

Modelling leatherback biphasic indeterminate growth using a modified Gompertz equation



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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.

1. 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, 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, 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, amongst 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

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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 chondroosseous (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 Virgin Islands) after intensive beach protection and nest relocation, which increased hatching production by an order of magnitude in the following decade. Genetic analysis from the same site suggested that first-time nesters are related, possibly being the genetic offspring of leatherbacks nesting in the 1980s, which points to an estimated age at maturity of <20 years (Dutton et al., 2005). Avens et al. (2009) suggested that Northwest Atlantic leatherbacks reach sexual maturity in 25–29 years based on skeletochronological analysis of the scleral ossicles as well as the use of a non-parametric smoothing spline model and the Von Bertalanffy growth function to determine growth rates and age at maturity. In the most recent study on leatherback growth and age at maturity, several leatherback turtles were maintained in captivity for nearly 2 years, ranging from hatchlings (6.31 cm SD 0.13 cm SCCL and 46.0 g SD 1 g) to juveniles (largest, 72.0 cm SCCL and 42.65 kg) (Jones et al., 2011). Curved carapace length (CCL) *sensu* Bolten (1999) is identical to the CCL_{ridge} *sensu* Robinson et al. (2017) and to the standard curvilinear carapace length (SCCL) *sensu* Georges and Fossette (2006). Using a global analysis of the relationship between absolute age and SCCL, Jones et al. (2011) fitted von Bertalanffy, Gompertz, and logistic growth functions to predict age at maturity for leatherbacks aged 16.1, 8.7, and 6.8 years, respectively. All these equations behave in a similar way, showing a quasi-exponential growth for very young individuals and an asymptote L_{∞} reached at adult stages.

However, we identified several potential biases in this procedure. First, adult females continue to show growth, which could decline for larger sizes but could still persist, thus producing a biphasic growth (Price et al., 2004). The three functions used in Jones et al. (2011) to model size versus age impose an asymptote L_{∞} at adult stage, but then L_{∞} is a biased estimate of size when resources are transferred from growth to reproduction. Second, nearly all the data for juveniles derive from individuals reared in captivity and fed *ad libitum*, whereas all the data for adults relate to individuals captured in the wild. Consequently, the growth of juveniles in captivity can be suspected to be scaled differently as compared to the growth of adults in the wild due to differences in food availability and temperature. This point is important, as the expected age at maturity falls precisely between these two categories of data, and thus no data are available to support the estimation.

Different methods described in the literature yield different sizes at maturity for leatherbacks. For example, Avens et al. (2009) used ages when individuals reached 125, 145, and 155 cm SCCL as the potential size at maturity. In other studies, the threshold carapace length for adult classification in leatherbacks was chosen to be 145 cm SCCL (Eckert, 2002; National Marine Fisheries Service, 2001). It should be noted, however, that females as small as 105 cm SCCL have already been seen nesting in Gandoca, Caribbean Coast of Costa Rica (Chaverri, 1999), 106 cm SCCL in Gabon, Africa (in Stewart et al., 2007), and 106 cm SCCL in French Guiana (this study).

Jones et al. (2011) defined size at maturity when 97.5% of the asymptote size L_{∞} was obtained, with L_{∞} being the asymptote of the von Bertalanffy, Gompertz, and logistic growth functions. Nevertheless, the value of 97.5% is not consistent amongst studies, with a range of 95.0 to 99.9% of the asymptote being used by different authors (Cailliet et al., 2006). Furthermore, most turtles mature at around 70% of maximum size, similarly to other reptiles (Shine and Iverson, 1995).

Our objective was to determine the growth patterns of leatherback turtles over their entire life-cycle. Longitudinal measurements from nesting females in French Guiana in the Northwest Atlantic regional management unit (RMU) (Wallace et al., 2010) are used to study growth at adult stage. First, size distribution of new nesters (neophytes) is compared to size distribution of females tagged in previous nesting season to detect a potential size increase at adult stage. Annual SCCL change was then estimated and modelled for females measured at several nesting season. These data are compared with those already published data for East Pacific RMU (Price et al., 2004). Finally, we develop a biphasic indeterminate growth model to describe the growth of leatherback turtles. The requirements to model marine turtle growth, which may be used in a much wider context such as population modelling, are as follows:

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

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

2. Materials and methods

2.1. 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 $(365.25(SCCL_{last} - SCCL_{first})/n \text{ days})$ with n days being the number of days between the first and last observations.

2.2. Biphasic indeterminate growth models

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

The differential of the Gompertz model is (x as size and t as time) (Laird, 1964):

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

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

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

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

No integrated form of the Eq. (2) exists. The parameters used for this model are:

- α is a constant related to the proliferative ability of cells that makes the individual grow;
- M is the size at which the transition between exponential juvenile growth and adult 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 a and b . 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 $\beta = 0$, this system of differential equations was similar to a Gompertz model as modified by Laird (1964).

The typical von Bertalanffy model (1938):

$$\frac{dx}{dt} = k(L_\infty - x) \tag{3}$$

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

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

2.3. Uniqueness of the solution of the biphasic indeterminate Gompertz model

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:

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

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 $\mathbb{R}^2 \rightarrow \mathbb{R}^2$ 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 $K'(t) \geq 0 \Rightarrow K(t) \geq K_0 > 0$.

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

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

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

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

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

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

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.

2.4. 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:

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

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

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

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 $t_2 - t_1$:

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

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

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

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

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

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

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

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.

2.5. 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.

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

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

We simultaneously implemented the Monte Carlo estimation of the Sobol indices for both first-order and total indices, which had the advantage of stabilising the variance (Jansen, 1999; Saltelli et al., 2010).

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	Δ AICc	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	Δ AICc	Akaike weight
Exponential decay	261.68	0.00	0.884
Constant	265.74	4.06	0.116
Zero	281.60	19.92	0.000

Sobol indices were calculated using 10,000 combinations of the values obtained from uniform distribution for α in $[0.001, 0.02]$, β in $[0.01, 0.1]$, M in $[90, 140]$, S in $[-20, 0]$, h in $[0.1, 1]$, K_0 in $[10, 50]$, and x_0 in $[4, 10]$. These ranges were obtained from a plausible range of values for each parameter, which were determined by manually changing the parameters and visually observing the dynamic changes. Parameter sensitivity for age was studied at SCCL 20, 50, 105, 130, and 150 cm and for size at 2, 5, 10, 20, and 40 years. This arbitrary choice of values covered a wide range of possible ages and SCCLs.

2.7. Fit of parameters using leatherback data

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

The h value was 1 for the data on leatherbacks reared in captivity and fed ad libitum, whereas a fitted value was used for field-captured leatherbacks. The logit of h value was 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: $SD = a \text{ SCCL} + b$, with a and b being positive.

Weekly average and standard deviation values for SCCL were

Table 2

Model selection based on AIC and Akaike weight. h_{ai} 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 Eqs. (2) and (4), respectively, with $\beta = 0$. Selected model is in bold.

Model	Habitat	AIC	Δ AIC	Akaike weight
Gompertz	h_{ab}, h_A, h_{ZP}	3262.22	1063.54	0.000
Gompertz	h_{ab}, h_{AZP}	3274.50	1075.83	0.000
Gompertz	–	3477.50	1278.83	0.000
Indeterminate Gompertz	h_{ab}, h_A, h_{ZP}	2198.67	0.0000	1.000
Indeterminate Gompertz	h_{ab}, h_{AZP}	2452.43	253.76	0.000
Indeterminate Gompertz	–	3086.99	888.30	0.000
von Bertalanffy	h_{ab}, h_A, h_{ZP}	2605.45	406.78	0.000
von Bertalanffy	h_{ab}, h_{AZP}	2866.50	667.83	0.000
von Bertalanffy	–	3028.06	829.39	0.000
Indeterminate von Bertalanffy	h_{ab}, h_A, h_{ZP}	2611.45	412.78	0.000
Indeterminate von Bertalanffy	h_{ab}, h_{AZP}	2870.50	671.83	0.000
Indeterminate von Bertalanffy	–	3034.06	835.39	0.000

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:

$$sd = \sqrt{\sum sd_i^2} \quad (5)$$

A comparison of fit statistics for the Gompertz or von Bertalanffy (Eqs. (1) and (3)) and indeterminate Gompertz or von Bertalanffy models (Eqs. (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 Eq. (1) with α , h , K , a , and b being fitted, and equal to 8 for Eq. (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 amongst 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 Nelder-Mead non-linear fitting algorithm (Nelder and Mead, 1965). The standard error for outputs was estimated using the delta method with the Hessian matrix as an approximation of the variance-covariance matrix. The delta method is a general method for approximating the moments of functions of asymptotically normal random variables with known variance (Oehlert, 1992). Alternatively, Bayesian posterior distribution for each parameter was estimated using iterations of MCMC parameter proposals. The initial values for the parameters were determined using maximum likelihood; no burn-in adaptation was used. Priors were all obtained from a uniform distribution with limits being very wide to ensure that a large range of parameter values could be checked (see Supplementary Material). Standard deviations for new proposals were chosen based on adaptive MCMC methodology (Rosenthal, 2011) as implemented in R package *HelpersMG*, version 4.0 (Girondot, 2020). The number of iterations required to estimate the quantile 0.025 to within an accuracy of ± 0.005 with probability 0.95 was calculated using an initial pilot 50,000 run (Raftery and Lewis, 1992). From this diagnostic, a run with 100,000 iterations was chosen. Convergence was first visually examined to ensure that the time series of the parameters were stationary, and then tested using the Heidelberg and Welch (1983) diagnostic. The standard error of the parameters was estimated after correction for autocorrelation (Roberts, 1996). Results from the MCMC were analysed using the R package *Coda*, version 0.19-1 (Plummer et al., 2011) and *HelpersMG*, version 4.0 (Girondot, 2020).

2.8. From growth pattern to age at maturity

Female age at maturity at the population scale can be obtained as the age at which the smallest females are seen nesting on the beach. The smallest nesting female was around 105 cm SCCL (this study, Chaverri, 1999; Stewart et al., 2007), but excluding this exceptional value, the SCCL distribution generally shows a lower value of around 130 cm (Fig. 1A). On the other hand, SCCL distribution of potential neophyte females is Gaussian with a mean of 158.10 cm and standard deviation of 8.23 cm (Fig. 1A).

3. Results

3.1. Biometry of nesting leatherbacks in Awala-Yalimapo, French Guiana

A total of 1061 different females were measured from 2011 to 2018: 622 females were observed for the first time based on the absence of

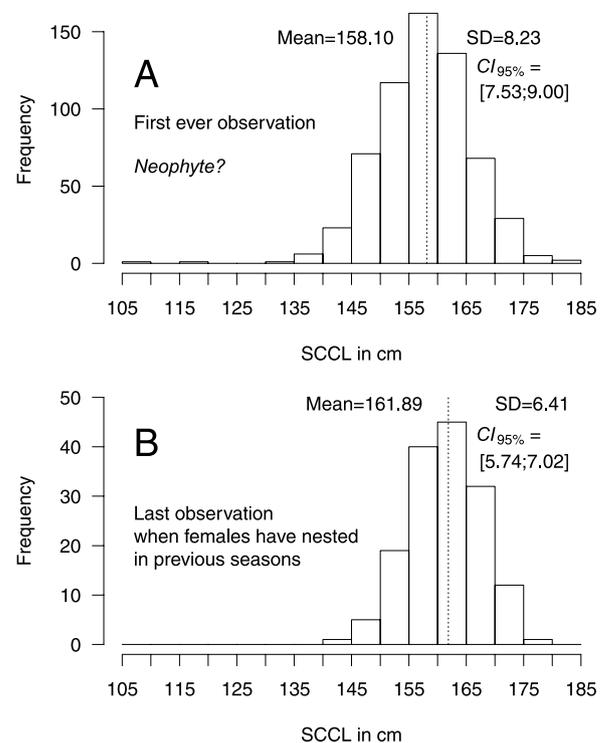


Fig. 1. Standard curvilinear carapace length (SCCL) distribution for nesting females on Awala-Yalimapo nesting beach (French Guiana) for (A) females seen nesting for the first time and being potential neophytes and (B) last observation for females seen nesting during previous nesting seasons.

PIT or monel tag, while 439 had already been tagged in the previous nesting seasons. Amongst these 1061 females, 187 were measured in several nesting seasons. The untagged females were not necessarily true neophytes, although tagged females were obviously true non-neophytes. The average SCCL was 159.43 cm (SD 7.84 cm), and the minimum and maximum sizes were 106 and 181 cm, respectively. When splitting the data into two groups based on whether the female was observed for the first time on the beach during a nesting season (Fig. 1A) or had already been tagged during a previous season (Fig. 1B), the size distributions strongly differed (difference 3.79 cm; BIC [Bayesian Information Criterion] weight = 6.10^{-8}). The BIC weight is the posterior probability that a single size distribution was sufficient to model the SCCL for the two groups (Girondot and Guillon, 2018). BIC was used instead of AIC because the true model was obviously amongst the tested models (i.e., size of two groups either differs or not).

When the same female was seen during different seasons, the model for average SCCL annual growth upon SCCL was an exponential decay for both West Atlantic leatherbacks nesting in French Guiana (Akaike weight = 0.991, Fig. 2A, Table 1) and the Pacific East leatherbacks nesting in Parque Nacional Marino Las Baulas, Costa Rica (Akaike weight = 0.884, Fig. 2B, Table 1) (data retrieved from Price et al., 2004). In both situations, the lower end of 95% confidence interval was different from 0 indicating a non-null growth even at larger 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.

3.2. Example of growth dynamics and parameter sensitivity

An example of the growth dynamic produced by the system of differential Eq. (2) is shown in Fig. 3 for $\alpha = 0.007$, $\beta = 0.067$, $M = 115.52$, $S = -7.55$, $h = 0.45$, $x_0 = 6.3$, and $K_0 = 28.88$. Sensitivity analysis highlights the relative influence of variables on the dynamics. In Fig. 3A, the contribution of variables to size for known age is shown. In

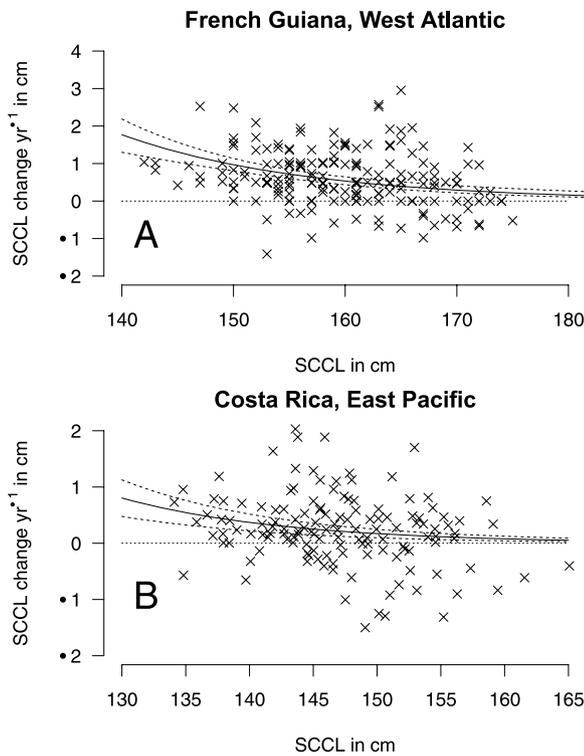


Fig. 2. Change in standard curvilinear carapace length (SCCL) in cm yr^{-1} for nesting females in the Northwest Atlantic (French Guiana, this study) and Pacific East (Costa Rica, Price et al., 2004) regional management units (as per Wallace et al., 2010). Solid lines represent the relation between SCCL 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.

Fig. 3B, the contribution of variables to age for known size is shown. As expected from Eq. (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 Fig. 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.

3.3. Parameter fitting

The biphasic indeterminate Gompertz model with fitted h_{ZP} and h_A (Eq. (2)) strongly out-performed all other models ($\Delta\text{AIC} > 200$, Table 1): the Gompertz model (Eq. (1)) can be excluded as a representation of leatherback growth with $\Delta\text{AIC} > 1000$, Akaike weight=0. The biphasic indeterminate Gompertz was also a highly supported model compared to the biphasic indeterminate von Bertalanffy model regardless of the number of habitat models. The model with fitted h_{ZP} (0.504) and h_A (0.275) strongly out-performed the model with a single fitted h (0.458) ($\Delta\text{AIC}=253$, Akaike weight=0) and the model with fixed $h = 1$ parameter ($\Delta\text{AIC}=888$, Akaike weight=0).

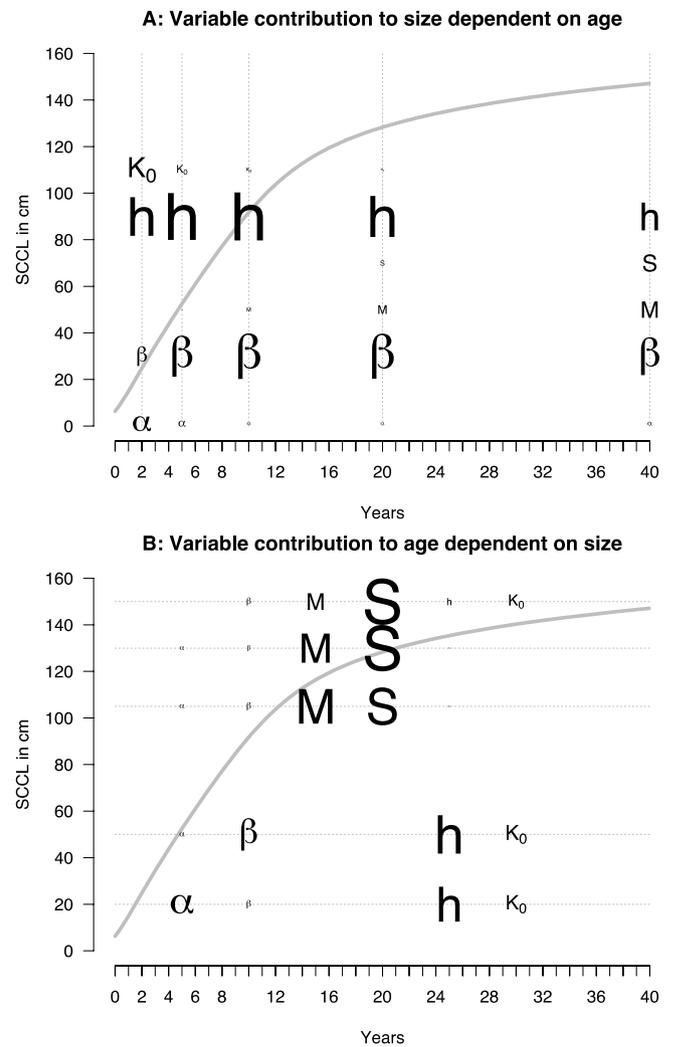


Fig. 3. An example of standard curvilinear carapace length (SCCL) growth with the total relative contribution of each variable (total contribution, including interaction, standardised to 1) for (A) SCCL at 20, 50, 105, 130, and 150 cm and (B) age at 2, 3, 10, 20, and 40 years. The contribution of x_0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

Habitat quality was therefore an important parameter to take into account.

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

3.4. Age at maturity

The size of the smallest leatherback females seen nesting on the beach was around 105 cm SCCL (Chaverri, 1999; Stewart et al., 2007) and 106 cm SCCL in our French Guiana dataset. This size can be reached between 6.2 to 7.5 years in natural conditions when $h = 0.504$ and between 11.3 to 13.6 years when $h = 0.275$. In the model, the age at which females reached the

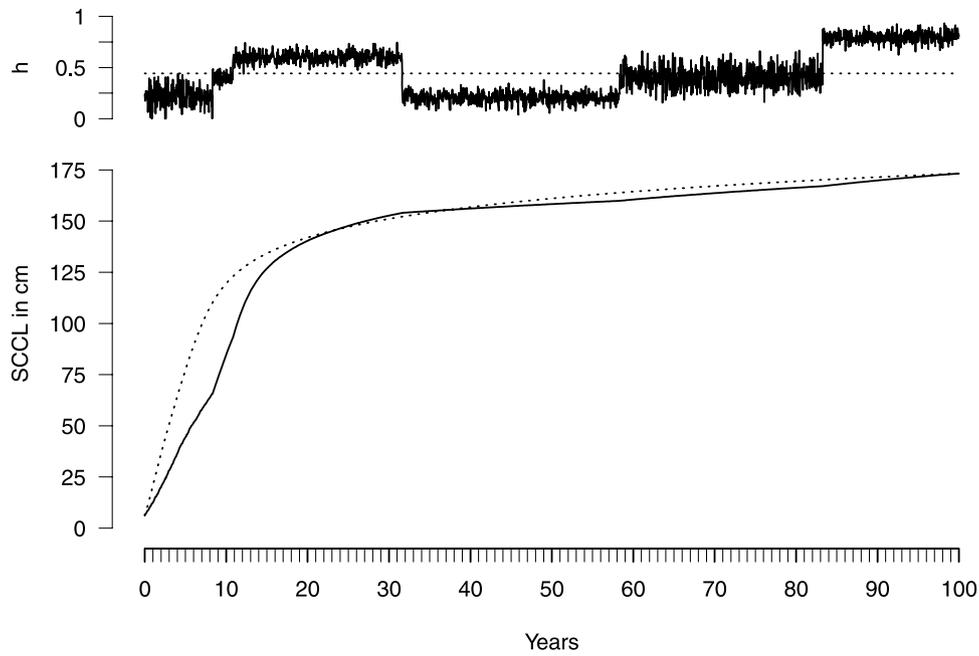


Fig. 4. Example of standard curvilinear carapace length (SCCL) growth when habitat quality h varies. Dotted lines represent the average habitat quality h and the corresponding growth dynamics. Note that the growth dynamics is different, but final size is the same.

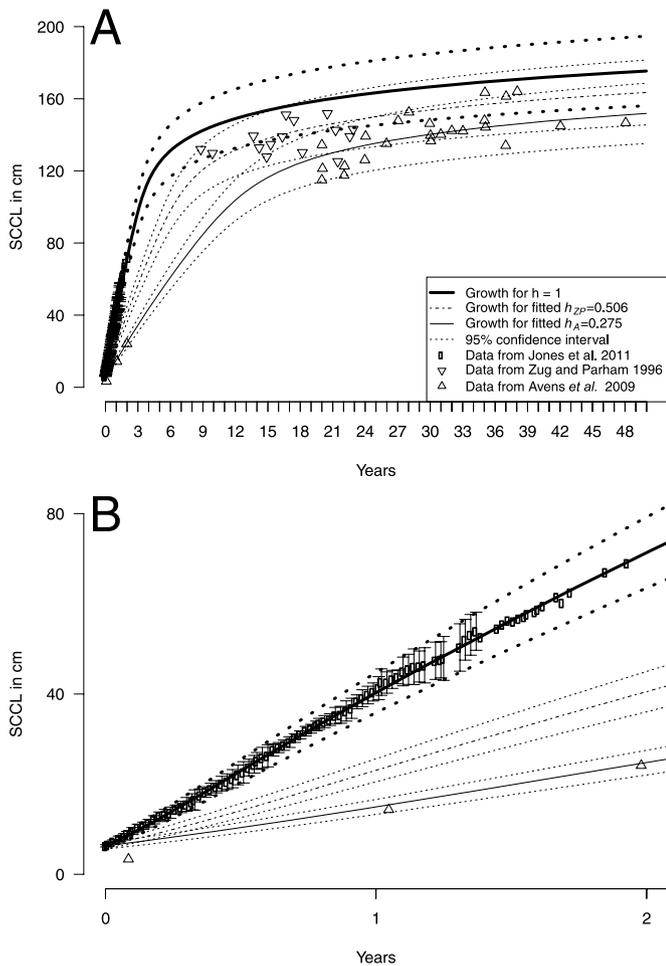


Fig. 5. Observed data of standard curvilinear carapace length (SCCL)-age for Northwest Atlantic leatherbacks and indeterminate Gompertz model of growth using $h = 1$ for leatherbacks in captivity and fitted h for leatherbacks captured in the wild (h is relative habitat quality).

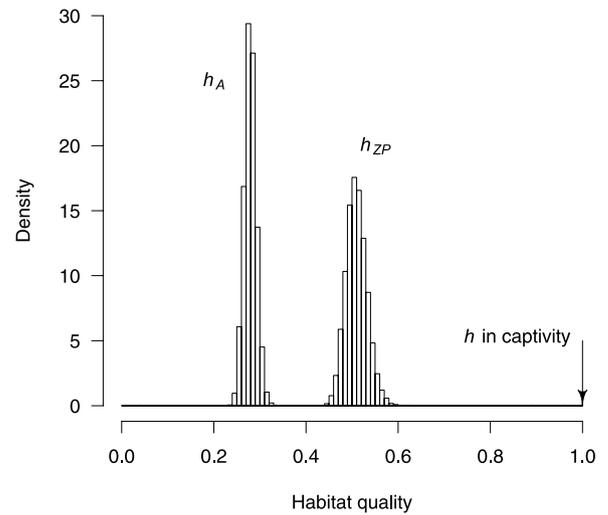


Fig. 6. Posterior distribution for 100,000 iterations of habitat quality (h) for data from Avens et al. (2009) (h_A), Zug and Parham (1996) (h_{ZP}), and Jones et al. (2011) (h in captivity).

size of 130 cm is between 9.6 and 14.9 years when $h = 0.504$ and between 17.5 and 27.1 years when $h = 0.275$. The mean SCCL for potential neophyte females (see the discussion below on capture probability and non-fidelity to nesting beaches) in French Guiana was between 157 and 158 cm (Fig. 1). This size can be reached between 24.7 to 61.7 years for $h = 0.504$ and 45.2 to 112.8 years for $h = 0.275$ (Fig. 7).

4. Discussion

We developed a new biphasic indeterminate growth model based on the Gompertz equation to investigate growth pattern of leatherback turtles. Furthermore, we showed that the model was improved by integrating habitat quality measured by the h parameter. Two groups of data provided two different estimates for h : 95% confidence interval for average habitat quality is between 0.250 and 0.304 for Avens et al. (2009) and between 0.465 and 0.555 for Zug and

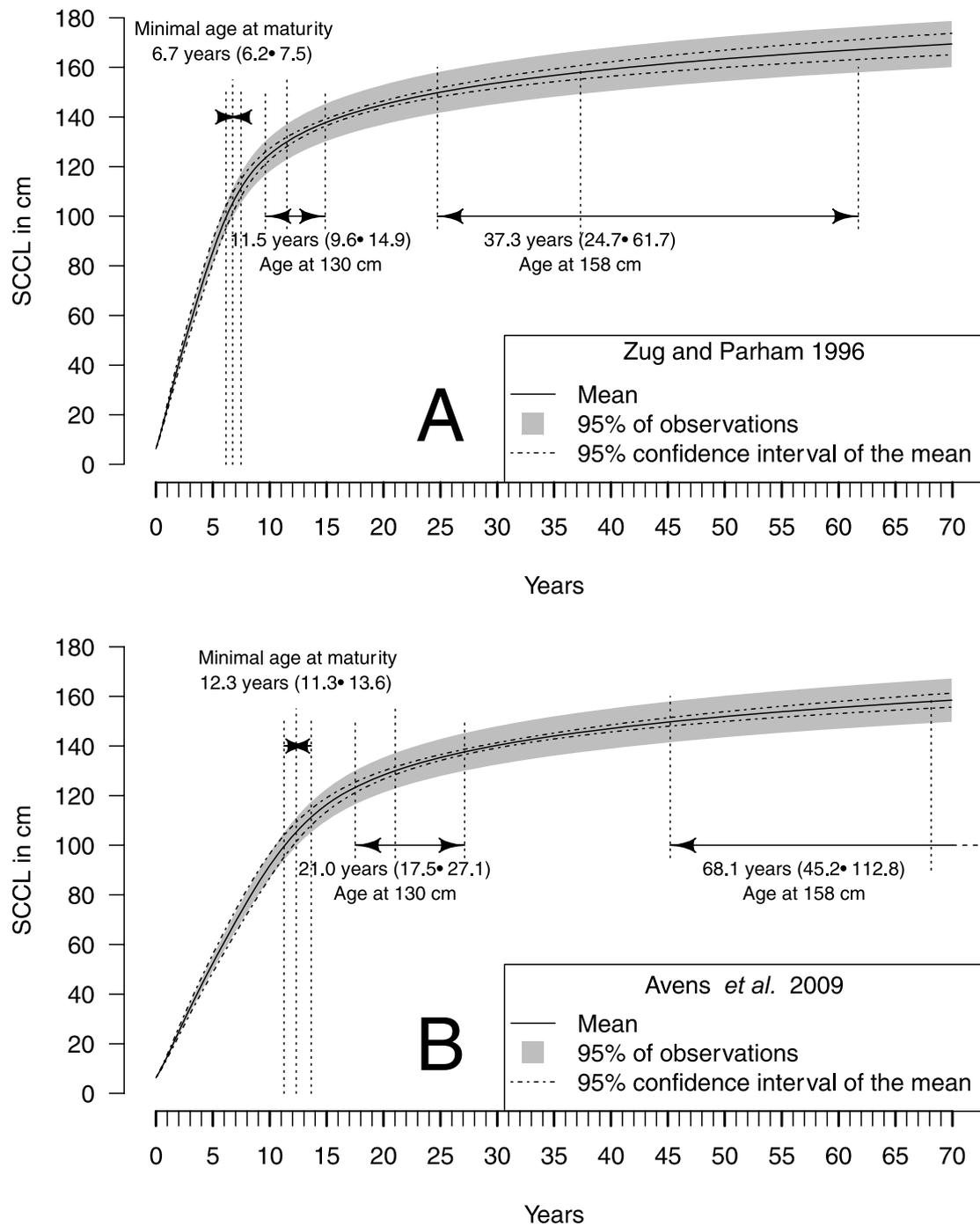


Fig. 7. Model of Northwest Atlantic leatherback growth in natural conditions (A: $h = 0.505$; B: $h = 0.275$) fitted using the indeterminate Gompertz model (Eqn (2)). The correspondence between standard curvilinear carapace length (SCCL) and range of possible ages (95% confidence interval) is shown for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

Parham (1996). It is difficult to determine if these differences are due to temporal, spatial, or methodological effects. We have no cues to choose amongst these hypotheses. It should be noted that the parameter h describing habitat quality has the same definition as the h parameter in Gaspar and Lalire (2017) for oceanic dispersion modelling. The distribution of the size of non-neophytes and females seen nesting on the beach for the first time was significantly different from the size of non-neophytes (Fig. 1), but the average difference was only 3.79 cm, with the potential neophyte being smaller. Of course, we cannot ascertain that individuals seen for the first time were true neophytes: they could have nested at another beach in a previous season or on this beach without being captured. It should be noted that Yalimapo-Awala beach

has been patrolled for 10 h per night on all nights during the nesting season for more than 10 years. Taking into account their high fidelity to the nesting beach (Girondot et al., 2007), at least a fraction of these females seen for the first time are probably true neophytes. The small size difference observed between neophyte and non-neophyte females was also noted in loggerheads (Tucek et al., 2014), indicating that growth at adult stage is very low. Data from the longitudinal field survey in French Guiana (Fig. 2A) as well as growth modelling (Fig. 5A) allowed us to clearly demonstrate that leatherbacks show indeterminate growth and thus confirm and extend previous findings on East Pacific leatherbacks (Price et al., 2004). The pattern described here for leatherback turtles could be general for marine turtles (Omeyer et al.,

2018).

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

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

5. 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.

6. Authors participation

Damien Chevallier organized and performed field work, contributed to manuscript writing.

Baptiste Mourrain performed analytical mathematical work and contributed to manuscript writing.

Marc Girondot designed the study, performed numerical mathematical work and contributed to manuscript writing.

Declaration of Competing Interests

The authors declare that they have no known competing financial

interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2020.109037](https://doi.org/10.1016/j.ecolmodel.2020.109037).

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