REGULAR PAPER

# Maturity of a giant: age and size reaction norm for sexual maturity for Atlantic leatherback turtles

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**Abstract**

Leatherback marine turtles are the largest extant turtles with some individuals measuring up to 2 m in carapace length. In addition, this species remains in oceanic habitat during much its life, making it difficult to investigate its ontogeny from hatchling to adult stage. Furthermore, distinct chondro-osseous (cartilage and bone) tissue morphology has led to speculation that sexual maturity may be reached as early as 3 years while others have estimated a minimum of 25 years to reach adulthood. Using a combination of reanalysis of the growth trajectories of juveniles maintained in captivity, and the age–size relationship of individuals in the field, we demonstrate and quantify the indeterminate growth of this species. Using comparisons of female size distribution on nesting beaches and stranded or captured-at-sea size distributions adjusted with a new asymmetric sigmoid function, we were able to model the size reaction norm for female sexual maturity. Combining these two models, we show that some females may reach maturity at 14 years in natural conditions, while others will take 50 years or more. Sexual maturity may even be reached at 5 years when individuals experience exceptionally good environmental conditions. This extreme plasticity in the age of sexual maturity has been demonstrated in loggerhead turtles in natural conditions and in green turtles in captivity. It may be a general life-history feature of marine turtles.

**KEYWORDS**
age at maturity, *Dermochelys coriacea*, indeterminate growth, leatherback, marine turtles

## 1 | INTRODUCTION

The age at sexual maturity is of particular interest in the science of conservation because demographic models are especially sensitive to fluctuations in this parameter (Lewontin, 1965). Recruitment to a breeding population is a gradual, complex process for long-lived species with delayed maturity. However, for these species, recruitment parameters may be difficult to estimate if mobility is high and detectability is low during the pre-breeding period (Jenouvrier et al., 2007). This is particularly true for marine species, which are difficult to monitor in the wild. Efforts to determine the age at maturity in marine turtles have been varied (Avens & Snover, 2013), with a variety of estimates, but arguably no definitive response proposed to date.

A key point that has not been adequately addressed until now is when an individual marine turtle can be considered to be sexually mature. At first glance, the answer seems abundantly evident: sexual maturity is normally and logically defined as the capacity to reproduce, that is the ability to produce functional gametes, not necessarily having reproduced successfully. However, using this definition, some sexually mature animals using this definition may not reproduce effectively for several reasons: This could be due to behavioural mismatch or some other factor that prevents an individual from finding a mate, or the lack of resource capitalization during pre-breeding migration if it is a capital breeder. Thus, a discrepancy in classification of sexual maturity is possible when based on the examination of the gonads in a dead stranded animal (Craven et al., 2019) or the

observation of an animal nesting on a beach. Furthermore, the appearance of secondary sexual characteristics, such a long tail in male marine turtles, can be decoupled from functional sexual maturity (Casale et al., 2005). Similarly, transition from oceanic to neritic habitat cannot be considered a criterion of sexual maturity as it occurs at 20–25 cm curved carapace length in *Chelonia mydas* in the northwestern Atlantic based on mark-recapture work (Bjorndal & Bolten, 1988) or at 25–35 cm straight carapace length (SCL) based on observations of a shift in stable isotopes composition (Reich et al., 2007), both of which are far smaller than the smallest nesting females (>80 cm SCL). The concept of age at sexual maturity is applied often at the scale of a group of individuals, but it is known that each individual could have its own response (Dieckmann & Heino, 2007). The concept of a single age at maturity for a group could be misleading if it does not include of range of possible values. Indeed, it can be measured as a confidence interval, although strictly speaking, inter-individual variation is not the same as a confidence interval.

Several proxies have been used to estimate the age at maturity in marine turtles. The time between the hatchling stage and the return as an adult has been determined in natural conditions only for loggerheads using tagging at the hatchling stage: the age at maturity can be as short as 6 years for a few individuals but 45 years or more for others (Tucek et al., 2014). Similar experiments have been done in Australia, but only anecdotical results (the first and only report of nesting was 29 years after being tagged as a hatchling) have been published so far from this experiment (Limpus, 2008). This result is consistent with a 34-year study of captive green turtles (*Chelonia mydas*), which followed individuals from hatching to maturity and beyond (Bjorndal et al., 2013).

An alternative method to estimate age of maturity uses information based on growth patterns. The life-history trade-off between growth and reproduction enforced by limited energy resources underlies the importance of resource allocation, according to the current theory (Stearns, 1992). In this scenario, the timing of the shift in resource allocation from growth to reproduction corresponds more or less to age at maturity. Attaining reproductive maturation is associated with a marked decrease in somatic growth in reptiles and amphibians, which corresponds with an abrupt decrease in the spacing between the lines of arrested growth (LAG) located in the outer edges of bones. Thus, the LAG at this transition zone was designated as the rapprochement LAG that signifies maturation (Avens et al., 2013, 2015, 2017). Age and size at maturation (ASM and SSM) were inferred from the age and SCL (straight carapace length) estimates associated with the rapprochement LAG.

The average size at maturity also can be inferred by back-calculating the average female size at breeding rookery from a growth curve (Casale et al., 2011; Casale et al., 2011; Frazer et al., 1994). It should be noted that until now, most growth curve equations (logistic or von Bertalanffy) used for sea turtle research have assumed determinate growth, whereas a recent review shows that growth is indeterminate in sea turtles (Omeyer et al., 2018).

For leatherback turtles, the pattern of growth between juvenile and adult stages has been used to infer age at maturity by different authors with different conclusions. Extremely rapid growth rates of 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 of this species (Rhodin, 1985). However, skeletochronological analysis suggested that leatherbacks could take as long as 13–14 years to sexually mature (Zug & Parham, 1996). Dutton et al. (2005) suggested that leatherbacks might reach maturity at 12–14 years, based on the increased returns at a nesting beach (St. Croix, US Virgin Islands) after intensive beach protection and nest relocation, which increased hatchling production by an order of magnitude relative to the previous decade. Genetic analysis from the same site suggested that first-time nesters are related and may have possibly been the genetic offspring of nesting leatherbacks first tagged 20 years ago, suggesting that age at maturity is less that this time lapse (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. A different study on leatherback growth and age at maturity was based on leatherback turtles that were maintained in captivity for nearly 2 years, ranging from hatchlings ($6.31 \pm 0.13$ cm straight carapace length (SCL) and $46.0 \pm 1$ g) to juveniles (largest, 72.0 cm SCL and 42.65 kg) (Jones et al., 2011). Using a global analysis of the relationship between absolute age and SCL, Jones et al. (2011) fitted von Bertalanffy, Gompertz and logistic growth functions to predict age at maturity for leatherbacks of 16.1, 8.7 and 6.8 years, respectively. All these equations behave similarly, showing a quasi-exponential growth for smaller individuals and an asymptote reached at larger, adult stages.

However, there are several potential biases in this approach. First, adult females continue to show growth, which could decline for larger size but still persist, producing a biphasic growth curve (Price et al., 2004). The three functions used by Jones et al. (2011) to model size versus age impose an asymptote $L_\infty$ at adult stage, but $L_\infty$ is a biased estimate of size when resources are transferred from growth to reproduction. Jones et al. (2011) used $L_\infty \times 0.975$ as an estimation of size at maturity with little clear justification. Second, the data for juveniles were derived from individuals reared in captivity and fed ad libitum, whereas the data for adults came for individuals captured in the field. Consequently, the growth of juveniles in captivity is likely different as compared to the growth of adults in the field, due to differences in food availability and temperature (Bjorndal et al., 2013). This point is important, as the expected age at maturity falls precisely between these two categories of data, and therefore, no data are available to validate the estimates provided.

The main objective of the present work is to provide consensus about the age at maturity for leatherback turtles. First, however, we must shift the paradigm from "age at maturity" to "reaction norm of sexual maturity" (Stearns & Koella, 1986). The size or age reaction norm for sexual maturity represents the probability that an individual is sexually mature based on its size or age. Indeed, there is not one

single age at maturity, because each individual has its own trajectory that is dependent not only on genetic characteristics but also on the environment. Second, we define new models to analyse the life history of leatherback turtles, taking into account their particularities, including potential high rate of growth, indeterminate growth, and large size and mass. Third, we analyse available data for the Atlantic leatherbacks using modelling and statistical tools to provide a more accurate estimate of size and a reaction norm for sexual maturity.

## 2 | MATERIALS AND METHODS

### 2.1 | Measurements of nesting leatherbacks

Data were collected during the nesting seasons in 2012 through 2018 at Awala-Yalimapo beach (5.7°N, 53.9°W), French Guiana, South America (Figure 1). Awala-Yalimapo beach is situated on the French side of the Maroni River, which separates French Guiana and Suriname. Monitoring programmes at this beach have been in place since the late 1970s (Girondot & Fretey, 1996). Nesting individuals have been extensively tagged using internal passive integrated transponder tags (Trovan Euroid), which facilitate individual identification. Between April and July, a 4 km stretch of beach where most nesting events occur (Girondot, 2010) was patrolled every night from 6:00p.m. to 7:00a.m. All tagged turtles encountered during these patrols were individually identified and measured during oviposition. Different measurements were obtained, but only SCL was used in this study to ensure consistency across studies. When a female was repeatedly seen during or between nesting seasons, only the first record was used to avoid pseudo-replication.

### 2.2 | Measurements of stranded or captured-at-sea leatherbacks

Four data sets of SCL of leatherbacks were used, one from unpublished information (stranded animals in North Carolina in USA) and three from published literature on turtles stranded or captured at

sea in the Mediterranean (Casale et al., 2003), captured at sea off Nova Scotia in Canada (James et al., 2007), and stranded animals along the French Atlantic coast (see supplementary material for the origin of data; Figure 1). Data from the French Atlantic coast include observations from 1979 to 2018 with SCL (Duguy, 1997) reported for 300 individuals (except for two individuals with only curved carapace length, CCL, being reported). Data with approximate size were not retained. Individuals were categorized as juveniles, males, females, unidentified or not reported. However, it should be noted that the definition of these categories was not consistent among the data sets. Only relatively fresh stranded individuals can be classified as males or females, using the sex specific structure of gonads, genital ducts or tail length. For example, a female as small as 96 cm SCL (Duguy, 1989) and a male as small as 76 cm SCL (Duguy, 1988) were classified for sex after dissection stranded dead individuals. For individuals captured off Nova Scotia in Canada, sex was assigned from tail length measurements collected from turtles with ≥145 cm CCL, to reduce potential error associated with visually sexing leatherbacks of smaller size classes (James et al., 2007). Juvenile individuals without secondary sexual characters, and particularly the male long tail, could be erroneously identified as females. The size/age at which a male's elongated tail becomes pronounced is currently unknown. Only individuals that were identified as "not males" were used in the analyses (i.e. all confirmed adult male data were excluded unless otherwise noted).

### 2.3 | Modelling the size reaction norm for sexual maturity

The size reaction norm for sexual maturity represents the probability that an individual of size x is sexually mature. The general form is a sigmoid function going from 0 for small x to 1 for large x. The exact form of the function is unknown, but there is no reason to assume that it is symmetric. Rather, it was anticipated that the transition was smooth for small size (few individuals are mature at small sizes, e.g. <110 cm), whereas the transition should be more abrupt for larger sizes, because nearly all individuals are expected to be
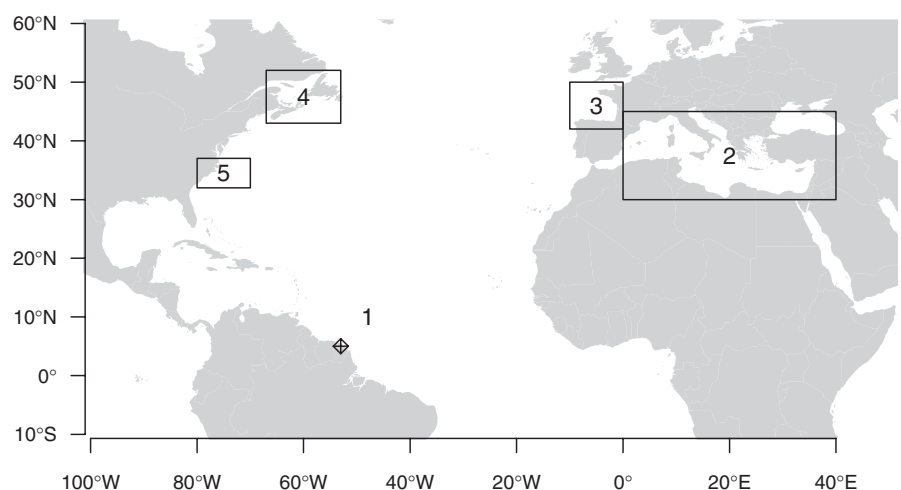


**FIGURE 1** Map showing approximate locations of leatherback data collection. 1—French Guiana nesting beach, 2—Mediterranean Sea, 3—French Atlantic coast including Manche, 4–Nova Scotia and 5–North Carolina coast

mature at large sizes, for example >160 cm. We therefore needed a flexible function, ruling out logistic, Hill or Weibull equations, which are all too constrained. We developed a new versatile sigmoid function based on a modification of logistic law. Let $f(x)$ being a logistic law: $f(x) = \left(1 + e^{4S(M-x)}\right)^{-1}$ with $f(x)$ being the probability to be mature at size $x$, $M$ being the size at which 50% of individuals are mature and $S$ the slope of the transition at $x = M$ $f(x = M) = 0.5$ and $f'(x = M) = S$. However, this model assumes a symmetric transition around $M$. The *A-logistic* model is a recently published asymmetric sigmoid model, with $K$ being a parameter controlling the asymmetry (Godfrey et al., 2003):

$$f(x) = \left(1 + \left(2^K - 1\right) e^{4S(M-x)}\right)^{-1/K}$$

As for a logistic model, $f(x = M) = 0.5$. When $K < 1$, the transitions from $M$ to the asymptotes showed more acute angles whereas when $K > 1$, and the transitions from $M$ to asymptotes showed more obtuse angles, as compared to logistic model on both sides of $M$. Hulin et al. (2009) observed that the *A-logistic* model requires that both transitions are either acute, or obtuse but that it was not possible to mix both conditions on each side of $M$. We propose here a new approach to alleviate this constraint.

The first-order derivative of the *A-logistic* model is as follows:

$$f'(x) = S \frac{4}{K} \left(2^K - 1\right) e^{4S(M-x)} \left(1 + \left(2^K - 1\right) e^{4S(M-x)}\right)^{-\frac{1}{K} - 1}$$

With $f'(x = M) = S \frac{4}{K} \left(2^K - 1\right) \left(2^{-K}\right)^{\frac{1}{K} + 1}$

It follows that slope at $x = M$ depends on both $S$ and $K$. As expected, when $K = 1$, $f'(x = M) = S$. In addition, different transitions towards the asymptotes below and above $M$ can be defined with $K = K_1$ for $x < M$ and $K = K_2$ for $x \geq M$. A smooth transition at $x = M$ requires the same $f'(x = M)$, regardless of the values of $K_1$ and $K_2$. Then, we search for $S_1$ and $S_2$ values (respectively, for $x < M$ and $x \geq M$) that ensure that $f'(x = M)$ is equal according to $K_1$ and $K_2$. It follows that:

$$S_1 = f'(x = M) \frac{\left(2^{-K_1}\right)^{-1/K_1 - 1} K_1}{4\left(2^{K_1} - 1\right)} \text{ and } S_2 = f'(x = M) \frac{\left(2^{-K_2}\right)^{-1/K_2 - 1} K_2}{4\left(2^{K_2} - 1\right)}$$

Being symmetric, a logistic law can be written in two ways:

$$f(x) = \left(1 + e^{4S(M-x)}\right)^{-1} = 1 - \left(1 + e^{4S(x-M)}\right)^{-1}$$

However, it does not apply for the A-logistic model $f(x) = \left(1 + \left(2^K - 1\right) e^{4S(M-x)}\right)^{-1/K}$ as.

$$\left(1 + \left(2^K - 1\right) e^{4S(M-x)}\right)^{-1/K} \neq 1 - \left(1 + \left(2^K - 1\right) e^{4S(x-M)}\right)^{-1/K}$$

However, both these forms are interesting as the influence of $K$ on the acute or obtuse transitions towards the asymptotes is reversed. When $K > 1$, the transition towards the asymptote is acute when $x < M$ and obtuse when $x > M$ for the form $\left(1 + \left(2^K - 1\right) e^{4S(M-x)}\right)^{-1/K}$. However, it becomes acute when $x > M$ and obtuse when $x < M$ for the form $1 - \left(1 + \left(2^K - 1\right) e^{4S(x-M)}\right)^{-1/K}$.

This property was used to define the flexible-logistic model that was named *flexit* model:

$$\begin{cases} x < M \ S_1 = \frac{2^{K_1 - 1} S K_1}{2^{K_1} - 1} & f(x) = \left(1 + \left(2^{K_1} - 1\right) e^{4S_1(M-x)}\right)^{-1/K_1} \\ x \geq M \ S_2 = \frac{2^{K_2 - 1} S K_2}{2^{K_2} - 1} & f(x) = 1 - \left(1 + \left(2^{K_2} - 1\right) e^{4S_2(x-M)}\right)^{-1/K_2} \end{cases}$$

It should be noted that $2^{K_i} - 1$ is always different from 0, and $\lim\limits_{K_i \to -\infty} S_i = 0$, and $\lim\limits_{K_i \to +\infty} S_i = S_i\infty$. $M$ is the size at which 50% of individuals are mature, and $S$ is the first-order derivative of the size reaction norm for sexual maturity at the size $x = M$.

Let $X$ be a series of SCL measured in stranded or captured-at-sea leatherbacks, and $B$ be a series of SCL measured in nesting leatherbacks (mature by definition). The $X$ series included both juveniles and mature individuals. 1 - *flexit*$(X; M, S, K_1, K_2)$ represents the probability that each element of $X$ is a mature individual. Then, we search for the parameters $M, S, K_1$ and $K_2$ that maximized likelihood of $X - X$ *flexit*$(X; M, S, K_1, K_2)$ being similar to $B$. Let $n_i$ be the number of individuals from $X$ between i and i + 1 cm and $p_i = n_i / \sum n$. It follows that $q_i = p_i$ (1 - *flexit*$(i + 0.5; M, S, K_1, K_2)$) is the expected proportion of mature individual in the $i$ class among all individuals. Let $b_i$ be the number of individuals from $B$ between i and i + 1 cm. The log likelihood of $X$ and $B$ in the *flexit* model with $M, S, K_1$ and $K_2$ is based on a multinomial model and is proportional to $\sum \log\left(q_i^{b_i}\right)$. The *flexit* model is included as a function in HelpersMG R package (version 3.7 and higher) (Girondot, 2020).

## 2.4 | Leatherbacks age and size

The conversion of the size reaction norm for sexual maturity into an age reaction norm for sexual maturity requires the use of a growth model to convert a particular size into a particular age. The model of indeterminate growth that has been developed specifically for marine turtles (Chevallier et al., 2020) is as follow:

$$\begin{cases} \frac{dx}{dt} = \alpha h \ln\left(\frac{K}{x}\right) x \\ \frac{dK}{dt} = \beta h \left(1 + e^{4S(M-x)}\right)^{-1} \end{cases}$$

No integrated form of this equation exists. Parameter $\alpha$ is a constant related to the proliferative ability of cells that ultimately contributes to the individual's growth, parameter $M$ is the size at which the transition between exponential juvenile growth and adult linear growth occurs, parameter $S$ controls the rate of transition between exponential juvenile growth and adult linear growth, parameter $\beta$ is the linear adult growth rate, and the effect of habitat quality, $h$, acts on both $\alpha$ and $\beta$. Habitat quality, $h$, acts as the proportion of the 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 and can represent individual

variations. It is interesting to note that the size reached after a time $t$ can be directly inferred using the size reached for the same time with $h$ being the average of all the $h$ during this time $t$ (Chevallier, Mourrain, et al., 2020).

This system of differential equations was numerically solved using the Runge–Kutta method of order 4. The Runge–Kutta methods are a family of implicit and explicit iterative methods used in temporal discretization for the approximate solutions of ordinary differential equations. The initial value was $x_0 = 6.3$ cm for SCL at hatchling stage (Jones et al., 2011), while the initial value for $K$, named $K_0$, was fitted to best adjust the observed data.

Data on the relationship between size and age of Atlantic leatherback turtles were retrieved from Table 1 in Jones et al. (2011) for leatherbacks raised in captivity from birth, as well as from printed figures in Zug and Parham (1996) and Avens et al. (2009) for stranded dead individuals aged using skeletochronological analysis of scleral ossicles. We chose not to use the data on growth in captivity published by Bels et al. (1988), as the individuals were probably in suboptimal conditions (Bels et al., 1988; Jones et al., 2011). Curved carapace length (CCL) measures were converted into SCL where necessary using the relationship SCL = (CCL/1.04) - 2.04 (Tucker & Frazer, 1991). The use of SCL rather CCL is preferred because the data are more homogeneous (Robinson et al., 2017).

The $h$ value had to be 1 for the data on leatherbacks reared in captivity and fed ad libitum, whereas a fitted $h$ value was used for field-captured leatherbacks.

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

Weekly average and standard deviation values for SCL 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 ($a\ \text{SCL} + b$) using:

$$sd = \sqrt{\sum sd_i^2}$$

## 2.5 | Parameter fitting

The same procedure was used to fit the age–size relationship for leatherbacks and size reaction norm of sexual maturity. In both cases, maximum likelihood and Bayesian Markov Chain using Monte-Carlo parameter proposition using Metropolis-Hasting algorithm were used to search for the parameters that best described the data.

The values of parameters, which maximized the likelihood of observed sizes within the model, were searched using the Nedler-Mead non-linear fitting algorithm (Nelder & Mead, 1965). The standard error for outputs was estimated using the delta method using 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

**TABLE 1** Synthesis of data. French Guiana data are from nesting females while others are from stranded animals or those captured at sea, including juveniles and adults. Skewness coefficient is $\mu_3/\sigma^3$ with $\mu_3$ being the third central moment, and $\sigma$ being the standard deviation. 95% confidence interval of skewness coefficient is based on 10,000 bootstrap replicates (Ankarali et al., 2009). A positive value indicated as P and a negative value indicated as N signifies that the distribution is enriched in smaller values (for P) or larger values (for N) as compared to normal distribution

| Location | Sex and stage categories | N | Min ; Max | Mean | SD | Skewness (95% CI) | |
|---|---|---|---|---|---|---|---|
| | | | **Straight carapace length distribution - SCL** | | | | |
| French Guiana nesting beach | Female | 551 | 106 ; 181 | 157.96 | 8.75 | −0.83 ( −1.88 ; 0.25 ) | |
| Mediterranean sea | Unavailable | 83 | 109 ; 176 | 135.99 | 16.04 | 0.43 ( 0.11 ; 0.72 ) | P |
| Nova Scotia | All | 108 | 106 ; 163 | 142.81 | 9.75 | −0.76 ( −1.29 ; −0.2 ) | N |
| Nova Scotia | Juvenile | 37 | 106 ; 140 | 132.38 | 7.56 | −1.26 ( −1.71 ; −0.54 ) | N |
| Nova Scotia | Juvenile + Female | 59 | 106 ; 160 | 138.38 | 10.33 | −0.35 ( −0.85 ; 0.2 ) | |
| Nova Scotia | Female | 49 | 141 ; 163 | 148.15 | 5.44 | 0.58 ( 0.28 ; 0.87 ) | P |
| Nova Scotia | Male | 22 | 140 ; 160 | 148.46 | 5.19 | 0.8 ( 0.6 ; 1.1 ) | P |
| North Carolina | All | 144 | 9 ; 182 | 138.44 | 20.64 | −1.88 ( −1.7 ; 0.78 ) | |
| North Carolina | Unknown | 83 | 9 ; 173 | 133.08 | 23.25 | −1.85 ( −1.69 ; 0.78 ) | |
| North Carolina | Unknown + Female | 122 | 9 ; 182 | 137.09 | 21.62 | −1.82 ( −1.69 ; 0.77 ) | |
| North Carolina | Female | 39 | 112 ; 182 | 145.62 | 14.56 | −0.01 ( −0.41 ; 0.37 ) | |
| North Carolina | Male | 22 | 124 ; 171 | 145.95 | 11.77 | 0.19 ( −0.07 ; 0.45 ) | |
| Atlantic French coast | All | 300 | 76 ; 203 | 140.77 | 17.26 | −0.29 ( −0.88 ; 0.3 ) | |
| Atlantic French coast | Unknown | 118 | 97 ; 174 | 135.02 | 17.31 | 0.01 ( −0.24 ; 0.25 ) | |
| Atlantic French coast | Unknown + Female | 208 | 96 ; 180 | 137.89 | 17.16 | −0.19 ( −0.47 ; 0.08 ) | |
| Atlantic French coast | Female | 90 | 96 ; 180 | 141.66 | 16.3 | −0.45 ( −0.78 ; −0.13 ) | N |
| Atlantic French coast | Male | 92 | 76 ; 203 | 147.29 | 15.73 | −0.51 ( −1.71 ; 0.97 ) | |

with known variance (Oehlert, 1992). Alternatively, Bayesian posterior distribution for each parameter was estimated using iterations of Markov Chain using Monte-Carlo parameter proposition. The initial values for the parameters were the ones determined using maximum likelihood, and then no burn-in adaptation was used. Priors were all obtained from a uniform distribution with limits being 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 3.6 and higher (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 run of 50,000 iterations (Raftery & Lewis, 1992). From this diagnostic, a 100,000 iterations run was chosen. Convergence was first visually examined to ensure that the time series of the parameters were stationary and then tested using the Heidelberger 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 packages *Coda*, version 0.19–1 (Plummer et al., 2011) and *HelpersMG*, version 3.7 (Girondot, 2020).

## 2.6 | From size to age reaction norm for sexual maturity

We have described how the size reaction norm for female sexual maturity was fitted by comparing the size distribution of stranded or captured-at-sea animals and nesting females size distributions. In addition, we have modelled the growth of animals where relationship between age and size. Each of these models was fitted using Bayesian MCMC methodology with 100,000 replicates. The distribution of the fitted parameters includes uncertainty both from the model itself and from the inter-individual variability. From these two relationships, it is straightforward to derive the age reaction norm for sexual maturity. The credibility interval for the age reaction norm for sexual maturity can be obtained by combining the 100,000 sets of parameters previously estimated for each of the models (size reaction norm for female sexual maturity and growth pattern); it also facilitates the production of 100,000 samples of the age reaction norm for sexual maturity from which quantiles were estimated.

## 3 | RESULTS

### 3.1 | Biometry of leatherbacks

A total of 1,399 measurements were obtained for nesting leatherback in French Guiana from 2012 to 2018. The average SCL was 157.96 cm (*SD* 8.75 cm), and the minimum and maximum sizes were 106 and 181 cm, respectively.

Biological data from 152 turtles, including 127 live-captured individuals during 8 seasons of fieldwork (1999 to 2006) off Nova Scotia, Canada, were available (James et al., 2007). A total of 411 records of leatherback turtles (*Dermochelys coriacea*) were reviewed for the whole of the Mediterranean (Casale et al., 2003). Among them, straight carapace length was reported for 83 individuals. A total of 300 records of stranded leatherbacks with carapace length measurements were available for French Atlantic coast and 144 for the North Carolina coast in USA. Data are summarized in Table 1 and in Figure 2.

### 3.2 | SCL reaction norm for sexual maturity

The straight carapace length reaction norm for sexual maturity fitted for the 4 regions with stranded leatherbacks is shown in Figure 3. The SCL in cm at which 50% of individuals are mature ranges from 145.7 to 155.8 cm, according to the data set with all 95% credibility interval overlapping. As no difference among different locations was found, all data sets were combined in a single Atlantic data set. The global model for leatherbacks in Atlantic is shown in Figure 4. The size at which 50% of individuals are mature ranges between 146.9 and 147.4 cm (95% credibility interval). These values are nearly identical if males are included in this analysis: 146.9 to 147.7 cm (95% credibility interval). The straight carapace length reaction norm for sexual maturity shows a strong asymmetry: the probability of attaining maturity slowly increased from 105 cm to 147 cm, but individuals >148 cm are virtually all mature. The repartition a posteriori into juveniles and adults in the four data sets used is shown in Figure 5.

### 3.3 | Growth curve of Atlantic leatherbacks

The plot of the observed size-age data and the fitted models for $h = 1$ and fitted $h$ is shown in Figure 6 ($h$ is a proxy of habitat quality). Large plasticity can be observed for the relationship between age and SCL. From this curve, it is impossible to directly infer average age at maturity (Chevallier, Mourrain, et al., 2020).

### 3.4 | Age reaction norm for sexual maturity

The combination of straight carapace length reaction norm for sexual maturity (Figure 4) with growth trajectories dependent on the habitat quality (Figure 6) can be used to estimate the age reaction norm for sexual maturity (Figure 7). The average age reaction norm for sexual maturity in natural habitats shows that 50% of individuals reach sexual maturity at 58 years (95% credibility interval from 55 to 70 years). However, 5% of these individuals in natural conditions could reach maturity at 13.8 years taking into environmental variability ($h$ temporal and spatial variation), genetic variability and their interaction (Figure 7). Alternatively, if an individual develops exclusively in poor-quality habitat (suboptimal food availability, low temperature), even after 100 years, the turtle will not reach the threshold of maturity (Figure 7). It is important

**FIGURE 2** Straight carapace length (cm) distribution for stranded or captured-at-sea animals that are identified as not males (histograms, scale in left axis) and for nesting females in French Guiana (bars, scale in right axis)
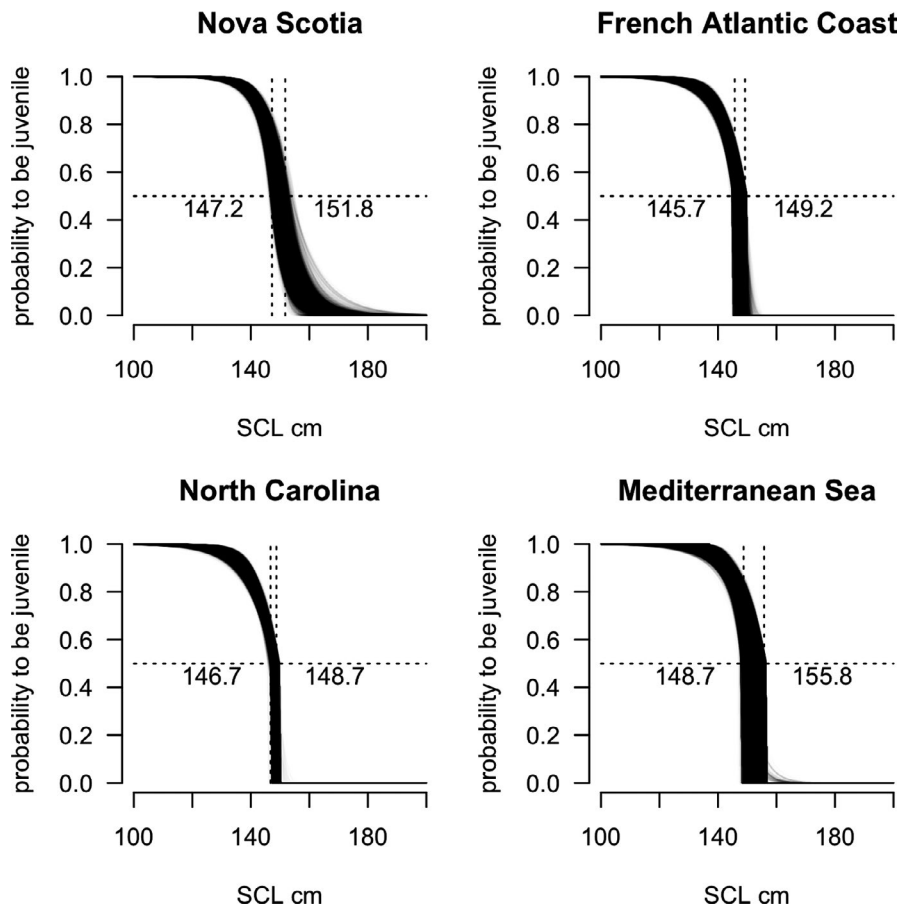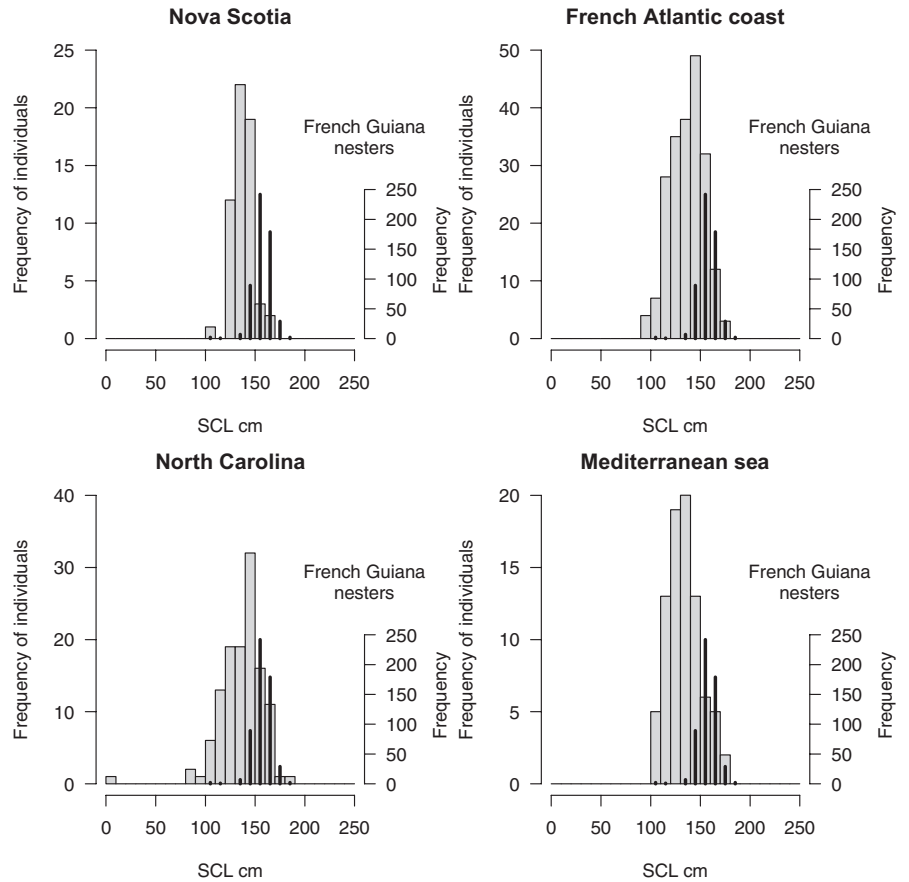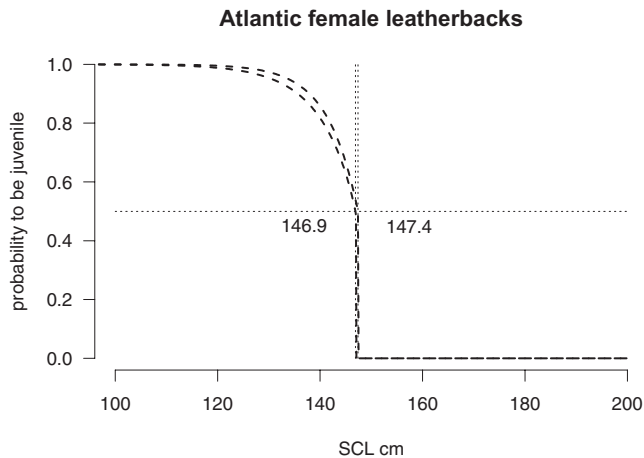
**FIGURE 3** Posterior distributions of straight carapace length reaction norm for female sexual maturity are based on 100,000 iterations of Markov Chain with Monte-Carlo sampling using Metropolis-Hastings algorithm. The values reported on the graphs are the 95% credibility intervals for the size at which 50% of females are mature

to recall that *h* is a measure of the average quality habitat experienced throughout the life of individual. For individuals that developed under experimental conditions being fed ad libitum, they will grow quickly enough that 5% of individuals could be mature in 5.4 years (Figure 7).

**Atlantic female leatherbacks**



**FIGURE 4** The posterior distribution of straight carapace length reaction norm for female sexual maturity for Atlantic leatherbacks based on 100,000 iterations of Markov Chain with Monte-Carlo sampling using Metropolis-Hastings algorithm. The values reported on the graphs are the 95% credible region for the size at which 50% of females are mature

## 4 | DISCUSSION

Over the past four decades, sea turtle researchers generally have characterized the "age at maturity" as a specific value, which is broadly applied to species or populations. While the age at maturity can be clearly defined for an individual sea turtle, it is unlikely to be constant for all individuals, given the diversity of environmental and genetic conditions experienced by different turtles within a population. We must shift the paradigm away from a constant "age at maturity" to "reaction norm of sexual maturity" (Stearns & Koella, 1986). This new approach to characterize sexual at maturity at the population level is a more realistic concept that includes variation across individuals and thereby allows new and more powerful ways to model the population dynamics of these species.

Our study suggests that 5% of female leatherback turtles may reach sexual maturity in 5.4 years for *h* = 1 (optimal conditions in captivity, fed ad libitum). Under normal conditions in the wild, 5% of females may reach maturity at 13 years, while the median age for sexual maturity is between 55 and 70 years (95% credible region; Figure 7). For individuals that are relegated exclusively to poor-quality habitats, they may never reach maturity, as they may die before a sufficient amount of time has elapsed for them to reach maturity. The proportion of females dying before reaching sexual maturity is unknown, because the annual survivorship for juveniles remains unknown. Our results suggest that the previously discordant estimates of the age at maturity of leatherbacks, proposed to
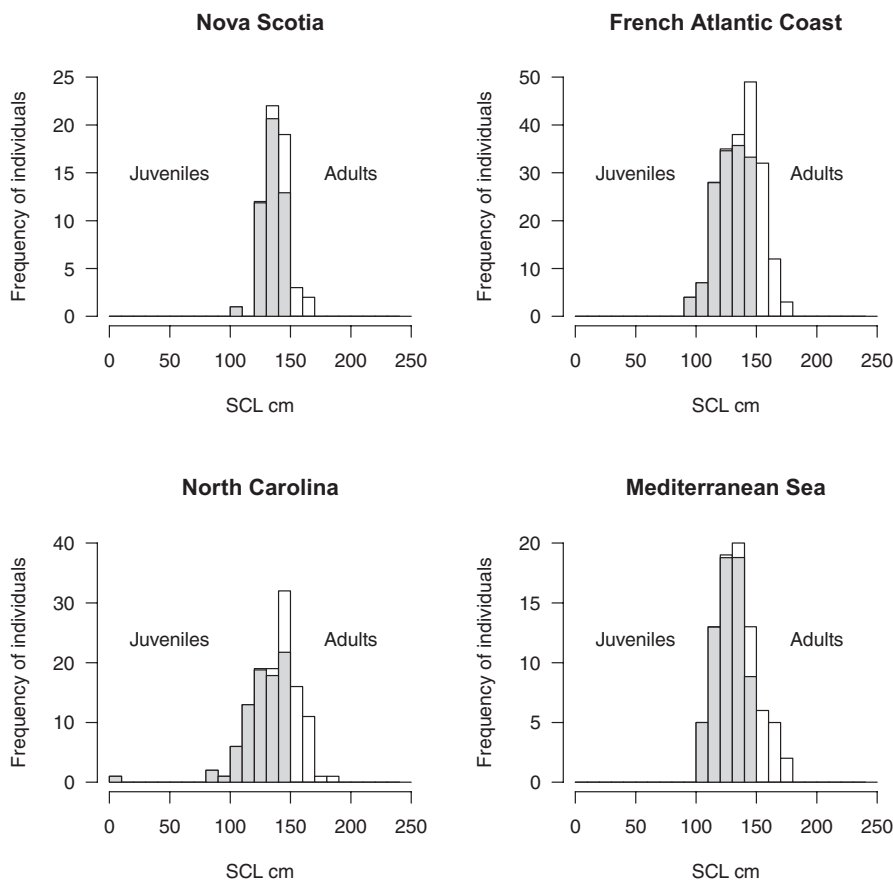


**FIGURE 5** Distribution of juvenile (grey) and adult identified as not males (white) stranded or captured-at-sea leatherbacks, based on the estimate of straight carapace length reaction norm for female sexual maturity
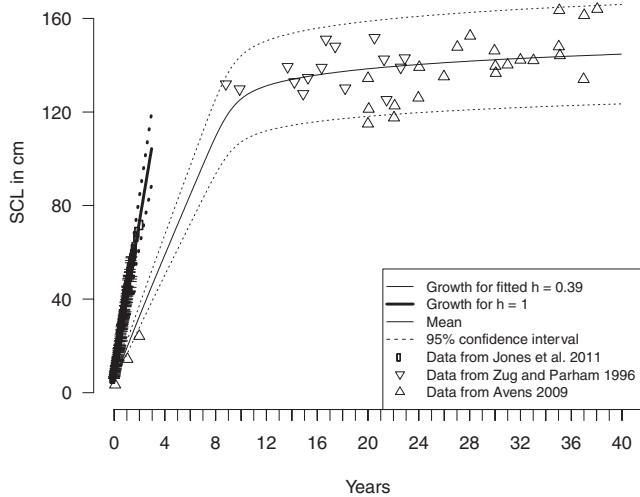
**FIGURE 6** Model of growth trajectory for leatherbacks in captivity and fed ad libitum ($h = 1$; $h$ being the habitat quality proxy) or in natural conditions (fitted $h$). The 95% credible region takes into account measurement errors, environmental variability (temporal and spatial variation for $h$), genetic variability and their interaction
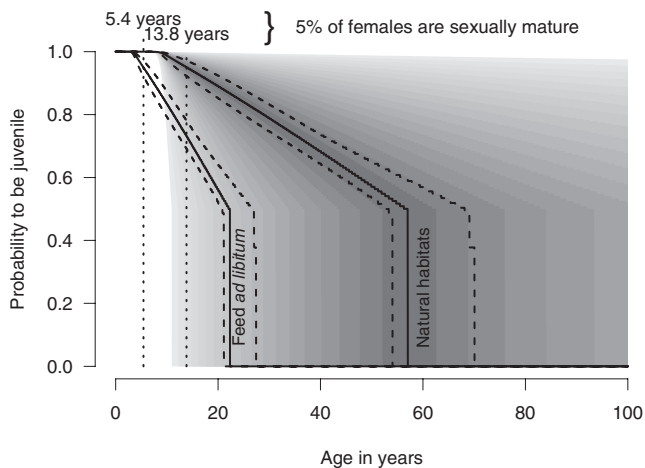


**FIGURE 7** Plain bold lines are the posterior distribution of the median age reaction norm for female sexual maturity for Atlantic leatherbacks, based on the combination of straight carapace length reaction norm for female sexual maturity (Figure 4) and model of growth for Atlantic leatherbacks (Figure 7). The greyed-in zone is the 95% credible region, taking into account measurement errors, environmental variability (temporal and spatial variation for $h$), genetic variability and their interaction for females in natural habitat. Each shade of grey represents a 5% credibility change. Dashed lines represent the uncertainty of the median due to the uncertainty of reaction norm parameters (Figure 4). Dotted lines represent the age at which 5% of the females are mature for individuals in captivity and fed ad libitum ($h = 1$, 5.4 years old) or in a natural habitat ($h = 0.39$, 13.8 years)

be as young as 2–3 years by some authors and more than 25 years by others, are actually all possible: there is a large phenotypic plasticity for this characteristic in leatherbacks. The demographic strategy of this species—and marine turtles in general—does not fit the

r-K continuum (Pianka, 1970). The longevity of adult female leatherbacks is potentially more than 10 years (Chevallier, Girondot, et al., 2020), which is typical of K-selection. A female produces around 500 eggs during a nesting season (Briane et al., 2007; Caut et al., 2006), and it can nest during as many as 10 nesting seasons, thus producing around 5,000 eggs during its reproductive lifetime.. This high egg productivity is typical of r-selection. The optimal conditions for the persistence of this kind of mixed demographic strategy remain unknown.

The precise identification of sexual phenotype is possible only when near fresh dead specimens are dissected. For this reason, we also fit the SCL reaction norm for sexual maturity pooling all data from juveniles, females, males and undetermined sex category. The age at which 50% of individuals are mature ranges from 146.9 to 147.7 cm (95% credibility interval), nearly the same as the value obtained when considering data only from juveniles, females and undetermined category: 146.9 to 147.4 cm (95% credibility interval). It indicates that there is no apparent sexual size dimorphism in this species.

The development of genetic tags for hatchling leatherback sea turtles (Dutton & Stewart, 2013) is a promising technique that may reveal the age of adult female turtles when they are first observed on the nesting beach. However, given that leatherbacks likely exhibit indeterminate growth and variable age at maturity, the first reproductive females observed with genetic tags derived from the hatchling stage may represent those individuals with the most rapid growth and fastest rate of maturity for this species. It is likely that more reproductive individuals with genetic tags will be subsequently identified, with slower rates of maturity, and thus long-term monitoring is needed on projects using genetic tags to fully reveal the range of age of maturity in this species.

Our result is of primary importance for the conservation of leatherbacks. Several populations of which appear to be on the brink of extinction in different part of the world include the Pacific coast (Spotila et al., 2000) or in West French Guiana where 95% of population has disappeared in 20 years (Chevallier, Girondot, et al., 2020). Extinction risk is inversely associated with maximum per capita population growth rate ($r_{max}$) (Mace et al., 2008). A comparative life-history analysis of 199 species has shown that age at maturity was the primary and negative correlate of $r_{max}$ (Hutchings et al., 2012). The maximum per capita population growth rate is also related to the capacity of a species to recover from a population crash (Mace et al., 2008). Our median estimate of 58 years at which 50% of individuals reach maturity suggests leatherback populations may not be able to quickly rebound from depleted levels. However, the demographic impacts of large developmental plasticity of sexual maturity are not fully understood. For example, the growth rate increases monotonically with the variance in survival rates, and the effect can be substantial, easily doubling the growth rate of slow-growing populations (Kendall et al., 2011). Ongoing monitoring of nesting populations of leatherbacks is needed not only for trends analysis but also contextualizing the importance of life-history parameters, such as age of maturity.

## CONFLICTS OF INTEREST

None.

## ETHICAL APPROVAL

Research was carried with authorization of French Ministry for Environment to capture, tag and measure animals.

## DATA AVAILABILITY STATEMENT

Original data sets and R scripts are included in the supplementary file.

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