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21 Declarations of interest: none

22

23 **Abstract**

24 Leatherback turtles (*Dermochelys coriacea*) are the largest extant marine turtle, with some  
25 individuals measuring more than 1.80 m carapace length. Given the exceptional size of this  
26 species and that females only return to land every few years to nest, it is difficult to  
27 investigate its ontogeny from hatchling to adulthood. Distinct chondro-osseous (cartilage  
28 and bone) tissue morphology has led to some speculation that sexual maturity may be  
29 reached as early as 3 years, while other studies suggest this could take as long as 25 years.  
30 Using a combination of longitudinal measurements obtained from nesting females in French  
31 Guiana as well as a reanalysis of the growth trajectories of juveniles maintained in captivity  
32 and the age-size relationship of individuals in the wild, we demonstrated that leatherback  
33 turtles exhibit a biphasic indeterminate growth pattern and continue to grow as adults.  
34 Using the fitted model, we showed that some individuals can reach maturity at 7 years in  
35 natural conditions, while others require 28 years or more. This extreme plasticity in age at  
36 sexual maturity was already demonstrated in loggerheads in natural conditions and in green  
37 turtles in captivity. This could be a general feature of marine turtles.

38

39 Keywords: *Dermochelys coriacea*, biphasic indeterminate growth, Gompertz, maturity,  
40 leatherback, marine turtles

41

42

## 43 **Introduction**

44 Growth strategies are central to our understanding of life-history theory as they determine  
45 body size and influence key life-history traits including survival, development, and  
46 reproduction (Roff, 2002; Stearns, 1992). As all organisms only have access to finite  
47 resources, they must balance their energy resources between growth and reproduction  
48 (Stearns, 1992). This also has an effect on an individuals' longevity (Roff, 2002; Stearns,  
49 1992). The timing of the shift in resource allocation more or less corresponds to age at  
50 maturity, while the cessation of growth when reproduction begins (i.e., determinate  
51 strategy) appears to optimize fitness (Kozłowski, 1992). However, the selection of a  
52 determinate strategy may be too weak to overwhelm random processes such as  
53 environmental stochasticity and genetic drift under low mortality conditions (Cichoń, 1999).  
54 Because indeterminate growth was not consistently defined in the literature and had a lack  
55 of consensus surrounding its definition, species that have been previously considered to  
56 exhibit in determinate growth may have been labelled erroneously or vice versa (Mumby et  
57 al., 2015). Reptiles are particularly affected by this issue (Congdon et al., 2013), caused  
58 partly by inadequate data. Even with a conservative definition of indeterminate growth, a  
59 too-small sample size in studies on growth can show spurious trends (Congdon et al., 2013).  
60 As such, relatively few reptile species can be definitively classified as indeterminate (Nafus,  
61 2015; Shine and Charnov, 1982).

62 Many models exist to estimate animal growth patterns (Bernstein et al., 2018; Kaufmann,  
63 1981), but the most frequently used are the logistic (Verhulst, 1838), von Bertalanffy (1938),  
64 and Gompertz (1825) models. Several variations based on these models have explicitly  
65 incorporated the cost of reproduction (Minte-Vera et al., 2016) or implemented a biphasic  
66 model into the von Bertalanffy model (Armstrong and Brooks, 2013; Day and Taylor, 1997;

67 Eaton and Link, 2011; Quince et al., 2008a; Quince et al., 2008b) or a polyphasic model into  
68 the logistic model (Peil and Helwin, 1981). Environmental factors such as temperature were  
69 incorporated into the Gompertz growth model applied to bacterial growth (Zwietering et al.,  
70 1991; Zwietering et al., 1994) and the von Bertalanffy model applied to fish growth  
71 (Kielbassa et al., 2010). Attempts to generalise these models often produce models that are  
72 too complex to be practical (Savageau, 1980).

73 To date, among the parametric models, only asymptotic growth models (Gompertz, von  
74 Bertalanffy, and logistic) have been applied to marine turtles, and more specifically, to  
75 leatherbacks (Avens et al., 2009; Jones et al., 2011). Data from a longitudinal field survey in  
76 East Pacific leatherbacks indicate that leatherbacks show growth while individuals are  
77 already at adult stages (Price et al., 2004). The pattern described for leatherback turtles is  
78 similar to what was found using 26 years of individual measurement data for green and  
79 loggerhead females nesting in Cyprus. Post-maturity growth persists in both species, with  
80 growth decreasing for approximately 14 years before plateauing around zero for a further  
81 decade in green turtles alone (Omeyer et al., 2018).

82 Age at maturity is often deduced from the growth pattern of marine turtles. At maturity,  
83 resource allocation shifts from growth to reproductive output, regardless of the nutrient  
84 availability or size at maturity (Bjorndal et al., 2013). Extremely rapid growth rates observed  
85 in captive leatherbacks have led to the speculation that these animals could reach sexual  
86 maturity within 2-3 years (Witham, 1977). A predicted age at maturity of 3-6 years was also  
87 inferred from chondro-osseous (cartilage and bone) morphology (Rhodin, 1985). However,  
88 skeletochronological analysis suggests that leatherbacks could take as long as 13-14 years to  
89 sexually mature (Zug and Parham, 1996). Dutton et al. (2005) suggested that leatherbacks  
90 reach maturity at 12-14 years based on increased returns at a nesting beach (St. Croix, US

91 Virgin Islands) after intensive beach protection and nest relocation, which increased  
92 hatchling production by an order of magnitude in the following decade. Genetic analysis  
93 from the same site suggested that first-time nesters are related, possibly being the genetic  
94 offspring of leatherbacks nesting in the 1980s, which points to an estimated age at maturity  
95 of <20 years (Dutton et al., 2005). Avens et al. (2009) suggested that Northwest Atlantic  
96 leatherbacks reach sexual maturity in 25-29 years based on skeletochronological analysis of  
97 the scleral ossicles as well as the use of a non-parametric smoothing spline model and the  
98 Von Bertalanffy growth function to determine growth rates and age at maturity. In the most  
99 recent study on leatherback growth and age at maturity, several leatherback turtles were  
100 maintained in captivity for nearly 2 years, ranging from hatchlings (6.31 cm SD 0.13 cm SCCL  
101 and 46.0 g SD 1 g) to juveniles (largest, 72.0 cm SCCL and 42.65 kg) (Jones et al., 2011).  
102 Curved carapace length (CCL) *sensu* Bolten (1999) is identical to the  $CCL_{\text{ridge}}$  *sensu* Robinson  
103 et al. (2017) and to the standard curvilinear carapace length (SCCL) *sensu* Georges and  
104 Fossette (2006). Using a global analysis of the relationship between absolute age and SCCL,  
105 Jones et al. (2011) fitted von Bertalanffy, Gompertz, and logistic growth functions to predict  
106 age at maturity for leatherbacks aged 16.1, 8.7, and 6.8 years, respectively. All these  
107 equations behave in a similar way, showing a quasi-exponential growth for very young  
108 individuals and an asymptote  $L_{\infty}$  reached at adult stages.  
109 However, we identified several potential biases in this procedure. First, adult females  
110 continue to show growth, which could decline for larger sizes but could still persist, thus  
111 producing a biphasic growth (Price et al., 2004). The three functions used in Jones et al.  
112 (2011) to model size versus age impose an asymptote  $L_{\infty}$  at adult stage, but then  $L_{\infty}$  is a  
113 biased estimate of size when resources are transferred from growth to reproduction.  
114 Second, nearly all the data for juveniles derive from individuals reared in captivity and fed *ad*

115 *libitum*, whereas all the data for adults relate to individuals captured in the wild.

116 Consequently, the growth of juveniles in captivity can be suspected to be scaled differently

117 as compared to the growth of adults in the wild due to differences in food availability and

118 temperature. This point is important, as the expected age at maturity falls precisely between

119 these two categories of data, and thus no data are available to support the estimation.

120 Different methods described in the literature yield different sizes at maturity for

121 leatherbacks. For example, Avens et al. (2009) used ages when individuals reached 125, 145,

122 and 155 cm SCCL as the potential size at maturity. In other studies, the threshold carapace

123 length for adult classification in leatherbacks was chosen to be 145 cm SCCL (Eckert, 2002;

124 National Marine Fisheries Service, 2001). It should be noted, however, that females as small

125 as 105 cm SCCL have already been seen nesting in Gandoca, Caribbean Coast of Costa Rica

126 (Chaverri, 1999), 106 cm SCCL in Gabon, Africa (in Stewart et al., 2007), and 106 cm SCCL in

127 French Guiana (this study). Jones et al. (2011) defined size at maturity when 97.5% of the

128 asymptote size  $L_{\infty}$  was obtained, with  $L_{\infty}$  being the asymptote of the von Bertalanffy,

129 Gompertz, and logistic growth functions. Nevertheless, the value of 97.5% is not consistent

130 among studies, with a range of 95.0 to 99.9% of the asymptote being used by different

131 authors (Cailliet et al., 2006). Furthermore, most turtles mature at around 70% of maximum

132 size, similarly to other reptiles (Shine and Iverson, 1995).

133 Our objective was to determine the growth patterns of leatherback turtles over their entire

134 life-cycle. Longitudinal measurements from nesting females in French Guiana in the

135 Northwest Atlantic regional management unit (RMU) (Wallace et al., 2010) are used to study

136 growth at adult stage. First, size distribution of new nesters (neophytes) is compared to size

137 distribution of females tagged in previous nesting season to detect a potential size increase

138 at adult stage. Annual SCCL change was then estimated and modelled for females measured

139 at several nesting season. These data are compared with those already published data for  
140 East Pacific RMU (Price et al., 2004). Finally, we develop a biphasic indeterminate growth  
141 model to describe the growth of leatherback turtles. The requirements to model marine  
142 turtle growth, which may be used in a much wider context such as population modelling, are  
143 as follows:

- 144 - Initial rapid growth similar to von Bertalanffy, Gompertz, and logistic growth  
145 functions;
- 146 - A slowdown when size reaches a particular threshold;
- 147 - Non-null growth at adult stage that can gradually slow down when size increases or is  
148 maintained;
- 149 - Habitat quality that acts on both the initial rapid growth and the growth at adult  
150 stage;
- 151 - Habitat quality that can change at any time during the growth process of an  
152 individual;
- 153 - A conversion into determinate growth using a simple parameter change.

154 As no current model met all our requirements, we decided to build a new one. The  
155 mathematical properties of the model are studied using Sobol sensitivity analysis. This  
156 model is then described in a context of varying habitat quality. The parameters of this model  
157 are fitted using observed captivity and field data in view of the origin of these individuals  
158 using the maximum likelihood and Bayesian Markov Chain Monte Carlo (MCMC) proposal  
159 methodology.

160

## 161 **Materials and methods**

### 162 *Measurements of nesting leatherbacks*



163 Field data for this study were obtained between 2011 and 2018 during the nesting seasons  
164 at Awala-Yalimapo beach (5.7°N, 53.9°W), French Guiana, South America. Awala-Yalimapo  
165 beach is situated on the French side of the Maroni River, separating French Guiana and  
166 Suriname. Monitoring programmes at this beach have been in place since the late 1970s  
167 (Girondot and Fretey, 1996). A 4 km stretch of the beach where most nesting events occur  
168 (Girondot, 2010) was continuously patrolled every night from 6:00pm to 7:00am between  
169 April and July. All tagged turtles encountered during these patrols were identified using  
170 internal passive integrated transponder (PIT) tags (Trovan Euroid). Nesting females were  
171 measured during oviposition. Different measurements were obtained, but only standard  
172 curvilinear carapace length (SCCL) was used in this study to ensure consistency across  
173 studies. Straight carapace length (SCL) measures were converted into SCCL where necessary  
174 using the relationship  $SCCL = (SCL + 2.04) \times 1.04$  (Tucker and Frazer, 1991). When a  
175 measured female was seen without a PIT, it was considered as a potential neophyte.  
176 Comparison of size distribution between neophyte nesters and experienced nesters could  
177 indicate if growth still occurred at adult stage. When a female was repeatedly measured  
178 during or between nesting seasons, only its first ( $SCCL_{first}$ ) and last ( $SCCL_{last}$ ) records were  
179 used to avoid pseudo-replication. The annual growth rate was then estimated using  
180  $(365.25 (SCCL_{last} - SCCL_{first}) / n. days)$  with *n.days* being the number of days between  
181 the first and last observations.

182

183 Biphasic indeterminate growth models

184 We concur with Day and Taylor (1997) that growth trajectory should be specified by two  
185 separate equations: a prematurity equation in which no surplus energy is devoted to  
186 reproduction and a post-maturity equation in which all (determinate growth) or some  
187 (indeterminate growth) surplus energy is devoted to reproduction. The new model was built  
188 as a modification of the Gompertz (Gompertz, 1825) and von Bertalanffy (von Bertalanffy,  
189 1938) models for growth by including a new differential equation for adult growth.  
190 The differential of the Gompertz model is ( $x$  as size and  $t$  as time) (Laird, 1964):

191 
$$\frac{dx}{dt} = \alpha \ln\left(\frac{K}{x}\right) x$$
 Eqn 1

192 And the integrated form is  $x = K e^{\ln\left(\frac{x_0}{K}\right)e^{-\alpha t}}$ .

193 With  $K$  being the asymptote (i.e., maximum size that can be reached with the available  
194 nutrients) and  $\alpha$  being a constant related to the proliferative ability of the cells. A simple  
195 solution to convert the model for the indeterminate growth rate was to change  $K$  during  
196 growth. To ensure that indeterminate growth decreases as  $x$  increases, a coupled system of  
197 differential equations was used:

198 
$$\begin{cases} \frac{dx}{dt} = \alpha h \ln\left(\frac{K}{x}\right) x \\ \frac{dK}{dt} = \beta h \left(\frac{1}{1+e^{(1/S)(M-x)}}\right) \end{cases}$$
 Eqn 2

199 No integrated form of the equation 2 exists. The parameters used for this model are:

- 200 -  $\alpha$  is a constant related to the proliferative ability of cells that makes the individual  
201 grow;  
202 -  $M$  is the size at which the transition between exponential juvenile growth and adult  
203 linear growth occurs;

- 204 -  $S$  controls the rate of transition between exponential juvenile growth and adult linear  
 205 growth;  
 206 -  $\beta$  is the linear adult growth rate;  
 207 -  $h$  is the habitat quality, and it acts on both  $\alpha$  and  $\beta$ . Habitat quality,  $h$ , acts as the  
 208 proportion of growth that is maintained in the corresponding habitat as compared to  
 209 maximum growth when  $h = 1$ . When  $h = 0$ , no growth occurs.

210 The change in  $h$  can be time-dependent or represent individual variations. Particularly in this  
 211 case,  $h$  will be used to distinguish individuals raised in captivity and fed *ad libitum* (then  
 212  $h = 1$ ) and wild individuals with fitted  $h$ . If  $\beta = 0$ , this system of differential equations was  
 213 similar to a Gompertz model as modified by Laird (1964).

214 The typical von Bertalanffy model (1938):

$$215 \quad \frac{dx}{dt} = k (L_{\infty} - x) \quad \text{Eqn 3}$$

216 can be modified to a biphasic indeterminate von Bertalanffy model using:

$$217 \quad \begin{cases} \frac{dx}{dt} = k h (L_{\infty} - x) \\ \frac{dL_{\infty}}{dt} = \beta h \left( \frac{1}{1 + e^{(1/S)(M-x)}} \right) \end{cases} \quad \text{Eqn 4}$$

218 Uniqueness of the solution of the biphasic indeterminate Gompertz model

219 The theorem of Cauchy-Lipschitz (also known as the theorem of Picard-Lindelöf) gives a set  
 220 of conditions under which an initial value problem (also named Cauchy problem) has a  
 221 unique solution. If we assumed a system of equations defined as:

$$222 \quad \begin{cases} (x'(t), K'(t)) = f(x, K) \\ (x(0), K(0)) = (x_0, K_0) \end{cases}$$

223 It was necessary to demonstrate that  $f$  was locally Lipschitz continuous: for  $y$  in  $\mathbb{R}^2$  a  
 224 neighbourhood  $U$  of  $y$  exists in which:

$$225 \quad \exists k > 0 \mid \forall (y_1, y_2) \in U \times U, \|f(y_1) - f(y_2)\| \leq k \|y_1 - y_2\|,$$

226  $f$  in  $\mathbb{R}^2 \rightarrow \mathbb{R}^2$  was defined by:

$$227 \quad f(x, K) = \begin{cases} f_1(x, K) = \alpha h \ln\left(\frac{K}{x}\right) x \\ f_2(x, K) = \beta h \frac{1}{1 + e^{S^{-1}(M-x)}} \end{cases}$$

228 Both  $x$  and  $K$  were positive as  $x_0 > 0, K_0 > 0$ . So, by definition  $K'(t) \geq 0 \Rightarrow K(t) \geq K_0 >$   
229  $0$ .

230 Furthermore,  $x'(t) > 0$  when  $0 < x < K_0 < K$  then  $x(t) > 0$ .

231 In  $\mathbb{R}^{+*} \times \mathbb{R}^{+*}$ , the partial derivatives were:

$$232 \quad \frac{\partial f_1}{\partial x} = \alpha h \left( \ln\left(\frac{K}{x}\right) - 1 \right)$$

$$233 \quad \frac{\partial f_1}{\partial K} = \alpha h \frac{x}{K}$$

$$234 \quad \frac{\partial f_2}{\partial x} = -\beta h \frac{e^{S^{-1}(M-x)}}{S(1 + e^{S^{-1}(M-x)})^2}$$

$$235 \quad \frac{\partial f_2}{\partial K} = 0$$

236  $f$  was then  $C^1$  in  $\mathbb{R}^{+*} \times \mathbb{R}^{+*}$  because its partial derivatives existed and were continuous.

237 According to mean value theorem,  $f$  was a locally Lipschitz function. Using the local Cauchy-

238 Lipschitz theorem, a unique solution exists for this Cauchy problem for  $x_0 > 0$  and  $K_0 > 0$ .

239 This implied that for a given set of parameters and habitat quality, there was only one

240 growth curve for the individual.

#### 241 *Biphasic indeterminate Gompertz growth model when $h$ varies*

242 We already proved that the solutions  $x(t)$  and  $K(t)$  of the biphasic indeterminate Gompertz

243 growth model on an interval  $[0, t_f]$  were unique (see previous demonstration).

244 If we assumed that  $x_0 < K_0$  and that there existed a first time  $t^*$  such that  $x(t^*) = K(t^*)$ ,  
 245 thus, this point verified:  $x'(t^*) = 0$  and  $K'(t^*) > 0$ .  $x(t)$  and  $K(t)$  being continuous, so  $\tau >$   
 246  $0$  existed such that  $\forall t \in ]t^* - \tau, t^* [, 0 < x'(t) < K'(t)$

247 When  $t < t^*$ , then  $x(t) < K(t)$  :

$$248 \quad x(t^*) = \int_{t^*-\tau}^{t^*} x'(t) dt + x(t^* - \tau) < \int_{t^*-\tau}^{t^*} K'(t) dt + K(t^* - \tau) = K(t^*)$$

249 A contradiction occurs: the point  $t^*$  such that  $x(t^*) = K(t^*)$  can never be reached.

250 Thus,  $x'(t) > 0$  and  $x(t)$  was a continuous function, and as a consequence,  $x$  was a bijective  
 251 function on the given interval  $[0, t_f]$ .

252 It followed that  $K'(t) > 0$  and that  $K(t)$  was also a continuous function. As a consequence,  
 253  $K$  was also a bijection on  $t$ .

254  $K$  can be written as a function of  $x$  :  $K = K \circ x^{-1}(x(t)) = \varphi(x)$

255 With  $\varphi$  being a continuous, positive, and strictly monotonic function.

256 An equivalent one-dimension problem to the initial differential problem was then:

$$257 \quad x'(t) = h g(x) = h \alpha \ln\left(\frac{\varphi(x)}{x}\right) x \text{ and } x(0) = x_0$$

258 We already proved that  $\forall t \in [0, t_f], x'(t) > 0$ . Let  $G$  be the primitive function of  $\frac{1}{g}$ , then:

$$259 \quad \frac{dx}{dt} = hg(x) \Rightarrow \frac{dx}{g(x)} = hdt \Rightarrow G(x(t)) - G(x_0) = ht$$

260  $G$  was a continuous and strictly increasing function, being the primitive function of a strictly  
 261 positive function. Thus,  $G$  was a bijective function, and  $G^{-1}$  was its inverse function. Then  
 262  $x(t)$  can be rewritten as  $x(t) = G^{-1}(ht + G(x_0))$ .

263 If we assumed that an individual was in a habitat of quality  $h_1$  during a time  $t_1$  and then in a  
 264 habitat of quality  $h_2$  during a time  $t_2 - t_1$ :

$$265 \quad x(t_1) = G^{-1}(h_1 t_1 + G(x_0))$$

266  $x(t_2) = G^{-1}(h_2(t_2 - t_1) + G(x(t_1)))$

267  $x(t_2) = G^{-1}(h_2(t_2 - t_1) + h_1 t_1 + G(x_0))$

268 The mean value of habitat encountered by this individual is:  $\bar{h} = \frac{h_1 t_1 + h_2(t_2 - t_1)}{t_2}$ . Now

269 consider another individual living in this mean habitat during a time  $t_2$ . Its final size will be:

270  $x(t_2) = G^{-1}(\bar{h} t_2 + G(x_0))$

271 The final sizes are identical for both individuals. This conclusion can be expanded by

272 recurrence to any situation  $\{(h_1, t_1), (h_2, t_2), \dots, (h_k, t_k)\}$  with

273 
$$\bar{h} = \frac{h_1 t_1 + h_2(t_2 - t_1) + \dots + h_k(t_k - t_{k-1})}{t_k}$$

274 Thus, when constant  $h$  was fitted for an individual, it can be interpreted as the average

275 habitat quality ( $\bar{h}$ ) experienced by this individual during its lifetime.

276 *Numerical solution of the biphasic indeterminate Gompertz growth model*

277 This system of differential equations was numerically solved using the Runge-Kutta method

278 of order 4 (Kutta, 1901; Runge, 1895). The Runge-Kutta methods are a family of implicit and

279 explicit iterative methods used in temporal discretisation for the approximate solutions of

280 ordinary differential equations implemented in deSolve R package version 1.24 (Soetaert et

281 al., 2010). The initial value was  $x_0 = 6.3$  cm for SCL at the hatchling stage (Jones et al., 2011),

282 while the initial value for  $K$ , named  $K_0$ , was fitted to best adjust the observed data.

283 *Sobol's method for parameter sensitivity (Sobol, 1993)*

284 Sensitivity analysis aims to determine how much the variability in the model output is

285 dependent on each of the input parameters, either a single parameter or an interaction

286 between different parameters. Sobol's method (2001) is based on the decomposition of the

287 model output variance into summands of variances using the same principal as the classical

288 analysis of variance (ANOVA) in a factorial design. However, Sobol sensitivity analysis is not

289 intended to identify the cause of input variability. It simply indicates its impact and extent on  
290 the model output. Sobol sensitivity analysis has the following features:

- 291 - No assumption between model input and output;
- 292 - Evaluation of the full range of each input parameter variation and interactions  
293 between parameters;
- 294 - High computation intensity as the main drawback.

295 We simultaneously implemented the Monte Carlo estimation of the Sobol indices for both  
296 first-order and total indices, which had the advantage of stabilising the variance (Jansen,  
297 1999; Saltelli et al., 2010). Sobol indices were calculated using 10,000 combinations of the  
298 values obtained from uniform distribution for  $\alpha$  in [0.001, 0.02],  $\beta$  in [0.01, 0.1],  $M$  in [90,  
299 140],  $S$  in [-20, 0],  $h$  in [0.1, 1],  $K_0$  in [10, 50], and  $x_0$  in [4, 10]. These ranges were obtained  
300 from a plausible range of values for each parameter, which were determined by manually  
301 changing the parameters and visually observing the dynamic changes. Parameter sensitivity  
302 for age was studied at SCCL 20, 50, 105, 130, and 150 cm and for size at 2, 5, 10, 20, and 40  
303 years. This arbitrary choice of values covered a wide range of possible ages and SCCLs.

#### 304 Fit of parameters using leatherback data

305 Data on the relationship between the size and age of Atlantic leatherback turtles were  
306 retrieved from Table 1 in Jones et al. (2011) as well as from the printed figures in Zug and  
307 Parham (1996) and Avens et al. (2009). We chose not to use the growth in captivity data  
308 published by Bels et al. (1988), as the individuals were probably in suboptimal conditions  
309 (Jones et al., 2011).

310 The  $h$  value was 1 for the data on leatherbacks reared in captivity and fed *ad libitum*,  
311 whereas a fitted value was used for field-captured leatherbacks. The logit of  $h$  value was  
312 used for fitting to ensure that  $h$  was always comprised between 0 and 1. We fitted or used a

313 common  $h$  for all the field data ( $h_{AZP}$ ), or a separate  $h$  for the data of Zug and Parham (1996)  
314 ( $h_{ZP}$ ) and Avens et al. (2009) ( $h_A$ ).

315 A Gaussian distribution of SCCL was used to estimate the likelihood of data within the model  
316 with the standard deviation being a fitted first-order function of size to model  
317 heteroskedasticity:  $SD = a \text{ SCCL} + b$ , with  $a$  and  $b$  being positive.

318 Weekly average and standard deviation values for SCCL were available for leatherbacks  
319 reared in captivity but not for their individual trajectories (Jones et al., 2011). Standard  
320 deviations of weekly measures were combined with the global heteroskedastic standard  
321 deviation ( $a \text{ SCL} + b$ ) using:

$$322 \quad sd = \sqrt{\sum sd_i^2} \quad \text{Eqn 5}$$

323 A comparison of fit statistics for the Gompertz or von Bertalanffy (Eqns 1 and 3) and  
324 indeterminate Gompertz or von Bertalanffy models (Eqns 2 and 4) was based on the Akaike  
325 information criterion (AIC), which is a measure of the quality of fit ( $L$ , for likelihood)  
326 penalised by the number of parameters:  $AIC = -2 \ln L + 2k$ . The number of parameters,  $k$ ,  
327 was equal to 5 for Eqn 1 with  $\alpha$ ,  $h$ ,  $K$ ,  $a$ , and  $b$  being fitted, and equal to 8 for Eqn 2, with  $\alpha$ ,  
328  $\beta$ ,  $h$ ,  $M$ ,  $S$ ,  $K_0$ ,  $a$ , and  $b$  being fitted; one parameter must be added if  $h_{ZP}$  and  $h_A$  were used  
329 instead of a single  $h$  parameter. The model with the lowest AIC has the stronger support  
330 (Akaike, 1974). The Akaike weight measures the probability that a given model is the best  
331 among the tested models (Burnham and Anderson, 2002).

332 Maximum likelihood and Bayesian MCMC parameter proposals were used to search for the  
333 parameters that best described the data.

334 The values of parameters that maximised the likelihood of observed sizes within the model  
335 were searched using the Nelder-Mead non-linear fitting algorithm (Nelder and Mead, 1965).



336 The standard error for outputs was estimated using the delta method with the Hessian  
337 matrix as an approximation of the variance-covariance matrix. The delta method is a general  
338 method for approximating the moments of functions of asymptotically normal random  
339 variables with known variance (Oehlert, 1992). Alternatively, Bayesian posterior distribution  
340 for each parameter was estimated using iterations of MCMC parameter proposals. The initial  
341 values for the parameters were determined using maximum likelihood; no burn-in  
342 adaptation was used. Priors were all obtained from a uniform distribution with limits being  
343 very wide to ensure that a large range of parameter values could be checked (see  
344 Supplementary Material). Standard deviations for new proposals were chosen based on  
345 adaptive MCMC methodology (Rosenthal, 2011) as implemented in R package *HelpersMG*,  
346 version 4.0 (Girondot, 2020). The number of iterations required to estimate the quantile  
347 0.025 to within an accuracy of  $\pm 0.005$  with probability 0.95 was calculated using an initial  
348 pilot 50,000 run (Raftery and Lewis, 1992). From this diagnostic, a run with 100,000  
349 iterations was chosen. Convergence was first visually examined to ensure that the time  
350 series of the parameters were stationary, and then tested using the Heidelberger and Welch  
351 (1983) diagnostic. The standard error of the parameters was estimated after correction for  
352 autocorrelation (Roberts, 1996). Results from the MCMC were analysed using the R package  
353 *Coda*, version 0.19-1 (Plummer et al., 2011) and *HelpersMG*, version 4.0 (Girondot, 2020).

#### 354 *From growth pattern to age at maturity*

355 Female age at maturity at the population scale can be obtained as the age at which the  
356 smallest females are seen nesting on the beach. The smallest nesting female was around  
357 105 cm SCCL (this study, Chaverri, 1999; Stewart et al., 2007), but excluding this exceptional  
358 value, the SCCL distribution generally shows a lower value of around 130 cm (Fig. 1A). On the

359 other hand, SCCL distribution of potential neophyte females is Gaussian with a mean of  
360 158.10 cm and standard deviation of 8.23 cm (Fig. 1A).

## 361 **Results**

### 362 *Biometry of nesting leatherbacks in Awala-Yalimapo, French Guiana*

363 A total of 1061 different females were measured from 2011 to 2018: 622 females were  
364 observed for the first time based on the absence of a PIT or monel tag, while 439 had  
365 already been tagged in the previous nesting seasons. Among these 1061 females, 187 were  
366 measured in several nesting seasons. The untagged females were not necessarily true  
367 neophytes, although tagged females were obviously true non-neophytes. The average SCCL  
368 was 159.43 cm (SD 7.84 cm), and the minimum and maximum sizes were 106 and 181 cm,  
369 respectively. When splitting the data into two groups based on whether the female was  
370 observed for the first time on the beach during a nesting season (Fig. 1A) or had already  
371 been tagged during a previous season (Fig. 1B), the size distributions strongly differed  
372 (difference 3.79 cm; BIC [Bayesian Information Criterion] weight=  $6.10^{-8}$ ). The BIC weight is  
373 the posterior probability that a single size distribution was sufficient to model the SCCL for  
374 the two groups (Girondot and Guillon, 2018). BIC was used instead of AIC because the true  
375 model was obviously among the tested models (i.e., size of two groups either differs or not).  
376 When the same female was seen during different seasons, the model for average SCCL  
377 annual growth upon SCCL was an exponential decay for both West Atlantic leatherbacks  
378 nesting in French Guiana (Akaike weight=0.991, Fig. 2A, Table 1) and the Pacific East  
379 leatherbacks nesting in Parque Nacional Marino Las Baulas, Costa Rica (Akaike weight=0.884,  
380 Fig. 2B, Table 1) (data retrieved from Price et al., 2004). In both situations, the lower end of  
381 95% confidence interval was different from 0 indicating a non-null growth even at larger  
382 size. The 95% confidence interval of the measures can be approximated by four times the

383 fitted standard deviation: 3 cm for French Guiana, West Atlantic data and 2.5 cm for Costa  
384 Rica, Pacific East data.

### 385 Example of growth dynamics and parameter sensitivity

386 An example of the growth dynamic produced by the system of differential equation 2 is  
387 shown in Figure 3 for  $\alpha=0.007$ ,  $\beta=0.067$ ,  $M=115.52$ ,  $S=-7.55$ ,  $h=0.45$ ,  $x_0=6.3$ , and  $K_0=28.88$ .  
388 Sensitivity analysis highlights the relative influence of variables on the dynamics. In Figure  
389 3A, the contribution of variables to size for known age is shown. In Figure 3B, the  
390 contribution of variables to age for known size is shown. As expected from Eqn 2, parameter  
391  $\alpha$  acts mostly during very early growth, while  $\beta$  acts later (Fig. 3A). Habitat quality ( $h$ ) has a  
392 special interest for ecologists, as it is a measure of the influence of ocean productivity.  
393 Habitat quality ( $h$ ) influences size for a given age regardless of the age (Fig. 3A), but it has  
394 almost no influence when age was inferred from size and size was large (Fig. 3B). From an  
395 ecological point of view, this result is important: if age is known, SCCL can be used as an  
396 indicator of ocean productivity experienced by an individual during its life.

397 A typical example of dynamic SCCL growth when  $h$  (habitat quality) changes during the life of  
398 an individual is shown in Figure 4. Note that the final size using the exact  $h$  dynamics  
399 (171.698 cm) or the mean of  $h$  values (171.706 cm) were very close as demonstrated in the  
400 Materials and Methods section, with this difference being due to numerical approximations.  
401 Thus, it is possible to summarize the growth of an individual using the average  $h$  value  
402 experienced by this individual during its all lifetime.

### 403 Parameter fitting

404 The biphasic indeterminate Gompertz model with fitted  $h_{ZP}$  and  $h_A$  (Eqn 2) strongly out-  
405 performed all other models ( $\Delta AIC > 200$ , Table 1): the Gompertz model (Eqn 1) can be  
406 excluded as a representation of leatherback growth with  $\Delta AIC > 1000$ , Akaike weight=0. The

407 biphasic indeterminate Gompertz was also a highly supported model compared to the  
408 biphasic indeterminate von Bertalanffy model regardless of the number of habitat models.  
409 The model with fitted  $h_{ZP}$  (0.504) and  $h_A$  (0.275) strongly out-performed the model with a  
410 single fitted  $h$  (0.458) ( $\Delta AIC=253$ , Akaike weight=0) and the model with fixed  $h = 1$  parameter  
411 ( $\Delta AIC=888$ , Akaike weight=0). Habitat quality was therefore an important parameter to take  
412 into account.

413 The fitted value for  $b = 0.0119$  was lower than its standard error  $SE\ b=0.0478$ , and as  $b$  had  
414 to be positive, the hypothesis of Gaussian distribution for parameters required for the delta  
415 method was violated (Oehlert, 1992). For this reason, the distributions of parameters were  
416 better estimated using the posteriors of Bayesian MCMC. Raftery and Lewis (1992)  
417 diagnostics indicate that around 100,000 iterations were necessary to estimate the posterior  
418 of  $h_{ZP}$  and  $h_A$  with  $\pm 0.005$  accuracy. Tests for stationary distributions (Heidelberger and  
419 Welch, 1983) for  $h_{ZP}$  and  $h_A$  were successfully passed with 100,000 iterations. The plot of the  
420 observed size-age data and fitted models for  $h = 1$  and fitted  $h_{ZP}$  and  $h_A$  is shown in Figure 5.  
421 Posterior distributions of  $h_{ZP}$  and  $h_A$  are shown in Figure 6.

#### 422 Age at maturity

423 The size of the smallest leatherback females seen nesting on the beach was around 105 cm  
424 SCCL (Chaverri, 1999; Stewart et al., 2007) and 106 cm SCCL in our French Guiana dataset.  
425 This size can be reached between 6.2 to 7.5 years in natural conditions when  $h = 0.504$  and  
426 between 11.3 to 13.6 years when  $h = 0.275$ . In the model, the age at which females reached  
427 the size of 130 cm is between 9.6 and 14.9 years when  $h = 0.504$  and between 17.5 and 27.1  
428 years when  $h = 0.275$ . The mean SCCL for potential neophyte females (see the discussion  
429 below on capture probability and non-fidelity to nesting beaches) in French Guiana was

430 between 157 to 158 cm (Fig. 1). This size can be reached between 24.7 to 61.7 years for  
431  $h = 0.504$  and 45.2 to 112.8 years for  $h = 0.275$  (Fig. 7).

432

### 433 **Discussion**

434 We developed a new biphasic indeterminate growth model based on the Gompertz  
435 equation to investigate growth pattern of leatherback turtles. Furthermore, we showed that  
436 the model was improved by integrating habitat quality measured by the  $h$  parameter. Two  
437 groups of data provided two different estimates for  $h$ : 95% confidence interval for average  
438 habitat quality is between 0.250 and 0.304 for Avens et al. (2009) and between 0.465 and  
439 0.555 for Zug and Parham (1996). It is difficult to determine if these differences are due to  
440 temporal, spatial, or methodological effects. We have no cues to choose among these  
441 hypotheses. It should be noted that the parameter  $h$  describing habitat quality has the same  
442 definition as the  $h$  parameter in Gaspar and Lalire (2017) for oceanic dispersion modelling.  
443 The distribution of the size of non-neophytes and females seen nesting on the beach for the  
444 first time was significantly different from the size of non-neophytes (Fig. 1), but the average  
445 difference was only 3.79 cm, with the potential neophyte being smaller. Of course, we  
446 cannot ascertain that individuals seen for the first time were true neophytes: they could  
447 have nested at another beach in a previous season or on this beach without being captured.  
448 It should be noted that Yalimapo-Awala beach has been patrolled for 10 hours per night on  
449 all nights during the nesting season for more than 10 years. Taking into account their high  
450 fidelity to the nesting beach (Girondot et al., 2007), at least a fraction of these females seen  
451 for the first time are probably true neophytes. The small size difference observed between  
452 neophyte and non-neophyte females was also noted in loggerheads (Tucek et al., 2014),  
453 indicating that growth at adult stage is very low. Data from the longitudinal field survey in

454 French Guiana (Fig. 2A) as well as growth modelling (Fig. 5A) allowed us to clearly  
455 demonstrate that leatherbacks show indeterminate growth and thus confirm and extend  
456 previous findings on East Pacific leatherbacks (Price et al., 2004). The pattern described here  
457 for leatherback turtles could be general for marine turtles (Omeyer et al., 2018).

458 As no general life-history pattern linked growth to age at maturity (Wenk and Falster, 2015),  
459 there was no justification for using any proxy (e.g.,  $x\%$  of  $L_\infty$ ) from the growth function to  
460 estimate age at maturity. Furthermore, age at maturity is a concept with a clear meaning for  
461 an individual, but at the scale of a group of individuals, only a range of ages at maturity  
462 should be proposed. We show here that in natural conditions ( $h=0.275$  or  $0.504$ ), the  
463 smallest females seen nesting on a beach (105 cm SCCL) could be aged between 6.2 and  
464 13.6 years. However, nesting females of this size are quite exceptional, and the more typical  
465 size of the smallest nesting females is around 130 cm. Such a size can be reached by females  
466 between 9.6 and 27.1 years in natural conditions. This large age range does not necessarily  
467 reflect the confidence interval of the estimate but may rather indicate large phenotypic  
468 plasticity.

469 The lowest age at maturity for females at the population scale can be obtained as the lowest  
470 age at which females are seen nesting on a beach. It is more difficult or even impossible to  
471 obtain an average, median, or highest age at maturity. Based on comparisons with  
472 loggerhead marine turtles in South Africa (Tucek et al., 2014), it is even possible that the  
473 concept of the highest age at maturity does not exist: if an individual grows very slowly due  
474 to an insufficiently rich environment, then it is possible that it may never attain an adequate  
475 size to reach sexual maturity. In such a situation, even the average or median age at  
476 maturity cannot be defined. Only the distribution of age at maturity among the nesting  
477 females can be estimated, but it is a biased measure of the distribution of age at maturity at

478 the scale of the population, because the slowest growing females could die before reaching  
479 sexual maturity. Indeed, the average annual adult survival probability  $0.789 \pm 0.009$  is low  
480 for leatherbacks in French Guiana (Chevallier et al., 2020).

481 The pivotal trade-off between growth and reproduction resource allocation occurs against a  
482 background of increasing mortality rates with age after maturity (Sgrò and Partridge, 1999).  
483 In this scenario, investing resources in reproduction rather than growth represents the most  
484 efficient strategy to improve individual fitness. However, the view that this scenario is  
485 universal has been challenged by relatively recent concepts such as negative senescence, in  
486 which the mortality rate declines after reproductive maturity similarly to how it declines  
487 during growth (Vaupel et al., 2004). In this case, investing in continued growth as well as  
488 reproduction is the optimal strategy, as the organism can experience the benefits of both a  
489 larger body size and improved fitness (Charnov, 1993). This pattern has been demonstrated  
490 in a longitudinal study on a freshwater turtle (Armstrong et al., 2018). Further fieldwork  
491 studies are nevertheless needed to show whether such a life-history strategy is relevant for  
492 marine turtles.

493

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514

#### 515 **Ethical standards**

516 The research was conducted with the authorisation of the French Ministry of Ecology,  
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518



519 **References**

520

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698



699 Table 1: Model selection based on AICc for pattern of annual growth rate upon SCCL for  
 700 French Guiana (West Atlantic) and Costa Rica (East Pacific) leatherbacks. The selected  
 701 models are in bold.

<b>West Atlantic</b>	AICc	$\Delta$ AICc	Akaike weight
<b>Exponential decay</b>	<b>434.12</b>	<b>0.00</b>	<b>0.991</b>
Constant	443.50	9.37	0.009
Zero	533.53	99.40	0.000
<b>East Pacific</b>	AICc	$\Delta$ AICc	Akaike weight
<b>Exponential decay</b>	<b>261.68</b>	<b>0.00</b>	<b>0.884</b>
Constant	265.74	4.06	0.116
Zero	281.60	19.92	0.000

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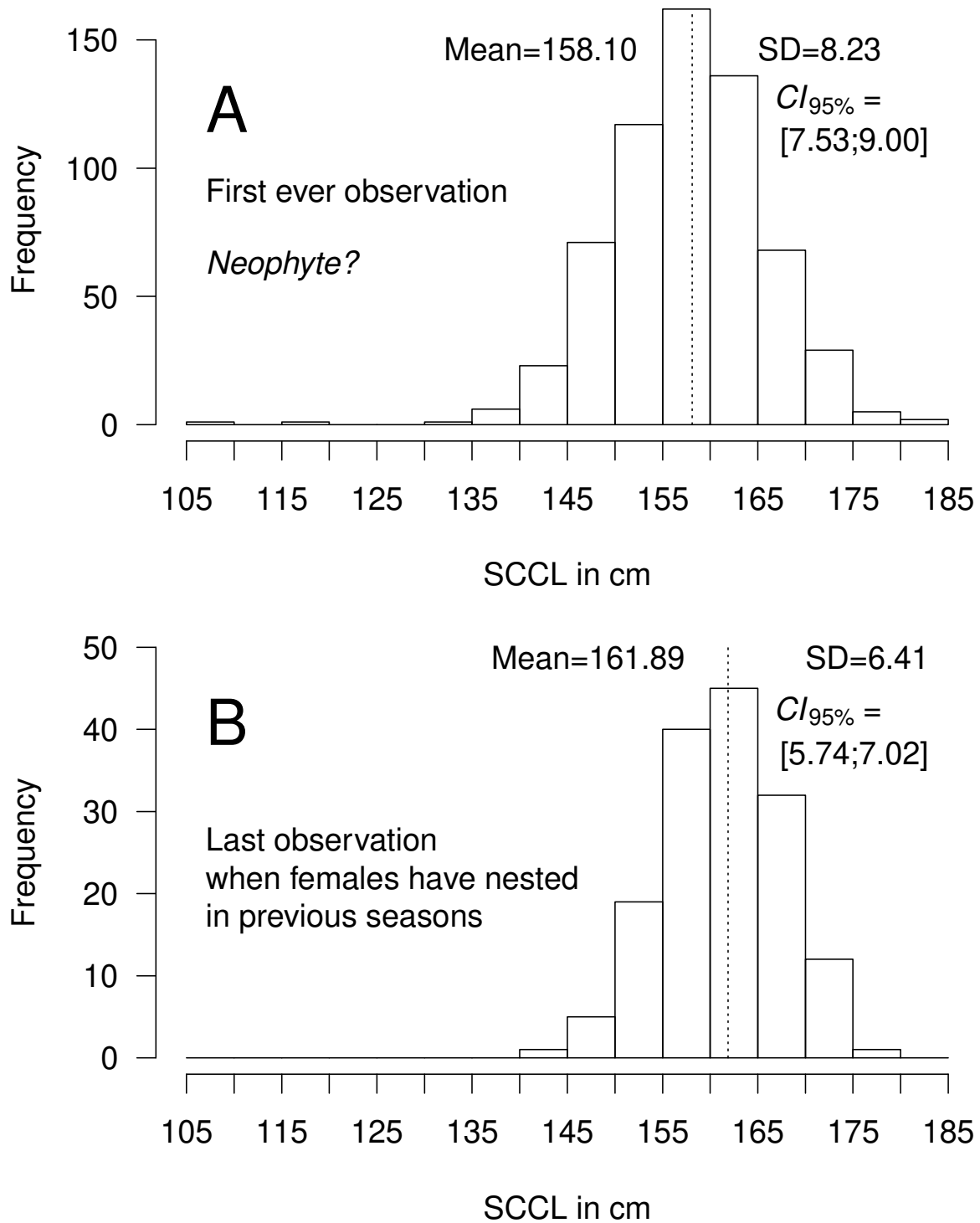
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704 Table 2: Model selection based on AIC and Akaike weight.  $h_{al}$  is the habitat quality when  
705 individuals are fed *ad libitum* ( $h=1$ ), while  $h_A$  is the fitted value for Avens et al. (2009) data  
706 and  $h_{ZP}$  for Zug and Parham (1996) data.  $h_{AZP}$  is the fitted value when a single habitat model  
707 is used for both datasets. The Gompertz and von Bertalanffy models are based on Eqn 2 and  
708 Eqn 4, respectively, with  $\beta = 0$ . Selected model is in bold.

Model	Habitat	AIC	$\Delta$ AIC	Akaike weight
Gompertz	$h_{al}, h_A, h_{ZP}$	3262.22	1063.54	0.000
Gompertz	$h_{al}, h_{AZP}$	3274.50	1075.83	0.000
Gompertz	-	3477.50	1278.83	0.000
<b>Indeterminate Gompertz</b>	<b><math>h_{al}, h_A, h_{ZP}</math></b>	<b>2198.67</b>	<b>0.0000</b>	<b>1.000</b>
Indeterminate Gompertz	$h_{al}, h_{AZP}$	2452.43	253.76	0.000
Indeterminate Gompertz	-	3086.99	888.30	0.000
von Bertalanffy	$h_{al}, h_A, h_{ZP}$	2605.45	406.78	0.000
von Bertalanffy	$h_{al}, h_{AZP}$	2866.50	667.83	0.000
von Bertalanffy	-	3028.06	829.39	0.000
Indeterminate von Bertalanffy	$h_{al}, h_A, h_{ZP}$	2611.45	412.78	0.000
Indeterminate von Bertalanffy	$h_{al}, h_{AZP}$	2870.50	671.83	0.000
Indeterminate von Bertalanffy	-	3034.06	835.39	0.000

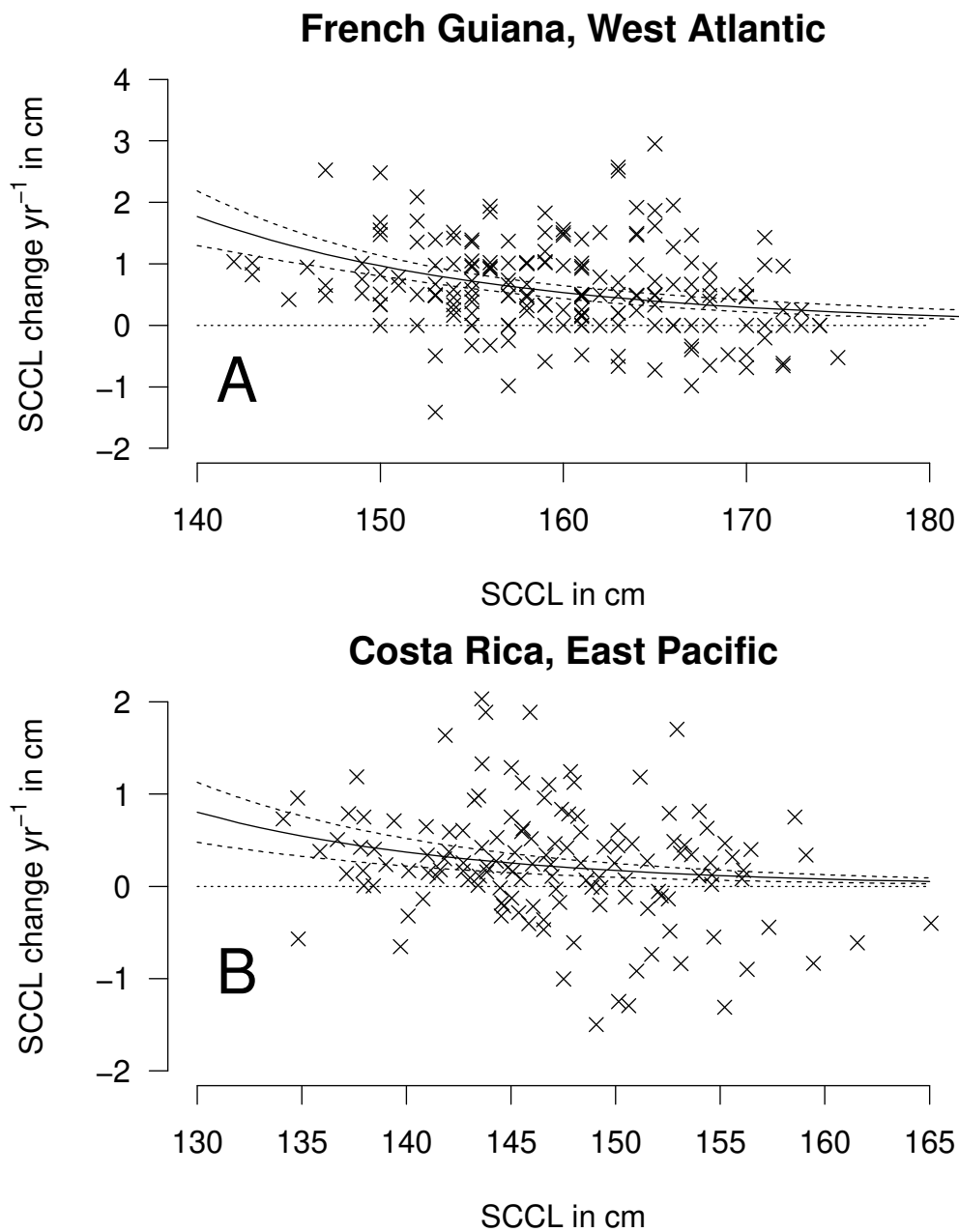
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710 Figure 1: Standard curvilinear carapace length (SCCL) distribution for nesting females on  
 711 Awala-Yalimapo nesting beach (French Guiana) for (A) females seen nesting for the first time  
 712 and being potential neophytes and (B) last observation for females seen nesting during  
 713 previous nesting seasons.



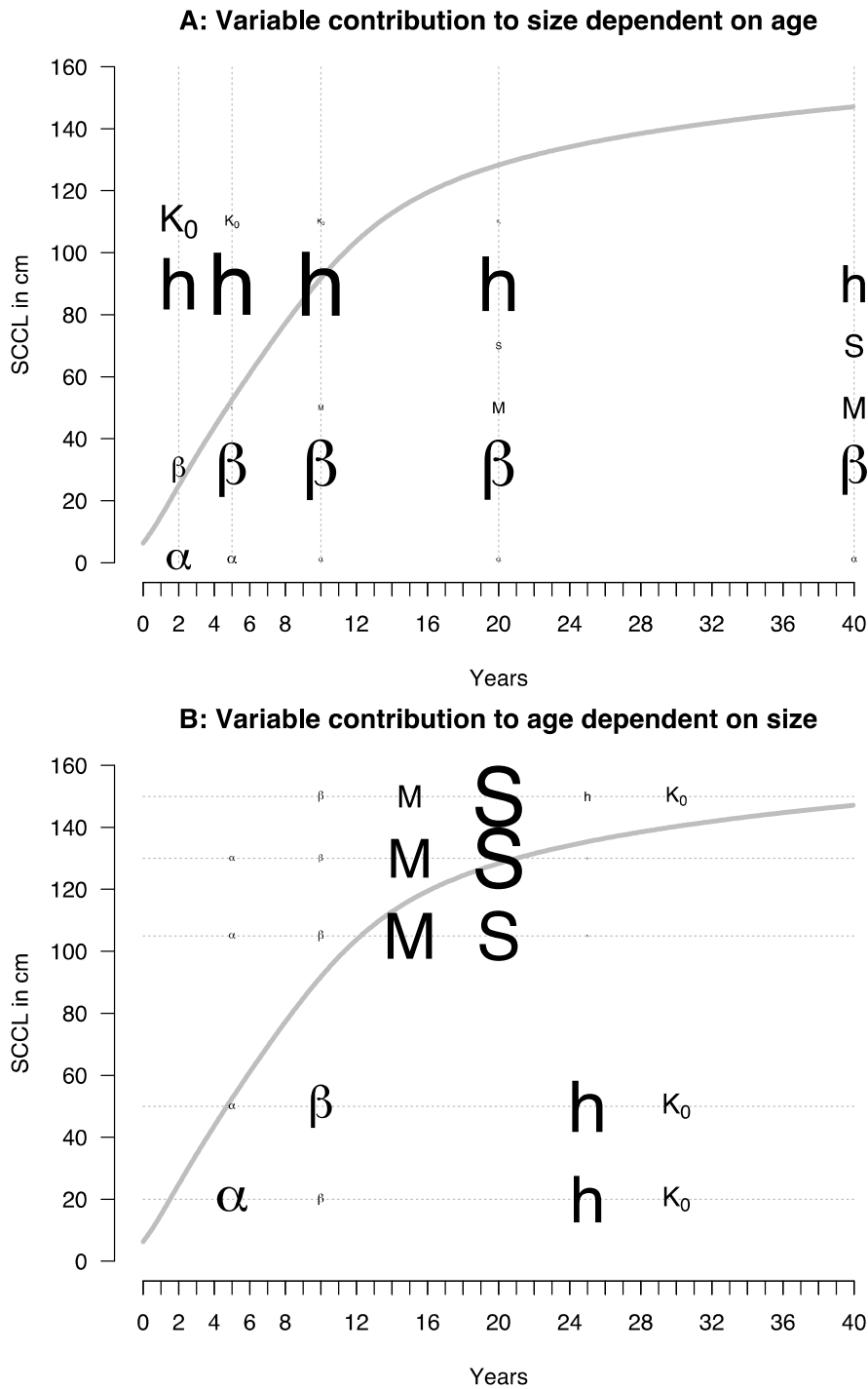
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715 Figure 2: Change in standard curvilinear carapace length (SCCL) in  $\text{cm yr}^{-1}$  for nesting females  
716 in the Northwest Atlantic (French Guiana, this study) and Pacific East (Costa Rica, Price et al.,  
717 2004) regional management units (as per Wallace et al., 2010). Solid lines represent the  
718 relation between SCCL and year change modelled as exponential decay (selected model  
719 based on AICc), and dashed lines are the 95% confidence interval. Dotted line represents the  
720 expected SCCL change if no growth occurs at adult stage.



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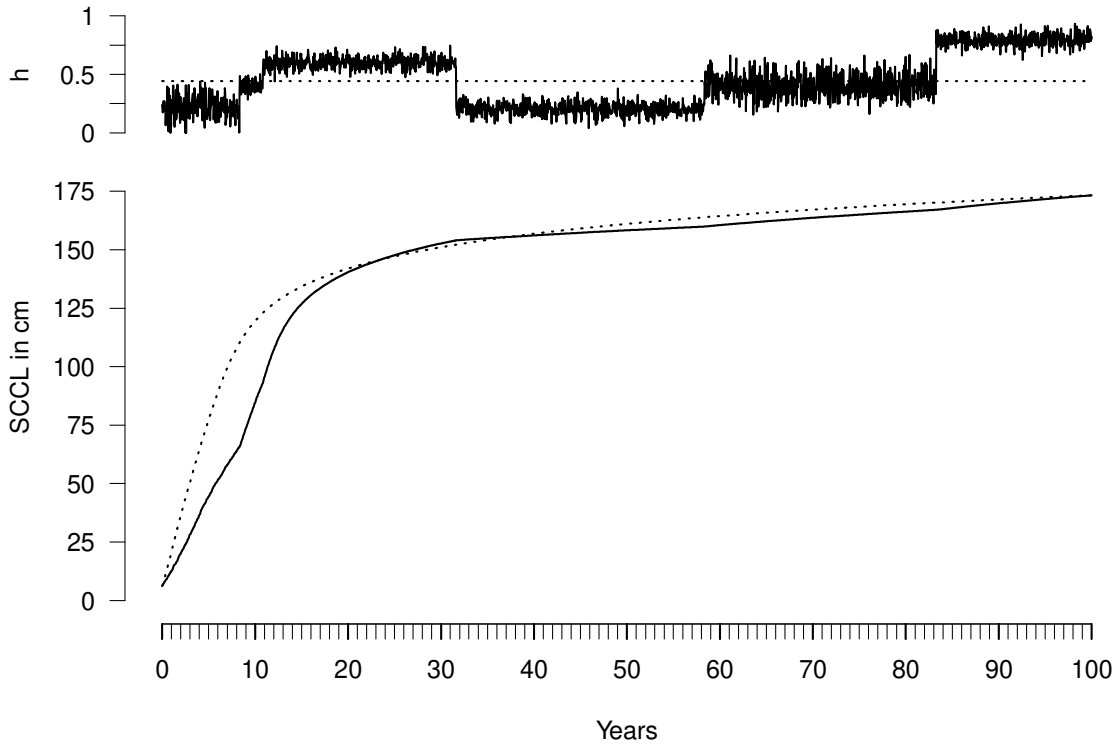
722 Figure 3: An example of standard curvilinear carapace length (SCCL) growth with the total  
 723 relative contribution of each variable (total contribution, including interaction, standardised  
 724 to 1) for (A) SCCL at 20, 50, 105, 130, and 150 cm and (B) age at 2, 3, 10, 20, and 40 years.  
 725 The contribution of  $x_0$  is always too low to be visible.



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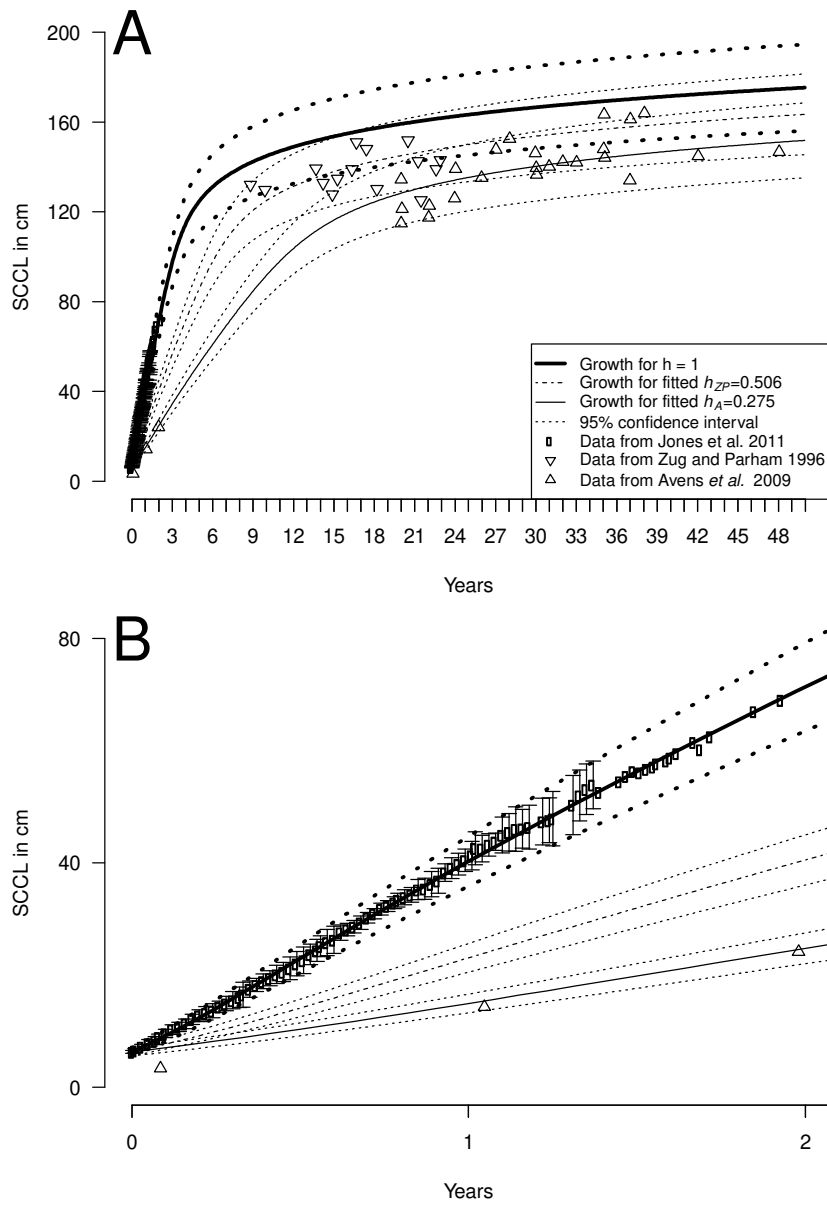
728 Figure 4: Example of standard curvilinear carapace length (SCCL) growth when habitat  
729 quality  $h$  varies. Dotted lines represent the average habitat quality  $h$  and the corresponding  
730 growth dynamics. Note that the growth dynamics is different, but final size is the same.



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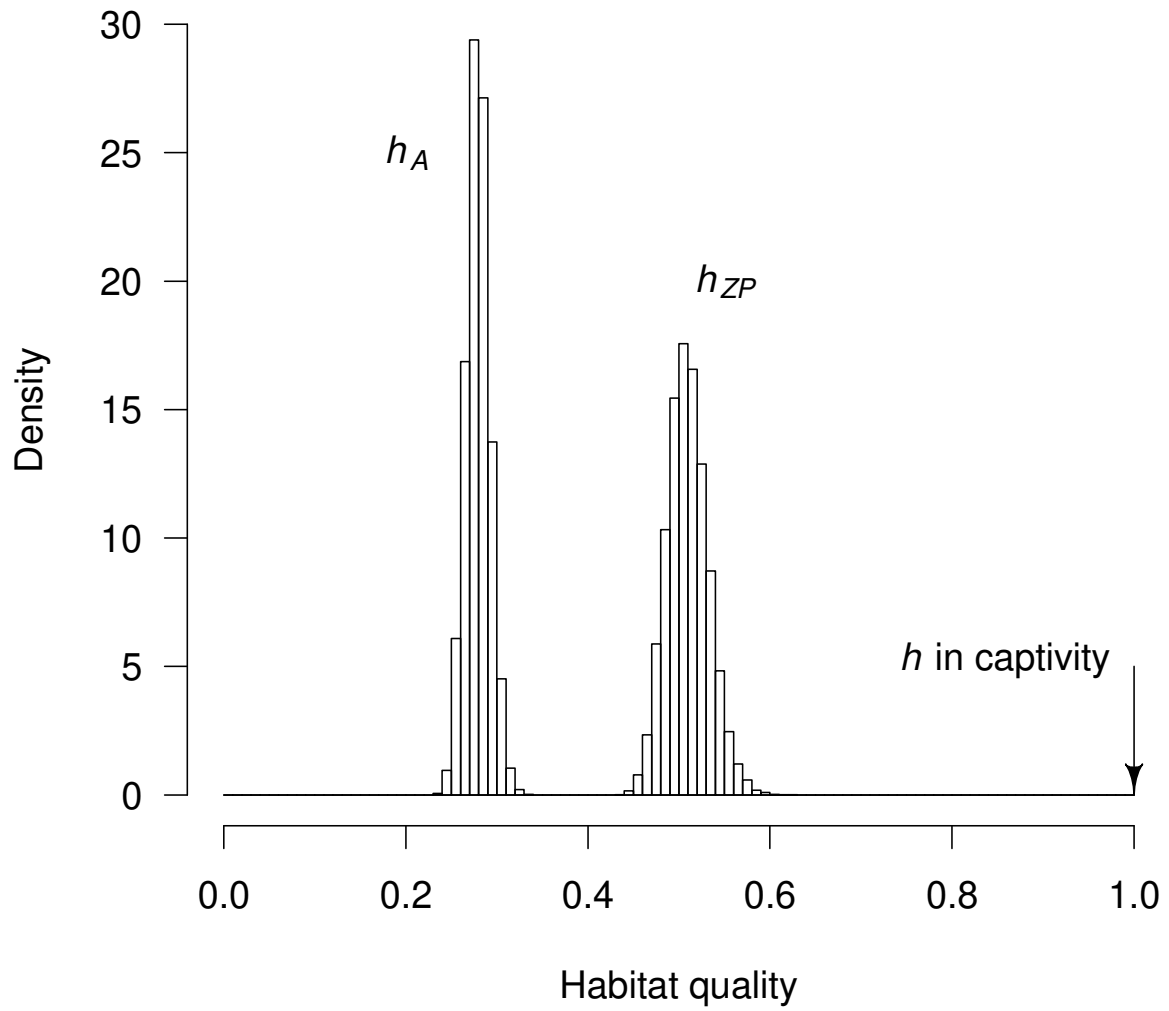
733 Figure 5: Observed data of standard curvilinear carapace length (SCCL)-age for Northwest  
734 Atlantic leatherbacks and indeterminate Gompertz model of growth using  $h = 1$  for  
735 leatherbacks in captivity and fitted  $h$  for leatherbacks captured in the wild ( $h$  is relative  
736 habitat quality).



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738

739 Figure 6: Posterior distribution for 100,000 iterations of habitat quality ( $h$ ) for data from  
740 Avens et al. (2009) ( $h_A$ ), Zug and Parham (1996) ( $h_{ZP}$ ), and Jones et al. (2011) ( $h$  in captivity).

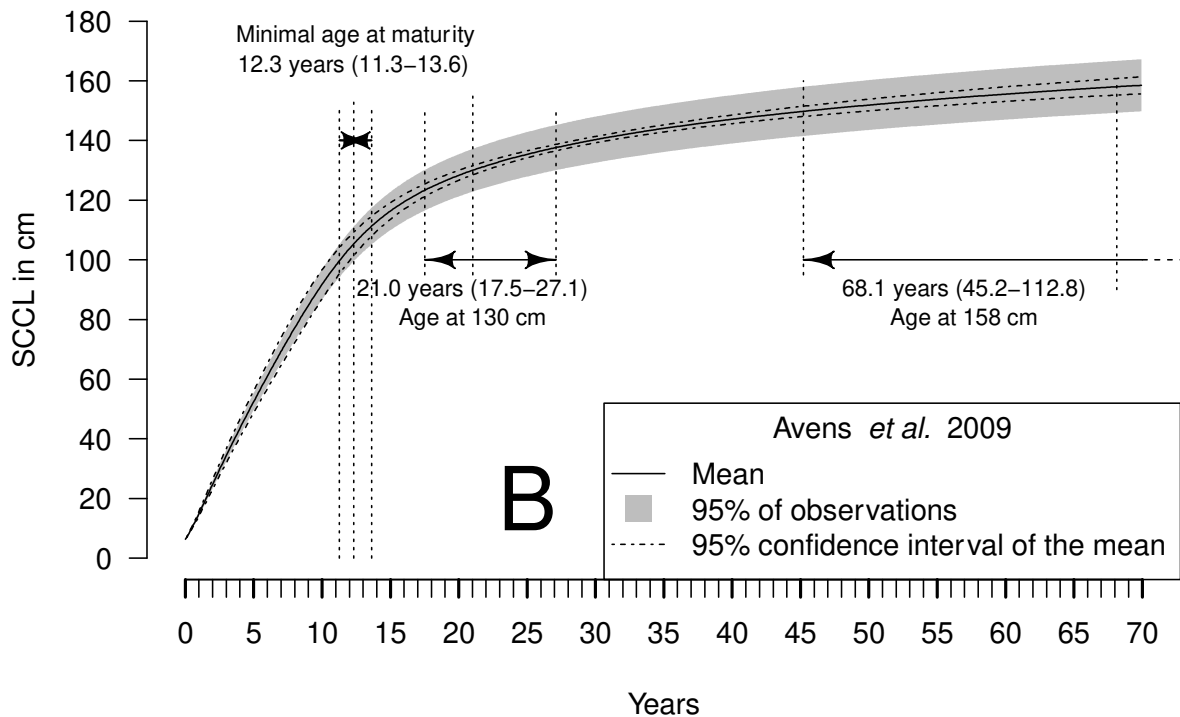
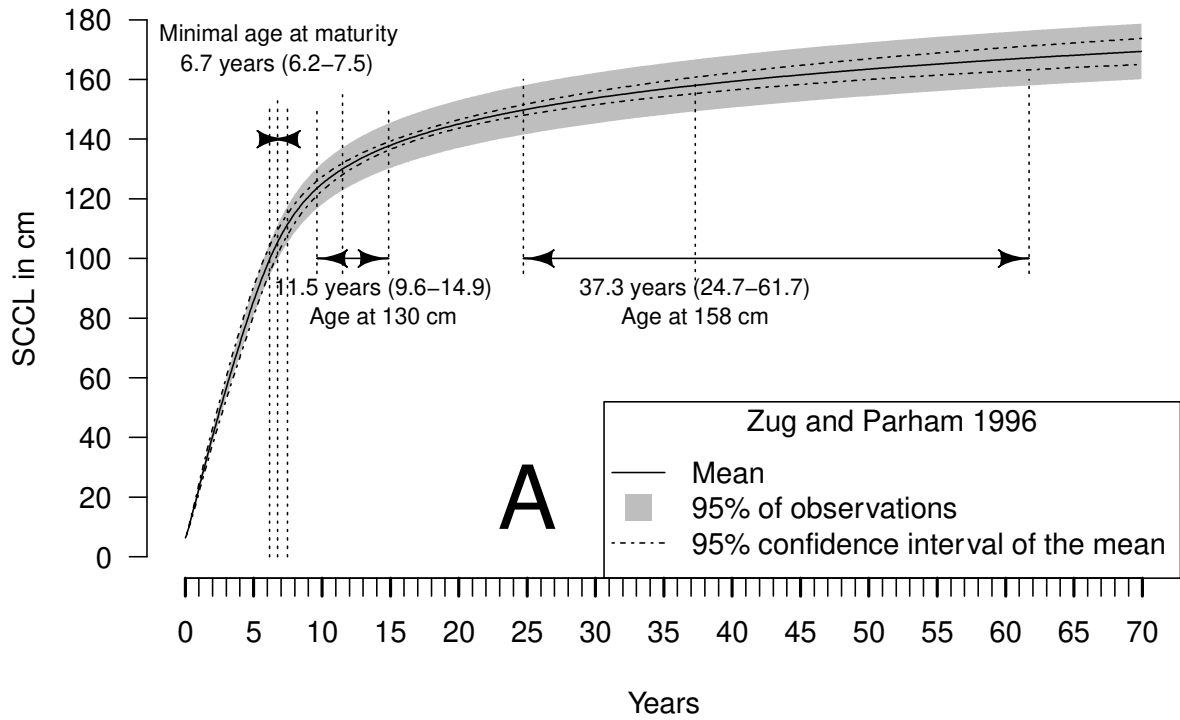


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743 Figure 7: Model of Northwest Atlantic leatherback growth in natural conditions (A:  $h = 0.505$ ;  
 744 B:  $h = 0.275$ ) fitted using the indeterminate Gompertz model (Eqn 2). The correspondence  
 745 between standard curvilinear carapace length (SCCL) and range of possible ages (95%  
 746 confidence interval) is shown for SCCL = 105, 130, and 158 cm.



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