and growth parameters is therefore fundamental for the sustainable management of their stocks.
25 Although demographic parameters have been assessed for bull shark (*Carcharhinus leucas*)
26 populations in several locations of the world, this information was missing so far around the
27 Reunion Island, in the South West Indian Ocean. To fill this gap of knowledge, age and growth
28 data was gathered from the vertebrae of 140 individuals of *C. leucas* (77 females and 63 males,
29 mostly adults) fished around the island between 2012 and 2019. After verification of the annual
30 deposition of growth band pairs on these structures using relative marginal increment analysis
31 on 40 individuals, band pairs were counted along the vertebral centrum for each individual.
32 Thanks to this approach, growth was shown to significantly differ between male and female *C.*
33 *leucas* around the reunion island, with respective von Bertalanffy growth model equations of
34 $L_t = 314(1 - e^{-0.0814(t+5.45)})$ and $L_t = 321.5(1 - e^{-0.0999(t+3.420)})$. Indeed, the females of
35 the species fished in this area were significantly ($p < 0.001$) larger than local males, with an

36 estimated difference in size of ~ 16.1 cm at 20 years old. They also apparently reach older ages,
37 with an estimated maximum age of 33.50 years, against 29.75 years only for the males. The
38 estimated size at birth around the island is larger than elsewhere in the world, varying from
39 92.30 to 100.00 cm depending on the method used. These results confirm that the population
40 of *C. leucas* around the Reunion Island exhibits a K-selected strategy, which makes it highly
41 vulnerable to fishing pressure.

42

43 **Keywords:**

44 Age determination, growth bands, Vertebrae, RMI analysis, Life history, Longevity

45

46 **Introduction:**

47 Sharks are often considered as key species in marine ecosystems, both because of their
48 high trophic impact as predators and because they contribute to the connection of distant
49 habitats through their migrations (Heithaus *et al.* 2008; Roff *et al.*, 2016). Most shark species
50 are targeted or taken as bycatch in a wide variety of fisheries worldwide (Campana *et al.*, 2016),
51 and a few are specifically targeted in shark control programs (McPhee 2014).

52 Depending on their reproductive strategies, some species are threatened with rapid
53 extinction whereas others might withstand long-term fishing if their catches are restricted by
54 adequate quotas throughout their distribution range (Dulvy *et al.* 2017). Accurate evaluation of
55 age and growth is fundamental in shark fisheries management (Campana *et al.* 2016; Goldman
56 2005; Musick *et al.* 1999) because inaccurate age estimates can lead to serious error in stock
57 assessments and possibly overexploitation (Campana, 2001). Precise size-at-age information is
58 also required for producing robust estimates of essential parameters such as natural mortality
59 and longevity (Goldman 2005).

60 The bull shark *Carcharhinus leucas* (Valenciennes, 1839) is a common tropical and
61 subtropical coastal shark (Garrick, 1982) that can temporarily enter freshwater systems
62 (Campagno, 1989). So far, its age and growth had been studied only in the Gulf of Mexico
63 (Branstetter and stiles, 1987; Cruz-Martinez *et al.*, 2005; Neer *et al.*, 2005), in South Africa
64 (Wintner *et al.*, 2002), in Australia (Tillet *et al.*, 2011) and in the Western North Atlantic
65 (Natanson *et al.*, 2014). These studies had shown that, like many other carcharhinids, *C. leucas*
66 are long-lived, attaining maximum ages of 30 to >50 years. Females typically grow to larger
67 sizes and mature later than males, and growth rates for both sexes are faster during the juvenile
68 stage (Branstetter and Stiles, 1987; Castro, 1983; Compagno, 1984; Natanson *et al.*, 2014;
69 Snelson *et al.*, 1984; Neer *et al.*, 2005; Tillet *et al.*, 2011; Werry, 2010; Wintner *et al.*, 2002).
70 However, *C. leucas* exhibit a wide variability in maximum age and length, growth rate and size
71 and age at maturity among sampling locations. These spatial differences, supported by recent
72 studies on the species' genetic structure (e.g. Pirog *et al.*, 2019a, Tillet *et al.*, 2011), suggest the
73 existence of separate populations within exploited stocks that are currently structured by
74 oceanic basins. This calls for more local studies on all the above-mentioned parameters, to
75 implement efficient conservation and management strategies for the different populations of

76 the species (Cailliet and Goldman, 2004), which face varied levels of fishing pressure. For
77 example, in the Western North Atlantic Ocean and the Gulf of Mexico, commercial fishing of
78 *C. leucas* stocks is not recent, and increased markedly in 1980s (Cortés *et al.*, 2002; Natanson
79 *et al.*, 2014). Meanwhile, along the eastern coast of South Africa, the main source of fishing
80 mortality is the local shark control program that started in 1966 to reduce the shark risk for sea
81 users (Cliff and Dudley, 1991).

82 Around the reunion island in the Western Indian Ocean, commercial shark fishing is
83 banned since 1999 due to a risk of food poisoning related to the presence of ciguatoxins (Quod
84 *et al.*, 2000). However, a spate of shark bites on humans since 2011 (Lagabrielle *et al.*, 2018;
85 Taglioni *et al.*, 2018) resulted in the implementation of a local shark control program in 2012,
86 to intercept sharks in coastal waters on the west coast of the island, close to the main local sites
87 of water-based activities (Guyomard *et al.*, 2019). This prompted research interest on the local
88 biology and ecology of *C. leucas*, one of the two species responsible for these incidences (Ballas
89 *et al.*, 2017) to avoid its local extinction as a result of the current shark control program. Despite
90 this, knowledge on the demographic parameters of the species is still very limited in this area
91 of the Indian Ocean. A recent study showed that male and female bull sharks around Reunion
92 Island reach sexual maturity at ca. 234 and 257 cm total length respectively, and the local
93 parturition period extends between October and December (Pirog *et al.*, 2019b). However, to
94 our knowledge, the present study is the first to report the age-length relationship and investigate
95 the growth of *C. leucas* around the Reunion Island. For this size-at-age data was gathered for
96 over 100 specimens of the species, by counting vertebral growth band pairs. Although it has
97 recently been pointed out as probably leading to a systemic underestimation of shark age (Harry
98 2018), this method remains the most commonly used for estimating age in sharks (Cailliet *et*
99 *al.* 2006; Panfili *et al.*, 2002). It was expected that its application to assess the demographic
100 parameters for *C. leucas* around the Reunion Island would bring in valuable knowledge for
101 efficiently protecting human lives through the local shark control program without threatening
102 the long-term maintenance of the local population and the ecosystem functions it sustains.

103

104 **Material and methods:**

105 **Study site and local population sampling**

106 The Reunion Island (21°08'S, 55°32'E) is a young volcanic island of 2,500 km² located
107 in the Western Indian Ocean (Figure 1), characterised by a very narrow island shelf and a
108 particularly small and discontinuous fringing coral reef on the leeward west coast. Between
109 December 2012 and July 2019, 163 individuals of *C. leucas* were caught along the west coast
110 of the island (Figure 1), within the frame of the local shark control program using bottom
111 longlines and drumlines with catch-alive system (SMART drumline, Guyomard *et al.*, 2019).
112 For 140 of these individuals (77 females and 63 males), biological information including sex,
113 mass, maturity stage, total length (L_t) and fork length (L_f) was recorded and a section of the
114 vertebral column was excised, approximately from below the anterior margin of the first dorsal
115 fin. Two near full-term embryos of 79 cm L_t , 1 male and 1 female, recovered from a pregnant
116 female caught in November (29/11/2016) were included in the growth analysis. As this size is

117 very close to the size of the smallest free-swimming specimen caught around the island (78 cm)
118 and to the maximum size-at-birth reported for the species locally (80 cm, Pirog et al. 2019b),
119 these two embryos were considered to be due to born in December 2016. Therefore, their size
120 was considered as that at birth and their age was estimated at -0.083 years (i.e. 1.00 month
121 before birth).

122

123 **Ethical statement**

124 All sharks were caught as part of the local shark control program organized since 2012
125 by the French government around the island. This program aims at reducing the shark risk close
126 to nautical activities and all catches are done by professional fishermen. The Reunion Island
127 University takes opportunity of these catches to organize the dissection of the sharks captured
128 in order to improve knowledge on the local biology and ecology of the species. As the death of
129 the sharks is not primarily related to the gathering of scientific knowledge and samples or data
130 are only taken from already dead animals, no ethical agreement is needed to conduct this
131 research.

132

133 **Vertebrae processing and sectioning**

134 For each fish, individual vertebrae were separated, stored frozen until processed, and
135 one was randomly selected for age estimation. Following common protocols (Cailliet and
136 Goldman, 2004), the centrum of each vertebra was cleaned by removing the neural arch and
137 any adherent soft tissues mechanically. When necessary, chemical cleaning by soaking the
138 vertebra in 5% sodium hypochlorite for 5 minutes was used to remove residual tissues, as it
139 does not affect the vertebra composition (Mohan *et al.*, 2017). The vertebrae were then rinsed
140 in a bath of distilled water during 10 minutes and cut in the middle (sections of ca. 600 μm
141 width) along the sagittal plane (Cailliet and Goldman, 2004) using a low-speed diamond saw
142 (Isomet; Beuhler). Each vertebral section was then photographed twice, first dry and then
143 immersed in 70% ethanol, under both reflected and transmitted lights using a binocular
144 (Olympus® SZX12). The resulting pictures were used for age estimation and growth rate
145 measurements, using the imageJ software. The radius of each vertebra centrum (R_{vc}) was
146 measured from the centrum focus to the distal margin of the *corpus calcareum* (Goldman,
147 2004).

148

149 **Centrum analysis and age verification**

150 Although the count of vertebrae increments for bull shark's age estimation has already
151 been verified in several previous studies (Branstetter and Stiles., 1987; Neer *et al.*, 2005; Tillet
152 *et al.*, 2011; Wintner *et al.*, 2002), verification of the approach is a crucial prerequisite in each
153 new location investigated (Panfili *et al.*, 2002). The Relative Marginal Increment analysis
154 (RMI) is the most common method for this, when tagging (or chemically marking) the fish and
155 recapturing them is impossible (Panfili *et al.*, 2002). In this study, we used it to verify age
156 estimates in our samples. For this, a sub-sample of individuals of both sexes and varied sizes
157 were selected for the unequivocal status of their vertebrae margins. For each of these

158 individuals, the width of the margin increment (i.e. the distance from the last growth band to
159 the centrum edge) was divided by the width of the last (previously) fully formed band pair
160 (Cailliet and Goldman, 2004). Resulting RMI values were then plotted as a function of the
161 month of capture to confirm the annual periodicity of band pair formation. Following Okamura
162 *et al.* (2013), a circular linear regression model with random effects was used to adjust three
163 models of growth periodicity (acyclic, annual and biannual cycle) to the RMI data. The model,
164 which best fits the data, was chosen using the Akaike information criterion (Burnham and
165 Anderson, 2002).

166

167 **Age determination and vertebral growth**

168 In sharks, birth leaves a noticeable mark on the vertebrae: the birth mark (BM)
169 identifiable as a marked change in the angle of the *corpus calcareum*. This mark, resulting from
170 the difference between fast intra-uterine and slower post-natal growth (Walter and Ebert 1991),
171 is commonly chosen to represent age 0 in sharks (Goldman, 2005). In this work, both the birth
172 mark radius, i.e. the distance from the centrum focus to BM, and the width of the following
173 growth band were measured on the *corpus calcareum* of each section.

174 To estimate age in this study, vertebral sections were randomly selected and analysed
175 without any a priori knowledge regarding fish sex or size. For each individual fish, age was
176 estimated by counting the number of band pairs (each formed by a pair of one opaque plus one
177 translucent growth bands) after the birth mark on the corresponding vertebral section. Two
178 separate readers independently made two non-consecutive counts of growth band pairs for each
179 fish. Count reproducibility between readers was estimated using the index of average
180 percentage error (APE; Beamish and Fournier, 1981) and the coefficient of variation (CV;
181 Chang, 1982). When the difference in age estimates between the two readers was less than 10%,
182 the mean of the two values was used, which can finally bring partial years (e.g. 0.5). Otherwise,
183 both readers re-analysed the section until a consensus was found. Age estimates were evaluated
184 for consistency within and between readers using age-bias plot (Campana *et al.*, 1995). Chi-
185 square tests of symmetry were used to determine whether difference between counts were due
186 to systematic bias or random error (Evans and Hoenig, 1998).

187 The relationship between R_{vc} and the shark's total length (L_t) was established using
188 Pearson correlation test. Sex-related differences for this relationship and for birth mark radius
189 were tested using an analysis of covariance (ANCOVA) and a Student test, respectively.
190 Average size at birth for *C. leucas* was estimated as the L_t value corresponding to the mean
191 birth mark width observed on the vertebrae when using the fitted R_{vc} - total length (L_t)
192 regression.

193

194 **Growth modelling and statistical analyses**

195 Sex-related differences in age and length were tested using non-parametric Wilcoxon tests,
196 since neither the normality nor the homoscedasticity of the data were confirmed. The von
197 Bertalanffy growth model (von Bertalanffy, 1938) was fitted on the whole dataset (both sexes

198 combined) and on the datasets produced for males and females, separately. For this, non-linear
199 least-squares regressions were implemented on R (Version 3.5.1, (C) 2018 The R Foundation
200 for Statistical Computing.) using the equation defined by von Bertalanffy (1938):

$$201 \quad L_t = L_\infty(1 - e^{-k(t-t_0)}),$$

202 where L_t = predicted length at time t , L_∞ = theoretical asymptotic length, k = growth coefficient
203 or growth completion rates and t_0 = theoretical age at zero length.

204 Sex-related differences in the parameters of this equation were assessed using analysis of
205 covariance (ANCOVA) on the log-transformed linear form of the growth regression. Ages at
206 maturity were determined following the L_{t50} criteria defined in Pirog *et al.* (2019b) for the bull
207 shark in Reunion Island. Longevity was defined as the age at which 95 % of L_∞ is reached
208 (Taylor, 1975).

209

210 **Results:**

211

212 RMI analysis on the vertebrae of 40 individuals ($L_t = 121\text{--}271$ cm) with unequivocal
213 margin status supported the hypothesis that growth band pairs on vertebral sections, consisting
214 each of one opaque and one translucent zone, are formed with an annual periodicity in the local
215 bull shark population, starting between December and January each year (Figure 2). The annual
216 cycle of growth-band pair deposition was further supported by the AIC values obtained for the
217 three models of growth periodicity tested (-76.27 for the annual cycle model, against -8.93 for
218 the acyclic and 12.18 for the biannual cycle ones).

219 Based on these findings, ages estimate from vertebrae reading in our sample ($N = 140$)
220 ranged between 0.2 and 33.5 years, for *C. leucas* specimens between 78 and 327 cm L_t and
221 from both sexes. This diversity allowed precisizing the local growth parameters of the species,
222 with important implications for the sustainable regulation of its stock around the reunion island.

223

224 **Precision in age estimates**

225 The average percentage error (APE) between readers A and B for two independent
226 counts was of 2.15% and the corresponding coefficient of variation (CV) was of 3.04%,
227 suggesting that age estimation was precise for both readers (Table 1). Nevertheless, the second
228 read was more precise than the first one for both readers and age estimates from reader B were
229 more consistent than those from reader A (Table 1). Therefore, reader B was used as the
230 reference (explanatory variable) for the comparison plot of ages assigned according to each
231 reader (age-bias plot, Figure 3). The age-bias plot indicates high agreement around the 1:1 line
232 and no systematic bias between readers (Figure 3). Chi-square tests of symmetry showed that
233 the little differences in age estimates between readers were only due to random errors ($n = 140$;
234 Bowker: $X^2 = 53.67$, $df = 54$, $p = 0.49$; Evans-Hoenig: $X^2 = 9.55$, $df = 8$, $p = 0.30$; McNemar:
235 $X^2 = 2.85$, $df = 1$, $p = 0.09$).

237 **Size-at-age distribution around the reunion island**

238 The mean total length (L_t) of the bull sharks used in this work was 246.40 ± 57.20 (mean
 239 \pm SD) cm. Females ($L_t = 78$ -327 cm) were significantly ($p < 0.001$) larger than males ($L_t = 101$ -
 240 310 cm), with mean lengths of 257.60 ± 60.97 and 232.80 ± 49.34 cm respectively. The average
 241 difference in size between them was of ~ 16.10 cm at 20 years old. Size frequency distributions
 242 were non-normal for both sexes, due to a lack of small sizes in the captures. Indeed, only 7 of
 243 the females and 4 males in our dataset were smaller than 150 cm and, in the 150-200 cm size-
 244 class, there were no female and only 9 males (Figure 4). The average age in the captures was
 245 of 15.11 ± 8.49 years (Figure 5), with females (0.20-33.50 years old) significantly ($p = 0.023$)
 246 older than males (0.25-29.75 years old) as mean ages for the two sexes were of 16.60 ± 8.98
 247 and 13.29 ± 7.54 years, respectively.

248 A significant and robust linear relationship was found between the radius of the
 249 vertebrae (R_{vc}) and the total length (L_t) of individuals (Pearson test; $n = 135$; $R^2 = 0.974$; p
 250 < 0.001 ; Figure 7) with no sex-related significant difference in its parameters (ANCOVA, $p =$
 251 0.09). Based on the width of the birth mark (BM), ranging from 34.52 to 43.87 mm (mean \pm
 252 SD: 39.11 ± 2.20 mm) with no significant difference between sexes (Wilcoxon test; $n = 137$;
 253 $W = 2729$; $p = 0.08$), the estimated range of body sizes at birth in our sample was estimated to
 254 be of 89.00 - 95.60 cm, around an average size of 92.30 ± 37.92 cm.

255

256 **Local growth equations and minimum and maximum sizes**

257 Von Bertalanffy growth equations for *C. leucas* in Reunion Island were estimated to be
 258 $L_t = 314(1 - e^{-0.0814(t+5.45)})$ for males and $L_t = 321.5(1 - e^{-0.0999(t+3.420)})$ for females
 259 (Table 2). Indeed, significantly different growth models were obtained for the two sexes
 260 (ANCOVA, $p < 0.001$). As a result, predicted local maximum sizes in the area (L_∞) differed
 261 between sexes, with estimates of 321 cm for the females and 314 cm for males (Table 2).
 262 Interestingly, while male *C. leucas* in our sample were all below 314 cm in size, three of the
 263 females captured in the area (of 322, 325 and 327 cm L_t) were larger than the maximum 321
 264 cm predicted by the Von Bertalanffy growth equation obtained for predicting their growth.
 265 Using the corresponding models, the longevity of the species (95% of L_∞ , Taylor, 1975) in the
 266 area was estimated to be 29.50 years (31.40 years for males and 26.30 years for females).
 267 Average ages at maturity were estimated to be of 11.30 and 12.70 years (from L_{150} of 234 and
 268 257 cm, Pirog et al., 2019) for males and females, respectively. Growth models including
 269 embryos did not differ significantly from those with only free-swimming individuals
 270 (ANCOVA, $p > 0.05$). Including the two embryos in the models however produced smaller
 271 estimates for both the global birth size, of 97.00 cm L_t instead of 100.00 cm L_t , and the
 272 asymptotic maximum size, of 307.3 cm L_t instead of 314 cm L_t for males and of 320.9 cm L_t
 273 instead of 321.5 cm L_t for females (Table 2, Figure 6). Therefore, both types of models are
 274 displayed in Table 2.

275

276 **Discussion:**

277 This study is the first to provide age and growth information for *C. leucas* around the
278 Reunion Island, and the second in the Western Indian Ocean, after Wintner *et al.* (2002) in
279 South Africa. Our results are consistent with previous findings on this species in other parts of
280 the world (Branstetter and Stiles, 1987; Cruz-Martinez *et al.*, 2004; Natanson *et al.*, 2014; Neer
281 *et al.*, 2005; Tillet *et al.*, 2011), and with the data gathered so far in other elasmobranchs (Cailliet
282 and Goldman, 2007; Cortés 2000). In particular, the low growth rate and the late age at maturity
283 found here for *C. leucas* are typical of large carcharhinid species (Cortés 2000). The von
284 Bertalanffy models obtained however suggest that life-history traits for the species in Reunion
285 Island differ from those observed in other locations (Branstetter and Stiles, 1987; Cruz-
286 Martinez *et al.*, 2004; Natanson *et al.*, 2014; Neer *et al.*, 2005; Tillet *et al.*, 2011), with the
287 exception of South Africa (McCord and Lamberth, 2010, Wintner *et al.* 2002) where similarly
288 high maximum sizes and sizes at birth were described (Table 3). These results corroborate a
289 recent study on *C. leucas* genetics, which suggested genetic isolation between *C. leucas*
290 populations from the Western Indian Ocean and those from the Western Atlantic and Western
291 Pacific Oceans (Pirog *et al.* 2019a). If true, this has important implications in terms of
292 population management for *C. leucas* around the island, where fishing mainly targets large
293 individuals.

294

295 **Verification and precision**

296 Age underestimation is common for sharks and rays when counting annual growth band
297 pairs on calcified structures (Harry, 2018). This is mainly due to the difficulty in distinguishing
298 growth band pairs for older ages, because seasonal growth bands tend to be narrower as a result
299 of the decrease in fish growth with age (Cruz-Martinez *et al.*, 2004; Natanson *et al.*, 2014). For
300 some species of sharks however, band pair deposition is annual for only a portion of the lifespan
301 (Natanson *et al.*, 2018; Passerotti *et al.*, 2014), a process being referred to as of the “missing
302 time” (Passerotti *et al.*, 2014). Factors that influence the differential rate of calcium deposition
303 in sharks’ vertebrae centra are not well understood yet. Changes in temperature, diet (Stevens,
304 1975) and stress-related activities such as migration (Pratt and Casey, 1983) have been
305 suggested. This highlights the importance of validating the method, including for old
306 specimens, before applying it for age estimation. In the present study, RMI analysis suggested
307 that growth band pairs, consisting each of an opaque plus a translucent zone, were formed
308 annually on the vertebrae of *C. leucas* specimens captured in Reunion Island, as already
309 observed for this species in other locations (Branstetter and Stiles, 1987; Neer *et al.*, 2005; Tillet
310 *et al.*, 2011; Wintner *et al.*, 2002). However, this analysis was performed on the vertebrae of 40
311 individuals only (28.58 % of our total sample) for which the last growth bands were easily
312 measurable. These fish were mainly small individuals, with sizes of 121-271 cm L_t , which calls
313 for caution when interpreting our age estimates, especially for large and old individuals. To our
314 knowledge, missing time has never been observed for *C. leucas* so far. However, other
315 validation methods such as tetracycline injection (Cailliet and Goldman, 2004; Panfili *et al.*,
316 2002) or capture-recapture might improve the accuracy of size-at-age estimates and lead to the
317 production of more robust models for local growth in the species. This being said, the

318 coefficient of variation (CV, Chang 1982) in this study did not exceed the 5% level
319 recommended by Campana (2001) and the APE, age-bias plot and symmetry tests produced are
320 among the most precise obtained for the species so far (Cruz-Martinez *et al.*, 2004; Neer *et*
321 *al.*, 2005; Wintner *et al.*, 2002). This substantiate our ability to correctly interpret vertebral band
322 pairs for *C. Leucas* in our study area and confirms previous conclusions that *C. leucas* is
323 relatively easy to age for a shark species.

324

325 **Size, growth and age of *Carcharhinus leucas* in Reunion Island**

326 Due to a combination of problems in sampling and growth band pairs reading on the
327 vertebrae, maximum predicted lengths in sharks are usually lower than those observed in the
328 field (Harry, 2018). This was the case here, and in most studies involving *C. leucas* worldwide,
329 exception made of one study in Northern Australia, where the maximum total length observed
330 for *C. leucas* (318 cm L_t) was smaller than the average maximum length ($L_\infty = 350.7$ cm)
331 predicted by the von Bertalanffy growth model (Tillet *et al.*, 2011). This might reflect an
332 artificial inflation of the L_∞ estimate though, due to the lack of large individuals in the local
333 dataset since parameter estimates with the von Bertalanffy equation are greatly influenced by
334 extreme values (Haddon 2001; Natanson *et al.*, 2014).

335 With total lengths up to 327 cm and an average predicted maximum size of 321.57 cm,
336 the *C. leucas* specimens caught around the Reunion Island are globally larger than those from
337 other locations (Table 3, Figure 8), as already pointed out by Blaison *et al.* (2015). Indeed,
338 studies in the Gulf of Mexico reported local maximum total lengths of 231.21 cm and 258.00
339 cm for female and male bull shark, respectively (Branstetter and Stiles, 1987; Cruz-Martinez *et*
340 *al.*, 2004; Neer *et al.*, 2005) and, to our knowledge, the largest individual of the species ever
341 observed was a female of 400.00 cm tagged in the Breede River, along the South Eastern coast
342 of South Africa (McCord and Lamberth, 2010). These results support the hypothesis that *C.*
343 *leucas* from Indian Ocean populations are larger than those from Atlantic ones (Pirog *et al.*
344 2019a, b). In sharks, life history traits can differ between conspecific populations, reflecting
345 spatial differences in population dynamics and resilience to exploitation (Dulvy *et al.* 2008).
346 This could explain the larger sizes observed in this work. However, all other life-history
347 parameters derived from the von Bertalanffy model fall within the range of the values from
348 other studies (Table 3). Alternatively, because until 2012 and the beginning of the shark control
349 program in Reunion Island, the local *C. leucas* population was barely fished, the presence of
350 large individuals in this population could reflects its pristine state. A last explanation could lie
351 in the use of different fishing gears (with different size-related selectivity) among locations.
352 Around the Reunion Island, the shark control program uses large hooks to target large
353 individuals and to limit bycatches (Guyomard *et al.*, 2019). Even if the size-related selectivity
354 cannot explain all differences, as in all studies both large and small individuals were caught, it
355 remains an important factor to consider.

356 The von Bertalanffy growth model is the most commonly applied in elasmobranch
357 studies (Cailliet and Goldman, 2004). It has been largely used to describe growth in *C. leucas*
358 (e.g. Branstetter and Stiles, 1987; Neer *et al.*, 2005), which explain its use for the present work.

359 Yet, it does not always provide the best fit with size-at-age data in fish (Cailliet and Goldman,
360 2004). Several models and multi-model combinations exist and can be used to describe shark
361 growth (Smart *et al.*, 2016). The use and comparison of these different models could improve
362 growth description for the local population of *C. leucas* in the future. For example, in the
363 Western North Atlantic, Natanson *et al.* (2014) found the Gompertz and the logistic models to
364 provide better descriptions of growth for *C. leucas* males and females, respectively. Still, such
365 model comparisons should be made with caution, as growth modelling in a given shark
366 population can provide different results depending on the age or length distribution in the
367 sample (Natanson *et al.*, 2014; Neer *et al.*, 2005). In particular, the lack of small and old
368 individuals in the sample can significantly influence growth model estimates (Goodman *et al.*,
369 2012; Haddon 2001; Natanson *et al.*, 2014; Neer *et al.*, 2005; Wintner *et al.*, 2002). This
370 highlights the need for a better scientific monitoring of the bull shark population around the
371 Reunion Island to improve the quality of the local size-at-age dataset.

372 In this study, *C. leucas* growth rate was found to differ between sexes, with a 3 to 5%
373 smaller maximum size predicted in the males than in the females. This confirms sex-related
374 differences in growth parameters already reported for the species at other locations (Figure 8,
375 Table 3), and is in agreement with the 10% size difference between sexes in favour of the
376 females observed by Cortès (2000) on 164 species of sharks and the 7% found by Garrick
377 (1982) on 24 species of the genus *Carcharhinus*. A characteristic of the dataset in the present
378 study though is the absence of females for the 150-200 cm L_t range. To our knowledge, this
379 sex-related difference in the size distribution (nine males and zero females) has never been
380 reported in other *C. leucas* populations. Scientific sampling efforts around the island in the
381 future should aim at determining whether this current size gap in the catches reflects a local
382 particularity in the behaviour or the ecology of 150-200 cm L_t females. Further investigations
383 could also help understanding the biology of *C. leucas* juveniles and sub-adults around the
384 island, which is still largely unknown. Indeed, small size classes (< 200 cm L_t) were poorly
385 represented in our samples for both sexes (Figure 4), probably because the large size hooks gear
386 used in the shark control program targets the largest individuals in the population. However,
387 because access to estuarine ecosystems is of key importance for both parturition and early
388 development in *C. leucas* (Werry *et al.* 2011), it is likely that the newborns and juveniles of the
389 species remain near the mouths of local perennial rivers, which are mostly located on the rainy
390 eastern coast of the island. As the focus for the shark control program is on the western coast
391 of the island, near coral reefs with limited freshwater inputs (Figure 1), this habitat preference
392 may also partly explain the low representation of small size classes in our sample.

393 Around the Reunion Island, both sexes of *C. leucas* were found to mature at ages
394 between 11 and 13 years, which falls within the values reported for the species at other locations
395 (Table 3), and between the ages at maturity found in Australia (Tillet *et al.* 2011) and in South
396 Africa (Wintner *et al.* 2002). The longevity estimates found (29.50 years) are also similar to
397 those previously reported at other locations (Table 3), with one noticeable exception: South
398 Africa, where longevity was estimated to be >50 years (Wintner *et al.* 2002).

399

400 **Size at birth of *Carcharhinus leucas* in Reunion Island**

401 Size at birth is particularly difficult to evaluate in *C. leucas*, due to the worldwide
402 variability in its life-history traits. The mean birth size reported for the species is of $78.33 \pm$
403 2.56 cm, but it is apparently larger (97.73 cm) in South Africa (Wintner *et al.*, 2002) than in the
404 Atlantic (70 - 80 cm, Branstetter and Stiles, 1987; Castro, 1983; Compagno, 1984; Natanson *et*
405 *al.*, 2014; Neer *et al.*, 2015; Rodriguez de la Cruz *et al.*, 1996; Snelson *et al.*, 1984). Around
406 the Reunion Island, Pirog *et al.* (2019b) estimated the birth size of the species to be between 70
407 and 80 cm, based on the analysis of 16 litters, and local anglers reported free-swimming
408 juveniles of 68 - 79 cm (T. Poirout, pers. obs.). In this study, the growth model predicted a birth
409 size of 100 cm, however this estimate decreased to 97 cm when including near full-term
410 embryos in the dataset. The lack of newborns and juveniles in our sample likely led to birth size
411 overestimation using von Bertalanffy growth modelling. Indeed, when using the local
412 relationship between R_{vc} and body total length (L_t) in the species, birth mark widths suggested
413 a mean birth size of 92.30 cm, which better fits with local field observations. Cortés (2000)
414 highlighted a universal positive correlation between female and offspring body sizes in sharks.
415 It seems plausible that in bull sharks as well, larger and older females produce larger offspring.
416 Larger female sizes in Reunion Island could therefore explain the local larger birth size, when
417 compared to most of the other study sites. This idea is also supported by the variability in birth
418 mark widths observed among vertebrae ($34.52 - 43.87$ mm), which might reflect individual
419 differences in mother sizes. Finally, the larger birth size estimates found in this study, but also
420 in South Africa (Wintner *et al.*, 2002), is an additional argument supporting the hypothesis of
421 a distinct population of bull sharks, with higher demographic parameters, in the Western Indian
422 Ocean.

423

424 **Shark risk and shark control program**

425 The results of this work confirm that bull sharks around the Reunion Island exhibit
426 typical characteristics of a K-selected fish population, with large maximum sizes, high
427 longevity, late maturity, low fecundity and slow growth for both sexes (Stearns, 1992). These
428 K-selected characteristics make populations particularly vulnerable to the removal of large and
429 mature individuals. Depending on the population size and its degree of connectivity with other
430 populations in the Indian Ocean, the on-going shark control program could significantly affect
431 the local population dynamics. As a matter of fact, the high abundance in the captures of old
432 individuals, larger than at most other locations where studies were conducted, suggests that,
433 until the beginning of the shark control program in 2012, the *C. leucas* population around the
434 island was relatively pristine. Knowledge on the local natural populations' dynamics is needed
435 however to appreciate whether the current fishing pressure acts as an additive or a compensatory
436 source of mortality (Allen *et al.*, 2006). Indeed, the local shark control only aims to eliminate
437 potentially dangerous specimens that would swim close to coastal areas where human activities
438 develop, so the idea is to only reduce the local population size to a threshold for which the
439 probability of shark bites will be close to nil. A long-term follow-up of the catches could help
440 identify trends in *C. leucas* body length and possible indirect effects of this targeted fishing
441 (Stevens *et al.*, 2000). Fishing pressure, especially on large individuals, can lead to changes in
442 the structure and life-history traits in some populations (Stevens *et al.*, 2000). In response to

443 demographic changes, changes in growth rate (Sminkey and Musick, 1995) or in reproductive
444 parameters (Holden, 1973, Walker *et al.*, 1998) can be observed in elasmobranch populations
445 (Roff *et al.*, 2018; Stevens *et al.*, 2000). Fecundity tends to increase with body size so that
446 populations with a higher proportion of larger fish have greater reproductive potential. A better
447 understanding of the general ecology of this species and a follow-up of its catches around
448 Reunion Island are essential to predict the consequences of the shark control program on the
449 risk of human attack by *C. leucas* and the local population dynamics of the species. It is also
450 vital to infer the possible impact of the program on the functioning of local ecosystems. Indeed,
451 large shark individuals are rare in most ecosystems, yet they have a unique functional role as
452 true apex predators (Roff *et al.* 2016). The removal of these individuals from the coastal habitats
453 around the Reunion Island could have unexpected consequences on the goods and services
454 provided by these ecosystems.

455

456

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603

604 **Contributions**

605 S.J. and A.D. designed the research; F.H., T.P. and L.J. contributed to data acquisition and
 606 generation; F.H. and M.L. prepared samples; F.H. analyzed the data and wrote the original draft,
 607 all authors contributed to the writing of the manuscript.

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610

611 Table 1 Average percentage of error (APE) and coefficient of variation (CV) in the age estimates obtained by
 612 two successive vertebra readings (first and second reads) by each of the two independent readers (A and B). In
 613 each case, n indicates the number of fish aged.

Reader	First read		Second read		n
	APE	CV	APE	CV	
A	-	-	1.94	2.74	140
B	-	-	0.80	1.13	140
A vs B	3.84	5.44	2.15	3.04	140

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615

616 Table 2 Summary of the biometric and growth parameters data for the 140 bull sharks from Reunion Island, with
 617 the inclusion or not of embryos in the von Bertalanffy model. All lengths (except BM) are in cm. L_T: Total
 618 Length; Age and longevity in years; BM: birth mark width in mm; L_∞, t₀ et k: parameters of von Bertalanffy
 619 growth model; L_{T50}: size at maturity for each sex (from Pirog *et al.*, 2019b).

Bull shark (C. leucas)	Free swimming individuals			Embryos included		
	Combined sexes	Males	Females	Combined sexes	Males	Females
Sample size	140	63	77	142	64	78
L_t min	78	101	78	78	79	78
L_t max	327	310	327	327	310	327
L_t mean	246.4	232.8	257.6	244.1	230.4	255.3
Age min	0.20	0.25	0.20	-0.083	-0.083	-0.083
Age max	33.5	29.7	33.5	33.5	29.7	33.5
Age mean	15.1	13.3	16.6	14.9	13.1	16.4
BM mean	39.11	38.70	39.44	39.11	38.70	39.44
L_∞	321.6	314	321.5	319.6	307.3	320.9
t₀	-4.231	-5.450	-3.420	-3.921	-4.551	-3.300
k	0.0889	0.0814	0.0999	0.0923	0.0911	0.1013
Estimated size at birth	100	112.4	93.1	97	104	91.2

Longevity	29.5	31.4	26.3	28.5	28.1	26.3
L_t 50	-	234	257	-	234	257
Age at maturity	-	11.34	12.7	-	11.18	12.63

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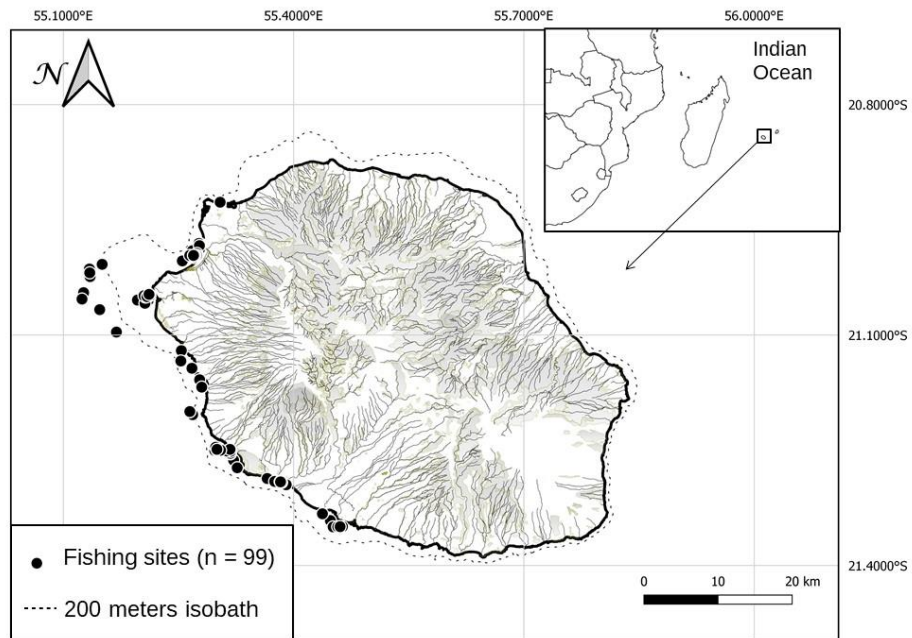
623 Table 3 Summary of main relative information on length, age and life history traits from different studies.

Bull shark (<i>C. leucas</i>)	Compagno (1984)	Branstetter and Stiles (1987)	Rodriquez de la Cruz et al. (1996)	Wintner et al. (2002)	Cruz- Martinez et al. (2004)	Neer et al. (2005)	Tillet et al. (2011)	Natanson et al. (2014)	This present study
L_t (cm) mean	NA	F=242-268 M=213-245	206.2	NA	NA	NA	NA	NA	F=257.6 M=232.8
L_t (cm) max	340	F=268 M=245	F=334	F=284 M=278	F=271 M=254	F=271,21 M=245.80	F=318 M=276	F=269 M=254	F=327 M=310
Age max (years)	14	F=24 M=21	NA	F=32 M=29	F=28 M=23	F=29 M=25	F=26 M=22	F=27 M=25	F=33.5 M=29.7
L_∞ T_0 K	NA	285 -3.00 0.076	NA	295,3 -5.120 0.071	256,4 -1.935 0.1397	377.7 -6.844 0.042	350,7 -2.485 0.082	259 NA NA	321.6 -4.231 0.0889
Length (cm) to maturity	250	F>225 M=210-220	F=204 M=190-200	F=249 M=246	F=204 M=190- 200	NA	NA	F=228 M=208	F=257 M=234
Age (years) to maturity	6	F>18 M=14-18	NA	F=21	F=10 M=9-10	NA	9.5	F=15 M=16	F=12.7 M=11.34
Gestation time (months)	10-11	10-11	10-11	NA	NA	NA	NA	NA	NA
Birth size (cm)	56-81	75	78	89-97	NA	56-97	NA	76	92-100
Number of pups	1-13	NA	1-22	NA	NA	NA	NA	NA	NA
Study locations	Symposis of world data	Northern Gulf of Mexico	Gulf of Mexico	South- Africa	Southern Gulf of Mexico	Northern Gulf of Mexico	North Australia	Western North Atlantic	Reunion Island

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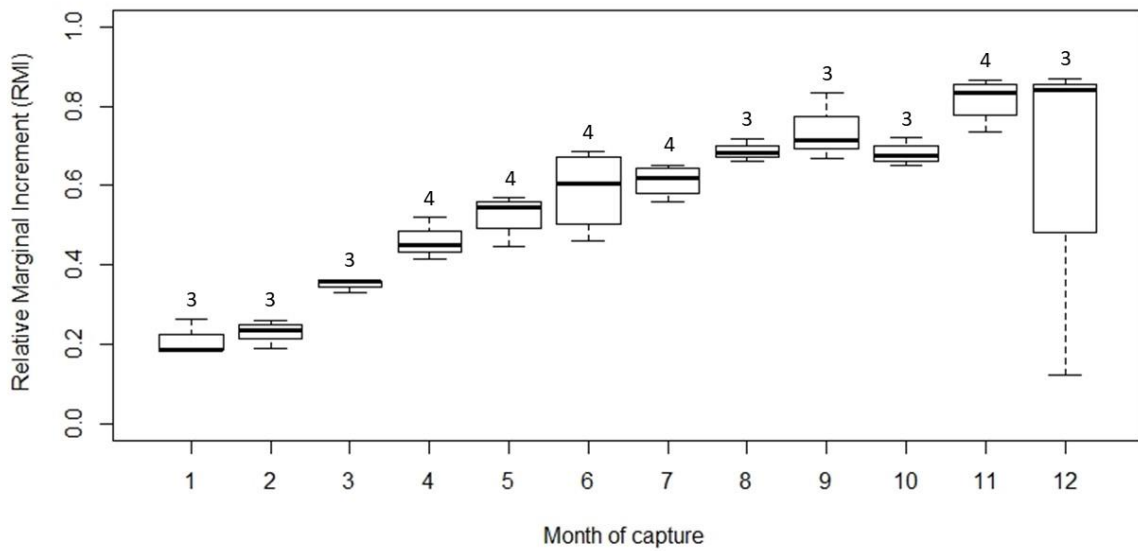
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627

628 *Figure 1 Fishing sites for the bull sharks (Carcharhinus leucas) captured around the Reunion Island between December 2012*
629 *and July 2019.*

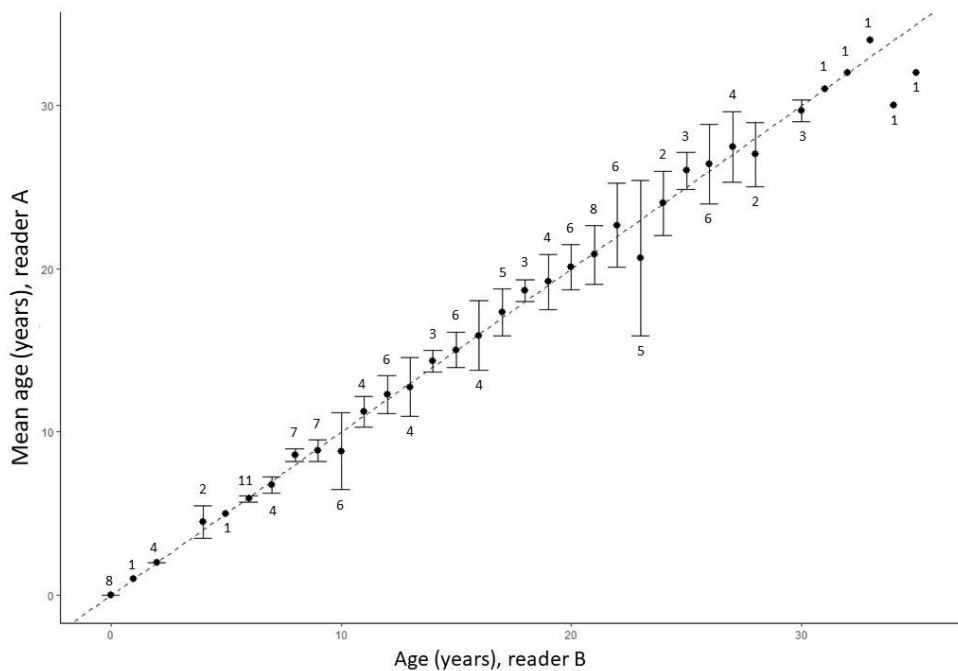
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631

632 *Figure 2 Relative marginal Increment (RMI) by month of capture for 40 individuals bull shark (Carcharhinus leucas). The*
633 *thick line in the boxplots represents the median value for each month, and box lower and upper margins represent the first and*
634 *third quartiles, respectively.*

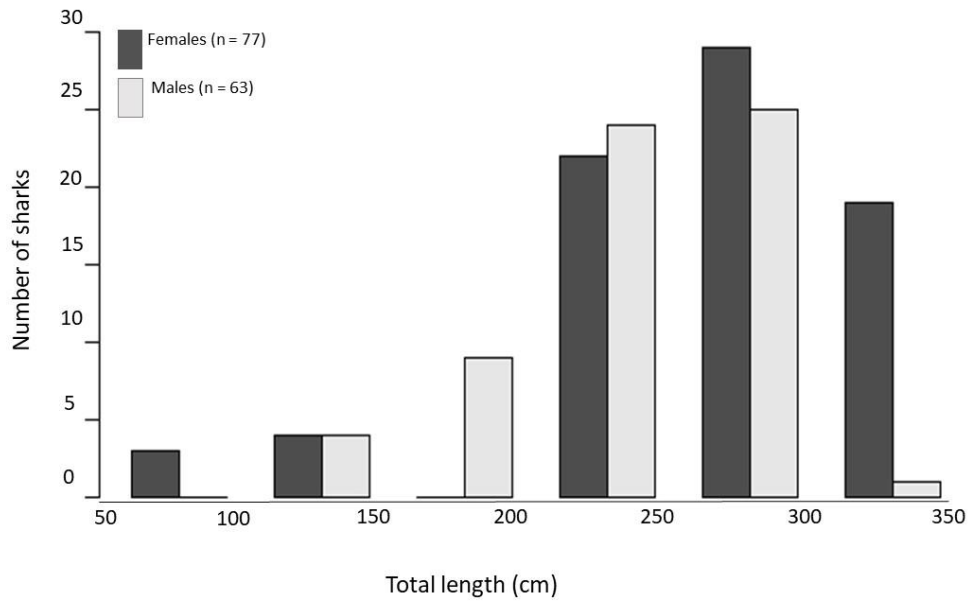
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637 *Figure 3 Reader-linked biases in age estimation from vertebral growth bands' counts in the 140 bull sharks (Carcharhinus*
638 *leucas) investigated in this work. Numbers along the 1:1 equivalence line (dotted line) indicate sample size for each age. Error*
639 *bars in each case represent the 95 % confidence intervals for the mean age assigned by reader B to all the fish assigned a*
640 *given age by reader A*

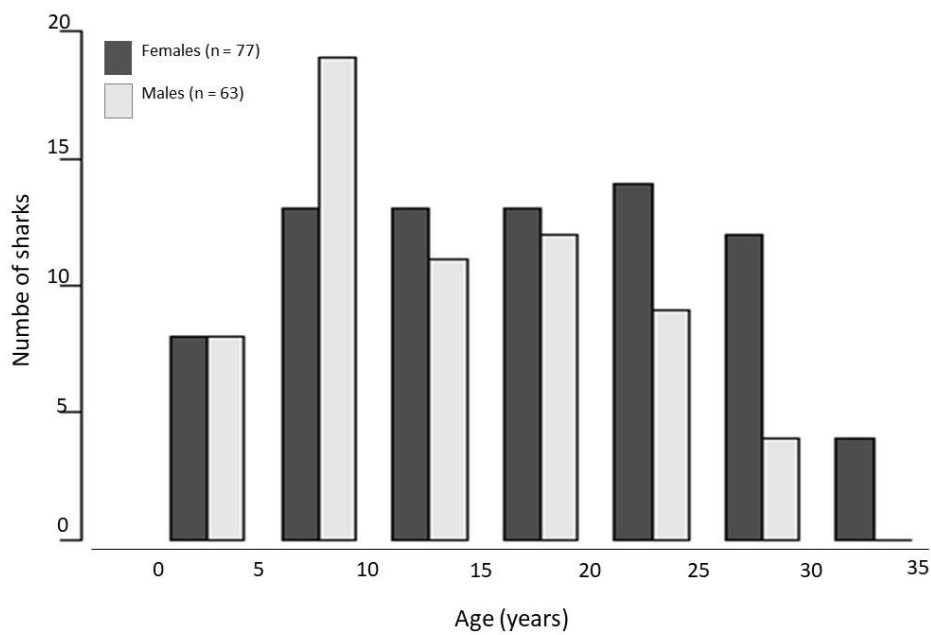
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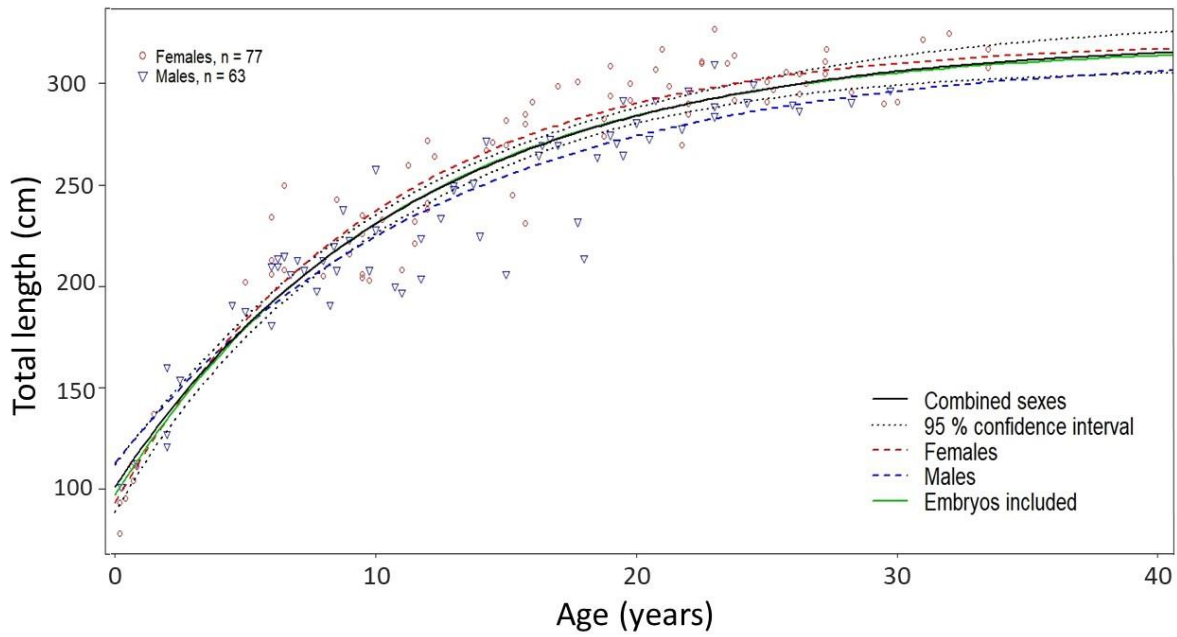
643 *Figure 4 Number of bull shark (Carcharhinus leucas) individuals studied by size class (L, cm) and sex.*

644



645

646 *Figure 5 Age distribution for the females (n=77) and males (n=63) bull shark (Carcharhinus leucas) caught around Reunion*
647 *island.*

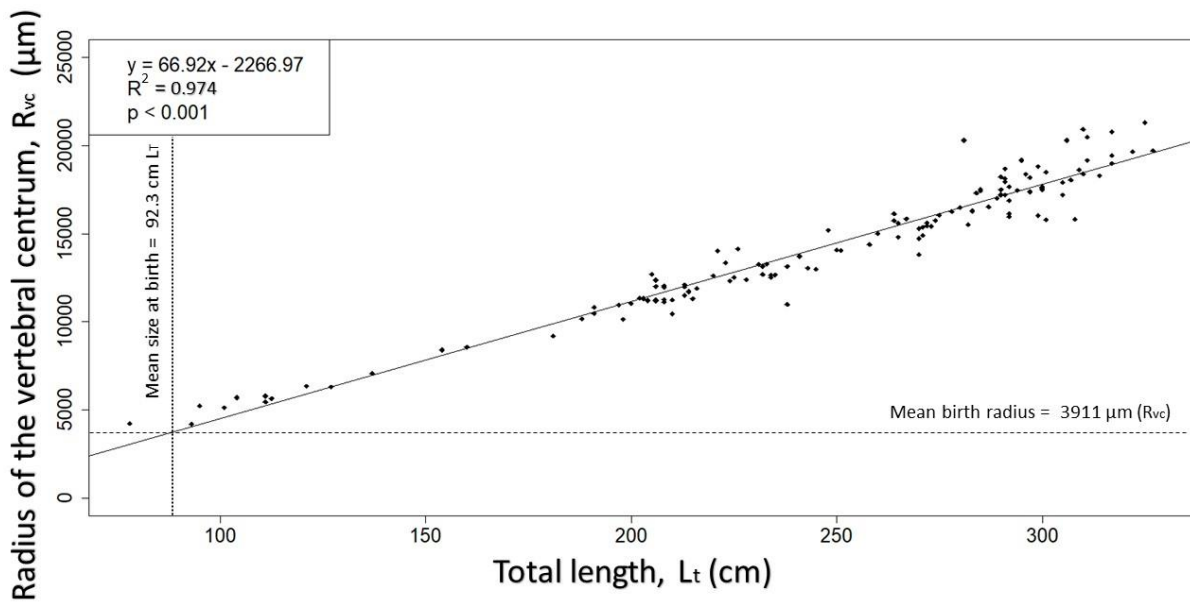


649

650 Figure 6 Fitted von Bertalanffy growth model for the bull shark (*Carcharhinus leucas*) in Reunion Island, for only
 651 free-swimming individuals (combined sexes, females and males) and for free-swimming with embryos included
 652 (only combined sexes).

653

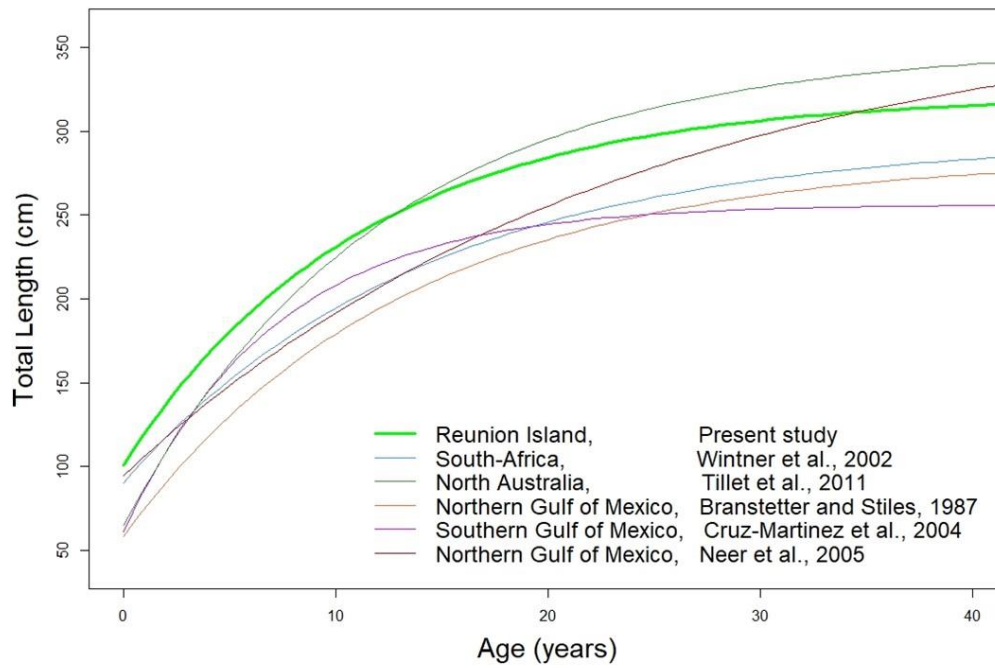
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655

656 Figure 7 Relationship between the radius of the vertebral centrum (R_{vc}) and the body total length (L_t) for 136 individuals of
 657 bull shark (*Carcharhinus leucas*). The horizontal dashed line represents the mean radius of the vertebral centrum (R_{vc}) of the
 658 birth mark and the vertical dashed line represents the mean size at birth (L_t).

659



660

661 *Figure 8 Comparison of the von Bertalanffy growth curve fitted for the bull shark (Carcharhinus leucas) in Reunion Island*
662 *(present study) with those obtained in other published studies*

663

664