

Age and growth of olive ridley sea turtles *Lepidochelys olivacea* in the main Brazilian nesting ground

Roberta Petitet^{1,2,*}, Larisa Avens³, Jaqueline C. Castilhos⁴, Paul G. Kinas⁵,
Leandro Bugoni¹

¹Laboratório de Aves Aquáticas e Tartarugas Marinhas, Instituto de Ciências Biológicas, Universidade Federal do Rio Grande (FURG), Campus Carreiros, Avenida Itália s/n, CP 474, 96203-900 Rio Grande, RS, Brazil

²Programa de Pós-Graduação em Oceanografia Biológica, Instituto de Oceanografia, Universidade Federal do Rio Grande (FURG), Campus Carreiros, Avenida Itália s/n, CP 474, 96203-900 Rio Grande, RS, Brazil

³Southeast Fisheries Science Center, Center for Coastal Fisheries and Habitat Research, NOAA National Marine Fisheries Service, 101 Pivers Island Road, Beaufort, NC 28516, USA

⁴Fundação Centro Brasileiro de Proteção e Pesquisa das Tartarugas Marinhas, Reserva Biológica de Santa Isabel s/n, Centro, 49190-000 Pirambu, SE, Brazil

⁵Laboratório de Estatística Ambiental, Instituto de Matemática, Estatística e Física, Universidade Federal do Rio Grande (FURG), CP 474, Avenida Itália s/n, CP 474, 96203-900 Rio Grande, RS, Brazil

ABSTRACT: Olive ridleys *Lepidochelys olivacea* are the most abundant sea turtles in the world, and their early life and adulthood offshore distributions make them less prone to anthropogenic coastal threats. However, primary use of oceanic habitat also results in olive ridley life history being the least studied of all sea turtle species. Here, age at maturation and growth rates of 68 olive ridleys washed ashore dead in northeastern Brazil were estimated through skeleto-chronological analysis of humerus bones. Turtles ranged from 58.0 to 77.0 cm in curved carapace length (CCL), with estimated ages between 14 and 26 yr old. As the sample comprised mostly adults, it was necessary to apply a correction factor from skeletochronological analysis of north-central Pacific olive ridley sea turtles to estimate the number of skeletal growth marks potentially lost at the bone's core. Mean age at sexual maturation was estimated to be 16 yr for a mean size at sexual maturation of 66.0 cm CCL. Growth models fit to the data showed a clear plateau of growth at 15 yr old, which likely coincides with the time when turtles begin directing energy toward reproduction instead of somatic growth. The olive ridley population in the study area is threatened in oceanic and neritic waters by longline and trawl fisheries, respectively. Despite this current threat, the number of nests has increased sharply for the past 16 yr, a time frame coincident with initiation of conservation actions on the beaches in 1982 and which corresponds with the mean age at maturity found in the current study.

KEY WORDS: Growth rate · Line of arrested growth · LAG · Life history · Maturation · Reptile · Skeletochronology · Skeletal growth mark

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Age and size are critical components of an animal's life history and key parameters to estimate somatic growth rates and age at maturation of a given popu-

lation (Bernardo 1993). Age at sexual maturation is one of the most significant data gaps in our knowledge of sea turtle demography (Bjorndal et al. 2013) and a parameter that must be estimated more rigorously to realistically infer extinction risks for sea tur-

tles (TEWG 2009). Generally, growth rate is related to age at sexual maturation for slow-growing animals; as the animal reaches maturity, growth rate starts to decrease over time, which reflects a switch in resource allocation to reproduction, rather than to somatic growth (Kozłowski 1992). Environmental conditions can also affect growth rates such that ectotherms from cold environments grow more slowly but reach larger sizes than at high temperatures (Kozłowski et al. 2004). Age determination, growth rates and particularly age-at-maturity data are essential parameters for population viability analysis (PVA). PVA uses measured or inferred life history data to predict the probability risk of extinction of a given population and project it forward using stochastic computer simulation for threatened species (Boyce 1992, Beissinger & Westphal 1998, Brook et al. 2000). The accuracy of parameters used in the models is a key aspect of precise PVA modeling (Brook et al. 2000).

Despite their importance, age and growth data are difficult to collect due to the complex pattern of migration exhibited by sea turtles throughout their life cycle, and therefore, many questions still remain. Although mark-recapture and captive growth studies can allow age and growth rate estimation, the former is related only to a short period of the overall sea turtle life cycle and the latter does not allow comparison with wild populations (Avens & Snover 2013, Bjørndal et al. 2013). Skeletochronological analysis is a type of age determination method involving skeletal growth mark counts, and in sea turtles, the method has been applied primarily to humerus bones and less often in scleral ossicles (Zug et al. 1986, Zug & Parham 1996). Furthermore, somatic growth rates can be estimated from each skeletal growth mark pair using the back-calculation method described by Snover et al. (2007a), enabling calculation of growth trajectories and consequently allowing detection of possible ontogenetic shifts based on growth rate oscillations (Snover et al. 2010).

Olive ridley sea turtles *Lepidochelys olivacea* spend most of their life cycle in oceanic waters, and are therefore classified as development type 3, oceanic developmental pattern (Bolten 2003). Olive ridley hatchlings emerge from nests, enter the sea, traverse the neritic zone and reach the oceanic zone where they spend their early and late juvenile stages until maturity (Reichert 1993). After maturation, this species recruits to the natal beaches to breed, followed by migration back to foraging grounds (Reichert 1993). This species displays 2 types of reproductive strategies: female turtles nest individually, and/or together in

groups comprising thousands of turtles (1000–500 000 animals), known as 'arribadas' (Plotkin 2007). Both solitary and arribada nesters typically have 2 clutches every nesting season, but the former has an interesting interval of 2 wk, while for the latter it seems to be 4 wk or more (Bernardo & Plotkin 2007).

Olive ridleys occur nearly circumglobally in tropical oceans (Reichert 1993). There are few studies of habitat use of juvenile olive ridleys, but in the Pacific Ocean, Polovina et al. (2004) demonstrated use of oceanic habitat from 15° to 26°N, with a water temperature regime between 23 and 28°C. In the western South Atlantic Ocean, off the northern Brazilian coast, Sales et al. (2008) reported that olive ridleys ranging from 35 to 80 cm in curved carapace length (CCL) were incidentally captured in the pelagic longline fishery mostly between 10°N and 10°S. Although this size range encompasses late juveniles and adult stages, most captured turtles were juveniles, based on the smaller size of olive ridleys nesting in Brazil (62.50 cm CCL) (Silva et al. 2007, Sales et al. 2008). This suggests that oceanic waters adjacent to northern Brazil are likely to be important habitats for juvenile olive ridleys (Sales et al. 2008). In contrast, adults in the same area seem to utilize both oceanic and neritic areas after the nesting season. Silva et al. (2011) demonstrated that post-nesting migrations of olive ridley occur in 3 different directions: while some individuals migrate to oceanic waters, others move to neritic waters northward or southward to feed. In Australia, French Guiana and Oman, following the nesting season, olive ridleys remain primarily in neritic areas and forage over the continental shelf (Whiting et al. 2007a, Rees et al. 2012, Plot et al. 2015). In contrast, in the eastern tropical Pacific Ocean, adults of this species seem to utilize more oceanic than neritic feeding grounds after nesting seasons (Plotkin 2010). Plot et al. (2015) proposed that these different patterns of post-nesting migration in olive ridley populations worldwide are due to environmental conditions in the areas adjacent to the reproductive sites.

In the South Atlantic Ocean, the largest nesting population of olive ridleys occurs in Gabon (Africa) followed by Suriname/French Guiana and Brazil, and smaller populations occur in Angola and the Republic of Congo (Metcalf et al. 2015). Within Brazil, Sergipe state in the northeast hosts the main nesting area for olive ridley sea turtles in the country, and the species is threatened by incidental mortality in the trawl fishery in this region (Silva et al. 2007, 2010). Since 1990, the number of trawl vessels has increased in areas close to olive ridley nesting beaches,

where adult males and females reside during reproductive seasons (Silva et al. 2010, 2011). This overlap causes increased mortality of adults, the life stage essential for persistence of sea turtle populations (Wallace et al. 2008). From 1994 to 1999, 283 sea turtles stranded dead on a small section (163 km) of the beach, and 56.9% were olive ridley sea turtles in the size range of adult nesting females (Silva et al. 2010). However, threats are not restricted to the neritic zone, as off the northeastern Brazilian coast, longline fisheries incidentally capture mostly olive ridley and leatherback (*Dermochelys coriacea*) sea turtles (Sales et al. 2008).

As the olive ridley is regarded as the most abundant sea turtle in the world, this species is not ranked as a 'conservation priority', and consequently, funding for research is scarce (Plotkin 2007). Additionally, its mainly oceanic distribution during early life and adulthood impedes access to individuals for study as compared to other, more coastal sea turtle species. As a result, few studies of this species have been conducted and published (Plotkin 2007). To date, only one age-determination study of olive ridley sea turtles has been reported: Zug et al. (2006) estimated the age of 26 specimens from the north-central Pacific through skeletochronology analysis of humerus bones. Turtles in the sample ranged from 20.5 to 64.4 cm in straight carapace length (SCL), and ages were estimated to be between 7.3 and 24.1 yr old (Zug et al. 2006). As olive ridleys from the north-central Pacific mature at 53 cm

SCL, a mean of 13 yr of age at first maturation was estimated (Zug et al. 2006).

In the current study, we estimate the age structure of olive ridley sea turtles stranded dead on the coast of Sergipe state in northeastern Brazil using skeletochronological analysis of humerus bones. In addition, size-at-age data yielded by the analysis are used to generate a growth curve to estimate age at first maturation and somatic growth rates for the first time for this major olive ridley population.

MATERIALS AND METHODS

Study area

Sampling took place along the coast of Sergipe state and south coast of Alagoas state in northeast Brazil, along 173 km of beach, between 10°31'S and 11°25'S, which is monitored by TAMAR-ICMBio (the Brazilian Sea Turtle Conservation Programme) in partnership with the Fundação Mamíferos Aquáticos (FMA). In the study area, there are 3 TAMAR-ICMBio stations (Ponta dos Mangues, Pirambu and Abaís beaches). Monitoring occurs along the whole Sergipe state coast, in addition to Pontal do Peba, in Alagoas state (Fig. 1). Despite being located in 2 states, the coastlines of both areas are contiguous and as a result are treated as a single area in this study. Sergipe state is the main Brazilian reproductive area for olive ridley

sea turtles, where 77% of Brazilian nests occur (6000 nests yr⁻¹) (Castilhos et al. 2011). Olive ridley sea turtles are known to form 'arribadas' (large nesting aggregations) (Pritchard 2007); however, at this location they are solitary nesters. Although breeding occurs mainly between September and March, olive ridley sea turtle nesting is observed all year round in low numbers (Silva et al. 2007). In 1982, when TAMAR-ICMBio began working in Sergipe state, almost all eggs were collected for human consumption; however, poaching decreased gradually over the years after the TAMAR-ICMBio station was established (Silva et al. 2007). While the number of nests has currently increased (Silva et al. 2007), trawl fishery activity is a significant threat in the area, causing high mortality of olive ridley adults (Silva et al. 2010).

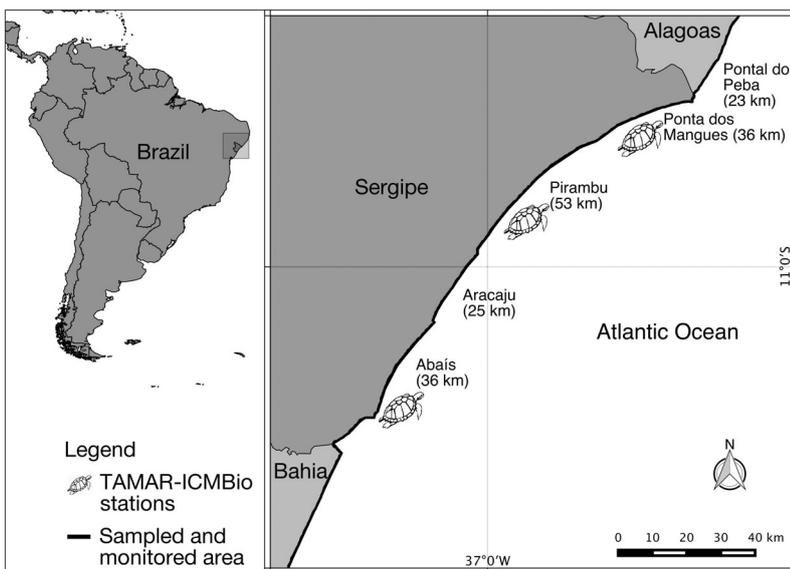


Fig. 1. Sampling locations of olive ridley sea turtles *Lepidochelys olivacea* stranded dead on the coast of Sergipe and Alagoas states, northeastern Brazil. Numbers in km indicate the extension of monitored coastal areas. Beaches in Alagoas were monitored from the nearby stations in Sergipe

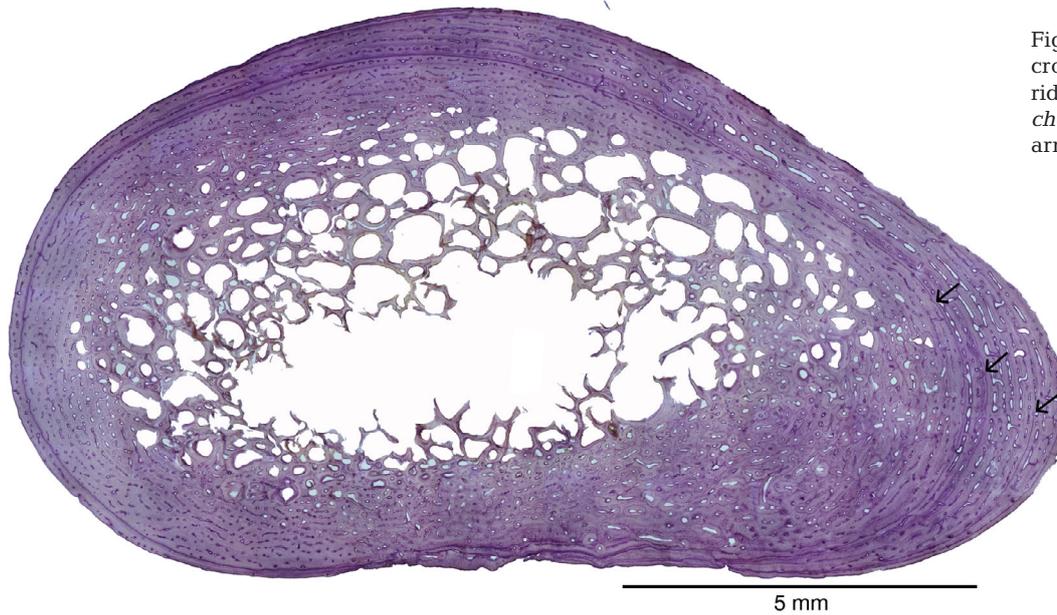


Fig. 2. Humerus (stained cross-section) from olive ridley sea turtle *Lepidochelys olivacea*. Black arrows: lines of arrested growth (LAGs)

Sample collection and preparation

From July 2010 to October 2012, humeri of olive ridleys stranded dead on the beach were collected for skeletochronological analysis. For every turtle, CCL was measured (Bolten 1999) with a flexible metric tape measure (± 0.1 cm). When possible, sex, presence of tags, formed eggs and tumor presence was recorded; if a turtle had a tumor, the sample was discarded. In addition, humeri of 14 fully developed hatchlings that failed to emerge from the nest surface and died at Pirambu beach were sampled.

Humerus bone samples were frozen and then transported to the Laboratório de Aves Aquáticas e Tartarugas Marinhas at the Universidade Federal do Rio Grande (FURG) in southern Brazil. Humeri were cleaned, measured and histologically processed according to methods detailed in Avens & Goshe (2007) and Petit et al. (2012), which resulted in a calibrated digital image of each entire processed humerus cross-section at 4 \times magnification (Fig. 2 & 3).

Age estimation

Each composite cross-section was analyzed as in Petit et al. (2012). A skeletal growth mark consists of a lightly stained area followed by a dark line of arrested growth (LAG), which appeared both as defined or diffuse (Zug et al. 1986). The interpretation of these LAGs 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, width of each LAG and humerus diameter, using ImageJ v.1.48 software.

The first growth mark is called the annulus and differs from others in that it is a diffuse band closest to the center of the bone; subsequent, more discrete LAGs are deposited along the outer circumference. Commonly, the annulus appears in young vertebrates only, because in large animals, resorption of older inner lines occurs as the individual develops and matures (Zug et al. 1986). The majority of sampled humeri were from adult olive ridleys, based on the size range of mature females from the main nesting area in Sergipe state (Silva et al. 2007), or the presence of eggs in the oviducts for stranded fe-

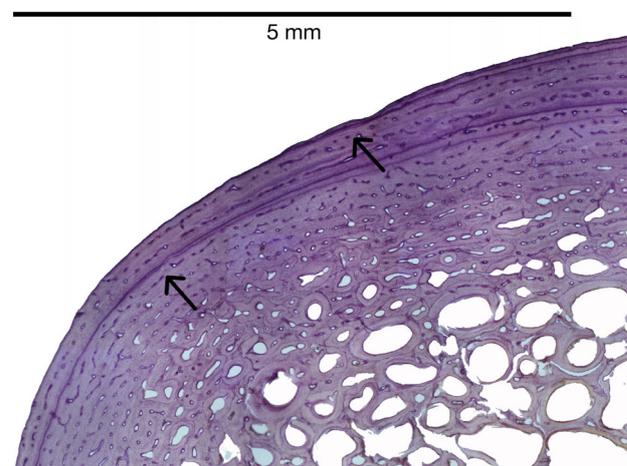


Fig. 3. Higher magnification of a portion of a humerus stained section from olive ridley sea turtle *Lepidochelys olivacea*. Arrows indicate where the lines of arrested growth (LAGs) are splitting

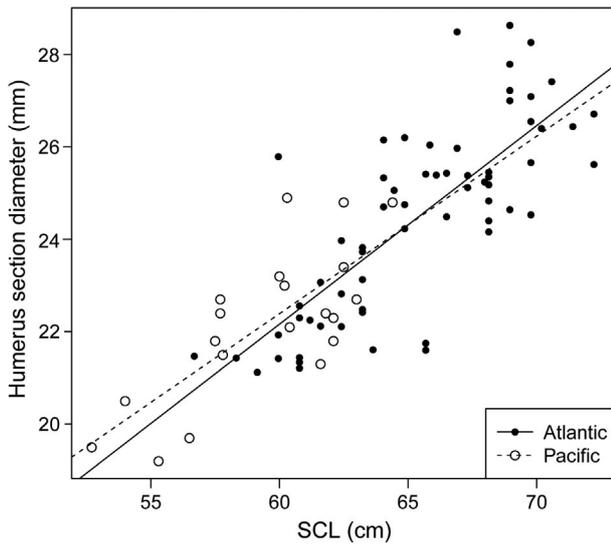


Fig. 4. Relationship between humerus section diameter (HSD) and straight carapace length (SCL) of olive ridley sea turtles *Lepidochelys olivacea* sampled in the Atlantic and Pacific Oceans. Solid line is the model ($SCL = a + b \cdot HSD$) fitted to the data set of olive ridleys from northeastern Brazil only. Dashed line is the same model, but data set is from olive ridleys from the Pacific, stranded at Hawaii archipelago

males. Because our sample did not contain juvenile turtles, annuli could not be found. Therefore, a correction factor was applied to estimate the number of lost LAGs in the resorption core of each section. This correction factor was based on data from olive ridley

turtles from the north-central Pacific Ocean, as reported in Zug et al. (2006). As populations are different between the Pacific and Atlantic basins, it was first necessary to determine whether turtles from the 2 populations have a similar growth. Thus, a linear model between humerus section diameter (HSD) vs. SCL was fitted, one for Pacific Ocean data (Zug et al. 2006) and another for Atlantic Ocean data (present study). Comparison of both linear models revealed that the 2 turtles groups exhibit very similar growth patterns, as the relationships were not significantly different (Fig. 4; $p = 0.652$).

Thereafter, a data set of size-at-age extracted from the growth model fitted to 26 specimens (20.5–64.4 cm SCL) along with the known mean hatchling size (~4 cm SCL) from the north-central Pacific Ocean were used to develop the correction factor. A grid was overlaid onto a growth model fitted (generalized smoothing spline model) to estimate SCL at discrete year intervals (Zug et al. 2006) (Fig. 5). Year was used as a proxy for LAG number, starting with the first year LAG (Fig. 5), and SCL was substituted into the relationship SCL vs. HSD provided by Zug et al. (2006) to yield an estimate of LAG diameter at size ($HSD = 0.332 + 0.385SCL$). Two models were then fit to the LAG diameter:LAG number pairs to characterize the relationship: the first model was a linear regression ($y = a + bx$) and the second model was a power function ($y = ax^b$), where y is the LAG diameter, x is the LAG number, a and b are the estimated parameters. Finally, we used the estimated parameters (a and b) and substituted resorption core diameter (y_{core}) for LAG diameter for each turtle in the sample to estimate the number of LAGs potentially lost to resorption (x_{core}). The age estimate for each turtle was therefore a combination of the number of growth layers observed in the outermost region of the bone section (x_{obs}), plus the predicted number of resorbed growth layers in the resorption core of the humerus ($x = x_{core} + x_{obs}$). As carapace measures were based in CCL, this measurement was converted to SCL based on the equation from Whiting et al. (2007b) (range: 65.0–75.2 cm CCL, $n = 85$; $SCL = 0.818CCL + 9.244$; $R^2 = 0.91$).

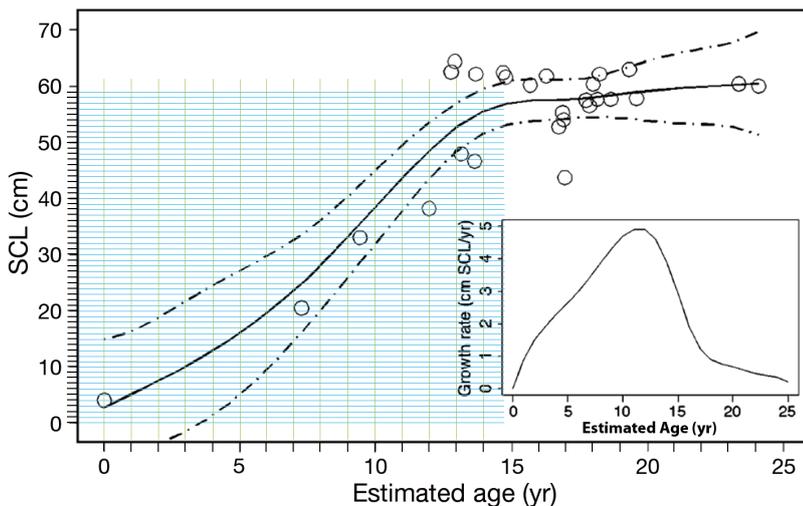


Fig. 5. Growth model fitted to size-at-age data of olive ridley sea turtles *Lepidochelys olivacea* from the Pacific Ocean, from Zug et al. (2006). Shaded area is the grid overlaid to extract the size-at-age data to estimate lost lines of arrested growth (LAG) of olive ridleys from the Atlantic. Adapted from Zug et al. (2006). SCL = straight carapace length. Dashed lines are the 95% interval of growth model. Open dots are the estimated age and inset shows growth rates of olive ridley sea turtles from Zug et al. (2006)

Age estimation was based on the assumption that 1 LAG represents 1 yr of age, as has been validated by known age specimens and marginal

increment analysis for the phylogenetically close Kemp's ridley *Lepidochelys kempii* (Snover 2002, Snover & Hohn 2004), and a marginal increment analysis to describe the pattern of skeletal growth mark deposition of a tropical sea turtle species, the hawksbill sea turtle *Eretmochelys imbricata* (Snover et al. 2013). Additionally, the pattern of annual LAG deposition has also been validated for 2 other sea turtle species: loggerhead *Caretta caretta* and green turtle *Chelonia mydas* (Klinger & Musick 1992, Coles et al. 2001, Snover et al. 2011) with known age specimen and tetracycline labeling, respectively. For the olive ridley, validation is difficult because they spend most of their life cycle in the oceanic zone. However, although the Kemp's ridley has a different life cycle from the olive ridley, the 2 species are closely related, having diverged only 2.5–3.5 million yr ago (Bowen et al. 1998). In addition, the 2 ridley sea turtle species share many characteristics: they are the smallest of all sea turtle species, with similar minimum female nesting size (~60 cm SCL) (Reichert 1993, Zug et al. 1997, Silva et al. 2007), and both species exhibit arribadas (Pritchard 2007). Therefore, it is likely that the olive ridley sea turtle deposits 1 LAG each year of life, as assumed in the current study.

Growth model

Schnute's growth model was fitted to the olive ridley sea turtles' size-at-age, as was done for loggerhead sea turtles in Petit et al. (2012). It is a general model that includes Pütter, von Bertalanffy, Richards, Gompertz and logistic growth models as special cases. The model proposed by Schnute (1981) is appropriate for the purpose of the present study, as the available size-at-age data for olive ridley sea turtles describes only 2 stages of their life cycle, hatchling and adults; therefore, the flexibility of this growth model to accommodate this is an advantage. Schnute's generic equation with 5 parameters is detailed in Schnute (1981) and Petit et al. (2012).

Growth rates

Growth rates were calculated based on the back-calculation method (Snover et al. 2007a) and incorporating the body proportional hypothesis (BPH) from Francis (1990). Four equations were fitted to check the best relationship between carapace length (in cm, SCL) and HSD (mm) (excluding hatchlings) as in Petit et al. (2012) for loggerhead sea turtles. The

mean hatchling carapace length used was 4.03 ± 0.17 (SD) cm SCL and the mean hatchling humerus diameter was 2.20 ± 0.02 mm. Then we used the BPH equation to back-calculate carapace length from the interior LAGs, as in the equation provided by Francis (1990) and Petit et al. (2012).

Annual somatic growth rates were calculated from each pair of successive LAG diameter measurements for each olive ridley in the sample, based on the assumption that 1 LAG represents 1 yr of age. In addition, as the sample comprised mostly adults, many olive ridley humerus sections showed LAGs spaced very closely together at the outer edge (Fig. 3). Such a decrease in LAG spacing corresponds to a decrease in growth rates, as a consequence of the onset of sexual maturity (Francillon-Vieillot et al. 1990, Guarino et al. 2008), when a turtle becomes anatomically and endocrinally capable of copulating and producing viable eggs (Caillouet et al. 2011). This phenomenon in the bones is termed 'rapprochement', and refers to the first decreasing interval between LAGs, previously observed in humeri of adult-sized turtles (Goshe et al. 2010, Snover et al. 2013, Avens et al. 2015) (Fig. 3). Therefore, size and age associated with the rapprochement LAG for a turtle were estimated when this line could be identified, as a proxy for estimated size at sexual maturation (SSM) and age at sexual maturation (ASM).

Statistical analysis

Inference was performed within a Bayesian statistical framework (Ellison 2004). In Bayesian analysis, estimates of unknown parameters are given as probability distributions denoted 'posteriors' (Gelman et al. 2003). We used non-informative priors for all estimated parameters and models fitted. Samples from the posterior distributions were drawn by Markov chain Monte Carlo (MCMC) and sampling importance resampling (SIR) (Gelman et al. 2003, Skare et al. 2003). In MCMC, a Markov chain is set up in such a fashion that the posterior is its long-run equilibrium distribution, while SIR aims at drawing a random sample from a target distribution. We used SIR only for the Schnute's growth model due to difficulties in obtaining acceptable convergence with MCMC.

All analyses were performed with R software (R Core Team 2014), and the JAGS program (<http://mcmc-jags.sourceforge.net> [accessed on 4 February 2015]) to specify models and perform the Bayesian analysis (Gilks et al. 1994). The R code for all ap-

Table 1. Values of Bayesian fits from power function model and linear regression between the diameter of the line of arrested growth (LAG) versus LAG number of olive ridley sea turtles *Lepidochelys olivacea* sampled in the Pacific Ocean by Zug et al. (2006). *a*, *b* and σ represent the posterior mean; values in brackets are 95% probability intervals. DIC = deviance information criterion; a smaller DIC indicates a better model fit

Parameter	Power function $y = ax^b$	Linear regression $y = a + bx$
a	0.27 [0.08–0.44]	0.17 [-0.02 to 0.36]
b	1.06 [0.93–1.18]	1.50 [1.44–1.55]
σ	0.34 [0.32–0.43]	0.81 [0.57–1.18]
DIC	1.30	37.58

lications is available in the Supplement at www.int-res.com/articles/suppl/m451p205_supp.pdf. Model selection was based on the deviance information criterion (DIC), in which the smallest values indicate the best fit (Spiegelhalter et al. 2002).

RESULTS

Age estimation

Age estimates for a total of 68 turtles with CCL between 58.0 and 77.0 cm (mean \pm SD: 69.1 \pm 4.56 cm) or SCL between 56.7 and 72.2 cm (mean \pm SD: 65.8 \pm 3.73 cm) were between 14 and 26 yr. The

sample comprised 25 females, 5 males and 38 turtles of undetermined sex, of which a sub-sample of 17 females was classified as sexually mature by the presence of formed eggs in the oviduct (n = 10) or detection of tags previously applied when the turtle had nested (n = 7). The power function model provided the best fit for the LAG diameter:LAG number relationship, according to the lower DIC value (Table 1). From the data set of Zug et al. (2006), the correction factor equation to estimate the number LAGs lost to resorption took the form:

$$LAG \text{ diameter (mm)} = 0.26 \times (LAG \text{ number})^{1.05} \quad (1)$$

Thus, within the equation, resorption core diameter values (y_{core}) were substituted for LAG diameters to provide the number of lost LAGs in the resorption area (x_{core}). The LAGs effectively observed in each humerus ranged from 3 to 9, while the estimated lost LAGs in the resorption core ranged from 11 to 16. LAG deposition patterns were similar to those of other sea turtle species, with a light band of fast bone growth followed by a dark line of slow growth, and the majority of the humerus sections presented split and double LAGs (Zug et al. 1986, Castanet & Smirina 1990) (Fig. 3).

Growth model

Schnute’s growth model fitted well to size-at-age data for olive ridley sea turtles in the current study (Fig. 6a), generating a curve similar to size-at-age data from the Pacific (Fig. 5). The curve had an

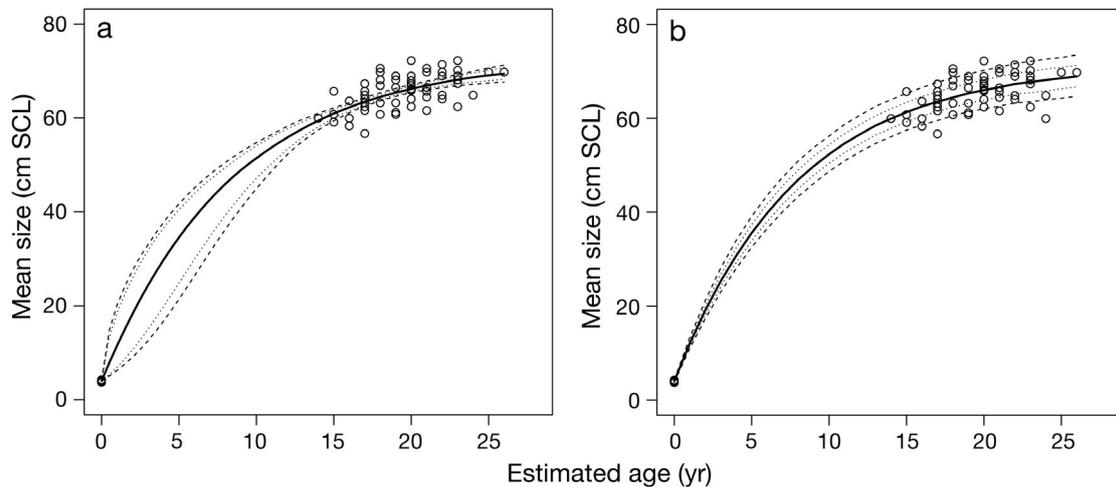


Fig. 6. Bayesian fit of (a) Schnute’s (1981) and (b) von Bertalanffy growth models to estimated age vs. size (straight carapace length, SCL) of olive ridley sea turtles *Lepidochelys olivacea* sampled in the Atlantic Ocean along northeastern Brazil. Black solid line is the curve generated from Schnute’s model; dashed and dotted lines are probability intervals of 95% and 80%, respectively

Table 2. Bayesian fit of Schnute's (1981) and von Bertalanffy growth models for straight carapace length (SCL) and estimated age data of olive ridley sea turtles *Lepidochelys olivacea* sampled in northeastern Brazil. Estimated parameters are posterior means; values in brackets are 95 % probability intervals. DIC = deviance information criterion to guide model selection; a smaller DIC indicates a better fit. nd = no data

Parameter	Schnute's model	Parameter	von Bertalanffy model
a	0.19 [0.09–0.31]	y_0	4.03 [3.93–4.14]
b	0.18 [–0.92 to 1.18]	k	0.13 [0.02–0.16]
y_1	4.03 [3.93–4.13]	y_∞	71.71 [68.12–76.25]
y_2	68.42 [66.75–70.35]	σ	0.05 [0.04–0.06]
σ	0.05 [0.04–0.06]	nd	nd
DIC	–407.8	DIC	347.2

inflection point (τ_i, y_i) and became S-shaped. The values of parameters a and b were similar to parameters of a von Bertalanffy growth model (von Bertalanffy 1957). The von Bertalanffy growth model requires a sample from all size classes ranging from hatchlings to old adults encompassing asymptotic size. Despite that our sample was restricted to mostly adults and 14 hatchlings, the von Bertalanffy model also fitted well, but the curve did not have an inflection point (Fig. 6b). The von Bertalanffy growth model equation took the form:

$$y_\tau = y_\infty [1 - \exp(-k(\tau - y_0))] \quad (2)$$

where y_τ is the size of the specimen at age τ ; in this case the size was the SCL in cm; k is the intrinsic growth rate and y_0 is the hypothetical age when length is equal to 0. Although both the Schnute's and von Bertalanffy growth models had similar parameter values (Table 2), Schnute's model had a smaller DIC than the von Bertalanffy model, suggesting that the former model had a better fit than the latter. As the von Bertalanffy model, in addition to the Pütter, Richards, Gompertz and logistic models, are special cases of the generalized growth model proposed by Schnute (1981), it was expected that Schnute's model would have a better fit than von Bertalanffy's. In addition, as the von Bertalanffy growth model is simpler than Schnute's, it calculated the age at maturation of olive ridleys from Eq. (2). The growth model fits demonstrated a gradual

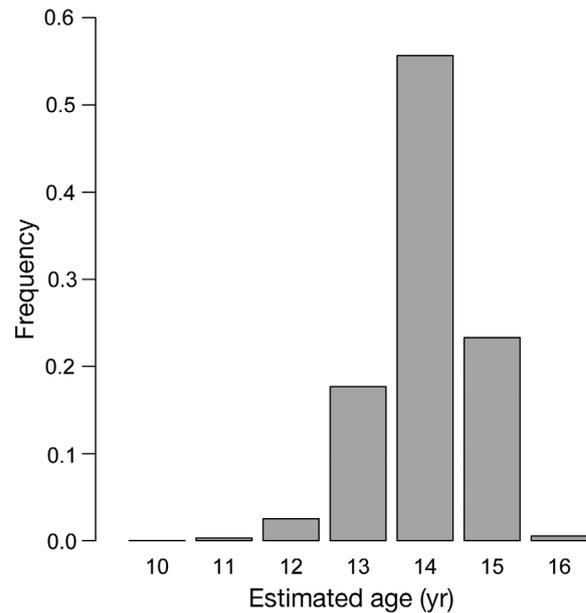


Fig. 7. Estimated distribution for age at maturation for olive ridley sea turtles *Lepidochelys olivacea* sampled in north eastern Brazil

decrease in growth at around 60 cm SCL, which corresponds with the lower end of the size range of olive ridleys recorded nesting at the main reproductive area in Brazil where humerus samples were obtained (Silva et al. 2007). For this size, mean age was estimated to be 14 yr, with a probability interval between 10 and 16 yr old. However, olive ridley sea turtles were estimated to have a 79 % of probability of maturing at 14–15 yr of age (Fig. 7).

Table 3. Bayesian fit of 4 models for straight carapace length (SCL) vs. humerus section diameter (HSD) of olive ridley sea turtles *Lepidochelys olivacea* sampled in northeastern Brazil. In each model, L is SCL and D is HSD; L_{op} = carapace length at hatching; D_{op} = humerus diameter at hatching. Estimated parameters are posterior means; values in brackets are 95 % probability intervals. DIC = deviance information criterion to select among models; a smaller DIC indicates a better fit

Model	Estimated parameters				DIC
	a	b	c	σ	
$L = L_{op} + b(D - D_{op})^c$		2.36 [2.12–2.70]	0.57 [0.46–0.64]	0.041 [0.035–0.049]	234.1
$L = L_{op} + b(D - D_{op})$		2.73 [2.69–2.76]		3.57 [3.01–4.25]	369.4
$L = a + bD^c$	16.91 [3.44–28.51]	4.38 [2.51–7.88]	0.76 [0.61–0.87]	2.53 [2.14–3.02]	323.5
$L = a + bD$	30.59 [22.80–39.82]	1.42 [1.04–1.73]		2.52 [2.13–3.01]	323.3

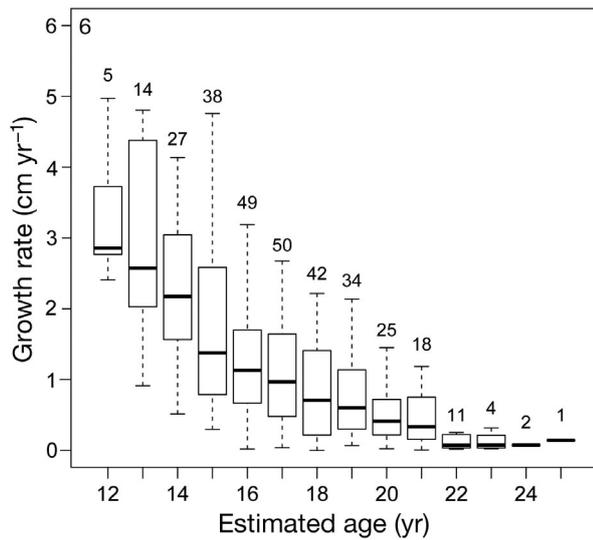


Fig. 8. Relationship between estimated age and annual growth rate based on back-calculated lengths from each growth mark diameter from each olive ridley sea turtle *Lepidochelys olivacea* sampled. Boxes are the range of growth rates; horizontal lines inside boxes are the means; vertical dashed lines are SD; numbers above boxes are sample sizes (i.e. numbers of lines of arrested growth or LAGs) corresponding with each age indicated along the x-axis

Growth rates

The best fit for back calculation was the equation which incorporated L_{op} , D_{op} and the constant c (Table 3). Therefore, this equation was used in the BPH equation from Francis (1990) and from Petitet et al. (2012) to calculate growth rates. The growth rate between each LAG pair showed a decrease from the inner LAG to the outer LAG (Fig. 8), suggesting that as turtles get older, growth rate decreases. The sample showed only growth rates from LAGs related to age estimates between 12 and 25 yr old. Although this range encompasses only the adult stage, it is clear that growth rates associated with early ages at maturation (12 yr) are higher than those corresponding with mean age at maturation (14–15 yr), when growth rates slow down (Fig. 8).

In 60 olive ridley humeri, the rapprochement LAG was identified, and the range of ages inferred by this approach was from 13 to 21 yr old (mean \pm SD: 16.6 \pm 1.80 yr), while estimated SCL varied between 56.1 and 68.6 cm (mean \pm SD: 63.3 \pm 3.34 cm) or CCL between 57.5 and 72.6 cm (mean \pm SD: 66.0 \pm 3.34 cm). The number of years after rapprochement (= period after maturation) ranged from 1 to 7 yr, in which growth rates decreased and became gradual (Fig. 9). The sub-sample of 17

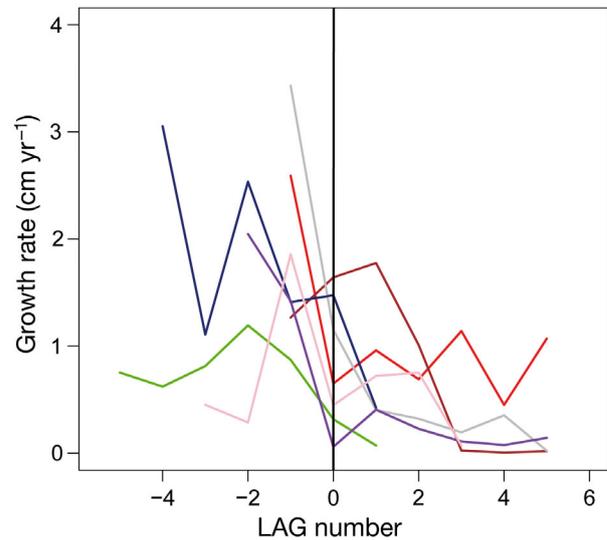


Fig. 9. Growth rates from 6 turtles from the sub-sample of 17 matured females of olive ridley *Lepidochelys olivacea*. Each line represents 1 individual; the line of arrested growth (LAG) 0 refers to the rapprochement (maturation) represented by the black straight line in the middle of the graph

mature females had ASM estimates between 15 and 21 yr old (mean \pm SD: 18 yr \pm 1.53 yr), at SSMs between 60.8 and 68.5 cm SCL (mean \pm SD: 65.5 \pm 2.78 cm) or 63.0 and 72.5 cm CCL (mean \pm SD: 68.8 \pm 3.40 cm).

DISCUSSION

Age estimation

We present the first study of age estimation for olive ridleys from the Atlantic Ocean, based on skeletochronological analysis and estimated for olive ridleys sized 56.7–72.2 cm SCL and ranging in age from 14–26 yr old. As the correction factor for lost LAGs applied was based on data from the north-central Pacific Ocean for turtles 7.3–24 yr old and 20.5–64.4 cm SCL in size (Zug et al. 2006), similar ages were expected for turtles of similar sizes in our samples from the Atlantic. However, there were some Atlantic olive ridleys in our sample of similar size or smaller whose age estimates were either younger or older than turtles from the Pacific. These discrepancies may have been in part due to methodological differences between the 2 studies; whereas Zug et al. (2006) analyzed undecalcified and unstained humerus cross-sections, the current study examined decalcified, thin-sectioned, stained hume-

rus cross-sections. Goshe et al. (2009) showed that in larger animals, the skeletochronological method without staining humerus sections might underestimate age due to the presence of closely spaced LAGs. As our sampling comprised mostly adults, with sections depicting double and split LAGs (Castanet et al. 1993, Snover & Hohn 2004, Petit et al. 2012), without staining, it would be impossible to read all lines (Figs. 2 & 3). However, for juveniles, there was no significant difference in the number of visible LAGs between stained and unstained bones (Goshe et al. 2009). As a result, use of the correction factor based on a data set of juveniles from Zug et al. (2006) was appropriate for the present study.

The frequency of growth mark deposition can potentially vary between and within individuals due to the influence of favorable and unfavorable environmental conditions, access to resources, abiotic factors and genetic contribution (Bjørndal et al. 2003, Petit et al. 2012). Formerly it was assumed that growth mark deposition in ectotherms was linked to variations in growth rates caused by seasonal fluctuations in temperature (Patnaik & Behera 1981). However, studies of tropical cold-blooded species, i.e. reptiles and amphibians, have demonstrated annual deposition of growth marks despite the absence of seasonal influences in the environment. Pal et al. (2009) and Zug & Rand (1987) showed annual deposition of LAGs in long bones (humerus, femur and third toe) from tropical lizards, fan-throated lizard *Sitana ponticeriana* and green iguana *Iguana iguana*, respectively. Scholz et al. (2010) demonstrated LAGs with seasonal growth pattern in a tropical amphibian, the West African caecilian *Geotrypetes seraphini*, which they interpreted as annually deposited marks. Although these are terrestrial animals, analyses have also supported deposition of annual LAGs in humeri of hawksbill and green sea turtles from the tropical Hawaiian archipelago (Snover et al. 2011, 2013). In addition to the more tropical sea turtle species, olive ridley humerus sections are also similar to those of loggerheads and Kemp's ridleys, which despite being temperate sea turtle species also have been demonstrated to exhibit annual LAG deposition (Klinger & Musick 1992, Coles et al. 2001, Snover & Hohn 2004). Given that olive ridley humerus sections in the present study showed LAG deposition characteristics similar to other sea turtles, this indicates that olive ridley bone growth may also have an annual cyclic pattern (Fig. 2).

The olive ridley, as well as the leatherback sea turtle, is more oceanic than other sea turtle species.

After hatching, olive ridleys spend all early life and late juvenile phases in the oceanic zone, after which they mature and recruit to nearshore areas for mating and nesting (Reichert 1993). The duration of the 'lost years', which is the period from hatchlings entering the sea until recruitment (Musick & Limpus 1996), is still unknown for these species. However, as the present study estimated a mean age of 14 yr old (range 10–16 yr) for the first maturation by the von Bertalanffy growth model, it can be estimated that the 'lost years' period for olive ridley sea turtle spans at least ~10 yr. After this time, they recruit to natal beaches, breed and/or nest, and migrate to a neritic or oceanic foraging ground (Plotkin 2010, Silva et al. 2011, Plot et al. 2015). The mean age at maturation estimated for olive ridleys in this study (~14 yr old) was similar to north-central Pacific olive ridleys (~13 yr old), despite that the minimum size for nesting females on Pacific Ocean beaches is 53 cm SCL (Zug et al. 2006), while for Atlantic Ocean beaches it is around 60 cm SCL or 62.50 cm CCL (Silva et al. 2007). Kemp's ridleys in the Gulf of Mexico have a mean age at maturation of 12 yr (range 9.9–16.7 yr) at around 60 cm SCL (Snover et al. 2007b), similar to olive ridleys from the Atlantic Ocean. Thus, it appears that despite ecological differences, such as a more benthic and coastal foraging in Kemp's ridley (Snover et al. 2007b), both species mature at similar ages.

ASM was also estimated using the von Bertalanffy growth model and from the rapprochement LAG; the former gave a range from 10 to 16 yr old (mean ~14 yr), while the second method gave between 13 and 21 yr old (mean ~16.6 yr). The von Bertalanffy growth model estimation was based on the minimum size of a nesting female (60.0 cm SCL) and the second approach was based on SCL back-calculated from the rapprochement LAG (56.1–68.6 cm SCL). However, as nesting females may mature before the first recorded nesting (Caillouet et al. 2011), individuals could mature at smaller sizes and earlier ages than our estimation. Because the model results showed smaller sizes and older ages at sexual maturity than the rapprochement LAG method, this discrepancy may be due to the limited growth after sexual maturity of sea turtles, and consequently SSM and ASM seem not to be correlated. After deposition of the rapprochement LAG, olive ridley sea turtle adult stage duration ranged from 1 to 7 yr, during which time they exhibited growth rates between 0 and 2.47 cm yr⁻¹ (mean ± SD: 0.69 ± 0.57 cm yr⁻¹). Thus, some individuals seem to have no growth after maturation, while others grew almost 2.5 cm. Therefore, SSM

and ASM from rapprochement LAG seem to be more reliable because there are large variations in female sizes, characteristic of sea turtle populations (Broderrick et al. 2003, Bjørndal et al. 2013). Moreover, for the sub-sample of 17 females confirmed as mature by formed eggs or tagging, the SSM estimates (60.8–68.5 cm SCL) fall within the range size of nesting females found at Sergipe coast (60.0–77.0 cm SCL), although these SSMs, corresponding with ASM estimates (15–21 yr), are greater than those yielded by the growth model.

Growth model and growth rate

Schnute and von Bertalanffy fits generated similar curves for Atlantic olive ridleys, with slower growth for turtles greater than 60 cm SCL (Fig. 6). At around this size, the turtles mature and presumably most resources consumed are directed toward reproduction instead of somatic growth (Bernardo 1993, Bjørndal et al. 2003). Similar growth patterns for larger olive ridley turtles in the Pacific were described by Zug et al. (2006) (Fig. 5). Colman et al. (2014) analyzed stomach contents from adult olive ridleys stranded dead along the Sergipe coast and found that of 30 turtles analyzed, 14 had empty stomachs and the remaining 16 had fed mostly on crustaceans (crabs and shrimps) and demersal fish. Even with benthic items holding higher caloric content than oceanic items, this high energy intake would be allocated to the energetic costs of reproduction, corresponding with observed low somatic growth rates for the adults sampled (Fig. 8).

Although little is known about the juvenile stage for olive ridleys, it is thought that in the Pacific Ocean, most juveniles inhabit the center of the Subtropical Gyre, characterized by warmer vertically stratified water and a deeper thermocline (Polovina et al. 2004). During this stage, the most common prey are pyrosomes and salps (Polovina et al. 2004), and it is likely that juveniles are feeding constantly and allocating energy to grow in size in order to minimize predation risks (Snover et al. 2007a). Zug et al. (2006) showed linear growth for olive ridley juveniles and consequently high growth rate (Fig. 5). The present study lacks juvenile samples, although it is clear in Fig. 8 that growth rates from inner LAGs are greater than LAGs related to the mean age-at-maturation (~16 yr old).

This growth scenario, with linear growth for juveniles and gradual growth for adults, is exhibited by all major ectothermic animal groups, which present

slow growth and late maturity, similar to all sea turtle species. In addition, most ectotherms grow more slowly in cold, but reach a larger adult size than at high temperatures (Kozłowski et al. 2004), as might be the case for the olive ridley, which reaches a maximum of 75 cm SCL, smaller than other temperate sea turtle species (Reichart 1993). This temperature effect is called the 'temperature-size rule', with large size in the cold attained by a prolonged growth period, which compensates for slow growth (Atkinson 1996). Moreover, this temperature effect differs from the effect of limited resources (growth retardation accompanied by smaller adult size; Kozłowski et al. 2004).

Implications for conservation

Estimated ages-at-maturation and growth rates are key parameters to support science-informed conservation actions of a given population. These estimates allow prediction of population resilience, but if the estimated is biased, it can lead to negative impacts (Avens et al. 2009). We estimated a mean age at maturation of 16 yr for the olive ridley sea turtle, greater than estimates for the north-central Pacific population (~13 yr old) (Zug et al. 2006). This means that at Sergipe state in northeastern Brazil, the olive ridley sea turtle would require at least 16 yr to recover from a negative impact. The estimated age-at-maturation is congruent with the step increase in the number of nests in the area, suggesting the effectiveness of protection of rookeries. TAMAR-ICMBio started protecting the nesting population in the area in 1982, and 16 yr later, in 1998, the number of nests started increasing (Silva et al. 2007). The nest monitoring effort has increased over the years, but, before protection, hunting of nesting female olive ridleys for meat and nest opening for egg consumption were common practices, which are nowadays prohibited (Castilhos et al. 2011). Thus, we are confident that the upward trend in the number of nests is a real increase in the population size.

Although the olive ridley sea turtle is the most abundant sea turtle species in the world (Plotkin 2007), this species is listed as Vulnerable by the IUCN Red List (IUCN 2015), with an inferred decreasing trend, and listed as Endangered in the Brazilian Red List (MMA 2014). Before 1982, in the present study area, this species was threatened by human consumption, while currently, olive ridleys are threatened throughout their annual and life cycles: in oceanic waters, mostly juveniles are inci-

dentally captured in pelagic longline fisheries, while in neritic waters, mostly adults are incidentally captured by shrimp trawlers (Sales et al. 2008, Silva et al. 2010). Moreover, olive ridleys washed ashore in this area are in the size range of adults, often with formed eggs in females (Castilhos & Tiwari 2006). In addition to potential effects on the population, caused by fisheries bycatch, the lack of planning for coastal development causes additional negative impacts, including moving sandy beaches (sand extraction and landfills), photopollution, vehicle traffic, human presence on the beaches, harbors, anchorages and jetties, occupation of the fringe by hotels and houses, and exploitation of oil and gas very close to beaches (Castilhos et al. 2011).

Our results have elucidated key aspects of olive ridley demography, such as age-at-maturation and growth rates, which are key parameters to PVA, to model prediction of extinction risk for this little-known, threatened species. Additional studies focused on the elusive juvenile stages, as well as studies integrating the role of individual threats to each life stage, would be important for accurate PVA analysis. Because the juvenile stages take place in oceanic waters, future studies benefiting from the study of individuals incidentally captured by pelagic longline fisheries, together with telemetry and stable isotope analysis of tissues from adults washed ashore, will further improve our understanding of habitat use and support effective conservation.

Acknowledgements. We acknowledge the TAMAR/ICMBio and FMA staffs for the humeri samples, with special thanks to Ederson Luiz Fonseca, Fabio Lira, Mari Weber, Jociery Vergara Parente, Bruno Almeida and veterinarians for their support. Bone sampling was possible due to the support of PRMEA (Regional Monitoring Program of Strandings and Abnormalities), a measure of environmental impact assessment required by federal environmental licensing for oil and gas exploration, conducted by IBAMA, Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis. The skeletochronology method was carried out with logistics provided by the Laboratório de Ecologia da Megafauna Marinha (Instituto de Oceanografia—FURG), with special thanks to Eduardo R. Secchi and Silvina Botta. R.P. received financial support from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). L.B. is a research fellow of the Brazilian CNPq, National Council for Scientific and Technological Development (Proc. No. 308697/2012-0). This research is part of the PhD thesis written by R.P. under the guidance of L.B.

LITERATURE CITED

- Atkinson D (1996) Ectotherm life history responses to developmental temperatures. In: Johnston IA, Bennett AF

- (eds) Animals and temperature: phenotypic and evolutionary adaptation. Cambridge University Press, Cambridge, p 183–204
- 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
- Avens L, Snover ML (2013) Age and age estimation in sea turtles. In: Wyneken J, Lohmann KJ, Musick JA (eds) The biology of sea turtles, Vol 3. CRC Press, Boca Raton, FL, p 97–133
- Avens L, Taylor JC, Goshe LR, Jones TT, Hastings M (2009) Use of skeletochronological analysis to estimate the age of leatherback sea turtles *Dermochelys coriacea* in the western North Atlantic. *Endang Species Res* 8:165–177
- Avens L, Goshe LR, Coggins L, Snover ML, Pajuelo M, Bjorndal KA, Bolten AB (2015) Age and size at maturation and adult stage duration for loggerhead sea turtles in the western North Atlantic. *Mar Biol* 162:1749–1767
- Beissinger SR, Westphal MI (1998) On the use of demographic models of population viability in endangered species management. *J Wildl Manag* 62:821–841
- Bernardo J (1993) Determinants of maturation in animals. *Trends Ecol Evol* 8:166–173
- Bernardo J, Plotkin PT (2007) An evolutionary perspective in the *arribada* phenomenon and reproductive behavioral polymorphism of olive ridley sea turtle (*Lepidochelys olivacea*). In: Plotkin PT (ed) Biology and conservation of ridley sea turtles. Johns Hopkins University Press, Baltimore, MD, p 59–87
- 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
- Bjorndal KA, Parsons J, Mustin W, Bolten AA (2013) Threshold to maturity in a long-lived reptile: interactions of age, size, and growth. *Mar Biol* 160:607–616
- 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. Publ No. 4. IUCN/SSC Marine Turtle Specialist Group, 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
- Bowen BW, Clarck AM, Abreu-Grobois FA, Chaves A, Reichart RJ (1998) Global phylogeography of the ridley sea turtles (*Lepidochelys* spp.) as inferred from mitochondrial DNA sequences. *Genetica* 101:179–189
- Boyce MS (1992) Population viability analysis. *Annu Rev Ecol Syst* 23:481–506
- Broderick AC, Glen F, Godley BJ, Hays GC (2003) Variation in reproductive output of marine turtles. *J Exp Mar Biol Ecol* 288:95–109
- Brook BW, O'Grady JJ, Chapman AP, Burgman MA, Akçakaya HR, Frankham R (2000) Predictive accuracy of population viability analysis in conservation biology. *Nature* 404:385–387
- Caillouet CW Jr, Shaver DJ, Landry AM, Owens DW, Pritchard PCH (2011) Kemp's ridley sea turtle (*Lepidochelys kempii*) age at first nesting. *Chelonian Conserv Biol* 10:288–293
- Castanet J, Smirina E (1990) Introduction to the skeletochronological method in amphibians and reptiles. *Ann*

- Sci Nat Zool 13 ser 11:191–196
- Castanet J, Francillon-Vieillot H, Meunier FJ, De Ricqlès A (1993) Bone and individual aging. In: Hall BBK (ed) Bone: bone growth, Vol 7. CRC Press, Boca Raton, FL, p 245–283
- Castilhos JC, Tiwari M (2006) Preliminary data and observations from an increasing olive ridley population in Sergipe, Brazil. *Mar Turtle Newsl* 113:6–7
- Castilhos JC, Coelho AC, Argolo JF, Santos EAP, Marcovaldi AM, Santos ASS, Lopez M (2011) Avaliação do estado de conservação da tartaruga marinha *Lepidochelys olivacea* (Eschscholtz 1829) no Brasil. *Biodiversidade Brasileira* 1:28–36
- Coles WC, Musick JA, Williamson LA (2001) Skeletochronology validation from an adult loggerhead. *Copeia* 2001:240–242
- Colman LP, Sampaio CLS, Weber MI, Castilhos JC (2014) Diet of olive ridley sea turtles, *Lepidochelys olivacea*, in the waters of Sergipe, Brazil. *Chelonian Conserv Biol* 13: 266–271
- Ellison AM (2004) Bayesian inference in ecology. *Ecol Lett* 7: 509–520
- Francillon-Vieillot H, Arntzen JW, Géraudie J (1990) Age, growth, and longevity of sympatric *Triturus cristatus*, *T. marmoratus* and their hybrids (Amphibia, Urodela): a skeletochronological comparison. *J Herpetol* 24:13–22
- Francis RICC (1990) Back-calculation of fish length: a critical review. *J Fish Biol* 36:883–902
- 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 LR, Avens L, Bybee J, Hohn AA (2009) An evaluation of histological techniques used in skeletochronological age estimation of sea turtle. *Chelonian Conserv Biol* 8: 217–222
- Goshe LR, 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
- Guarino FM, Di Giá I, Sindaco R (2008) Age structure in a declining population of *Rana temporaria* from northern Italy. *Acta Zool Hung* 54:99–112
- IUCN (2015) The IUCN Red List of Threatened Species, version 2015.1. www.iucnredlist.org/details/11534/0 (accessed 3 June 2015)
- Klinger RC, Musick JA (1992) Annular growth layers in juvenile loggerhead turtles (*Caretta caretta*). *Bull Mar Sci* 51:224–230
- Kozłowski J (1992) Optimal allocation of resources to growth and reproduction: implications for age and size at maturity. *Trends Ecol Evol* 7:15–19
- Kozłowski J, Czarnoleski M, Danko M (2004) Can optimal resource allocation models explain why ectotherms grow larger in cold? *Integr Comp Biol* 44:480–493
- Metcalfe K, Agamboué PD, Augowet E, Boussamba F and others (2015) Going the extra mile: ground-based monitoring of olive ridley turtles reveals Gabon hosts the largest rookery in the Atlantic. *Biol Conserv* 190:14–22
- MMA (Ministério do Meio Ambiente) (2014) Répteis - *Lepidochelys olivacea* (Eschscholtz, 1829) - Tartaruga-oliva. In: Lista de espécies da fauna Brasileira ameaçadas de extinção. www.icmbio.gov.br/portal/biodiversidade/fauna-brasileira/lista-de-especies/6630-especie-6630 (accessed on 3 June 2015)
- 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
- Pal A, Swain MM, Rath S (2009) Long bone histology and skeletochronology in a tropical Indian lizard, *Sitana ponticeriana* (Sauria: Agamidae). *Curr Herpetol* 28:13–18
- Patnaik BK, Behera HN (1981) Age determination in the tropical agamid garden lizard, *Calotes versicolor* (Daudin), based in bone histology. *Exp Gerontol* 16: 295–307
- Petitet R, Secchi ER, Avens L, Kinan PG (2012) Age and growth of loggerhead sea turtles in southern Brazil. *Mar Ecol Prog Ser* 456:255–268
- Plot V, Thoisy B, Georges JY (2015) Dispersal and dive patterns during the post-nesting migration of olive ridley turtles from French Guiana. *Endang Species Res* 26: 221–234
- Plotkin PT (2007) Introduction. In: Plotkin PT (ed) Biology and conservation of ridley sea turtles. Johns Hopkins University Press, Baltimore, MD, p 3–5
- Plotkin PT (2010) Nomadic behaviour of the highly migratory olive ridley sea turtle *Lepidochelys olivacea* in the eastern tropical Pacific Ocean. *Endang Species Res* 13: 33–40
- Polovina JJ, Balazs GH, Howell EA, Parker DM, Sekil MP, Dutton PH (2004) Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central north Pacific Ocean. *Fish Oceanogr* 13:36–51
- Pritchard PCH (2007) *Arribadas* I have known. In: Plotkin PT (ed) Biology and conservation of ridley sea turtles. Johns Hopkins University Press, Baltimore, MD, p 7–21
- R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org
- Rees AF, Al-Kiyumi A, Broderick AC, Papathanasopoulou N, Godley BJ (2012) Conservation related insights into the behaviour of the olive ridley sea turtle *Lepidochelys olivacea* nesting in Oman. *Mar Ecol Prog Ser* 450: 195–205
- Reichert HA (1993) Synopsis of biological data on the olive ridley sea turtle *Lepidochelys olivacea* (Eschscholtz, 1829) in the western Atlantic. NOAA Tech Memo NMFS-SEFSC-336
- Sales G, Giffoni BB, Barata PCR (2008) Incidental catch of sea turtles by the Brazilian pelagic longline fishery. *J Mar Biol Assoc UK* 88:853–864
- Schnute J (1981) A versatile growth model with statistically stable parameters. *Can J Fish Aquat Sci* 38:1128–1140
- Scholz S, Orlik M, Gonwouo LN, Kupfer A (2010) Demography and life history of a viviparous Central African caecilian amphibian. *J Zool* 280:17–24
- Silva ACCD, Castilhos JC, Lopez GG, Barata PCR (2007) Nesting biology and conservation of the olive ridley sea turtle (*Lepidochelys olivacea*) in Brazil, 1991/1992 to 2002/2003. *J Mar Biol Assoc UK* 87:1047–1056
- Silva ACCD, Castilhos JC, Santos EAP, Brondízio LS, Bugoni L (2010) Efforts to reduce sea turtle bycatch in the shrimp fishery in northeastern Brazil through a co-management process. *Ocean Coast Manag* 53:570–576
- Silva ACCD, Santos EAP, Oliveira FLC, Weber MI, Batista JAF, Serafini TZ, Castilhos JC (2011) Satellite-tracking reveals multiple foraging strategies and threats for olive

- ridley turtles in Brazil. *Mar Ecol Prog Ser* 443:237–247
- Skare O, Bolviken E, Holden L (2003) Improved sampling-importance resampling and reduced bias importance sampling. *Scand J Stat* 30:719–737
 - Snover ML (2002) Growth and ontogeny of sea turtle using skeletochronology: methods, validation and application to conservation. PhD dissertation, Duke University, Durham, NC
 - 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 Bull* 102:682–692
 - Snover ML, Avens L, Hohn AA (2007a) Back-calculating length from skeletal growth marks in loggerhead sea turtles *Caretta caretta*. *Endang Species Res* 3:95–104
 - Snover ML, Hohn AA, Crowder LB, Heppell SS (2007b) Age and growth in Kemps ridley sea turtles: evidence from mark-recapture and skeletochronology. In: Plotkin PT (ed) *Biology and conservation of ridley sea turtles*. Johns Hopkins University Press, Baltimore, MD, p 89–105
 - Snover ML, Hohn AA, Crowder LB, Macko SA (2010) Combining stable isotopes and skeletal growth marks to detect habitat shifts in juvenile loggerhead sea turtles *Caretta caretta*. *Endang Species Res* 13:25–31
 - Snover ML, Hohn AA, Goshe LR, Balazs GH (2011) Validation of annual skeletal marks in green sea turtles *Chelonia mydas* using tetracycline labeling. *Aquat Biol* 12: 197–204
 - Snover ML, Balazs GH, Murakawa SKK, Hargrove SK, Rice MR, Seitz WA (2013) Age and growth rates of Hawaiian hawksbill turtles (*Eretmochelys imbricata*) using skeletochronology. *Mar Biol* 160:37–46
 - Spiegelhalter DJ, Best NJ, Carlin BP, van der Linde A (2002) Bayesian measure of model complexity and fit. *J R Stat Soc B* 64:583–639
 - TEWG (Turtle Expert Working Group) (2009) An assessment of the loggerhead turtle population in the western north Atlantic Ocean. NOAA Tech Memo NMFS-SEFSC-575
 - von Bertalanffy L (1957) Quantitative laws in metabolism and growth. *Q Rev Biol* 32:217–231
 - Wallace BP, Heppell SS, Lewison RL, Kelez S, Crowder LB (2008) Impacts of fisheries bycatch on loggerhead turtles worldwide inferred from reproductive value analyses. *J Appl Ecol* 45:1076–1085
 - Whiting SD, Long JL, Coyne M (2007a) Migration routes and foraging behaviour of olive ridley turtles *Lepidochelys olivacea* in northern Australia. *Endang Species Res* 3:1–9
 - Whiting S, Long J, Hadden K, Lauder A, Koch A (2007b) Insights into size, seasonality and biology of a nesting population of the olive ridley turtle in northern Australia. *Wildl Res* 34:200–210
 - Zug GR, Parham J (1996) Age and growth in leatherback turtles, *Dermochelys coriacea* (Testudines: Dermochelyidae): a skeletochronological analysis. *Chelonian Conserv Biol* 2:244–249
 - Zug GR, Rand S (1987) Estimation of age in nesting female *Iguana iguana*: testing skeletochronology in a tropical lizard. *Amphibia-Reptilia* 8:237–250
 - Zug GR, Wynn AH, Ruckdeschel C (1986) Age determination of loggerhead sea turtles, *Caretta caretta*, by incremental growth marks in the skeleton. *Smithson Contrib Zool* 427:1–34
 - 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, Chaloupka M, Balazs GH (2006) Age and growth in olive ridley sea turtles (*Lepidochelys olivacea*) from the north-central Pacific: a skeletochronological analysis. *Mar Ecol* 27:263–270

Editorial responsibility: Susanne Schüller,
Oldendorf/Luhe, Germany

Submitted: July 17, 2015; Accepted: October 27, 2015
Proofs received from author(s): December 2, 2015