

Age and growth of juvenile green turtles *Chelonia mydas* in the western South Atlantic Ocean

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ABSTRACT: The green turtle *Chelonia mydas* has a circumtropical distribution and is globally endangered. This long-lived, migratory turtle has a spatially complex life cycle that encompasses initial development in oceanic habitat, with subsequent recruitment to neritic habitat. In the coastal waters of the western South Atlantic Ocean, juvenile green turtles are a notable component of the marine megafauna. As a result of incidental capture and other anthropogenic causes, dead specimens are commonly found stranded on beaches. Knowledge of age and growth is critical to understanding population life history and dynamics, as well as for conservation planning. We applied skeletochronology to estimate age and growth rates for green turtles stranded throughout 16 yr (1994 to 2010) in southern Brazil. Curved carapace length (CCL) ranged from 31 to 61 cm (mean = 41 cm) and estimated ages from 2 to 13 yr (mean = 5 yr, mode = 3 yr). Green turtles recruit to the neritic environment in this area around 30 cm CCL and aged 2 to 3 yr, remaining in this region until reaching about 50 cm and 7 yr. The mean growth rate of the whole sample was 3.7 cm CCL yr⁻¹, and both age and size had a significant influence on growth.

KEY WORDS: Skeletochronology · Growth rates · Recruitment · Sea turtle

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INTRODUCTION

The somatic growth rate of an animal, including changes in growth rate throughout life, is an important element for better understanding the demography and life history patterns of different species (Bjorndal & Bolten 1988). While growth and age data can be directly acquired for many organisms, this information is not readily available for most sea turtle populations due to their long life span and extensive migrations, and the difficulty in performing direct observations in the marine environment (Zug & Glor 1998). As a result, dead stranded sea turtles may become a valuable source of information through skeletochronological analysis, as first suggested by

Zug et al. (1986). With this technique, it is possible to rapidly and widely access a population's age and growth parameters through analysis of growth marks deposited in bones as animals grow and age (Avens & Snover 2013).

In the western South Atlantic Ocean, along the southern coast of Brazil (south of 25°S), there are no sea turtle rookeries, but the region is used regularly by leatherbacks, loggerheads and green sea turtles as an important feeding area, at least during some portion of their lives (Di-Bernardo et al. 2003, Barata et al. 2004, Lenz et al. 2016). Juvenile green turtles *Chelonia mydas* are commonly found stranded, or washed ashore debilitated or dead, along the 600 km of sandy beaches along the southernmost coast of Brazil

(Bugoni et al. 2001). The cause of death of such animals seems to be related to the ingestion of anthropogenic residues and interaction with coastal fisheries (Bugoni et al. 2001, Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul unpubl. data).

The green turtle is a typically nektonic, migratory and solitary animal, which may aggregate in feeding and breeding areas (Márquez 1990). It has a circum-tropical distribution, mainly concentrated within the 40° N and 40° S latitudes, and is globally Endangered (Hirth 1997, Seminoff 2004). The global population is genetically structured, and different rookeries and feeding grounds may retain distinct genetic composition, biological characteristics and conservation status (Bowen & Karl 2007). Its life cycle is characterized by an initial development in the pelagic zone, followed by later development in the neritic zone (Bolten 2003), where it performs periodic migrations between feeding and breeding habitats.

Although age and growth data are needed to better understand sea turtle population trends and the potential impacts of management actions, this information is not readily available through direct observation, and as a result, indirect methods of study are needed. Skeletochronological analysis, or analysis of skeletal growth marks, has been applied to numerous turtle species and has provided a better understanding of growth patterns and age distributions (reviewed by Avens & Snover 2013). Deposition of annual lines of arrested growth (LAGs) of green turtles has been validated by oxytetracycline marking (Snover et al. 2011, Goshe et al. 2016), mark-recapture (Goshe et al. 2010, Avens et al. 2012) and on individuals with known ages (Goshe et al. 2010). In addition, the positive relationship between bone growth and somatic growth has been demonstrated in green turtles of the western North Atlantic (Goshe et al. 2010, 2016, Avens et al. 2012). Apart from yielding age estimates, skeletochronology also yields growth rates for multiple years, as each growth mark represents an annual cycle (Goshe et al. 2010). Available data indicate that green turtle growth rates differ among populations in the North Atlantic and Pacific, being higher in the Atlantic (Bjørndal et al. 2000). Mean growth rates of green turtles from the western North Atlantic varied from 3 to 5 cm yr⁻¹ after their transition to the neritic habitat (Zug & Glor 1998). Another variable aspect among green turtle populations is the age and size at which juveniles recruit to the neritic environment, which occurs between 3 and 9 yr and at carapace length from 25 to 35 cm, but seems to occur earlier in the turtles inhabiting the western North Atlantic (Zug & Glor 1998, Zug et al. 2002, Reich et al. 2007).

Despite the need for green sea turtle age and growth data, this information is lacking or still poorly addressed for a number of areas, including the western South Atlantic, where the species suffers with increasing levels of incidental capture and marine pollution. In this study, we estimate the recruitment age to neritic environments, the age structure and the somatic growth rates of juvenile green turtles found on the southern coast of Brazil. This region is influenced by the Brazil–Malvinas Confluence Zone (Subtropical Convergence of the Southwestern Atlantic), an oceanographic complex area, characterized by high biological productivity and strong anthropogenic pressure posed by industrial fisheries and continental pollution. Our results expand the knowledge of green turtle life history in the South Atlantic, allowing for comparisons with other areas, besides supporting better local and global conservation strategies for this threatened species.

MATERIALS AND METHODS

Sample collection

Humerus bones for skeletochronological analysis were collected along the northern coast of the State of Rio Grande do Sul, in the extreme south of Brazil (Fig. 1), in an area covering 270 km of sandy beaches between Lagoa do Peixe, Mostardas municipality (31° 22' S, 51° 02' W), and Mampituba River, Torres municipality (29° 19' S, 49° 43' W). Collection was made possible through a partnership between the Universidade Federal do Rio Grande do Sul (UFRGS) and the Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul (GEMARS). Between 1994 and 2010, 188 green turtles stranded dead in these areas; each was measured (curved carapace length, CCL) and the humerus was collected. The humeri of 70 of these turtles were selected, macerated in water to remove the soft tissues, then dried and stored. Values for CCL and humerus section diameters are presented throughout the text as means ± SD.

Skeletochronology

Humeri were prepared for the growth mark analysis following Snover & Hohn (2004). A 3–5 mm transverse section was removed from the humerus, distal to the deltopectoral crest using a manual hacksaw. Each section was decalcified using a commercial decalcifier solution (RDO, Apex Engineering Prod-



Fig. 1. Study area on the northern coast of the State of Rio Grande do Sul, Brazil. The humerus samples of green turtles stranded dead were collected in the 270 km of sandy beaches (black line) between Lagoa do Peixe and Mampituba River (squares)

ucts Corporation) for 6 to 12 h, depending on the size of the cross-section. Following decalcification, sections were maintained in water overnight, then thin sections were cut with a cryostat (Leica CM 1850) at 25 μ m thickness and approximately -12°C . These were stained with Ehrlich's hematoxylin diluted with distilled water (1:1) and mounted on microscope slides in 100% glycerin.

Identification, counting and measurements of LAGs that demarcate the outer edges of individual skeletal growth marks were based on Goshe et al. (2010). Each section was photographed (Leica DFC 290HD camera, software Leica Application Suite [LAS] version 3.4.1) in sequential portions with a light microscope (Leica DM750) or stereomicroscope (Leica S6D). The partial images were then merged to yield high-resolution mosaics (Fig. 2). Identification, counting and measurement of LAGs was performed using these mosaics.

Each section was analyzed independently by 2 readers (A.J.L. and L.A.) to obtain consensus regarding the position and number of LAGs. The diameter of each LAG and diameter of the whole humerus section were measured with the software ImageJ 1.46 (Research Services Branch, National Institute of Mental Health, Bethesda, MD, USA). LAGs were numbered sequentially starting from the innermost LAG and continuing to the outer edge of the humerus section (Fig. 2). LAGs were interpreted according to Castanet & Smirina (1990) and Snover & Hohn (2004). Each LAG was examined around the

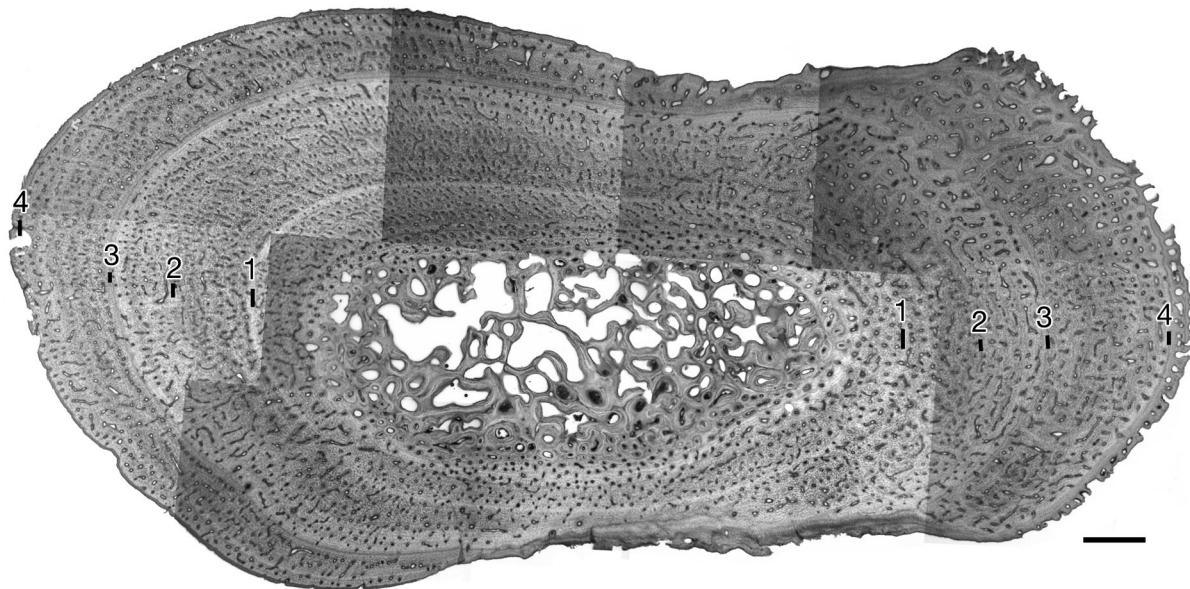


Fig. 2. Mosaic assembled from sequential photographs of a humerus section of green turtles. Lines of arrested growth (LAGs) are marked with black lines with their respective numbers. Line 1 represents the annulus. Scale bar: 1 mm

entire circumference of the bone section for validation. When a LAG divided into 2 or more lines, each line was counted as 1 independent skeletal growth mark (Snover & Hohn 2004).

Age estimation

As LAGs are deposited concentrically, older LAGs are observed near the medullary region, while recent LAGs are visualized near the outer margin of the bone (Zug et al. 1986). In decalcified and stained sections, bone growth marks appear as wide zones of light coloration followed by darker growth lines defined as LAGs (Goshe et al. 2010). A diffuse annulus has been recorded in the first year of life of some species of sea turtles, with well-defined LAGs starting at the end of the second year and in the following years (Snover & Hohn 2004, Goshe et al. 2010, Avens et al. 2012, 2013). Therefore, for the turtles that retained the annulus, age is equal to the number of LAGs recorded.

On the periphery of the medullary cavity, at the core of the humerus bone, resorption due to bone remodeling can completely eliminate some LAGs deposited during the first years of life, leading to underestimation of individual age if only direct LAG counts are used (Castanet & Smirina 1990). The absence of the annulus was regarded as a sign of resorption; therefore, it was necessary to estimate the number of lost LAGs. Turtles that retained the annulus were used to develop a correction factor that allowed estimation of the number of lost LAGs in turtles that exhibited resorption (Goshe et al. 2010, Avens et al. 2012). The diameter of each LAG was plotted against the corresponding LAG number, and regression models were tested to determine the relationship that best describes the data, according to Goshe et al. (2010), with the best-fitting model chosen based on r^2 values. To estimate the number of lost LAGs, the diameter of the LAG in the model's equation was replaced by the diameter of the innermost LAG of the turtle that showed resorption. To obtain the individual's age, the estimated number of resorbed LAGs was added to the number of observed LAGs.

Back-calculation and growth rates

The spacing between successive LAGs is not constant throughout life, but reveals the variation of bone and body growth and is a record of individual growth curves over time (Castanet & Smirina 1990). Through

analysis of humeri of loggerhead and green turtles that had been tagged and measured some time prior to stranding, it has been demonstrated that the diameter of LAGs can be converted into estimates of carapace length, representing the size of the turtle at the time a given LAG was deposited (Snover et al. 2007, Goshe et al. 2010, 2016, Avens et al. 2012). To enable prediction of CCL from LAG diameters, the relationship between CCL and the diameter of the humerus section was modeled using the following nonlinear equation, according to Snover et al. (2007):

$$\text{CCL} = \text{CCL}_h + b(D - D_h)^c \quad (1)$$

where CCL is the curved carapace length of the individual; CCL_h is the CCL of the hatchling; D is the diameter of the humerus section; D_h is the diameter of the humerus section of the hatchling; b is an angular coefficient; and c is a proportionality coefficient. Values of CCL_h and D_h were obtained from green turtles from the North Atlantic, as no data are available for Brazilian populations ($\text{CCL}_h = 5.2$ cm, NOAA Beaufort Laboratory, unpubl. data; $D_h = 2.47$ mm, Goshe et al. 2010).

After applying Eq. (1) to obtain the values of b and c , it is possible to apply the back-calculation model below to estimate the individual's CCL for each LAG, that is, for each year of life. This model is known as the body proportional hypothesis (BPH) and was developed by Francis (1990) and adapted for use with sea turtles by Snover et al. (2007):

$$\text{CCL}_{\text{est}} = [f(D_{\text{lag}})] \times [\text{CCL}_{\text{final}}] \times [f(D_{\text{final}})] \quad (2)$$

where CCL_{est} is the estimated CCL; $f(D_{\text{lag}})$ is Eq. (1) applied to the diameter of the specific LAG; $\text{CCL}_{\text{final}}$ is the CCL of the turtle at the time of death; and $f(D_{\text{final}})$ is Eq. (1) applied for the humerus diameter at the time of death.

After obtaining the estimated CCL of the individual for each LAG, it was possible to determine annual growth rates by calculating the difference between adjacent pairs of CCL estimates (Avens et al. 2012, 2013, Goshe et al. 2016). Individual growth values were grouped according to age and estimated CCL (10 cm CCL size classes), and mean growth rates for each size class were calculated. To be able to compare data from the present study with data from other published papers, which present straight carapace length (SCL), conversion from CCL to SCL was conducted using Eq. (3) derived for green turtles from the US Atlantic coast (Goshe et al. 2010) and Gulf of Mexico (Avens et al. 2012). The descriptive information for the turtles on which the dataset is based is as follows: SCL mean = 36.2 ± 11.7 cm (range = 14.8 –

101.4 cm, n = 602), CCL mean = 38.0 ± 12.5 cm (range = 16.7–107.4 cm, n = 602, $r^2 = 0.99$):

$$\text{CCL} = 1.064 \times \text{SCL} - 0.4579 \quad (3)$$

Each back-calculated growth rate was assigned to the mean carapace length (CCL) calculated for the growth interval, as well as the age estimate and calendar year assigned to the initial LAG for the LAG pair used to calculate the growth rate. To account for incorporation of multiple annual growth intervals from each turtle and potential non-linear relationships, generalized additive mixed models (GAMMs) were applied to investigate the potential influence of continuous covariates such as size (CCL), age and year on somatic growth response. The GAMMs included turtle ID as a random, individual-specific effect, incorporated an identity link and robust quasi-likelihood function, and were implemented using the *mgcv* and *nlme* packages in the statistical program R version 3.1.1 (Wood 2006, R Core Team 2014). Significance of continuous covariates was determined using non-parametric *F*-ratio tests. Because high concavity was found between CCL and age (0.75), it was necessary to incorporate these variables into separate models ($\text{GAMM}_{\text{CCL}+\text{Year}}$ and $\text{GAMM}_{\text{Age}+\text{Year}}$). Stepwise removal of covariates in subsequent model runs was conducted and model fits were evaluated using Akaike's information criterion (AIC) values.

RESULTS

Age estimation

The CCL of green turtles stranded along the southern coast of Brazil between 1994 and 2010 ranged from 29 to 74.5 cm (mean = 39.2 ± 5.7 cm, n = 188). The size distribution of the subsample (mean CCL =

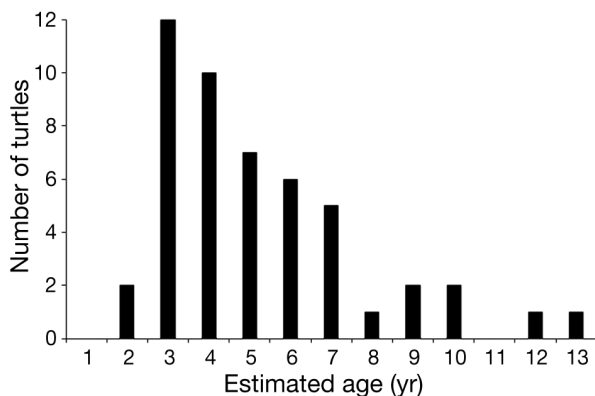


Fig. 3. Age distribution of the green turtles from the southern coast of Brazil, estimated by skeletochronology (n = 49)

41 ± 5.8 cm, range = 30.6–62 cm, n = 70) did not differ statistically from the entire sample (Kolmogorov-Smirnov = 0.156; p = 0.169). Out of the total sample of 70 humeri, it was possible to estimate age for 49 individuals; 21 humerus sections were discarded due to problems during processing or difficulties with identifying LAGs. Age estimates ranged from 2 to 13 yr (mean = 5 yr; Fig. 3). There was a positive relationship between carapace length and age ($r^2 = 0.47$, p < 0.0001; Fig. 4). Among the analyzed humeri, 42 retained the annulus, which represents the end of the first year of growth. These individuals ranged in size from 30.6 to 57.3 cm CCL and retained 2 to 8 LAGs. For these individuals, the number of LAGs is equal to their age. The relationship between LAG diameter and LAG number for the turtles that retained the annulus (Fig. 5) was best characterized by the following equation ($r^2 = 0.77$, n = 169 LAGs):

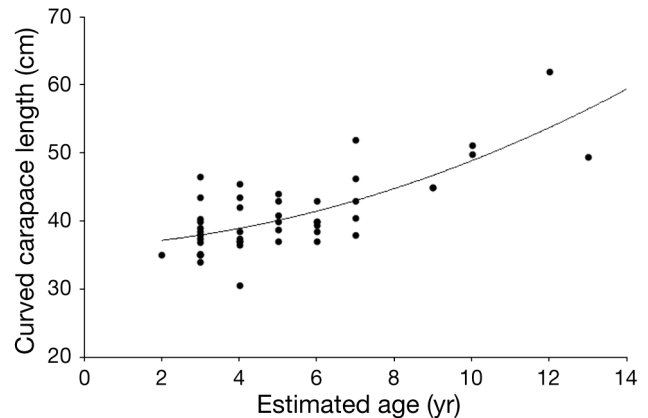


Fig. 4. Relationship between curved carapace length and estimated age for green turtles on the southern coast of Brazil ($r^2 = 0.55$, p < 0.0001, n = 49). The solid line represents the polynomial equation

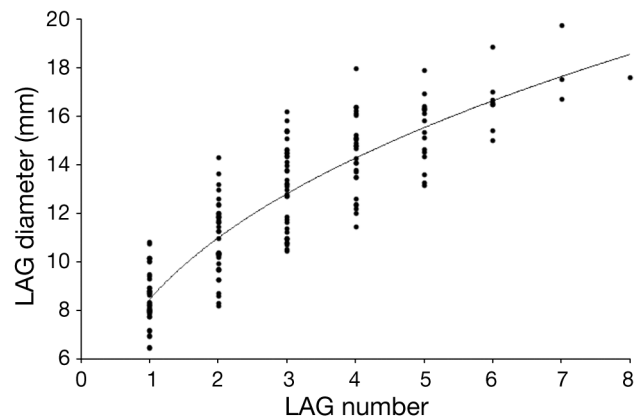


Fig. 5. Relationship between diameter and number of lines of arrested growth (LAGs) of green turtles from the southern coast of Brazil that retained the annulus ($r^2 = 0.77$, n = 169 LAGs)

$$\text{LAG diameter} = 8.4972 \times (\text{LAG number})^{0.3757} \quad (4)$$

This equation enabled us to estimate the number of LAGs lost due to bone reabsorption for individuals that did not retain the annulus by substituting the inner measurable LAG diameter in the equation as a proxy for resorption core diameter. The age estimated for individuals that did not retain the annulus ranged between 7 and 13 yr, while the CCL ranged from 38 to 62 cm (mean = 48.1 cm).

Back-calculation and growth rates

The diameter of each LAG was used to back-calculate CCL for each year of life. Application of the model described by Eq. (1) for 70 pairs of CCLs and diameters yielded values for the parameters *b* and *c* of 3.012 and 0.922, respectively. Next, a CCL back-calculation was performed for the diameter of each LAG using Eq. (2). Annulus diameter ranged from 6.47 to 10.83 mm (mean = 8.57 ± 1.14 mm). Back-calculation of CCL corresponding to the diameter of

the annulus indicated that turtles attained 22.2 cm (±2.73 cm) in the first year of life.

Growth rates were back-calculated for 43 turtles from 155 annual growth increments and were then grouped by size class and age (Tables 1 & 2). It was not possible to calculate growth rates for all individuals, because 2 estimated sequential carapace lengths are required to calculate an annual rate, which was not available for all turtles or years. The mean somatic annual growth rate for the entire sample was 3.7 cm CCL yr⁻¹. Results of GAMM analysis indicated that the model that best fit the data incorporated only age, followed by the model that incorporated only CCL, but each covariate had a significant influence on growth response (Table 3). Individual, random effects were also significant (log-likelihood ratio test

Table 1. Growth rates by size class obtained by back-calculation of the curved carapace length (CCL) from humerus diameters (n = 155 growth intervals) for 44 green turtles from the southern coast of Brazil. n: sample size (no. of growth intervals)

Size class (CCL, cm)	n	Mean growth rate (cm yr ⁻¹)	SD	Minimum	Maximum
20–29.9	37	4.43	2.22	0.84	11.24
30–39.9	82	3.89	2.54	0.007	10.67
40–49.9	33	2.82	1.75	0.45	7.65
50–59.9	3	3.03	1.8	1.5	5.02

Table 2. Growth rates by age obtained from the curved carapace length (CCL) back-calculation from humerus diameters (n = 155 growth intervals) of 44 green turtles from the southern coast of Brazil. n: sample size (no. of growth intervals)

Estimated age (yr)	n	Mean growth rate (cm yr ⁻¹)	SD	Minimum	Maximum
2	32	5.66	2.15	2.17	11.24
3	33	4.59	2.27	0.84	9.74
4	27	3.62	2.26	0.06	7.65
5	19	2.72	1.74	0.08	5.85
6	14	2.89	1.45	0.45	5.02
7	10	2.17	2.10	0.10	6.63
8	6	1.70	0.90	0.47	3.24
9	6	1.23	0.71	0.10	2.23
10	3	2.60	0.70	1.86	3.26
11	2	2.59	0.0001	2.58	2.6
12	2	3.21	2.55	1.41	5.02
13	1	1.89	–	–	–

Table 3. Statistical output from generalized additive mixed models (GAMMs) used to investigate the potential influence of different covariates on growth response of green turtles from southern coast of Brazil. Edf: estimated degrees of freedom; CCL: curved carapace length; Year: calendar year

Model	Adjusted r ²	AIC	Smooth terms				Parametric coefficients				
			Variable	Edf	F	Prob(F)	Variable	Estimate	SE	t	Prob(t)
GAMM _{CCL+Year} (n = 155)	0.17	699	CCL (cm)	4.33	6.91	<0.001	Intercept	3.81	0.18	20.77	<0.001
			Year	1.00	0.92	0.34					
GAMM _{CCL} (n = 155)	0.17	696	CCL (cm)	4.34	6.78	<0.001	Intercept	3.83	0.19	20.2	<0.001
GAMM _{Age+Year} (n = 155)	0.29	670	Age (yr)	2.53	24.67	<0.001	Intercept	3.77	0.16	23.75	<0.001
			Year	1.00	0.86	0.36					
GAMM _{Age} (n = 155)	0.29	667	Age (yr)	2.55	24.98	<0.001	Intercept	3.77	0.16	23.69	<0.001

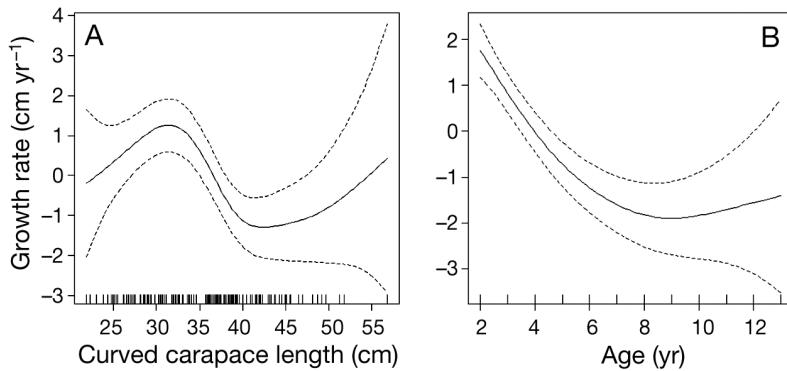


Fig. 6. Summary of generalized additive mixed model (GAMM) growth response relative to the potential covariates (A) curved carapace length (CCL) and (B) age of green turtles from southern coast of Brazil. Within each plot, the solid line represents mean growth response (on a scale centered around 0) for the covariate conditioned on other covariates included in the model and dashed lines represent the extent of the 95% Bayesian credible interval. Short, vertical lines above the horizontal axis (rug plot) signify the distributions of covariate values

$p < 0.001$). Growth response relative to CCL was variable, increasing overall through approximately 32 cm CCL, subsequently decreasing, and beginning to increase again around 42 cm CCL, although confidence intervals became very wide at this point, limiting interpretation of the trend (Fig. 6A). In contrast, growth response decreased from ages 2 to 9 yr, after which it began to increase slightly; however, again, the breadth of the confidence interval limits interpretation (Fig. 6B).

DISCUSSION

Age estimation

This study describes the age structure and growth rates of juvenile green turtles in the western South Atlantic Ocean. It is worth noting that 81% of the green turtles' humeri retained the annulus, a diffuse LAG that represents the end of the first year of growth (Snover & Hohn 2004). For these individuals, age is equivalent to the number of LAGs observed, which increased accuracy of age estimates and allowed development of a robust correction factor to compensate for LAG resorption for those humeri in which an annulus was not observed. The power equation that best described the relationship between LAG number and diameter (Eq. 4) is similar to the one found by Goshe et al. (2010) for sea turtles on the east coast of the USA.

Genetic data indicated that Ascension (British Overseas Territory), Aves (Surinam) and Trindade

(Brazil) green turtle rookeries are the main contributors to the feeding area stocks inhabiting the western South Atlantic (Proietti et al. 2012). Considering the minimum size of female green turtles nesting at Trindade Island (90 cm CCL; Almeida et al. 2011), all green turtles recorded at the study area were juveniles. Most (77%) green turtles found stranded in southern Brazil were estimated to be between 3 and 7 yr old (Fig. 3). After hatching, turtles go to the sea and remain in the pelagic environment for a variable time span, after which they recruit to neritic habitats in temperate or tropical zones (Musick & Limpus 1997). Little is known about the oceanic juvenile stage of life, which is generically characterized as the 'lost years' (Bolten 2003). It can be

inferred that the smaller green turtles found in southern Brazil are in a stage of recruitment from the pelagic to the neritic environment, which seems to occur between the ages of 2 and 7 yr and at around 30–40 cm of length. These data indicate that, in the western South Atlantic, the 'lost years' for green turtles comprise at least 2 yr. The recruitment age identified in this study is comparable to those reported from study areas in the western North Atlantic such as central Florida (3–6 yr; Zug & Glor 1998), the Bahamas (3–5 yr; Reich et al. 2007) and the east coast of the USA (1–7 yr; Goshe et al. 2010). However, in the Pacific, it seems that green turtles recruit to the neritic environment at a larger size (35–37 cm) and a little later (6–9 yr) than those in the Atlantic (Zug et al. 2002).

The minimum recruitment size in southern Brazil (~30 cm CCL or 28.6 cm SCL) is slightly larger than that identified in the North Atlantic (minimum 18.1 cm SCL; Avens et al. 2012). Although recruitment in the North Atlantic may occur when individuals are at least 18 cm SCL, most individuals recruit to neritic waters at greater than 30 cm SCL (Zug & Glor 1998), which corresponds to the size of specimens found in southern Brazil. Juvenile green turtles less than 50 cm CCL found in neritic environments off the south coast of Brazil, Uruguay and Argentina are omnivorous, in transition between a carnivorous and herbivorous diet (Bugoni et al. 2003, Carman et al. 2012, Vélez-Rubio et al. 2016). In these areas, green turtles larger than 45 cm CCL exhibit a gradual increase in the occurrence of macroalgae in their diet with increasing size (Vélez-Rubio et al. 2016). These

data confirm that individuals found in southern Brazil are in the recruitment stage, making a gradual habitat and diet transition.

The green turtles occurring in the study area have a narrow size range, with 94% measuring between 29 and 50 cm CCL, indicating that this area is a temporary development habitat mainly used by green turtles between 3 and 7 yr of age. Telemetry and stable isotope analysis revealed that green turtles smaller than 50 cm CCL move between Uruguayan, Argentine and south Brazilian waters (Carman et al. 2012, Vélez-Rubio et al. 2016). We can hypothesize that after recruiting to the neritic environments off the south coast of Brazil, juvenile green turtles inhabit these areas for some years, making these seasonal migrations, and moving definitively to northern areas of development in Brazil after reaching about 50 cm and at around 7 yr of age. Along the Brazilian coast there are records of juveniles in feeding areas with a larger size range than reported here (state of Santa Catarina: mean CCL = 49.9 cm, range 32–83 cm, Reisser et al. 2013; state of São Paulo: mean CCL = 40.6 cm, range 27–96 cm, Gallo et al. 2006; state of Paraíba: mean CCL = 56.5 cm, range 26 cm up to adults, Mascarenhas et al. 2005; Fernando de Noronha: mean CCL = 49.4 cm, range 32.5–60 cm, Bellini & Sanches 1996).

Growth

The size reached by the green turtles in their first year of life in the South Atlantic Ocean, as inferred from back-calculation (22.2 ± 2.7 cm), indicates fast growth during this period. Studies of captive green turtles demonstrate that individuals 8 mo old can reach up to 23 cm CCL (Wood & Wood 1993). Growth rates of captive specimens are higher than those of wild specimens (Zug & Glor 1998), but these observations verify that this species is able to grow larger than 20 cm before reaching 1 yr of age.

Among the growth rates already reported for the 20–29 cm size class (Table 4), those measured for green turtles in southern Brazil are among the highest (mean 4.3 cm yr⁻¹). Boulon & Frazer (1990) reported a higher somatic growth rate (6.9 cm yr⁻¹) for this size class from Caribbean green turtles, but

with a sample size of only 4. Zug et al. (2002) reported 4.4 cm yr⁻¹ ($n = 9$) for this size class in Hawaiian green turtles, similar to our results. The 20–29 cm size range in the western South Atlantic is represented by turtles that are either still in the pelagic stage or initiating recruitment to the neritic environment, during which time they still exhibit a carnivorous diet, which could explain the higher growth rates. The oceanic zone of southern Brazil has a high biological productivity due to interactions between the oligotrophic Brazil Current and the Malvinas Current, with nutrient-rich waters and continental discharge (Seeliger & Odebrecht 1998) which may favor juvenile growth at this stage of life. Furthermore, predation is the primary source of small-sized turtle mortality in the pelagic environment, which leads to increased energetic input toward somatic growth to achieve safer sizes as quickly as possible (Snover et al. 2007).

Green turtles of the western North Atlantic commonly exhibit mean somatic growth rates of 3–5 cm yr⁻¹ after entering neritic habitats (Zug & Glor 1998). In the Pacific, some studies reported low growth rates for the 40–49 cm class (0.4 cm yr⁻¹, Green 1993; 0.8 – 1.6 cm yr⁻¹, Sampson et al. 2015), while Zug et al. (2002) reported higher growth rates for Hawaiian green turtles. The growth rates recorded in this study are within the general pattern found in the western Atlantic (3.7 cm yr⁻¹). Several green turtle populations in the Atlantic and the Pacific show a non-monotonic somatic growth, with rates increasing until 50–70 cm and subsequently decreasing (e.g. Limpus & Chaloupka 1997, Balazs & Chaloupka 2004, Kubis et al. 2009, Avens et al. 2012, Sampson et al. 2015). In this study we were not able to evaluate

Table 4. Comparison of size-class-specific growth rates (straight carapace length [SCL], cm yr⁻¹) of Atlantic populations of green turtles. Growth rates were obtained by skeletochronology or mark-recapture. Only size classes (in cm) analyzed in this study were included. Values in parentheses are no. of growth intervals

Population	Mean growth rate per size class			
	20–29.9	30–39.9	40–49.9	50–59.9
Skeletochronology				
Southern Brazil (present study)	4.3 (45)	3.5 (85)	2.5 (24)	4.7 (1)
Gulf of Mexico (Avens et al. 2012)	3.1 (145)	3.5 (207)	4 (158)	3.7 (89)
Florida (Zug & Glor 1998)	3.1 (23)	4.4 (70)	4.8 (68)	5.3 (40)
East US Coast (Goshe et al. 2010)	3 (118)	2.1 (93)	2.5 (54)	2.7 (34)
Mark-recapture				
Bahamas (Bjorndal & Bolten 1988)	–	8.8 (10)	4.9 (40)	3.1 (67)
Virgin Islands (Boulon & Frazer 1990)	6.9 (4)	5 (26)	4.7 (12)	3.5 (5)
Florida (Kubis et al. 2009)	1.8 (50)	2.3 (168)	1.6 (44)	–
Florida (Kubis et al. 2009)	1.2 (16)	2.1 (119)	2.5 (112)	2.6 (35)

size classes larger than 60 cm and sample size was small for the 50–59 cm category. Thus, we can only make inferences for the better-sampled size classes (20–49 cm), which appear to show a non-monotonic growth decline with an increase overall through approximately 32 cm CCL, subsequent decrease, and additional increase again at around 42 cm CCL.

In Brazil, only one other study presents growth rates of green turtles; Torezani et al. (2010) analyzed the growth rates of juveniles 27–47 cm in CCL measured through mark-recapture. The growth rates of individuals that were considered to be in good health ($n = 60$) were 3.11 and 2.91 cm yr⁻¹ (estimates yielded by 2 different methods; Torezani et al. 2010). This mark-recapture study was carried out in an area of green turtle aggregation at an effluent discharge canal for a steel industry from southeast Brazil, therefore representing unusual ecological conditions. Although comparisons should be made with caution, due to the unusual conditions experienced by that study population, we verify that the growth rates reported by Torezani et al. (2010) are similar to our results (30–39 cm = 3.93 cm yr⁻¹; 40–49 cm = 2.82 cm yr⁻¹).

As sea turtle age data are sparse, few studies present growth rates relative to the age of individual turtles. However, Zug & Glor (1998) demonstrated an increase in somatic growth between 3 and 6 yr of age for juvenile green turtles along the Florida coast in the southeast USA, relative constancy between 7 and 10 yr of age, and then a decline. Avens et al. (2012) also described the relationship between growth rates and age for juvenile green turtles in the northeastern Gulf of Mexico, reporting a tendency for growth rates to increase up to 11 yr of age and then subsequently decrease. In the present study, we observed declining growth rates between 2 and 9 yr of age and a small increase between 10 and 12 yr of age (Fig. 6B, Table 2). However, as only a small number of growth rates could be calculated for the age class between 10 and 13 yr, the confidence interval around the mean is broad and limits interpretation. A larger sample size for turtles ≥ 10 yr of age could enlighten this situation.

A remarkable aspect of sea turtle growth observed in the present study (see growth rate range of each age or size class in Tables 1 & 2) is the great individual variability within age and size classes. This variability could result from numerous biotic and abiotic factors and, as it was not possible to evaluate all of these potential covariates in the present study, this may have decreased the explanatory power of the GAMMs (Table 3). However, even for green turtles

raised in captivity, under the same conditions with a high proteic diet, growth rates vary greatly (Bjørndal et al. 2013). In a mixed genetic pool, as is the case for populations at feeding areas in southern Brazil (Proietti et al. 2012), immature green turtles of the same size and age may grow at different rates, even if sharing the same foraging area (Bjørndal et al. 2000).

Variation in growth rates may also be related to differences in food availability among foraging sites (Bjørndal et al. 2000, Kubis et al. 2009) and the quality of food (macroalgae or vascular plants). After recruiting to the neritic zone, green turtles become herbivorous, feeding mainly on macroalgae and marine monocotyledons (Bjørndal 1997). Juvenile green turtles found on the south coast of Brazil, Uruguay and Argentina are omnivorous, exhibiting a gradual increase in the occurrence of macroalgae in their diet, indicating a transition period from the young oceanic carnivorous diet to a neritic adult herbivorous diet (Bugoni et al. 2003, Carman et al. 2012, Vélez-Rubio et al. 2016). Despite exhibiting regional high marine productivity, only few sites with conditions suitable for macroalgal and monocotyledon development are found along a large area on the coast of Rio Grande do Sul and south Santa Catarina, in southern Brazil (Baptista 1977). Areas such as the coast of Florida, the Caribbean and the Bahamas offer a variety of herbivorous resources for turtles, following recruitment to neritic habitat (Bolten et al. 1992, Bjørndal et al. 2000, Kubis et al. 2009). The lack of resources in the Rio Grande do Sul coast may underlie the observed reduction in growth rates following recruitment and may also be an indication that green turtles only remain in this area for a short time because they cannot find sufficient food to sustain further development. Another factor that may be related to the decline in growth rates is the high level of plastic ingestion observed for green turtles in this area. Bugoni et al. (2001) reported plastic waste intake by 60% of the green turtles analyzed in the state of Rio Grande do Sul ($n = 38$). Vélez-Rubio et al. (2016) found marine debris in 51.9% of the stomach contents analyzed from the Uruguay coast ($n = 74$). However, this percentage may be even higher, reaching 90% of individuals according to a more recent study in Rio Grande do Sul coast (C. T. Rigon, unpubl. data). Although there is not much clear evidence that demonstrates the effects of plastic ingestion at a population level (Nelms et al. 2015), the ingestion of plastic debris may cause sublethal effects, decreasing the productivity (growth and reproduction) of turtles (Bjørndal 1997).

The results of the present study elucidate some aspects of the biology and life history of green turtles in the South Atlantic, identifying recruitment ages and growth rates of juveniles. We expect our findings to contribute to the development of better conservation strategies at both local and global levels. However, as knowledge of marine turtles in the South Atlantic is still scarce, much effort is still needed to comprehensively describe and understand the age and growth patterns in this region, especially in feeding areas. We emphasize the need for further studies to identify patterns of habitat use, seasonal movements, temporal variation in somatic growth rates and characterization of population sex ratio, to better characterize this population and facilitate management and conservation efforts.

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