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Modelling leatherback biphasic indeterminate growth using a modified Gompertz equation

Running page head: Leatherbacks indeterminate growth

Damien Chevallier[1], Baptiste Mourrain[2] and Marc Girondot[2*]

[1] – Institut Pluridisciplinaire Hubert Curien, Département Ecologie, Physiologie et Ethologie, UMR 7178, CNRS-Unistra, 23 rue Becquerel, 67087 Strasbourg Cedex 2, France

[2] – Laboratoire Écologie, Systématique, Évolution, Université Paris-Sud, AgroParisTech, CNRS, Université Paris Saclay, 91405 Orsay, France

* Corresponding author

Orcid number: 0000-0001-6645-8530

Email: marc.girondot@u-psud.fr

Phone: +33 1 69 15 72 30

+33 6 20 18 22 16

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Abstract

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

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

Introduction

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

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

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

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

Age at maturity is often deduced from the growth pattern of marine turtles. At maturity, resource allocation shifts from growth to reproductive output, regardless of the nutrient availability or size at maturity (Bjorndal et al., 2013). Extremely rapid growth rates observed in captive leatherbacks have led to the speculation that these animals could reach sexual maturity within 2-3 years (Witham, 1977). A predicted age at maturity of 3-6 years was also inferred from chondro-osseous (cartilage and bone) morphology (Rhodin, 1985). However, skeletochronological analysis suggests that leatherbacks could take as long as 13-14 years to sexually mature (Zug and Parham, 1996). Dutton et al. (2005) suggested that leatherbacks 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_{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_∞ at adult stage, but then L_∞ 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_∞ was obtained, with L_∞ 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*

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

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

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

193 With *K* being the asymptote (i.e., maximum size that can be reached with the available
194 nutrients) and α 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 $$\begin{cases} \frac{dx}{dt} = \alpha \, h \, ln\left(\frac{K}{x}\right) x \\ \frac{dK}{dt} = \beta \, h \left(\frac{1}{1+e^{(1/S)(M-x)}}\right) \end{cases} \qquad \text{Eqn 2}$$

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

200 - α 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;

- *S* controls the rate of transition between exponential juvenile growth and adult linear growth;
- β is the linear adult growth rate;
- *h* is the habitat quality, and it acts on both α and β. Habitat quality, *h*, acts as the proportion of growth that is maintained in the corresponding habitat as compared to maximum growth when *h* = 1. When *h* = 0, no growth occurs.

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

The typical von Bertalanffy model (1938):

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

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

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

<u>*Uniqueness of the solution of the biphasic indeterminate Gompertz model*</u>

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

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

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

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

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

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

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

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

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

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

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

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

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

f was then C^1 in $\mathbb{R}^{+*} \times \mathbb{R}^{+*}$ because its partial derivatives existed and were continuous. According to mean value theorem, *f* was a locally Lipschitz function. Using the local Cauchy-Lipschitz theorem, a unique solution exists for this Cauchy problem for $x_0 > 0$ and $K_0 > 0$. This implied that for a given set of parameters and habitat quality, there was only one growth curve for the individual.

Biphasic indeterminate Gompertz growth model when h varies

We already proved that the solutions $x(t)$ and $K(t)$ of the biphasic indeterminate Gompertz growth model on an interval $[0, t_f]$ were unique (see previous demonstration).

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

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

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

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

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

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

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

With φ being a continuous, positive, and strictly monotonic function.

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

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

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

$$\frac{dx}{dt} = hg(x) \Longrightarrow \frac{dx}{g(x)} = hdt \Longrightarrow G\big(x(t)\big) - G(x_0) = ht$$

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

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

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

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

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

The mean value of habitat encountered by this individual is: $\overline{h} = \frac{h_1 t_1 + h_2(t_2 - t_1)}{t_2}$. Now consider another individual living in this mean habitat during a time t_2. Its final size will be:

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

The final sizes are identical for both individuals. This conclusion can be expanded by recurrence to any situation $\{(h_1, t_1), (h_2, t_2), \cdots, (h_k, t_k)\}$ with

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

Thus, when constant *h* was fitted for an individual, it can be interpreted as the average habitat quality ($\bar{h}$) experienced by this individual during its lifetime.

Numerical solution of the biphasic indeterminate Gompertz growth model

This system of differential equations was numerically solved using the Runge-Kutta method of order 4 (Kutta, 1901; Runge, 1895). The Runge-Kutta methods are a family of implicit and explicit iterative methods used in temporal discretisation for the approximate solutions of ordinary differential equations implemented in deSolve R package version 1.24 (Soetaert et al., 2010). The initial value was x_0 = 6.3 cm for SCL at the hatchling stage (Jones et al., 2011), while the initial value for *K*, named K_0, was fitted to best adjust the observed data.

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

Sensitivity analysis aims to determine how much the variability in the model output is dependent on each of the input parameters, either a single parameter or an interaction between different parameters. Sobol's method (2001) is based on the decomposition of the model output variance into summands of variances using the same principal as the classical 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 α in [0.001, 0.02], β 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

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

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

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

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

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

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

The values of parameters that maximised the likelihood of observed sizes within the model were searched using the Nedler-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 ±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

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

Example of growth dynamics and parameter sensitivity

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

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

Parameter fitting

The biphasic indeterminate Gompertz model with fitted h_{ZP} and h_A (Eqn 2) strongly out-performed all other models (ΔAIC > 200, Table 1): the Gompertz model (Eqn 1) can be excluded as a representation of leatherback growth with ΔAIC > 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) (ΔAIC=253, Akaike weight=0) and the model with fixed h = 1 parameter
411 (ΔAIC=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 ±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 is 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_∞) 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

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

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

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Ethical standards

The research was conducted with the authorisation of the French Ministry of Ecology, Sustainable Development and Energy to capture, tag, and measure the animals.

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

West Atlantic	AICc	ΔAICc	Akaike weight
Exponential decay	**434.12**	**0.00**	**0.991**
Constant	443.50	9.37	0.009
Zero	533.53	99.40	0.000
East Pacific	AICc	ΔAICc	Akaike weight
Exponential decay	**261.68**	**0.00**	**0.884**
Constant	265.74	4.06	0.116
Zero	281.60	19.92	0.000

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

Model	Habitat	AIC	ΔAIC	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
Indeterminate Gompertz	**h_{al}, h_A, h_{ZP}**	**2198.67**	**0.0000**	**1.000**
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

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

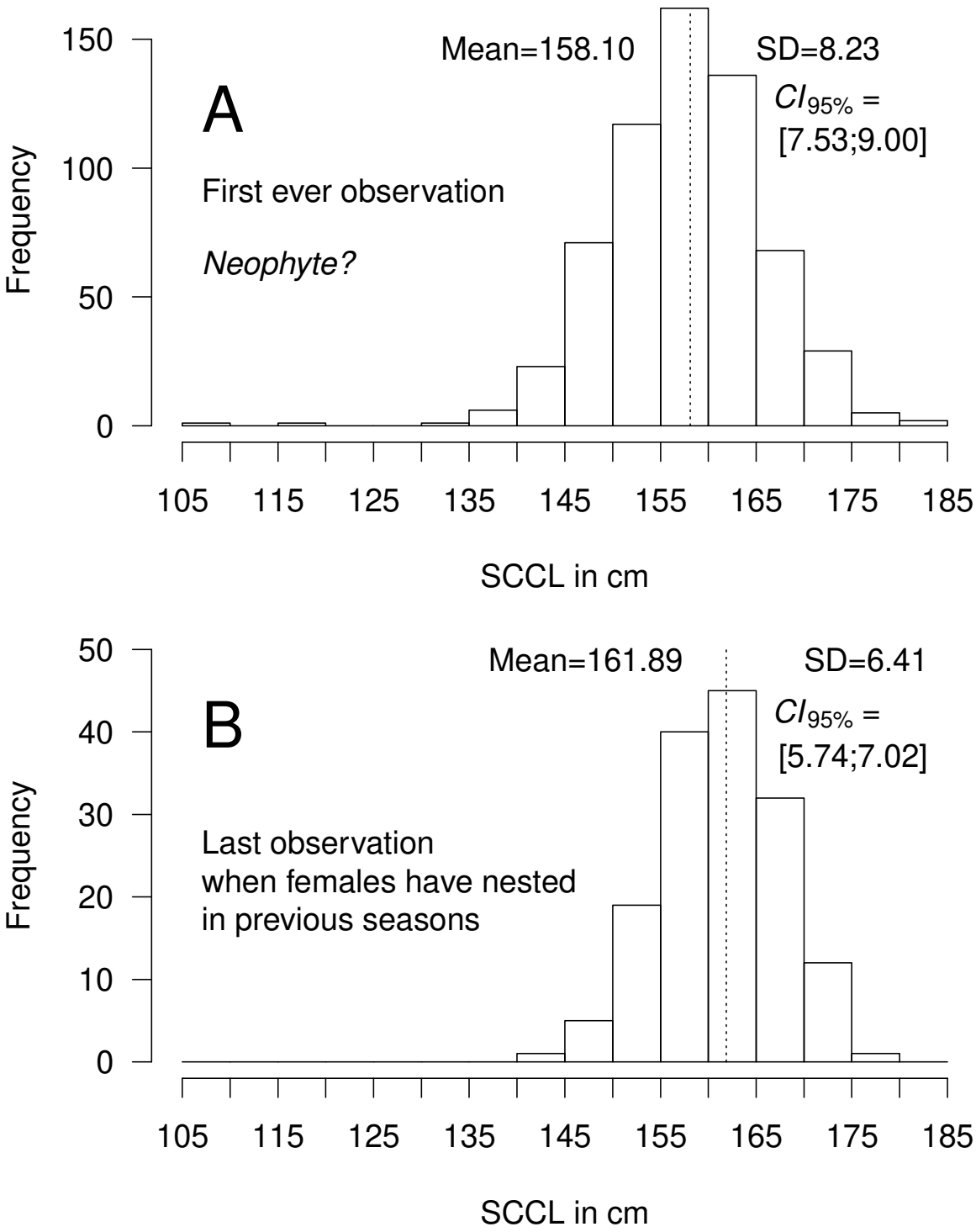

Figure 2: Change in standard curvilinear carapace length (SCCL) in cm yr^{-1} for nesting females in the Northwest Atlantic (French Guiana, this study) and Pacific East (Costa Rica, Price et al., 2004) regional management units (as per Wallace et al., 2010). Solid lines represent the relation between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

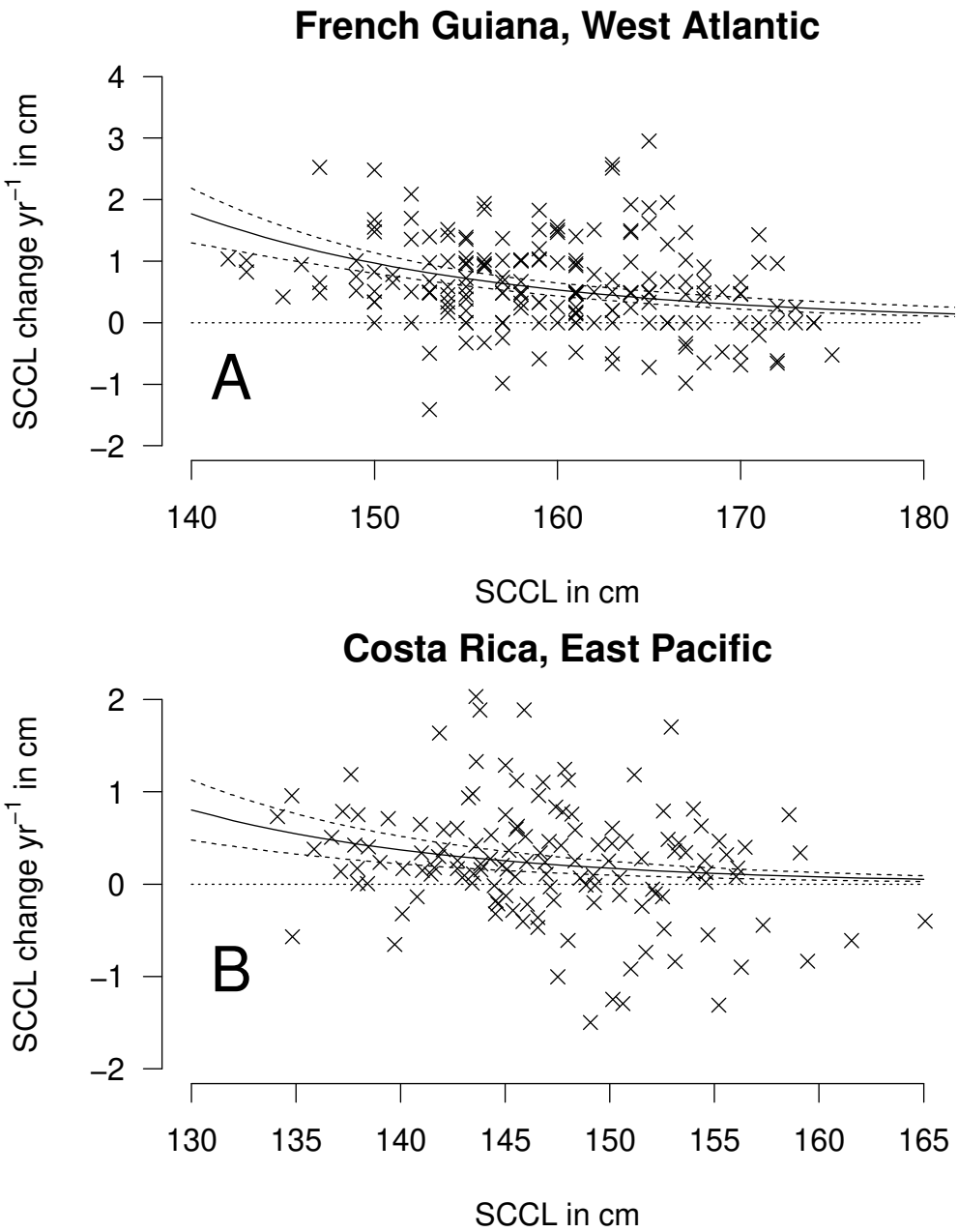

Figure 3: An example of standard curvilinear carapace length (SCCL) growth with the total relative contribution of each variable (total contribution, including interaction, standardised to 1) for (A) SCCL at 20, 50, 105, 130, and 150 cm and (B) age at 2, 3, 10, 20, and 40 years. The contribution of x_0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

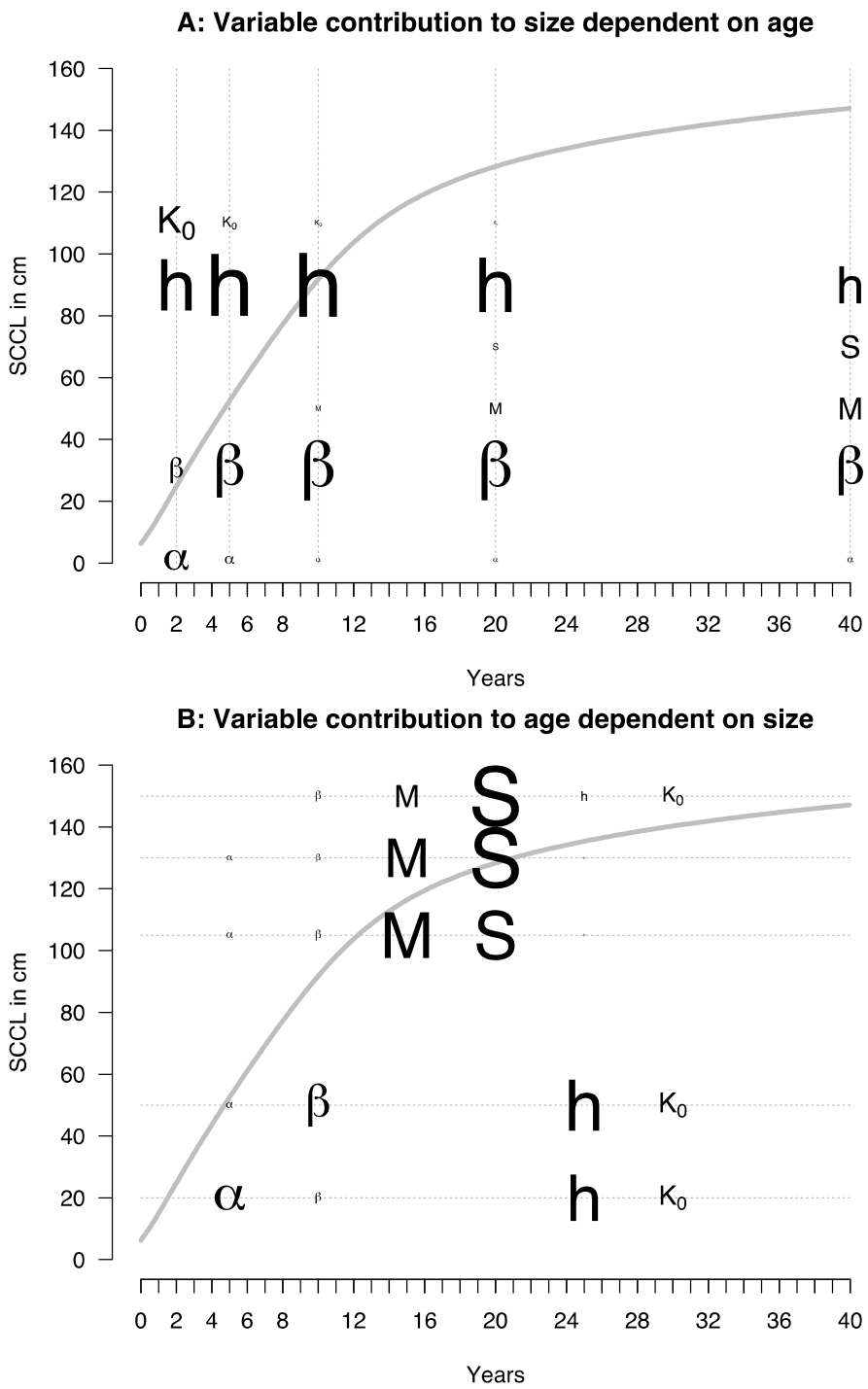

Figure 4: Example of standard curvilinear carapace length (SCCL) growth when habitat quality *h* varies. Dotted lines represent the average habitat quality *h* and the corresponding growth dynamics. Note that the growth dynamics is different, but final size is the same.

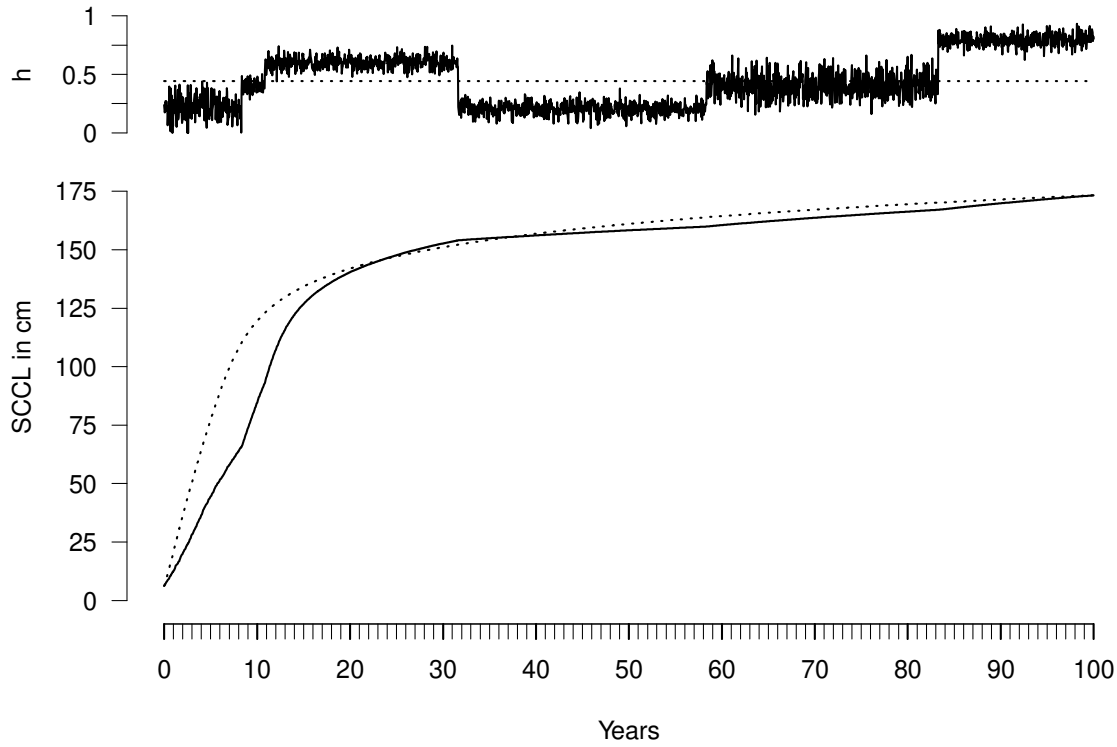

Figure 5: Observed data of standard curvilinear carapace length (SCCL)-age for Northwest Atlantic leatherbacks and indeterminate Gompertz model of growth using *h* = 1 for leatherbacks in captivity and fitted *h* for leatherbacks captured in the wild (*h* is relative habitat quality).

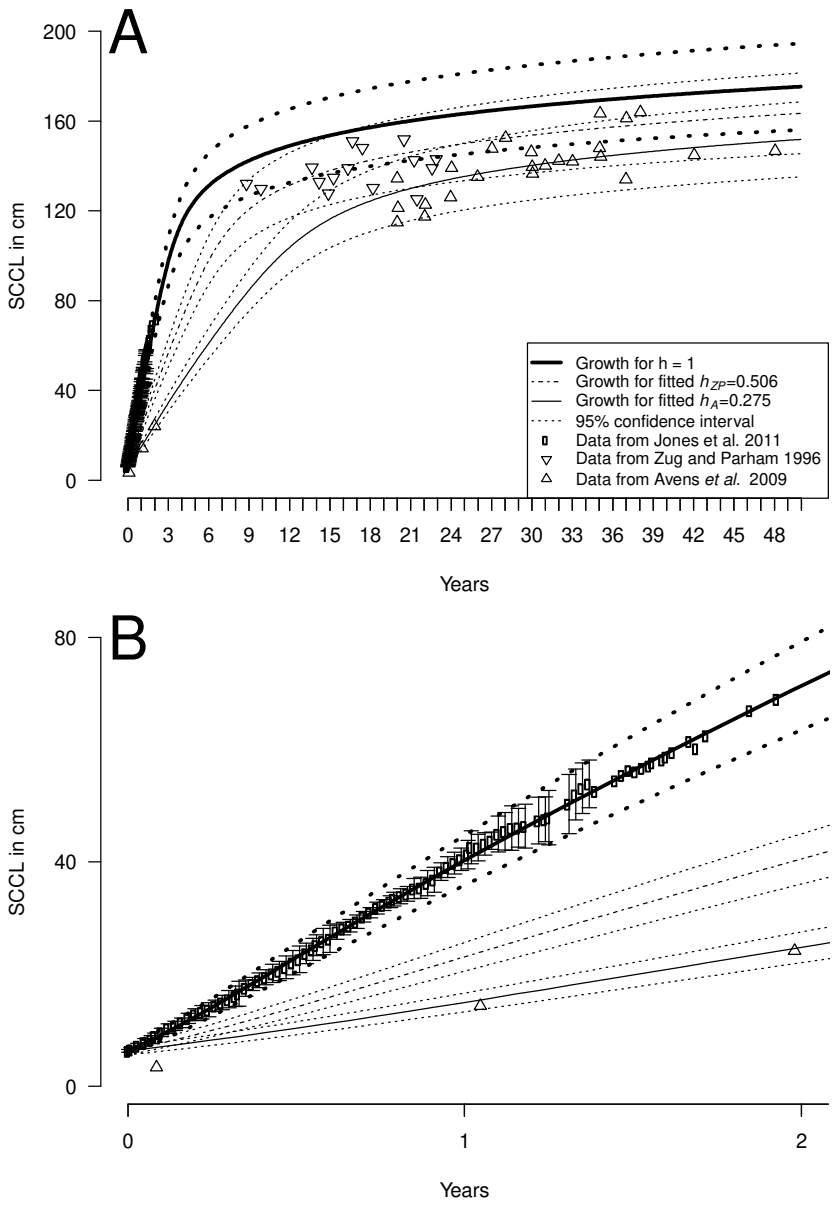

Figure 6: Posterior distribution for 100,000 iterations of habitat quality (*h*) for data from Avens et al. (2009) (h_A), Zug and Parham (1996) (h_{ZP}), and Jones et al. (2011) (*h* in captivity).

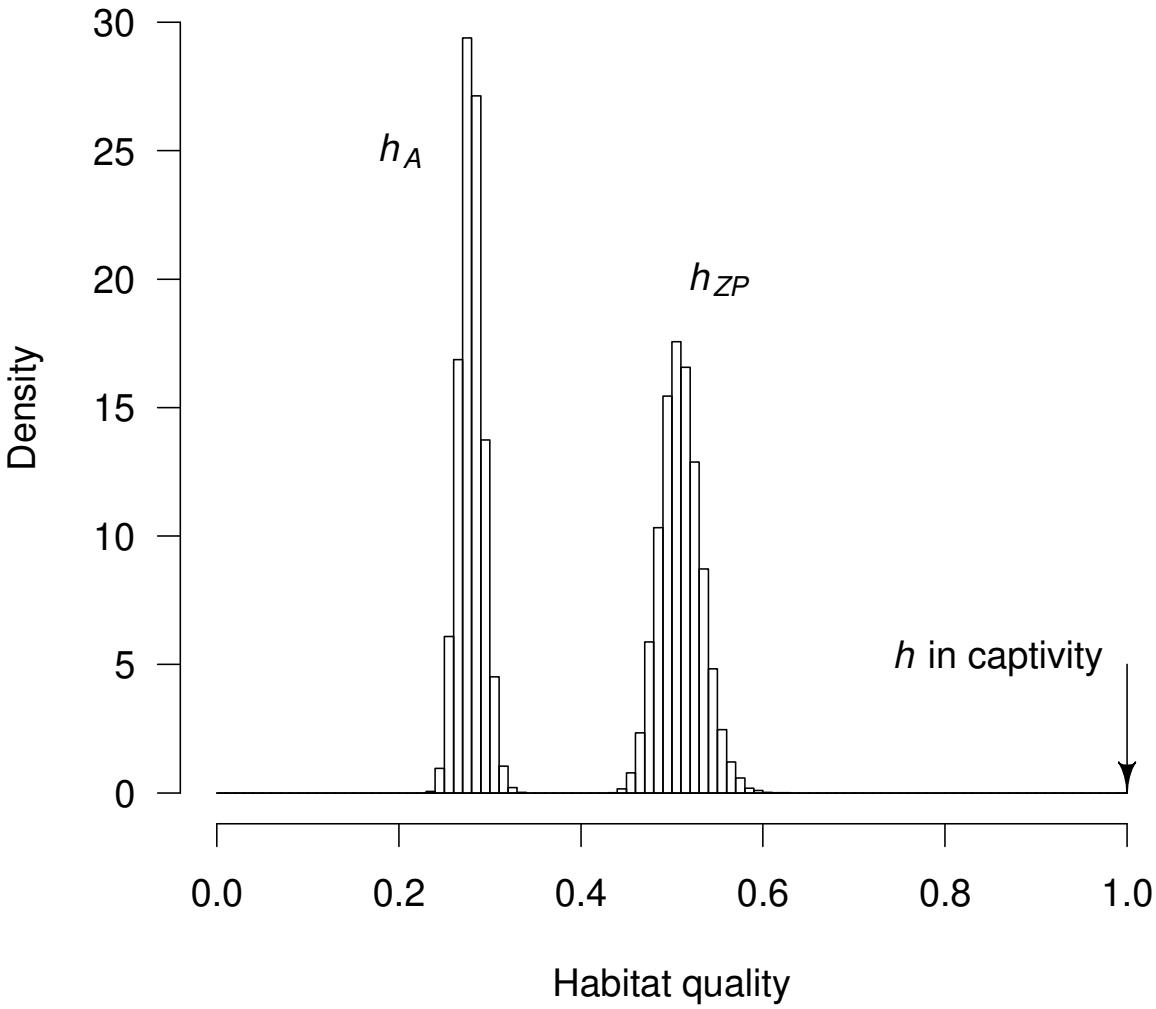
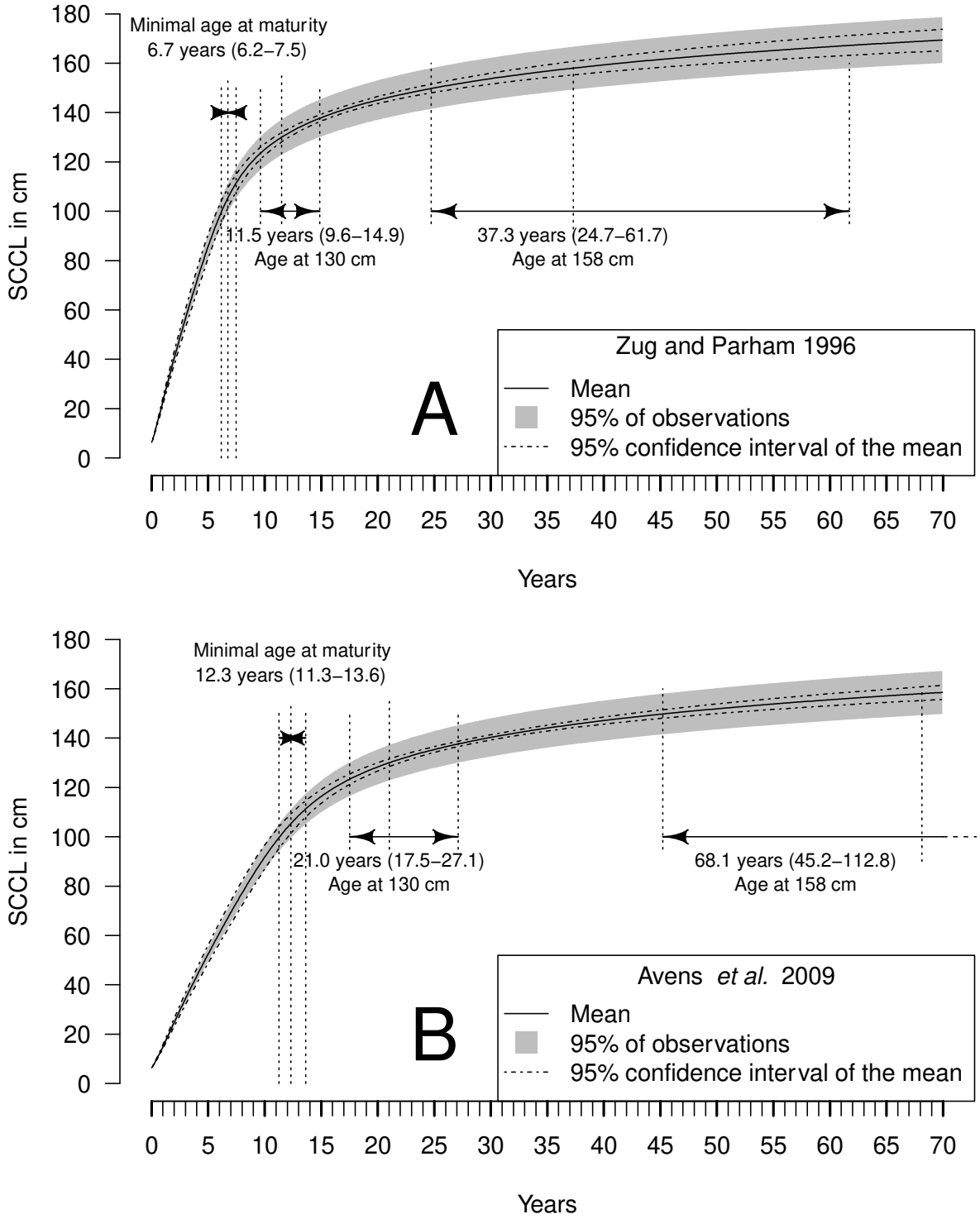
Figure 7: Model of Northwest Atlantic leatherback growth in natural conditions (A: *h* = 0.505; B: *h* = 0.275) fitted using the indeterminate Gompertz model (Eqn 2). The correspondence between standard curvilinear carapace length (SCCL) and range of possible ages (95% confidence interval) is shown for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