

Age and growth of loggerhead sea turtles in southern Brazil

Roberta Petitet^{1,2,4,*}, Eduardo R. Secchi³, Larisa Avens⁵, Paul G. Kinas²

¹Programa de Pós-graduação em Oceanografia Biológica, Instituto de Oceanografia, ²Laboratório de Estatística Ambiental, Instituto de Matemática, Estatística e Física (IMEF), and ³Laboratório de Tartarugas e Mamíferos Marinhos, Instituto de Oceanografia; Universidade Federal do Rio Grande (FURG), Avenida Itália km 8, CEP 96201-900, Rio Grande, Rio Grande do Sul, Brazil

⁴Centro de Recuperação de Animais Marinhos - CRAM-FURG, Rua Capitão Heitor Perdigão, no. 10, CEP 96200-580, Centro, Rio Grande, Rio Grande do Sul, Brazil

⁵NOAA Fisheries, Southeast Fisheries Science Center, Center for Coastal Fisheries and Habitat Research, 101 Pivers Island Road, Beaufort, North Carolina 28516, USA

ABSTRACT: The juvenile and subadult stages of loggerhead sea turtles *Caretta caretta* are poorly studied in Brazil. We present age estimates and a growth model for loggerhead sea turtles in the South Atlantic Ocean obtained through skeletochronological analysis of humeri from both neritic and oceanic stage individuals. The age estimation was based on the number of growth marks in the humerus; however, for larger turtles early growth marks were resorbed and therefore it was necessary to use a correction factor to account for the lost growth marks. The estimated ages indicate that the oceanic stage lasts 8 to 19 yr (average: 11.5 yr). Schnute's growth model was fit to age-at-length data, as its shape is versatile and it does not require data from all life stages (i.e. hatchlings through adults near asymptotic size). However, because the shape of Schnute's curve was almost linear for the age window comprising our data, a linear regression ultimately provided a better fit to the data, yielding an age at maturation estimate of 32 yr. Somatic growth rates were calculated through incorporation of the Body Proportional Hypothesis into conversion of growth mark measurements to estimates of carapace length. Growth rates from neritic stage South Atlantic loggerheads were similar to those reported for neritic loggerhead sea turtles from the North Atlantic Ocean, but were lower than those of oceanic loggerheads from the South Atlantic Ocean. This finding suggests that local environmental conditions influence loggerhead sea turtles' growth rates as well as the energy expenditure during migrations, energy allocation and genetic origin.

KEY WORDS: Age · Growth · Skeletochronology · Bayesian inference · Schnute's curve · *Caretta caretta*

— Resale or republication not permitted without written consent of the publisher —

INTRODUCTION

Age structure is one of the parameters that influences the dynamics of a given population. Furthermore, age-related data are essential for calculating natural growth rates and age at sexual maturity, which are needed to develop conservation management plans for endangered sea turtle species (Bjornald & Bolten 1988, Zug et al. 2002). However, these

data are challenging to collect owing to the complex pattern of migration exhibited by sea turtles throughout their life cycle (Musick & Limpus 1996), and therefore, many questions relating to this matter still remain.

The loggerhead sea turtle *Caretta caretta* is one of the 7 species of sea turtles and is widely distributed throughout the oceans. Throughout its range, the loggerhead faces a number of threats to its survival and

is therefore classified as 'endangered' in the IUCN Red List of Endangered Species of Fauna and Flora proposed by the International Union for Conservation of Nature and Natural Resources (IUCN 2010). Like other species of sea turtles, loggerheads have complex life histories (Musick & Limpus 1996, Bolten 2003). In general, as soon as they enter the sea, they swim to oceanic zones in offshore waters where they spend the first years of their life, which are termed the 'lost' years, as it is a difficult phase of the turtle's life cycle to research (Musick & Limpus 1996). Thereafter, when the curved carapace length (CCL) reaches approximately 46 to 64 cm, they recruit as juveniles to foraging areas in the neritic zone (Bjorndal et al. 2000). Upon maturation, adults then start migrating between foraging and breeding areas (Bolten 2003).

Demographic parameters such as mortality, recruitment, interhabitat dispersal, annual remigration, and sex-, size- and age-specific growth rates can be provided by mark–recapture data and used to model a population (Chaloupka & Musick 1996). Although this method has been used with all sea turtle species throughout the world (Bjorndal et al. 2000, Chaloupka & Limpus 2002, Reisser et al. 2008, Revelles et al. 2008, Casale et al. 2009), it requires intensive long-term field work (Casale et al. 2007). Consequently, results became available only in the long-term.

In contrast, skeletochronological studies have been validated and applied to *Caretta caretta* (Zug et al. 1986, Klinger & Musick 1992, Parham & Zug 1997, Snover & Hohn 2004, Casale et al. 2011a,b), allowing estimation of age from growth increments formed in the humerus bone (Parham & Zug 1997). This approach allows for understanding some age-based parameters, similar to mark–recapture; however, the skeletochronological method has the potential to yield results more rapidly. Furthermore, if marks are deposited annually and a proportional relationship exists between bone and somatic growth (Klinger & Musick 1992, Snover & Hohn 2004), then it is possible to obtain growth rates from each skeletal growth increment. This, in turn, allows estimation of growth rates over multiple years and detection of ontogenetic changes due to life stage intrinsic dynamics (Snover 2002).

Regardless of the means by which growth information is obtained, fitting a growth model to the age data is essential to characterize the general growth pattern for a given population and to estimate the age of individuals based on their size. In the literature, there are an extensive number of growth mod-

els to contemplate, such as Pütter, von Bertalanffy, Richards, Gompertz or logistic models. However, these growth models exhibit a limit or asymptote (Schnute 1981), which necessitates that sampling include all ages throughout the life cycle; otherwise it is not possible to adequately fit these growth models to the data. For sea turtles, the most commonly used growth models are the von Bertalanffy, Gompertz and logistic models; however, for most of these studies, it was necessary to estimate ages for post-hatchlings and early juveniles, and as well as for adults approaching asymptotic length, in order to generate reasonable growth curves (Klinger & Musick 1995, Zug et al. 1995, 2002, Bjorndal et al. 2000, Snover 2002, Goshe et al. 2010). Schnute (1981) developed a general growth model that encompasses many specific models (like those cited above) as special cases, allowing the fit of a growth model even if only data from a limited age window of the complete life cycle is available.

Along the Brazilian coast, most studies of loggerhead sea turtles focus on adult females on nesting beaches, and the majority of nesting occurs in the states of Bahia and Espírito Santo (Marcovaldi & Chaloupka 2007). Although information for immature individuals during their oceanic and neritic stages is fragmentary, it is known that the southern coast of Rio Grande do Sul state, southern Brazil, is an important foraging area for both stages of *Caretta caretta* (Martinez-Souza 2009, Barros 2010). Although the carcasses of loggerheads are frequently washed ashore (Monteiro et al. 2006), little is known about the species demography in this area, including the age and growth data essential for understanding population dynamics of loggerheads in the South Atlantic Ocean. In this study, skeletochronological data are used to describe growth patterns of loggerheads washed ashore or incidentally caught in pelagic longline fisheries off southern Brazil.

MATERIALS AND METHODS

Study area

Sample collection took place on the south coast of Rio Grande do Sul, southern Brazil, between Lagoa do Peixe (31°20'S, 51°05'W) and Arroio Chuí (33°45'S, 53°22'W), spanning 355 km of beach (Fig. 1). This stretch of beach was monitored once a week, between November 2008 and December 2009, to collect humeri from sea turtles washed ashore for skeletochronological analysis. Humeri collected from

loggerheads incidentally caught by the longline fisheries in the oceanic zone of southern Brazil, between 29° and 38° S latitude and 45° and 51° W longitude (Fig. 1) were also analyzed. For every turtle, the curved carapace length (CCL) was measured (Bolten 1999) with a flexible metric tape (± 0.1 cm).

Sample preparation

Humeri were dissected and macerated, i.e. soaked in water for 2 to 3 wk until the soft tissue was removed, and the bones were then air-dried for ~2 wk. After cleaning the bone, 7 morphometric measurements were recorded by using digital calipers (± 0.1 mm): (1) maximal length, (2) longitudinal length, (3) proximal width, (4) delto-pectoral process width, (5) medial width, (6) distal width, (7) thickness, and (8) weight (Zug et al. 1986). The histological method

used to prepare humerus sections used for skeletochronological analysis was based on Avens & Goshe (2007). As the stain quickly faded from the histologically processed cross sections, 5 \times magnified pictures were taken of sequential portions of the sections with a Spot Insight QE digital camera fitted to an Axiovert 135 binocular inverted microscope. The partial images of each histological section were combined using Adobe Photoshop Elements 8.0, resulting in a high resolution composite digital image of the entire section that was archived and used for growth mark analysis.

Growth layers

Each digital image from the cross-section was labeled with a random number before counting growth marks. Each section was interpreted by one

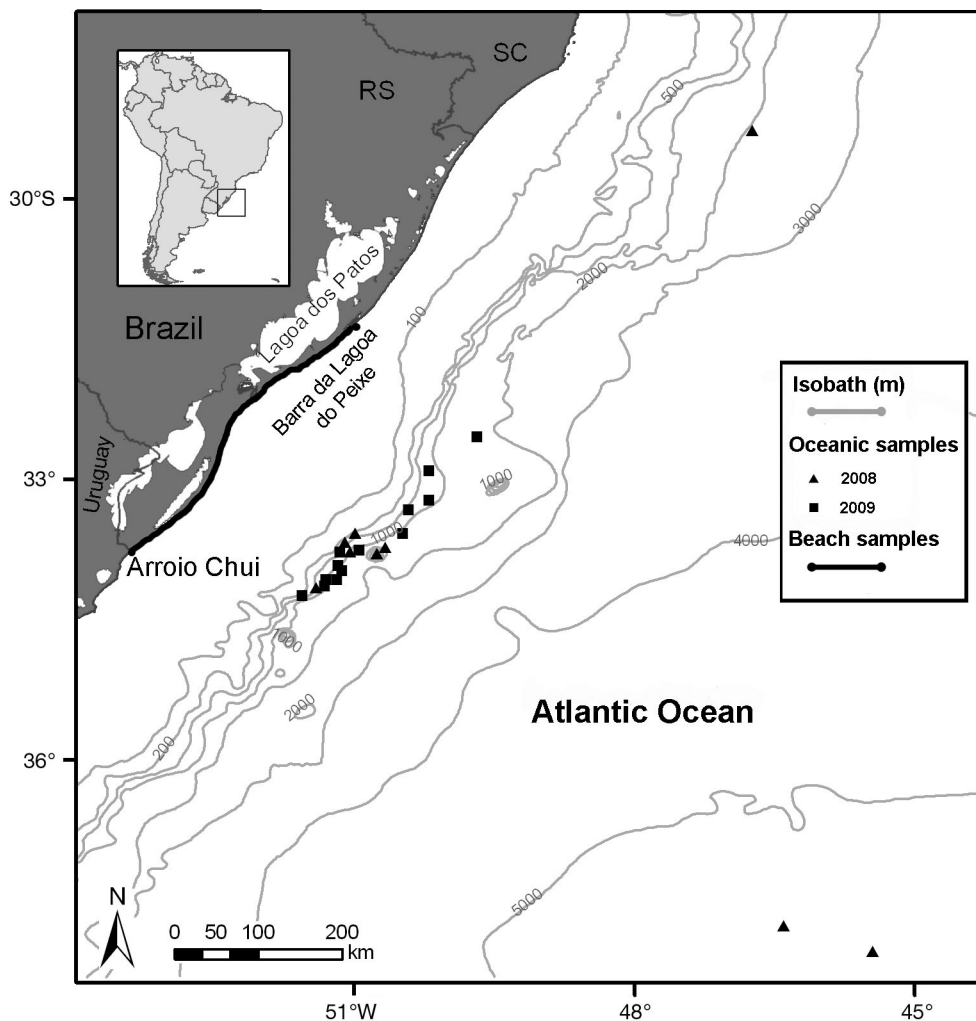


Fig. 1. *Caretta caretta*. The 2 sampling locations of dead loggerhead sea turtles: (1) neritic individuals stranded at the coast south of Rio Grande do Sul, southern Brazil; (2) oceanic individuals caught by the longline fisheries in the south of Rio Grande do Sul, southern Brazil (adapted from Barros 2010). RS: Rio Grande do Sul; SC: Santa Catarina

reader in 3 independent readings performed on different occasions and later compared to increase the accuracy. If the number of growth marks varied between readings, a fourth reading was done. In the cross-sections a growth mark consisted of a lightly stained area followed by a dark line of arrested growth (LAG), which appeared as defined or diffuse (Zug et al. 1986). When these layers were continuous along the humerus circumference, the line was counted as one LAG, if there were 2 dark lines following the same direction closely spaced along the entire circumference, this was counted as a double LAG representing one LAG (Fig. 2a). However, if there was a dark line that split into multiple lines in some region of the bone circumference, each multiple line was counted as one LAG (Fig. 2b). The interpretation of double and split lines was based on Castanet Smirina (1990) and Snover & Hohn (2004). An axis parallel to the dorsal edge of the humerus was used to measure the resorption core, each LAG and each humerus diameter using Spot Camera 3.5.0.0 software.

Age estimation

The first growth mark (annulus) appears closest to the center of the bone and later growth marks are deposited sequentially along the outer circumference (Zug et al. 1986) (Fig. 2c). Snover & Hohn (2004) validated that, for Kemp's ridley sea turtles *Lepidochelys kempii*, this earliest growth mark is shaped as

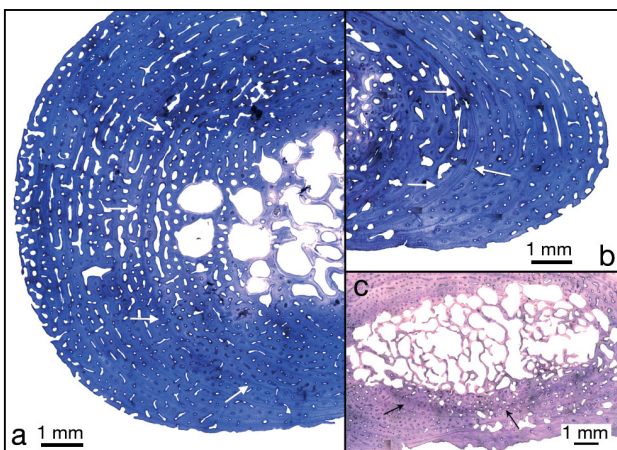


Fig. 2. *Caretta caretta*. Interpretation of lines of arrested growth (LAG; arrows) from loggerhead humerus: (a) double line, counted as one LAG; (b) one dark LAG that split into 5 lines, counted as 5 LAGs; (c) first year mark (denoted as annulus)

a diffuse line and we assumed that the pattern holds for loggerhead sea turtles as well. Accepting that the bone growth is cyclic (Zug et al. 1986), and that for *Caretta caretta* each growth mark indicates 1 yr of life (Klinger & Musick 1992, Coles et al. 2001, Bjorn-dal et al. 2003), the age was defined as the number of LAGs for the turtles that retained an annulus. However, in large individuals, the early periosteal layers are entirely replaced by remodeling and endosteal growth (denoted 'lost LAGs') (Zug et al. 1986). The number of lost LAGs within the resorption cores was calculated based on the age-estimation protocol proposed in Parham & Zug (1997) as a correction factor. According to Zug et al. (2006), age estimation by a correction factor is more plausible biologically because age and size are dissociated. This correction factor derives from a relationship between the number of growth layers (x) and the corresponding growth layer diameters (y). In a first step, for turtles that retained an annulus, the pairs (x, y) were measured with numbered lines from the inner to outer edge of the bone. Two models: (1) linear regression $y = a + bx$ and (2) power function $y = ax^b$ were fitted to the data set.

To estimate model parameters, 2 different error structures were assumed (Faraway 2006). The first, denoted 'naïve', assumes that $y_i = A + bx_i + v_i$ or $y_i = ax_i^b + e^{v_i}$, where v_i are independent normal random variables with mean 0 and variance σ^2 for a total of n pairs of data (y_i, x_i), $i = 1, \dots, n$ and $a = \ln A$. The second, denoted 'hierarchical', in line with the data-collecting process, takes the inter- and intraindividual variability into account. Hence, this error structure assumes that $y_{ij} = A_i + b_i x_{ij} + v_{ij}$ or $y_{ij} = a_i x_{ij}^{b_i} e^{v_{ij}}$ where, within individual $i = 1, \dots, m$, the variables v_{ij} are independent normal random variables with mean 0 and variance σ_i^2 for a total of n_i pairs of data (y_{ij}, x_{ij}), $j = 1, \dots, n_i$ and $n = \sum_{i=1}^m n_i$. Furthermore, the pair of parameters (a_i, b_i) are individual-specific and modeled as independent normal random variables with mean and variance ($\mu_{a_i}, \sigma_{a_i}^2$) and ($\mu_{b_i}, \sigma_{b_i}^2$), respectively. The naïve models have 3 parameters a (or A), b and σ , while the hierarchical models have 5 parameters ($\mu_{a_i}, \mu_{b_i}, \sigma_{a_i}, \sigma_{b_i}$ and σ).

In a second step, for turtles without an annulus, the resorption core diameters were measured (y_{core}), and the corresponding number of lost lines inferred by reverse prediction (x_{core}). Therefore, the number of growth layers observed in the outermost region of the bone section (x_{obs}) plus the predicted number of resorbed growth layers represented in the resorption core of the humerus is the turtle's estimated age ($x = x_{\text{core}} + x_{\text{obs}}$).

Back-calculation and growth rates

Back-calculation is a technique developed to estimate the length of a fish at an earlier time and is based on body length measurements and the size of hard parts (typically otoliths) used to assess age obtained at the time of death. From these data, the body length for all previously formed marks within the hard structure is estimated (Francis 1990). Smedstad & Holm (1996) applied and validated the method for Atlantic cod *Gadus morhua*. In sea turtles, the back-calculation method has been applied and validated for loggerheads and green sea turtles *Chelonia mydas* (Snover et al. 2007, Goshe et al. 2010, Casale et al. 2011a).

We fitted 4 models to find the best relationship between curved carapace length and humerus diameter, as did Snover et al. (2007) for North Atlantic loggerheads: (1) $L = I_{op} + b(D - d_{op})^c$; (2) $L = I_{op} + b(D - d_{op})$; (3) $L = a + bD^c$; and (4) $L = a + bD$, where L is CCL, D is the diameter of the humerus, I_{op} is a given CCL of the turtle at hatching, d_{op} is a given diameter of the humerus at hatching and c is the allometric coefficient, which is equal to 1 for Models 2 and 4. For I_{op} and d_{op} , we used the hatchling mean straight carapace length (SCL) of 4.6 cm in Snover et al. (2007) converted to CCL based on the linear regression equation in Avens & Goshe (2007) ($SCL = 0.923(CCL) - 0.189$; $I_{op} = 4.77$ cm).

Once the best model is established, back-calculation provides estimates of size (CCL) for growth layer (LAG) diameters within the humerus. Thereafter, the 'Body Proportional Hypothesis' (BPH) was applied. This hypothesis says that the ratio between true size (L and model-estimated size $\hat{L} = f(D)$ for the associated humerus diameter (D) and a given model f , is the same for all values of D (Francis 1990, Snover et al. 2007). Under BPH, and taking the best-fitted model as f , the back-calculated length (L_b) for a given diameter D_b is:

$$L_b = [f(D_b)] [L_{final}] [f(D_{final})]^{-1} \quad (1)$$

where L_{final} is the CCL of a turtle at death; and $f(D_{final})$ is the back-calculated CCL, based on humerus diameter.

To calculate the average yearly growth rate for each turtle, the diameter of the innermost LAG was measured and the corresponding CCL back-calculated with Eq. (1) and then subtracted from the CCL for the outermost LAG; the difference was divided by $k + 1$, where k is the number of LAGs in between.

Growth model

There are a number of published growth models, including the Pütter, von Bertalanffy, Richards, Gompertz and logistic growth models, among others. All these models are special cases of a generalized model proposed by Schnute (1981). Logistic and von Bertalanffy growth models have been applied to skeletochronological and mark-recapture growth data for loggerhead sea turtles (Frazer & Ehrhart 1985, Klinger & Musick 1995, Zug et al. 1995, Bjørndal et al. 2000, Snover 2002). However, Schnute's (1981) model is fitted here to age at length owing to its generality in shape. Since the set of data included in the present analysis covers only a specific age window of the turtle's life cycle, the flexibility of this model is a possible advantage. Schnute's (1981) generic equation with 4 parameters takes the form

$$y_\tau = \left\{ \gamma_1^b - [\gamma_2^b - \gamma_1^b] \times \left[\frac{1 - e^{-a(\tau - \tau_1)}}{1 - e^{-a(\tau_2 - \tau_1)}} \right] \right\}^{\frac{1}{b}} \quad (2)$$

where y is the size of the specimen at age τ , in this case the size was the CCL. The parameters τ_1 and τ_2 are the ages fixed by the researcher, with the restriction that $\tau_2 > \tau_1$, which are usually the youngest and oldest ages present in the sample, respectively. The parameters γ_1 and γ_2 are the expected sizes at ages τ_1 and τ_2 , respectively, with the restriction that $0 < \gamma_1 < \gamma_2$. The parameters a and b define the shape of the curve and can be positive, negative or equal to zero. Parameter a is related to the curve slope and its unit is τ^{-1} and parameter b does not have a unit. Specific combinations of these 2 parameters lead to different growth models; for example, the von Bertalanffy curve when $a > 0$ and $b = 1$. The 5 parameters to be estimated are a , b , γ_1 , γ_2 , and σ , where σ is the SE of residuals. A linear regression ($CCL = A + Bx$) was also fitted, where $x = (\text{age} - 15)s_x^{-1}$ is the standardized distance at 15 yr of age, the full age closest to the mean age in the sample.

Statistical analysis

Inference was performed within a Bayesian statistical framework. In Bayesian analysis, estimates of unknown parameters are given as probability distributions denoted 'posteriors' (Gelman et al. 2003). These posteriors are obtained by the integration of the data likelihood with other relevant information expressed in prior probability distributions, using

Bayes' theorem. When analytical solutions are not feasible, posteriors are approximated by random samples taken from it. If the inclusion of external information is not possible or desirable, appropriate non-informative or 'open-minded' priors are chosen instead.

We used non-informative priors in all but Schnute's (1981) growth model, for which the prior for the parameter vector (a , b , $\log \gamma_1$, $\log \gamma_2$, $\log \sigma$) was a 5-dimensional Student's distribution with 10 df, centered at the mode of the log likelihood and with a scale matrix equal to the inverse-Hessian. Although informative, this prior is considered open-minded in the sense that all possible parameter values have positive prior probability. Samples from the posterior distributions were drawn by the method of Markov chain Monte Carlo (MCMC) (Gelman et al. 2003). In MCMC, a Markov chain is set up in such a fashion that the posterior is its long run equilibrium distribution.

Posterior means were used as parameter estimates unless otherwise stated. Uncertainty about these estimates were expressed in 95% posterior probability intervals with lower and upper limits equal to the quantiles 2.5 and 97.5% of the posterior sample, respectively. A posterior probability interval is the Bayesian analog to conventional confidence intervals (Ellison 2004, McCarthy 2007). Model selection was based on the deviance information criterion (DIC) (Spiegelhalter et al. 2002). All analyses were performed with software R (R Development Core Team 2008) and OpenBugs (Thomas et al. 2006), which is an application of BUGS language (The BUGS Project, www.mrc-bsu.cam.ac.uk/bugs/ [accessed 8 December 2008]) to specify models and perform the Bayesian analysis (Gilks et al. 1994). The R-code on all applications can be obtained on request from the first author.

RESULTS

A total of 69 humeri were collected, 49 from loggerhead turtles washed ashore and 20 from turtles incidentally caught in pelagic longline fisheries. Sizes of stranded turtles ranged from 45.5 to 102.0 cm CCL (mean \pm SD = 74.81 \pm 11.59 cm), while individuals caught in the ocean ranged from 47.0 to 66.5 cm CCL (58.92 \pm 5.00 cm) (see Table 3). The sample

was divided into oceanic and neritic individuals, i.e. the former being caught in the longline fishery operating 150 km from shore and the latter stranded dead on mainland beaches. This separation is based on different diets. Barros (2010) found only oceanic prey in 33 out of 35 stomachs in the oceanic turtles, while both benthic and oceanic prey were found in neritic turtles ($n = 42$). Data from the oceanic and neritic sea turtles were combined for growth analysis, because they were considered to be from the same population (Reis et al. 2010). The individuals were classified as 'possible' adults or juveniles based on the size range (83.0 to 120.0 cm CCL) of mature loggerheads from the nearest nesting area (Baptistotte et al. 2003).

Age estimation

Of the 69 humeri (neritic samples plus oceanic samples), only 13 humeri retained a diffuse annulus representing the first-year mark (Snover & Hohn 2004) and these turtles retained between 8 to 13 LAGs. The hierarchical power function model provided the best fit to age-at-death data, based on DIC (Table 1). With posterior means as parameter point estimates, the equation took the form:

$$\text{LAG diameter (mm)} = 2.18 \times (\text{LAG number})^{0.35} \quad (3)$$

For the 56 turtles without an annulus, the LAG diameter (y) was replaced by the resorption core diameter (y_{core}) and the equation solved for lost LAGs (x_{core}). The estimated age for oceanic turtles varied between 8 and 19 yr, which indicates the oceanic stage duration for loggerheads in the South Atlantic. For stranded turtles, estimated ages were between 9 and 24 yr.

Table 1. *Caretta caretta*. Bayesian fits of the 4 models for line arrested growth (LAG) of turtles versus line number data. The letters a , b and symbol σ represent the posterior mean; values within brackets are the 95% probability intervals. DIC is the deviance information criteria; a smaller DIC indicates a better fit

Parameter	— Naïve model —		— Hierarchical model —	
	$y = a + bx$	$y = ax^b$	$y = a + bx$	$y = ax^b$
a	9.11 (8.5, 9.7)	2.18 (2.1, 2.2)	8.98 (7.8, 9.9) ($\sigma_a = 2.21$ [1.4, 3.5])	2.18 (2.0, 2.3) ($\sigma_a = 0.21$ [0.1, 0.3])
b	1.16 (1.1, 1.3)	0.35 (0.3, 0.4)	1.18 (1.0, 1.3) ($\sigma_b = 0.27$ [0.2, 0.4])	0.35 (0.3, 0.4) ($\sigma_b = 0.08$ [0.05, 0.13])
σ	1.70 (1.5, 1.9)	0.12 (0.10, 0.13)	0.75 (0.7, 0.9)	0.04 (0.03, 0.05)
DIC	504.9	-170.7	321.1	-430.0

The comparison between estimated lost LAGs from the naïve and hierarchical power models shows an increased over-estimation of the naïve model in comparison with the hierarchical model for older ages (Fig. 3a). However, this difference is less pronounced for the overall age estimation (Fig. 3b).

Back-calculation and growth rates

The best-fitted model incorporated the biological intercepts l_{op} , d_{op} , and constant c . While the other 3 models provided reasonable fits to the data, the first model obtained the lowest DIC (Table 2, Fig. 4). This model was fitted to the complete age-at-length data set, because when applied separately, the fit was similar for the 2 samples (Fig. 4). Thus, the growth rates were calculated for the combined data.

The relationships between growth rates and size (CCL), as well as growth rate and estimated age, were negative ($r = -0.29$ and $r = -0.65$, respectively), suggesting that turtle growth rates decrease as age and size increase (Fig. 5). However, based on a linear model fit (not shown), the relationship between size and growth rate was not significant ($p = 0.393$), although the average growth rate for oceanic loggerheads was slightly higher than for neritic turtles ($p = 0.088$) (Table 3).

Growth models

Schnute's (1981) growth model had a good fit for the relationship between estimated age and carapace length data. Because the data did not include earlier ages (hatchling and small juveniles) and older adults, Schnute's curve was almost a straight line (Fig. 6a). The much simpler linear model fit well to the data (Fig. 6a) and had a slightly lower DIC than Schnute's model (Table 4), suggesting that within this 'age window' growth is nearly linear. Parameter A is the average size (cm) of an individual at age 15 yr (Fig. 6c, Table 4). Parameter B was divided by s_x to become B_y , the average yearly growth (cm yr⁻¹), resulting in a posterior mean of 2.04 cm yr⁻¹, similar to the average growth

Table 2. *Caretta caretta*. Bayesian fit of 4 models for carapace length versus humerus diameter. In each model L is curved carapace length and D the humerus diameter; l_{op} = carapace length at hatching; d_{op} = humerus diameter at hatching. Estimated parameters are posterior means; values within brackets = 95 % probability intervals. DIC = deviance information criterion to select among models; a smaller DIC indicates a better fit

Model	Parameter estimates				DIC
	a	b	c	σ	
$L = l_{op} + b(D - d_{op})^c$		1.30 (1.1, 1.5)	0.92 (0.8, 1.0)	0.07 (0.05, 0.08)	170.4 –
$L = l_{op} + b(D - d_{op})$		2.86 (2.8, 2.9)		4.06 (3.5, 4.7)	393.9
$L = a + bD^c$	0.57 (0.0, 4.4)	3.69 (2.8, 44)	0.92 (0.9, 1.0)	3.90 (3.3, 4.7)	391.7
$L = a + bD$	5.22 (-0.3, 9.7)	2.62 (2.4, 2.8)		3.91 (3.3, 4.6)	393.2

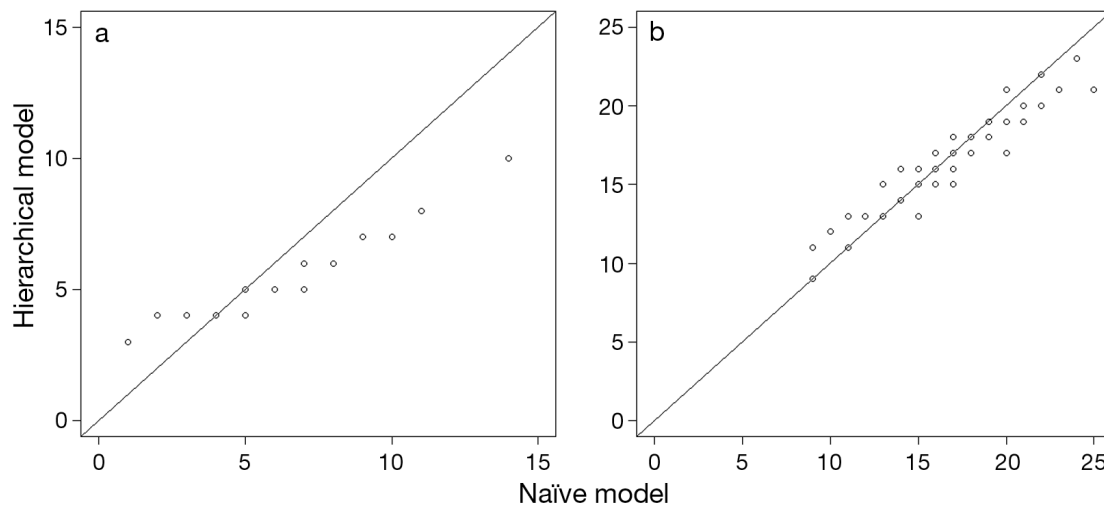


Fig. 3. *Caretta caretta*. Estimated (a) lost LAGs and (b) estimated age for turtles without an annulus obtained from the naïve model versus hierarchical model. Circles along the diagonal line represent selected estimates from both models

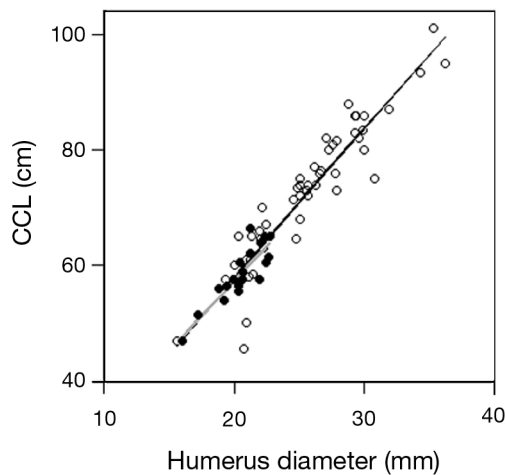


Fig. 4. *Caretta caretta*. Relationship between curved carapace length (CCL) and humerus diameter ($n = 69$). Grey solid line: model $[CCL = l_{op} + b(D - d_{op})^c]$ fitted only to the oceanic turtle data set (\bullet , $n = 20$). Black solid line: same model fitted only to the neritic turtle data set (\circ , $n = 49$). l_{op} : CCL at hatching; d_{op} : humerus diameter at hatching; b : slope of the line; c : allometric coefficient

rate obtained from back-calculation (2.45 cm yr^{-1}) (Fig. 6b, Table 4).

As the much simpler linear model had a lower DIC than Schnute's (1981) model, we used the former for estimating the age distribution of turtles within the size range of mature loggerheads from the Brazilian coast (83.0 to 123.0 cm CCL) (Baptistotte et al. 2003). The estimated age distribution was based on the assumption that this size range has an approximate normal distribution with the mean equal to 102.5 cm and the SD equal to 5.3 cm, and that the linear regression is acceptable up to the maximum size. Uncertainty in the parameter estimates of the linear age-at-size relation was included by use of the poste-

Table 3. *Caretta caretta*. Number (n) of turtles from neritic (beach) and oceanic (pelagic longline fisheries) zones and mean respective growth rates (range in brackets) by size classes of curved carapace length (CCL). –: no data

Size class (cm)	Neritic		Oceanic	
	n	Growth rate (cm yr^{-1})	n	Growth rate (cm yr^{-1})
40–49	2	2.39 (1.8–3.0)	1	3.37
50–59	4	2.82 (1.9–3.7)	10	3.51 (2.2–4.4)
60–69	11	2.55 (1.4–4.6)	9	2.79 (1.1–4.5)
70–79	16	2.55 (1.7–3.5)	–	–
80–89	13	2.53 (1.2–4.1)	–	–
90–99	2	–	–	–
100–109	1	–	–	–

rior distribution. The simulated age distribution resulted in a mean age at maturation for the loggerhead sea turtle population at 31.8 yr (± 3.47 yr; 95% probability interval: 25.7–39.2) (Fig. 7).

DISCUSSION

Age estimation

The size range and age estimates of oceanic loggerhead sea turtles in the South Atlantic were lower than for neritic ones inhabiting nearshore areas along the coast of southern Brazil. Bjorndal et al. (2000) suggested that loggerheads from the North Atlantic Ocean recruit to the neritic zone at ~46.0 to 64.0 cm CCL, which is similar to our findings for the South Atlantic Ocean. We show that oceanic turtles ranged from 47.0 to 65.5 cm CCL while those from the neritic area were predominantly >70 cm CCL. A few neritic individuals fell within the size range of oceanic turtles. They may

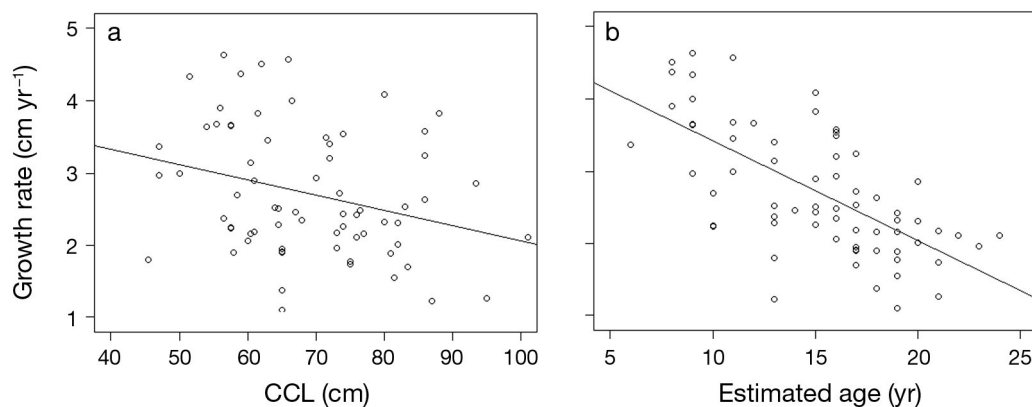


Fig. 5. *Caretta caretta*. Relationship between growth rates and (a) curved carapace length (CCL) ($r = -0.29$) and (b) estimated age ($r = -0.65$). $n = 69$

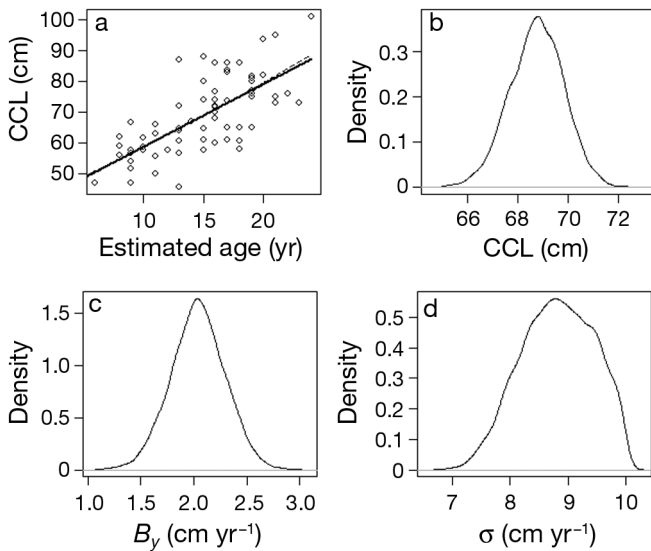


Fig. 6. *Caretta caretta*. (a) Bayesian fit of Schnute's (1981) model (dashed line) and linear model (solid line) to estimated age versus size (curved carapace length, CCL) of turtles. Posterior distribution of (b) average CCL at 15 yr of age, (c) parameter B_y , (d) residual SD (σ) all for the linear model

Table 4. *Caretta caretta*. Bayesian fit of Schnute's (1981) growth model and linear model for curved carapace length (CCL) and estimated age data. Estimated parameters are posterior means; values brackets = 95% probability intervals. DIC = deviance information criterion to select among models; a smaller DIC indicates a better fit. -: no data

— Schnute's model —		— Linear model —	
a	0.02 (-0.1, 0.2)	A	68.71 (66.5, 70.9)
b	0.04 (-0.7, 1.5)	B	2.04 (1.5, 2.5)
γ_1	49.04 (37.6, 58.0)	σ	8.81 (7.6, 9.9)
γ_2	88.53 (79.3, 100.2)	-	-
σ	8.73 (7.2, 10.4)	-	-
DIC	502.7	DIC	499.9

have been new recruits in transition from the oceanic to the neritic zone, as observed by Casale et al. (2008). Or, alternatively, they represented discards from longline fisheries, although this is less likely given that the fishing ground is at least 150 km from shore. Moreover, Monteiro et al. (2006) reported that most stranded loggerheads (average, 74.3 cm CCL) showed cuts on the carapace produced by sharp objects, entanglement in fishing lines, hooks or nets, due to interactions with fisheries that operate in coastal waters, such as bottom trawling or gill-netting. However, Barros (2010) found 3 out of 18 turtles washed ashore (50.0 to 69.9 cm CCL) with only oceanic prey items in their stomachs, suggesting that these strandings might have been caused by other factors.

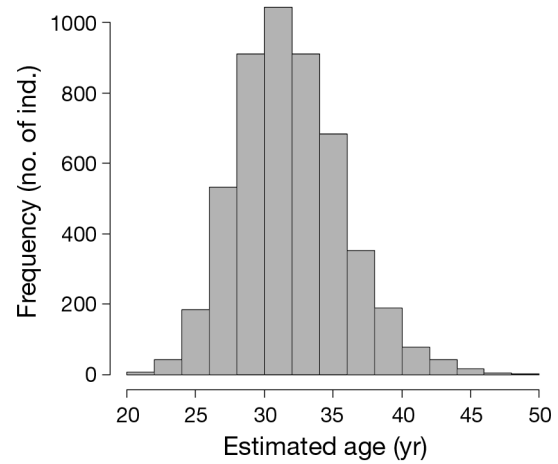


Fig. 7. *Caretta caretta*. Estimated age at maturation for the South Atlantic loggerhead sea turtle population

For North Atlantic loggerhead sea turtles, the age range for the oceanic stage has been estimated through skeletochronological analysis to be between 9 and 24 yr (Snover 2002). We estimated the age range of the western South Atlantic loggerhead population from 8 to 19 yr (average, 11.5 yr). While estimates by Snover (2002) and by our study are similar, Bjorndal et al. (2000) estimated ages from 6.5 to 11.5 yr by using length-frequency analysis in the North Atlantic Ocean, suggesting that methodology may influence the estimates.

Differences in the calculation of lost LAGs can explain minor differences between Snover et al. (2007) and our studies. Several methods that calculate the loss of periosteal layers have been applied in skeletochronology studies: correction factor, ranking and simple deduction based on the smallest turtle (Parham and Zug 1997; Zug et al. 1997, 2002, 2006, Bjorndal et al. 2003, Goshe et al. 2010). However, the individuals and interindividual variation of LAG deposition in specimens from the same population has never been taken into account. This variation is expected owing to the stochastic nature of the environmental conditions experienced by turtles during the many years in their oceanic phase until they recruit to neritic habitat (Bjorndal et al. 2003).

The hierarchical power model was more stable in comparison with the naïve alternative, because it estimated ages lower for larger and higher for smaller turtles (Fig. 3). Moreover, this model had lower residual variance (Fig. 3, Table 1) owing to the incorporation of σ_a and σ_b , which are related to parameters μ_a and μ_b respectively, which take into account the variation in LAG deposition. Further-

more, the application of Bayesian inference provided further accuracy to estimated ages because they were based on predictive probabilities over all possible ages given the whole data set (Ellison 2004).

Growth rate

Growth rates were greater for oceanic than for neritic loggerhead turtles, even for turtles within the same size range. Some neritic turtles within the size range of new recruits had growth rates similar to oceanic turtles, suggesting that the former could have been in their transition between both zones (Table 3) (Hawkes et al. 2006, Hatase et al. 2007). However, McClellan & Read (2007) recently demonstrated that this ontogenetic shift for loggerheads is not as absolute as previously thought.

Growth rates can vary significantly, both within and among individual turtles, as well as among foraging areas (Bolten 2003, Braun-McNeill et al. 2008), potentially owing to a variety of factors such as water temperature, food resources, energy expenditure during migrations and genetic origin (Goshe et al. 2010). Water temperature influences the physiology of reptiles (Moon et al. 1997), as feeding behavior, locomotor movements or hormone levels are negatively affected at high or low temperatures (Milton & Lutz 2003). Schwartz (1978) reported that turtles halt feeding and start floating when temperatures fall below 10°C, which influences their growth rates. However, the growth rates for neritic loggerheads in the southwestern Pacific Ocean (Great Barrier Reef: 1 to 2 cm yr⁻¹ CCL at 15°C in winter, and Moreton Bay: 2 to 3 mm yr⁻¹ CCL at 15°C; Read et al. 1996, Limpus & Limpus 2003), western North Atlantic (2.1 to 4.8 cm yr⁻¹ SCL at 13.3 to 28°C; Coles & Musick

2000, Snover 2002, Braun-McNeill et al. 2008) and western South Atlantic Ocean (1.5 to 4.5 cm yr⁻¹ CCL at 12.5 to 23°C) indicate that temperature is not the main factor underlying differences in growth rates among feeding areas. Turtles have the ability to move into regions of preferred temperature for physiological maintenance (Coles & Musick 2000, Hawkes et al. 2007, Schofield et al. 2009). Recent studies, such as Hawkes et al. (2007) and Mansfield et al. (2009), demonstrate that loggerheads migrate to lower latitudes in winter and to higher latitudes in summer in the North Atlantic Ocean. In contrast, there is no evidence that loggerhead turtles in Moreton Bay undertake south–north, summer–winter, non-breeding migrations (Musick & Limpus 1996). Instead, they become lethargic and spend longer time on the bottom, growing more slowly as a result (Limpus & Limpus 2003).

Before recruitment to the neritic zone, loggerheads inhabit stochastic environments characterized by extreme variation (Bjorndal et al. 2003) and the growth rates of these turtles may vary between individuals and populations. Bjorndal et al. (2000) reported growth rates that are higher than the growth rates obtained in the present study (Table 5). This variation might be explained by the different environmental conditions, such as water temperature and food resource, experienced by the turtles in the oceanic habitat of each ocean basin. Furthermore, loggerheads from the North Atlantic oceanic zone exhibit compensatory growth, which is an increase in growth when the conditions are favorable (Bjorndal et al. 2003).

Migration patterns of the loggerhead turtle populations in the South Atlantic Ocean are little understood. Nevertheless, it is possible that the energy expended during seasonal and inter-nesting migra-

Table 5. *Caretta caretta*. Growth rates for loggerhead sea turtle populations (straight carapace length [SCL], cm yr⁻¹) by size classes. RS: Rio do Grande do Sul, Brazil; NC: North Carolina, USA; GA: Georgia, USA; SC: skeletochronology; MR: mark-recapture; LF: length frequency analysis. Values within brackets = 95% probability interval (S Atlantic and RS) or 95% confidence interval (N Atlantic and GA) or SE (NC). – no data

SCL (cm)	Oceanic			Neritic			
	S Atlantic ^a SC	N Atlantic ^b MR	LF	RS ^a SC	NC ^c SC	GA ^d SC	NC ^e MR
40–49	3.6 (3.1, 4.0)	4.0 (3.4, 4.6)	3.9	2.2 (1.7, 2.8)	4.7 (±0.37)	3.6 (2.6, 4.3)	
50–59	3.1 (2.0, 4.3)	6.1	3.1	2.4 (1.8, 3.4)	3.9 (±0.31)	3.3 (1.7, 5.2)	1.81 (±1.15)
60–69	2.1 (1.0, 3.7)	2.9 (2.8, 3.0)	–	2.4 (1.6, 4.2)	3.2 (±0.24)	2.9 (2.2, 4.1)	2.16 (±1.61)
70–79	–	–	–	2.3 (1.6, 3.8)	2.1 (±0.37)	(1.6, 2.4)	2.41 (±0.51)
80–89	–	–	–	2.1 (1.1, 3.5)	–	(0.9, 3.5)	–
90–100	–	–	–	2.0	–	–	–

^aThe present study, curved carapace length converted to straight carapace length based on Avens & Goshe (2007). ^bBjorndal et al. (2000). ^cSnover (2002). ^dParham & Zug (1997). ^eBraun-McNeill (2008)

tion may influence growth rates. The wide seasonal water temperature variation in southern Brazil (Garcia 1998) may induce the northward migration of loggerhead during cold months, as was observed for green sea turtles (Hawkes et al. 2007, R. Petitet unpubl. data). Moreover, the turtles within the size range of mature loggerheads along the Brazilian coast (83.0 to 120.0 cm CCL) (Baptistotte et al. 2003) may perform seasonal migrations between foraging (southern Brazil) and nesting grounds (Espírito Santo State), thus contributing to the slow growth rates of this group (Table 3). Satellite telemetry would potentially improve the understanding of the migration and distribution patterns of loggerhead sea turtles in southern Brazil, which is an important foraging area for the western South Atlantic population (Martinez-Souza 2009, Barros 2010).

Martinez-Souza (2009) and Barros (2010) have observed that oceanic loggerheads feed mostly on salps and pyrosomes and suggested that these turtles feed constantly to balance the low energy budget of this food source. Thus, the trend for oceanic growth rates to be higher than those of neritic turtles ($p = 0.088$) may be due to the amount of food intake and the need for high growth rates to minimize predation risks (Snover et al. 2007). Although in the neritic zone, loggerheads feed upon prey with higher energy content (Barros 2010), their growth rates are lower in comparison. As it has been reported that larger turtles have lower growth rates (Klinger & Musick 1995, Goshe et al. 2010), the difference between our growth rate data and Moreton Bay studies may be due to the size range of recruits. In Australia, loggerhead turtles recruit to neritic habitat when their average CCL is 78.62 cm (Limpus & Limpus 2003), which is a much larger size than those estimated for the turtles in the South (~58.9 cm CCL, the present study) or North Atlantic Oceans (~53.0 cm CCL, Bjorndal et al. 2000). The low growth rate for Moreton Bay turtles (2.3 mm yr⁻¹ CCL) may be because the animals are already fairly large when they recruit to neritic habitat.

In addition to the various factors described above, growth rates may vary depending on the calculation method. As the BPH method was validated by Snover et al. (2007) for loggerheads, the calculation of growth rates became more accurate (Table 5). Skeletochronological analysis can potentially yield annual growth rates over multiple years, whereas mark-recapture studies produce a growth rate estimate related

merely to the variable time interval between capture and recapture.

Growth model

Schnute's (1981) growth model resulted in an almost straight line (Fig. 4), probably because the data set incorporated only a small 'age window' of the loggerhead sea turtle's life cycle. Furthermore, the majority of individuals were classified as juveniles (Limpus & Limpus 2003). Juvenile turtles appear to grow faster than adults (Bjorndal et al. 2003) perhaps as rapid size increase may protect them from predation (Snover & Hohn 2004).

An important advantage of Schnute's (1981) growth model is the versatility to adapt its shape according to the age window for which data are available. In contrast, to fit the more conventional von Bertalanffy growth model, a sample from all size classes ranging from hatchlings to old adults encompassing asymptotic size, is required. Such a data set is difficult to gather owing to the extensive migration pattern characteristic of the sea turtle's life cycle and the uncertainty remaining with regard to the 'lost years' (Carr 1987). In spite of these difficulties, the logistic or the von Bertalanffy growth models have usually been applied in most sea turtle growth studies (Frazer & Ehrhart 1985, Klinger & Musick 1995, Zug et al. 1995, Bjorndal et al. 2000, Snover 2002).

Based on the linear model, the estimated age at maturation was ~32 yr (Fig. 7). Snover (2002) reported a mean of 30.8 yr for age at maturation, and Bjorndal et al. (2000) estimated it took 26.5 yr for reaching a CCL of 87 cm, which is considered to be the minimum size at which loggerheads from the North Atlantic Ocean become mature. These estimates and those from Klinger & Musick (1995) (22 to 26 yr) are within the credibility interval of our estimates; however, the estimates strongly depend on the mean estimated size of mature loggerhead turtles in the population (Table 6).

Table 6. *Caretta caretta*. Estimated age at maturation in 4 different loggerhead turtle populations. VA: Virginia, USA; PT: Azores, Portugal; NC: North Carolina, USA; RS: Rio Grande do Sul, Brazil

Method	Population	Age at maturation (yr)	Source
Mark-recapture	VA	22–26	Klinger & Musick (1995)
Length frequency	PT	26.5	Bjorndal et al. (2000)
Sceletochronology	NC	30.8	Snover (2002)
Sceletochronology	RS	31.8	Present study

CONCLUSIONS

The south coast of Rio Grande do Sul is an important development area for oceanic juvenile loggerhead sea turtles (8 to 19 yr) as well as for neritic juveniles and adults (9 to 24 yr). Growth rates decreased with an increase in both age and size, reflecting the difference between growth rates of individuals in the oceanic and neritic zones. During the post-hatching to late juvenile stage, growth is linear, and the age at maturation is ~30 yr.

Skeletochronological analysis is a powerful tool to provide age- and growth-related data for characterizing sea turtle population dynamics throughout the world. This study is the first to describe age and growth for *Caretta caretta* in the South Atlantic and provides invaluable information for assessing loggerhead sea turtle population dynamics in southern Brazil.

Acknowledgements. We acknowledge the National Marine Fisheries Service, Sea Turtle Aging Laboratory, NOAA Fisheries, of skeletochronological training, with special thanks to A. Hohn, L. Goshe and M. Godfrey. We acknowledge the Núcleo de Educação e Monitoramento Ambiental (NEMA) and Centro de Recuperação de Animais Marinhos (CRAM-FURG) for the humeri samples. Some samples were collected and the age determined with the logistics provided by the Laboratório de Tartarugas e Mamíferos Marinhos (Instituto de Oceanografia—FURG). This paper is a contribution of the Research Group 'Ecologia e Conservação da Megafauna Marinha—EcoMega/CNPq'. E.R.S. was supported by CNPq (PQ 305219/ 2008-1). R.P. received financial support from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). This research is part of the Master's dissertation written by R.P. under the guidance of P.G.K.

LITERATURE CITED

- Avens L, Goshe LR (2007) Comparative skeletochronological analysis of Kemp's ridley (*Lepidochelys kempii*) and loggerhead (*Caretta caretta*) humeri and scleral ossicles. *Mar Biol* 152:1309–1317
- Baptistotte C, Thomé JCA, Bjorndal KA (2003) Reproductive biology and conservation status of the loggerhead sea turtle (*Caretta caretta*) in Espírito Santos state, Brazil. *Chelonian Conserv Biol* 4:523–529
- Barros J (2010) Alimentação da tartaruga-cabeçuda (*Caretta caretta*) em habitat oceanic e nerítico no Sul do Brasil: composição, aspectos nutricionais e resíduos sólidos Antropogênicos. MSc dissertation, Universidade Federal do Rio Grande
- Bjorndal KA, Bolten AB (1988) Growth rates of juvenile loggerheads, *Caretta caretta*, in the southern Bahamas. *J Herpetol* 22:480–482
- Bjorndal KA, Bolten AB, Martins HR (2000) Somatic growth model of juvenile loggerhead sea turtles *Caretta caretta*: duration of pelagic stage. *Mar Ecol Prog Ser* 202:265–272
- Bjorndal KA, Bolten AB, Dellinger T, Delgado C, Martins HR (2003) Compensatory growth in oceanic loggerhead sea turtles: response to a stochastic environment. *Ecology* 84: 1237–1249
- Bolten AB (1999) Techniques for measuring sea turtles. In: Eckert KL, Bjorndal KA, Abreu-Grobois FA, Donnelly M (eds) Research and management techniques for the conservation of sea turtles. IUCN/SSC Marine Turtle Specialist Group, Publication No. 4, Washington, DC, p 1–5
- Bolten AB (2003) Active swimmers—passive drifters: the oceanic stage of loggerheads in the Atlantic system. In: Bolten AB, Witherington BE (eds) Loggerhead sea turtles. Smithsonian Institution, Washington, DC, p 63–78
- Braun-McNeill J, Epperly SP, Avens L, Snover ML, Taylor JC (2008) Growth rates of loggerhead (*Caretta caretta*) sea turtles from the western North Atlantic. *Herpetol Conserv Biology* 3:273–281
- Carr A (1987) New perspectives on the pelagic stage of sea turtle development. *Conserv Biol* 1:103–121
- Casale P, Mazaris AD, Freggi D, Basso R, Argano R (2007) Survival probabilities of loggerhead sea turtles (*Caretta caretta*) estimated from capture-mark-recapture data in the Mediterranean Sea. *Sci Mar* 71:365–372
- Casale P, Abbate G, Freggi D, Conte N, Oliverio M, Argano R (2008) Foraging ecology of loggerhead sea turtles *Caretta caretta* in the central Mediterranean Sea: evidence for a relaxed life history model. *Mar Ecol Prog Ser* 372:265–276
- Casale P, Mazaris AD, Freggi D, Vallini C, Argano R (2009) Growth rates and age at adult size of loggerhead sea turtles (*Caretta caretta*) in the Mediterranean Sea, estimated through capture-mark-recapture records. *Sci Mar* 73:589–595
- Casale P, Conte N, Freggi D, Cioni C, Argano R (2011a) Age and growth determination by skeletochronology in loggerhead sea turtles (*Caretta caretta*) from the Mediterranean Sea. *Sci Mar* 75:197–203
- Casale P, Mazaris AD, Freggi D (2011b) Estimation of age at maturity of loggerhead sea turtles *Caretta caretta* in the Mediterranean using length frequency data. *Endang Species Res* 13:123–129
- Castanet J, Smirina E (1990) Introduction to the skeletochronological method in amphibians and reptiles. *Ann Sci Nat Zool* 13e Sér 11:191–196
- Chaloupka MY, Limpus CJ (2002) Survival probability estimates for the endangered loggerhead sea turtle resident in southern Great Barrier Reef waters. *Mar Biol* 140: 267–277
- Chaloupka MY, Musick JA (1996) Age, growth, and population dynamics. In: Lutz PL, Musick JA (eds) The biology of sea turtles. CRC Press, Boca Raton, FL, p 233–276
- Coles WC, Musick JA (2000) Satellite sea surface temperature analysis and correlation with sea turtle distribution off North Carolina. *Copeia* 2000:551–554
- Coles WC, Musick JA, Williamson LA (2001) Skeletochronology validation from an adult loggerhead. *Copeia* 2001:240–242
- Ellison AM (2004) Bayesian inference in ecology. *Ecol Lett* 7: 509–520
- Faraway JJ (2006) Repeated measures and longitudinal data. In: Faraway JJ (ed) Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models. Chapman & Hall/CRC, Boca Raton, FL, p 185–199

- Francis RICC (1990) Back-calculation of fish length: a critical review. *J Fish Biol* 36:883–902
- Frazer NB, Ehrhart LM (1985) Preliminary growth rates for green, *Chelonia mydas*, and loggerhead, *Caretta caretta*, turtles in the wild. *Copeia* 1985:73–79
- Garcia CAE (1998) Oceanografia física. In: Seelinger U, Odebrecht C, Castello JP (eds) Os ecossistemas costeiros e marinhos do extremo sul do Brasil. *Ecoscintia*, Rio Grande, p 104–106
- Gelman A, Carlin JB, Stern HS, Rubin DB (2003) Bayesian data analysis, 2nd edn. Chapman & Hall, London
- Gilks WR, Thomas A, Spiegelhalter DJ (1994) A language and program for complex Bayesian modeling. *Statistician* 43:169–177
- Goshe L, Avens L, Scharf FS, Southwood AL (2010) Estimation of age at maturation and growth of Atlantic green turtles (*Chelonia mydas*) using skeletochronology. *Mar Biol* 157:1725–1740
- Hatase H, Omuta K, Tsukamoto K (2007) Bottom or mid-water: alternative foraging behaviours in adult female loggerhead sea turtles. *J Zool* 273:46–55
- Hawkes LA, Broderick AC, Coyne MS, Godfrey MH and others (2006) Phenotypically linked dichotomy in sea turtle foraging requires multiple conservation approaches. *Curr Biol* 16:990–995
- Hawkes LA, Broderick AC, Coyne MS, Godfrey MH, Godley BJ (2007) Only some like it hot—quantifying the environmental niche of the loggerhead sea turtle. *Divers Distrib* 13:447–457
- IUCN (International Union for Conservation of Nature and Natural Resources) (2010) IUCN red list of threatened species, version 2010.3. www.iucnredlist.org (accessed 22 September 2010)
- Klinger RC, Musick JA (1992) Annular growth layers in juvenile loggerhead turtles (*Caretta caretta*). *Bull Mar Sci* 51:224–230
- Klinger RC, Musick JA (1995) Age and growth of loggerhead turtles (*Caretta caretta*) from Chesapeake Bay. *Copeia* 1995:204–209
- Limpus CJ, Limpus DJ (2003) Biology of the loggerhead turtle in western South Pacific Ocean foraging areas. In: Bolten AB, Witherington BE (eds) *Loggerhead sea turtles*, 1st edn. Smithsonian Institution, Washington, DC, p 63–78
- Mansfield KL, Saba VS, Keinath JA, Musick JA (2009) Satellite tracking reveals a dichotomy in migration strategies among juvenile loggerhead turtles in the Northwest Atlantic. *Mar Biol* 156:2555–2570
- Marcovaldi MA, Chaloupka M (2007) Conservation status of the loggerhead sea turtle in Brazil: an encouraging outlook. *Endang Species Res* 3:133–143
- Martinez-Souza G (2009). *Ecologia alimentar da tartaruga marinha cabeçuda (Caretta caretta) no oceano Atlântico Sul Ocidental, Uruguai*. MSc dissertation, Universidade Federal do Rio Grande
- McCarthy MA (2007) Bayesian methods for ecology. Cambridge University Press, Cambridge
- McClellan CM, Read AJ (2007) Complexity and variation in loggerhead sea turtle life history. *Biol Lett* 3:592–594
- Milton SL, Lutz PL (2003) Physiological and genetic responses to environment stress. In: Lutz PL, Musick JA, Wyneken J (eds) *The biology of sea turtles*, Vol 2. CRC Press, Boca Raton, FL, p 163–197
- Monteiro DS, Bugoni L, Estima SC (2006) Strandings and sea turtle fisheries interactions along the coast of Rio Grande do Sul State, Brazil. In: Book of abstracts. Twenty-sixth annual symposium on sea turtle biology and conservation, 3–8 April 2006, Island of Crete. International Sea Turtle Society, Athens, p 257 (Abstract)
- Moon DY, Mackenzie DS, Owens DW (1997) Simulated hibernation of sea turtles in the laboratory. I. Feeding, breathing frequency, blood pH, and blood gases. *J Exp Zool* 278:372–380
- Musick JA, Limpus CJ (1996) Habitat utilization and migration in juvenile sea turtles. In: Lutz PL, Musick JA (eds) *The biology of sea turtles*. CRC Press, New York, NY, p 137–163
- Parham JF, Zug JR (1997) Age and growth of loggerhead sea turtles of coastal Georgia: an assessment of skeletochronological age-estimates. *Bull Mar Sci* 61:287–304
- R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org
- Read MA, Grigg GC, Limpus CJ (1996) Body temperature and winter feeding in immature green turtles, *Chelonia mydas*, in Moreton Bay, southeastern Queensland. *J Herpetol* 30:262–265
- Reis EC, Soares LS, Vargas SM, Santos FR and others (2010) Genetic composition, population structure and phylogeography of the loggerhead sea turtle: colonization hypothesis for the Brazilian rookeries. *Conserv Genet* 11:1467–1477
- Reisser J, Proietti M, Kinas PG (2008) Photographic identification of sea turtles: method description and validation, with an estimation of tag loss. *Endang Species Res* 5:73–82
- Revelles M, Camiñas JA, Cardona L, Parga M and others (2008) Tagging reveals limited exchange of immature loggerhead sea turtles (*Caretta caretta*) between regions in the western Mediterranean. *Sci Mar* 72:511–518
- Schnute J (1981) A versatile growth model with statistically stable parameters. *Can J Fish Aquat Sci* 38:1128–1140
- Schofield G, Bishop CM, Katselidis KA, Dimopoulos P, Pantis JD, Hays GC (2009) Microhabitat selection by sea turtles in a dynamic thermal environment. *J Anim Ecol* 78:14–21
- Schwartz FJ (1978) Behavioral and tolerance response to cold water temperatures by three species of sea turtle (Reptilia: Cheloniidae) in North Carolina. In: Henderson GE (ed) *Proc Fl Interegion Conf Sea Turtle* 24–25 July 1976. Jensen Beach, FL. *Mar Res Publ* 33:16–18
- Smedstad OM, Holm JC (1996) Validation of back-calculation formulae for cod otoliths. *J Fish Biol* 49:973–985
- Snover ML (2002) Growth and ontogeny of sea turtles using skeletochronology: methods, validation and application to conservation. PhD dissertation, Duke University, Durham
- Snover ML, Hohn AA (2004) Validation and interpretation of annual skeletal marks in loggerhead (*Caretta caretta*) and Kemp's ridley (*Lepidochelys kempii*) sea turtles. *Fish Res* 102:682–692
- Snover ML, Avens L, Hohn AA (2007) Back-calculating length from skeletal growth marks in loggerhead sea turtles *Caretta caretta*. *Endang Species Res* 3:95–104
- Spiegelhalter DJ, Best NJ, Carlin BP, van der Linde A (2002) Bayesian measure of model complexity and fit. *J R Stat Soc B Stat Methodol* 64:583–639
- Thomas A, O'Hara B, Ligges U, Sturtz S (2006) Making BUGS open. *R News* 6(1):12–17

- Zug GR, Wynn AH, Ruckdeschel CA (1986) Age determination of loggerhead sea turtle, *Caretta caretta*, by incremental growth marks in the skeleton. *Smithson Contrib Zool* 427:1–34
- Zug GR, Balazs GH, Wetherall JA (1995) Growth in juvenile loggerhead sea turtles (*Caretta caretta*) in the North Pacific pelagic habitat. *Copeia* 1995:484–487
- Zug GR, Kalb HJ, Luzar SJ (1997) Age and growth in wild Kemp's ridley sea turtles *Lepidochelys kempii* from skeletochronological data. *Biol Conserv* 80:261–268
- Zug GR, Balazs GH, Wetherall JA, Parker DM, Murakawa SKK (2002) Age and growth of Hawaiian green sea turtles (*Chelonia mydas*): an analysis based on skeletochronology. *Fish Bull* 100:117–127
- Zug GR, Chaloupka M, Balazs GH (2006) Age and growth in olive ridley seaturtles (*Lepidochelys olivacea*) from the North-central Pacific: a skeletochronological analysis. *Mar Ecol* 27:263–270

Editorial responsibility: Hans-Heinrich Janssen, Oldendorf/Luhe, Germany

*Submitted: February 18, 2011; Accepted: February 17, 2012
Proofs received from author(s): May 25, 2012*