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# Age and size at maturation- and adult-stage duration for loggerhead sea turtles in the western North Atlantic

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**Abstract** Age at maturation data are integral to understanding dynamics of threatened and endangered sea turtle populations. However, full characterization of this parameter requires information regarding variability in growth rates and both size and age at maturation potentially resulting from diverse environmental and biological influences. To address the need for these data, skeletochronological analysis was conducted for US Atlantic loggerhead sea turtles *Caretta caretta*. The influence of different covariates on back-calculated growth rates for the years 1976–2010 was investigated, and while growth decreased overall with size and age, at larger sizes, male growth rates were higher than those of females. Growth varied significantly by calendar year, increasing from 1990 to 1996/1997 and subsequently decreasing through the end of the study period. Mean sizes [cm straightline carapace length (SCL)] corresponding to the "rapprochement" skeletal growth mark associated with maturation were 90.5 for females (range 75.0–101.3) and 95.8 for males (range 80.6–103.8). Ages at maturation estimated from (1) the rapprochement skeletal growth mark; (2) back-calculated SCL-at-age data; and (3) bootstrapping and fitting Fabens modified von Bertalanffy growth curve to back-calculated growth data were very similar between approaches, but demonstrated a wide possible range. Mean age predictions associated with minimum and mean maturation SCLs were 22.5–25 and 36–38 years for females and 26–28 and 37–42 years for males. Post-maturation longevity (i.e., adult-stage duration) was similar for males and females, ranging from 4 to 46 years (mean 19 years).

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## Introduction

The need for estimates of age at sexual maturation (ASM) to refine population models integral to assessment and management of protected sea turtle populations has been repeatedly emphasized over the past several decades (Crouse et al. 1987; Heppell et al. 2003; NRC 2010). However, as indicated by this recurring, long-term emphasis, comprehensive ASM data have been difficult to obtain, due in large part to the relatively slow somatic growth and highly migratory behavior exhibited by many sea turtle populations (Avens and Snover 2013). Sea turtle ASM estimates have been predominantly generated by applying parametric growth curves (e.g., von Bertalanffy, logistic, Gompertz) to somatic growth data either measured during mark-recapture studies or inferred from skeletal growth increment widths (reviewed by Avens and Snover 2013). The size-at-age relationships described by these growth curves are then used to predict ASM assuming reproductive maturation occurs at a specific size. As male size at sexual maturation (SSM) data is lacking and population models

focus on female fecundity, the SSM value typically used to estimate ASM is a single minimum, or more often mean, carapace length observed for nesting females in a population (reviewed by Avens and Snover 2013).

Although some animal populations appear to exhibit strict thresholds for ASM or SSM due to genetic, anatomic, and/or energetic constraints, it is more often the case that individuals both among and within populations mature across a range of ages and sizes (Stearns 1992; Bernardo 1993). An organism's life history represents a series of trade-offs between somatic growth, maintenance, movements, and reproduction, while under the constraint of resource limitation, whereby an individual should devote only sufficient energetic resources toward maintenance and growth to reach a SSM that maximizes lifetime reproductive output (Gadgil and Bossert 1970). ASM represents a balance between delaying maturation long enough to approach optimal SSM, but not so long that the probability of surviving long enough to reproduce is minimized (Gadgil and Bossert 1970). The time required to reach a particular size in turn depends on somatic growth rate, which can vary according to mortality pressures and genetic and environmental influences integrated over pre-maturation life span (Bernardo 1993; Kawecki and Stearns 1993). Due to these complex, interacting factors, every individual is likely to exhibit its own trajectory with respect to growth, development, and maturation schedule (Bernardo 1993).

Sea turtles exhibit a "bet-hedging" life-history strategy, where delayed maturation with corresponding increased SSM, adult survival, and iteroparity is thought to occur in response to stochastic reproductive conditions (e.g., variable hatchling mortality on dynamic nesting beaches) (Sæther et al. 1996; Heppell et al. 1999). The need to delay ASM to reach large SSM is also compatible with observations that female sea turtle reproductive output increases with size (van Buskirk and Crowder 1994). Regional sea turtle populations comprise considerable diversity in genetic composition (Jensen et al. 2013), migratory behavior and habitat use (Musick and Limpus 1997; Plotkin 2003), and mortality pressures (Lewison et al. 2013). Combinations of these influences are likely to underlie the extremely variable somatic growth rates observed within and among both individuals and populations (e.g., Braun-McNeill et al. 2008; Bjorndal et al. 2013b), which in turn have the potential to broaden the possible scope of ASM and SSM. Recent data indicate that captive green sea turtles (*Chelonia mydas*) reared together under the same conditions exhibit a wide range in both ASM and SSM (Bjorndal et al. 2013a). Great variability has also been observed for a small number of wild, known-age nesting Kemp's ridleys assumed to be neophyte nesters (*Lepidochelys kempii*) (Caillouet et al. 2011) and captive Kemp's ridleys (Bjorndal et al. 2014). As a result, although point estimates of

ASM and SSM available to date for sea turtles are informative, additional data are needed regarding potential variability to allow accurate parameterization of population models (NRC 2010).

In addition to promoting increased ASM and SSM, stochastic conditions resulting in highly variable survival of offspring can select for increased reproductive life span (Stearns 1992). For sea turtles, data yielded by long-term saturation tagging studies (e.g., Dahlen et al. 2000; Humburg and Balazs 2014) and inference through the assumption of constant survivorship of nesting females (Frazer 1983a) suggest reproductive longevity may span at least 2 or 3 decades. However, no information regarding adult-stage duration is available for male sea turtles. Consequently, information regarding reproductive longevity remains sparse and further study is needed to gain insight into the duration and variability of individual reproductive contributions and how these might influence population dynamics.

To address these data needs for loggerhead sea turtles (*Caretta caretta*) in the NW Atlantic, we conducted analyses of skeletal growth increments (skeletochronology; reviewed by Avens and Snover 2013) to characterize size-at-age relationships and growth patterns, as well as mean and variability in ASM and SSM. In addition, we investigated post-maturation longevity to provide insight into the possible mean and range of adult-stage duration for loggerheads in this region.

## Methods

### Sample collection and processing

Through cooperation with the National Sea Turtle Stranding and Salvage Network, humerus bones were collected from the front flippers of large juvenile and adult loggerhead sea turtles that stranded along the Atlantic coast of the USA. All turtles from which humeri were taken were either dead at stranding or alive and subsequently euthanized if rehabilitation was not deemed possible; no turtles were killed for the purpose of this study. When possible, sex was determined by the examination of the gonads during necropsy; for adults >95 cm SCL that were not necropsied, sex was inferred from tail length. Straightline carapace length from the nuchal notch to the longest posterior tip (SCL) and stranding location were also collected for each individual when possible. In cases where only curved carapace length (CCL) measurements were available, SCL was calculated using Eq. (1) from Snover et al. (2010).

Humeri were prepared and histologically processed according to the methods of Avens and Snover (2013) and Avens et al. (2013) to yield a digital image of each stained

humerus cross section at 4× magnification. The location and number of the lines of arrested growth (LAGs) that demarcate the outer edges of growth marks within each digital image were independently determined by two readers (LA, LRG), who then worked together to reach consensus where characterizations differed. Each LAG and humerus section diameter (HSD) was measured along the antero-posterior axis of the cross section (Avens and Snover 2013).

## Validation analysis

Application of skeletochronological analysis to a skeletal structure to investigate age and growth is contingent upon several assumptions (Avens and Snover 2013), primarily (1) knowledge of the frequency with which LAGs are deposited in the bone and (2) verification of a predictable, proportional relationship between bone and somatic size and/or growth. Although previous studies of samples from bone-marked, known-age, and tagged loggerhead turtles have demonstrated that typically one LAG is deposited each year in the humerus bone (reviewed by Avens and Snover 2013; Avens et al. 2013) and SCL can be reliably estimated from LAG diameters (Snover et al. 2007; Avens et al. 2013), these studies have predominantly involved mid-sized juveniles. As a result, we applied the methods of Avens et al. (2013) to humeri obtained from large juvenile and adult loggerheads that had been tagged and measured more than a year prior to stranding to test these assumptions for larger turtles as well. LAGs were assigned calendar years based on three different assumptions of annual LAG deposition frequency (1 LAG/year, 2 LAGs/year, and 1 LAG every 2 years) and the LAG predicted to have been deposited closest to the time of tagging under each scenario was identified. The relationship between HSD and SCL measurements for all life stages from hatchling to adult was characterized by combining data collected using identical methods from Avens et al. (2013) with measurements obtained during the current study. This relationship, adjusted for each individual through the application of the body proportional hypothesis (BPH; Francis 1990) as modified for sea turtles (Snover et al. 2007; Avens et al. 2013), was used to estimate SCL at tagging from the diameter of the proposed tagging LAG. Estimated and measured SCLs for each turtle under each deposition frequency scenario were compared using a Wilcoxon signed-rank test. Close correspondence between estimated and measured values would provide support for the annual frequency of LAG deposition used to predict the LAG at tagging and allow age estimation using that frequency (see "Age estimation" section below). In addition, convergence between estimated and measured SCL would validate somatic growth rate

calculation through conversion of LAG diameters to SCL estimates (see "Somatic growth" section below).

## Age estimation

All humeri from large juvenile and adult loggerheads exhibited resorption, or destruction of the diffuse LAG (annulus) denoting the end of the first year of growth, as well as other early LAGs toward the bone's core. As a result, it was necessary to apply a correction factor based on the relationship between early LAG numbers and diameters for small- and mid-sized juvenile loggerheads in this same population (Avens et al. 2013) to estimate the number of missing LAGs per resorption core of a given size. Because resorption core boundaries tend to be indistinct, the diameter of the innermost, measurable LAG was used as a proxy for resorption core diameter. The estimated number of resorbed LAGs was added to the number of observed LAGs to yield a total age estimate. Each final age estimate was adjusted according to mean hatch date for the population and stranding date, to the nearest 0.25 years (Avens et al. 2013).

The validated relationship between HSD and SCL was used to estimate SCL for every measurable LAG in each humerus, and age and calendar year were also assigned to each LAG. To provide size-at-age representation for all life stages in this study population, large juvenile and adult SCL and age-estimate data from the current study were combined with the small- to mid-sized juvenile data collected using identical methods from Avens et al. (2013). A generalized additive mixed model (GAMM) (Wood 2006) that accounted for multiple but varying data points from each turtle was used to fit a nonparametric smoothing spline to the age and SCL-estimate datasets for males and females. This model included SCL as the continuous response variable, age as the fixed covariate, and individual turtle ID as a random effect. Spline fits and 95 % credible bands were then used to estimate ages at different SCLs associated with reproductive maturation for male and female loggerhead sea turtles in the western North Atlantic (Frazer 1983b; Frazer and Ehrhart 1985; Bjorndal et al. 2000, 2001; Snover 2002; TEWG 2009; Vaughan 2009). When only CCL was reported, it was converted to an estimate of SCL using Eq. (1) from Snover et al. (2010) to allow comparison with results from the current study. This GAMM, as well as those applied to model growth (see "Somatic growth" section below), incorporated an identity link and robust quasi-likelihood error function and was implemented using the *mgcv* and *nlme* packages in the statistical program R version 3.1.1 (Wood 2006; R Core Team 2014). Significance of model factors was determined by *t* ratio statistical inference (in the case of nonparametric covariates) and nonparametric *F* ratio test (for continuous covariates).

## Somatic growth

Following the methods of Avens et al. (2013), annual growth rates for each humerus were calculated by taking the difference between successive SCL estimates generated from LAG pairs and each value was assigned to (1) the mean SCL for the growth increment, as well as (2) the calendar year and (3) age estimate for the initial LAG. GAMMs were applied to characterize the potential influence of different covariates on somatic growth rates (the model response variable) for large juvenile and adult loggerheads >80 cm SCL, including fixed effects such as age, SCL, and calendar year (continuous covariates), sex (discrete covariate), and turtle ID as a random, individual-specific effect. Because of high co-concurvity between age and SCL, these factors were separated into two different models (Avens et al. 2012, 2013); GAMM$_{>80\_Age}$ included age, calendar year, and sex and GAMM$_{>80\_SCL}$ incorporated SCL, calendar year, and sex. In addition to describing the overall temporal trend for large juveniles and adults, size class-specific patterns (80–89.9, 90–99.9, 100–109.9) were characterized using linear mixed-effect models implemented using the *nlme* package in the statistical program R version 3.1.1 (R Core Team 2014).

Back-calculated growth rates from the current study were then also combined with those of the smaller neritic juvenile loggerheads from Avens et al. (2013) and incorporated into two additional GAMMs (GAMM$_{All\_Age}$ and GAMM$_{All\_SCL}$) to evaluate growth patterns relative to SCL, age, and calendar year for all neritic samples. In addition, the combined juvenile (neritic and oceanic) and adult growth rates were modeled to estimate age at maturation, for comparison with the results yielded by the explicit SCL and age-estimate relationship (see "Age estimation" section above). An alternative model of somatic growth was constructed using methods initially described by Fabens (1965), and assuming turtle growth is described by the von Bertalanffy (1938) growth function, for which growth rate is a decreasing linear function of size. The paired annual growth rate and initial size data required by the Fabens model were provided by the annual growth rates and back-calculated SCLs associated with every measurable LAG in each humerus section. To address likely nonindependence of back-calculated growth increment data among multiple observations from individual turtles, the data were repeatedly sampled to extract a single paired data point from each turtle. These nonparametric bootstrap samples were then used to estimate the von Bertalanffy parameters $k$ and $L_\infty$ via the Fabens method. This procedure was employed 1000 times to characterize the uncertainty in the von Bertalanffy parameters and to estimate the minimum, mean, and maximum ASM (see "Age estimation" section, above).

## Adult-stage duration

In some amphibians and reptiles, onset of reproductive activity has been demonstrated to coincide with a decrease in LAG spacing within bones, a phenomenon termed "rapprochement" (El Mouden et al. 1997; Francillon-Viellot et al. 1990; Guarino et al. 2008). Although a lack of humerus samples from individuals with fully documented reproductive histories has prevented direct validation of the relationship between onset of reproductive maturation and rapprochement in sea turtles, an abrupt decrease in LAG spacing has previously been observed in humeri of adult-sized turtles (Snover 2002; Goshe et al. 2010; Snover et al. 2013). As reproductively active loggerhead sea turtles exhibit very low growth rates (Frazer 1983a) and validation analyses of humeri from tagged turtles have demonstrated correspondence between bone and somatic measures (Snover et al. 2007; Avens et al. 2013; current study), this decrease in increment spacing is consistent with attainment of reproductive maturity. In the current study, onset of rapprochement was identified first through visual inspection of the posterior lateral edge of each humerus section, as this lateral aspect tended to exhibit less resorption and greater LAG clarity (Fig. 1). In addition, when the extent of resorption allowed measurement of pre-and post-rapprochement LAG diameters, pre- and post-rapprochement growth rates estimated through conversion of LAG diameters to SCL were statistically compared for individuals (Paired *t* test) and for all grouped data (Mann–Whitney rank-sum test). Size (SCL) at maturation for each turtle exhibiting rapprochement was estimated by applying the validated BPH-corrected relationship between HSD and SCL to convert the rapprochement LAG diameter to SCL. Adult-stage duration was estimated by counting the number of LAGs deposited from the rapprochement LAG to the outer edge of the bone and calculating the time period represented by this number using the validated frequency of yearly LAG deposition. Although the extent of LAG compaction at the lateral edges of the bone where diameters were measured impeded counting at this location, LAGs diverged toward the ventral aspect of the cross section (Fig. 1). As a result, LAGs were counted ventrally and then tracked to either lateral edge to determine the location and extent of lateral LAG convergence and determine placement for diameter measurement. The relationship between growth and size at maturation was determined by using SCL at rapprochement as a proxy and determining the extent of its correlation with (1) mean growth for all measurable increments pre- and post-rapprochement; (2) mean growth for 4 years pre- and post-rapprochement (Bjorndal et al. 2013a); and (3) estimated mean lifetime growth rates prior to rapprochement (Bjorndal et al. 2013a). Mean lifetime growth rate for each turtle was calculated by subtracting the mean SCL of
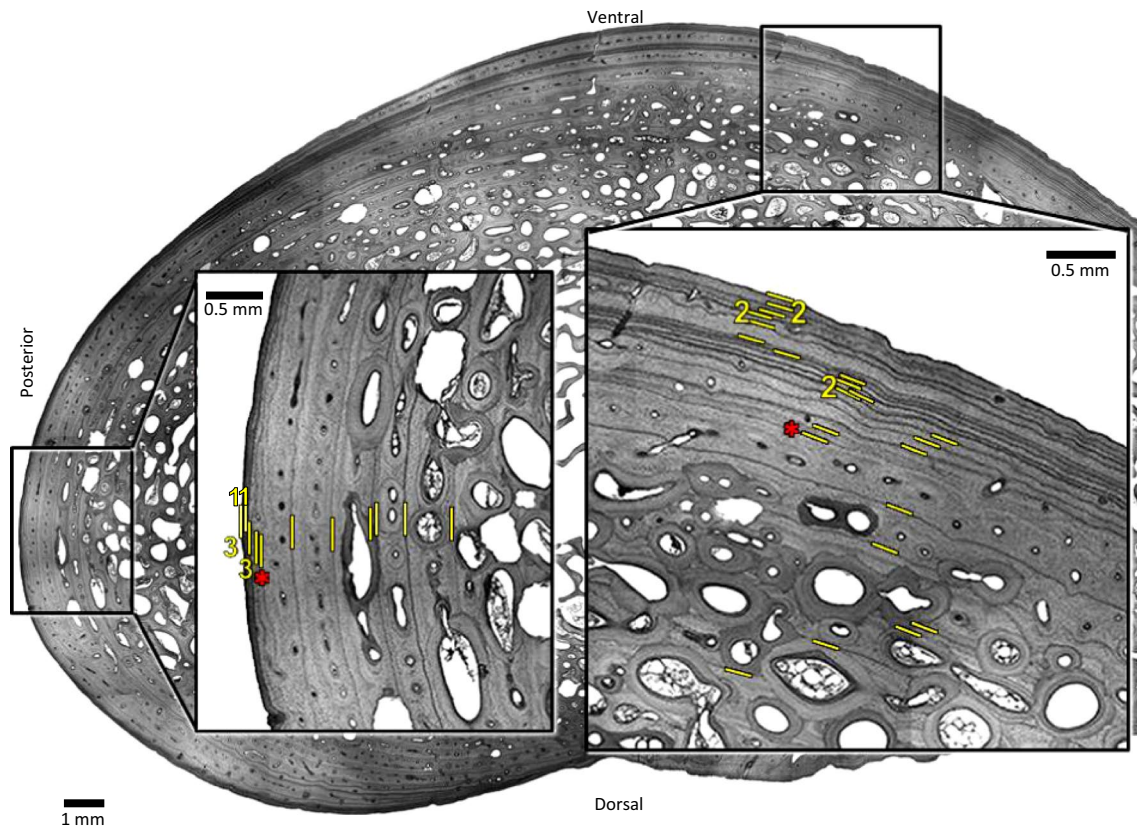
**Fig. 1** Image of histologically processed humerus cross section from a male loggerhead 91.9-cm straightline carapace length (SCL); although processed sections are typically *colored blue*, the image is presented in *black* and *white* to highlight notation in the section. *Lines* of arrested growth (LAGs) that delimit skeletal growth marks are labeled with *yellow bars* and *yellow numbers* denote convergence of multiple LAGs. The *red asterisk* at both the posterior margin and ventral edge is placed at the LAG marking the onset of rapprochement, or the abrupt decrease in LAG spacing consistent with slowing or cessation of somatic growth associated with reproductive maturation. At both the ventral and posterior margins, 19 LAGs are present between the rapprochement LAG and the edge of the bone

hatchling loggerheads in this population (4.6 cm; Avens et al. 2013) from the estimated SCL at rapprochement and dividing this value by the estimated age at rapprochement.

## Results

A total of 67 humeri from large juvenile and adult loggerheads were processed and analyzed, and these data were combined with those obtained using identical methods for 20 humeri from loggerheads >80 cm SCL previously incorporated into the analyses of Avens et al. (2013). The total sample size for large juveniles and adults was therefore 87 humeri from known-sex loggerheads (44 female and 43 male) ranging from 80.0 to 108.2 cm SCL (mean = 94.3 ± 7.8 cm SD), collected during the years 1999–2011 (mean = 2006 ± 2.8 years SD) (see *Supplementary material, Table 1 for geographic distribution and relative sample sizes*). To provide SCL-at-age and growth rate data for all loggerhead life-history stages, the samples

from >80 cm SCL turtles were combined with those from loggerheads <80 cm SCL processed and analyzed using identical methods in Avens et al. (2013). This yielded a total sample of 313 humeri turtles from 8.2 to 108.2 cm SCL (mean = 64.5 ± 21.7 cm SD) collected during the years 1996–2011 (mean = 2003 ± 4.2 years SD).

### Validation analysis

The relationship between SCL and HSD for all loggerhead life stages was determined to be positive and allometric, as found in Avens et al. (2013), but with slope ($b$) = 2.88 and the allometric proportionality coefficient ($c$) = 0.96. No significant difference in the SCL–HSD relationship was found between adult males and females (ANOVA $p = 0.473$). Twelve loggerheads that stranded at ≥80 cm SCL in the sample had been previously tagged and had SCL measured ≥1 year prior to stranding. For these turtles, measured SCL and SCL estimated through conversion of the diameter of the LAG predicted to
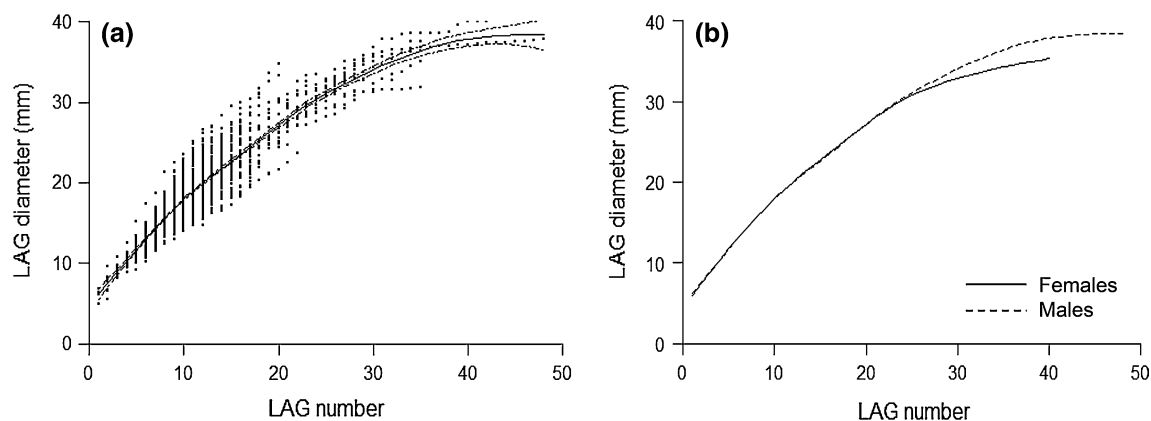
**Fig. 2** Correction factors based on generalized additive mixed models (GAMMs) applied to line of arrested growth (LAG) number: LAG diameter relationships used to account for any LAGs lost to resorption at the core of the humerus. **a** Smoothing spline and 95 % confidence interval fit to all data; **b** smoothing splines fit to female (*solid line*) and male (*dashed line*) data

have been deposited closest to time of tagging using the BPH-corrected allometric equation and assuming 1 LAG was deposited each year were not significantly different ($p = 0.36$, Wilcoxon signed-rank test) and mean difference was 0.6 cm SCL (*Supplementary material, Table 2*). By contrast, predicted and measured SCLs under the other two deposition scenarios were significantly different (1 LAG every 2 years, $p = 0.01$; 2 LAGs per year, $p < 0.01$). These results further validate the assumptions of (1) annual LAG deposition (i.e., 1 LAG per year) for age estimation and (2) application of the validated, BPH-corrected allometric relationship to convert LAG diameters to SCL estimates, as well as annual growth rate calculation by taking the difference between successive SCL-estimate pairs.

## Age estimation

The second-order correction factor described by Avens et al. (2013) allowed estimation of the number of resorbed LAGs for 33 of the loggerheads in the >80 cm SCL sample. As a result, a third-order correction factor was developed by using the second-order correction factor to estimate the number of resorbed LAGs and assign LAG numbers to the remaining LAGs in this subset of 33 humeri, according to the methods of Avens et al. (2013). Although smoothing splines fit to the LAG number and LAG diameter data demonstrated no difference for turtles of both sexes <80 cm SCL, after this point, the relationship diverged for males and females (Fig. 2a, b). Sex-specific third-order correction factors were therefore applied to estimate age for turtles >80 cm SCL. Resorption cores of 6 turtles exceeded the extent of the third-order correction factor, and therefore age estimates were not generated for these turtles; instead, these samples were solely used for growth rate

back-calculation and rapprochement analyses resulting in different sample sizes for models incorporating age versus growth data (e.g., Table 1). The mean estimated number of resorbed LAGs for the total sample ($n = 307$ humeri) was $10 \pm 13$ SD (median = 5; min = 0; max = 54).

Age estimates for loggerhead turtles >80 cm SCL ranged from 18 to 77 years (mean = 45 years $\pm$ 17 SD; median = 44 years), with 18–77 year for females (mean = $46.2 \pm 18.8$ SD) and 21–70 years for males (mean = $43.7 \pm 15.2$ SD). Conversion of every measurable LAG diameter to a SCL estimate using the validated, BPH-corrected allometric equation for the total sample of 313 turtles yielded 2799 SCL-at-age estimates. GAMM spline fits to the overall (Fig. 3a) and sex-specific (Fig. 3b) paired SCL and age estimates were significant ($p < 0.001$ in all cases), and log-likelihood ratio test results indicated random, individual effects were also significant ($p < 0.001$). Sex-specific spline fits and confidence intervals were used to estimate age at minimum and mean SCLs observed for adult male and female loggerheads in the southeastern USA, as well as those yielded by the current study (*see description of estimating SCL from rapprochement LAGs, below*) (Table 2). Mean spline ASM estimates for minimum and mean SSMs predicted from rapprochement were 22.5 and 36.5 years for females and 26 and 40 years for males (Table 2). Spline ASM predictions for a broader range of SSMs drawn from the published literature were 22–39 years for females and 24.5–40 years for males. However, the total range of possible age estimates for loggerheads at these proposed SSMs was 14–50 years for females and 18–63 years for males (Table 2).

Back-calculated SCL-at-age data for loggerheads >80 cm SCL yielded 1007 annual growth increments, and GAMM results (GAMM$_{>80\_Age}$, GAMM$_{>80\_SCL}$) revealed a significant influence of SCL, age, calendar year, and sex on growth response for these turtles (Table 1; *Supplementary*

**Table 1** Summary of statistical output from the generalized additive mixed models (GAMMs) applied to analyze the influence of different potential covariates on growth response for all back-calculated growth data

| Model | Adjusted $R^2$ | AIC | Smooth terms | | | | Parametric coefficients | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Variable | Edf | $F$ | Prob ($F$) | Variable | Estimate | SE | $t$ | Pr > $|t|$ |
| GAMM$_{>80\_Age}$ ($n = 814$) | 0.46 | 1165 | Age (years) | 5.32 | 77.26 | <0.001 | Constant | 0.3 | 0.06 | 5 | <0.001 |
| | | | Year | 3.28 | 8.03 | <0.001 | Sex$_{male}$ | 0.26 | 0.08 | 3.17 | 0.002 |
| GAMM$_{>80\_SCL}$ ($n = 1007$) | −0.13 | 1283 | SCL (cm) | 2.34 | 130.51 | <0.001 | Constant | 0.16 | 0.11 | 1.48 | 0.139 |
| | | | Year | 1 | 0.69 | 0.406 | Sex$_{male}$ | 0.33 | 0.14 | 2.28 | 0.023 |
| GAMM$_{All\_Age}$ ($n = 2670$) | 0.39 | 9364 | Age (years) | 5.38 | 88.38 | <0.001 | Constant | 2.14 | 0.07 | 29.36 | <0.001 |
| | | | Year | 2.72 | 4.92 | 0.003 | Sex$_{male}$ | −0.02 | 0.12 | −0.16 | 0.876 |
| | | | | | | | Sex$_{unk}$ | −0.13 | 0.1 | −1.21 | 0.227 |
| GAMM$_{All\_SCL}$ ($n = 2863$) | 0.43 | 9778 | SCL (cm) | 7.1 | 79.42 | <0.001 | Constant | 2.04 | 0.08 | 26.72 | <0.001 |
| | | | Year | 2.56 | 4.2 | 0.009 | Sex$_{male}$ | −0.02 | 0.12 | −0.18 | 0.856 |
| | | | | | | | Sex$_{unk}$ | −0.12 | 0.11 | −1.08 | 0.281 |

"Edf" denotes the estimated degrees of freedom; SCL is straightline carapace length; "unk" refers to data from turtles whose sex was not determined through necropsy or morphometrics. Sample sizes for the two model types (Age vs. SCL) differ because resorption prevented age assignment for six of the largest turtles in the study
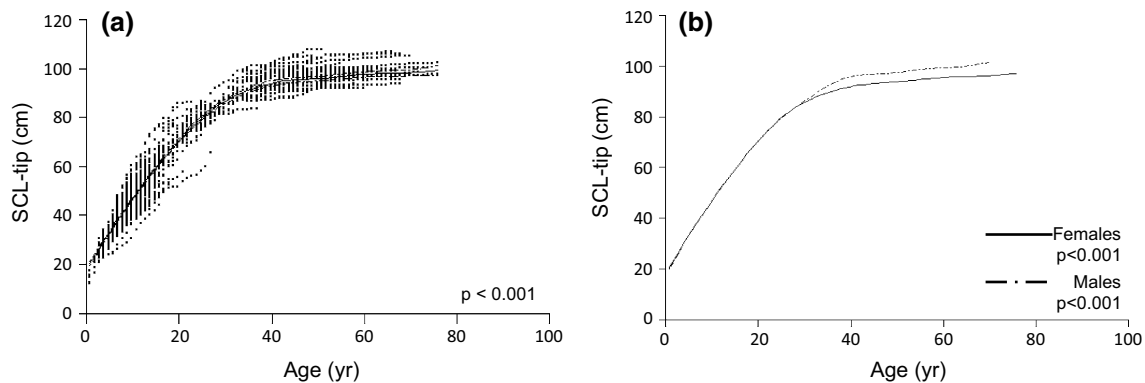


**Fig. 3** Generalized additive mixed model (GAMM) smoothing splines fit to straightline carapace length (SCL) and age estimates back-calculated using skeletochronology for every measurable line of arrested growth (LAG) for 313 loggerhead sea turtles from current study and Avens et al. (2013); **a** all data ($n = 2799$); **b** combined data for juveniles <80 cm SCL with sex-specific data for turtles >80 cm SCL (*solid line* females, $n = 2387$; *dashed line* males; $n = 2364$)

*material, Fig. 1*), and random effects were significant as well ($p < 0.001$, log-likelihood ratio test). Linear mixed-effect model fits demonstrated a consistent and significant decrease in growth rates for all size classes >80 cm SCL from 1975 to 2010 ($p = 0.003$, 80–89.9 cm; $p < 0.001$, 90–99.9 and 100–109.9 cm) (*Supplementary material, Fig. 2*). Estimated growth rates for all loggerhead juvenile and adult size classes were very similar to those yielded by mark-recapture growth studies conducted throughout the same geographic region during a comparable time frame (Fig. 4; Table 3). Combined growth data from the current study and Avens et al. (2013) comprised 2921 annual growth increments associated with 8.8–108.1 cm SCL (mean = $63.9 \pm 25.7$ cm SD), ages 0–75.75 years (mean = $21.0 \pm 18.3$ years SD), and the years 1975–2010

(mean = $1997 \pm 6$ years SD). Because two successive SCL estimates were needed to generate each growth increment, sample size differed between SCL-at-age and growth models (Fig. 3; Table 1). GAMM$_{All\_Age}$ and GAMM$_{All\_SCL}$ incorporating data from all neritic strandings revealed significantly decreasing growth relative to age and SCL overall (Fig. 5a, b). However, the relationship with SCL exhibited a transient increase in growth response ~45–55 cm SCL, approximately at the size when oceanic juveniles are expected to transition to neritic habitat (Avens et al. 2013). Although wide confidence intervals for growth response 1975–1985 prevented reliable interpretation of temporal trends during that time, growth response increased from 1990 to 1996/1997 and then declined through 2010 (Fig. 5c). Random effects were found to be significant for

**Table 2** Summary of estimates of straightline carapace length (SCL) and curved carapace length (CCL) at maturation (size at sexual maturation, SSM) and corresponding ages at sexual maturation (ASM) drawn from published literature (italic)

| Source for SCL at maturation (SSM) | SCL | CCL | Previous ASM estimates | Rapprochement LAG ASM | Spline age | Spline 95 % CI | Total age range | Bootstrap VB age |
|---|---|---|---|---|---|---|---|---|
| *Females* | | | | | | | | |
| Frazer (1983a, b) and Frazer and Ehrhart (1985) | *74* | *80* | *12[a], 13[b]; 29.9[b], 30[a]* | | 22 | 21–23 | 14–25 | 24 |
| Atlantic US Current Study Min | 75 | 82.9 | – | 22.75 | 22.5 | 22–23 | 15–25 | 25 |
| NW Atl Min (NMFS and USFWS 2008) | *81.8* | 87 | *26.5[c,d]* | | 26.5 | 26–28 | 23–30 | 30 |
| NW Atl Min (TEWG 2009) | 82 | 87.2 | – | | 27 | 26–28 | 23–30 | 30 |
| Frazer (1983a, b) | *87.1* | *94.1* | *21.7[b], 28.0[b]* | | 31.5 | 30–33 | 28–33 | 34 |
| Snover (2002) and Vaughan (2009) | *90* | *97.3* | *30.8[e]; 33.9 ± 3.6 SD[f]* | | 35.5 | 34–38 | 32–38 | 37 |
| Atlantic US Current Study Mean | 90.5 | 97.6 | – | 36.1 | 36.5 | 34–39 | 33–47 | 38 |
| NW Atl Mean (TEWG 2009) | *91.2* | *98.2* | *45 (38–52)[g]* | | 38 | 35–40 | 33–47 | 38 |
| Frazer and Ehrhart (1985) | *92* | *99.5* | *30[a], 47[a]* | | 39 | 35–44 | 32–50 | 39 |
| Frazer (1983a, b) | *92.2* | *99.7* | *31.4[b], 46.4[b]* | | 39 | 35–44 | 32–50 | 39 |
| *Males* | | | | | | | | |
| NW Atl Min (NMFS and USFWS 2008) | *78.4* | *83* | – | | 24.5 | 24–25 | 18–28 | 27 |
| Atlantic US Current Study Min | 80.6 | 88.2 | – | 26.75 | 26 | 25–27 | 19–32 | 28 |
| Atlantic US Current Study Mean | 95.8 | 102.7 | – | 37.1 | 40 | 37–46 | 31–63 | 42 |

Estimates of SSM from the current study based on SCLs associated with rapprochement LAGs (e.g., Figure 1) are interspersed in non-italicized cells. Ages at maturation (ASM) for all proposed SSMs estimated from (1) mean age associated with rapprochement LAG (rapprochement LAG ASM); (2) smoothing spline and 95 % confidence interval fit to back-calculated SCL-at-age data (spline ASM, 95 % CI, total age range); (3) bootstrapping and fitting Fabens modified von Bertalanffy growth curve to back-calculated growth data (bootstrap VB ASM)

[a] Frazer and Ehrhart (1985); [b] Frazer (1983b); [c] Bjorndal et al. (2000); [d] Bjorndal et al. (2001); [e] Snover (2002); [f] Vaughan (2009); [g] Scott et al. (2012)

these models as well ($p < 0.001$, log-likelihood ratio test). Bootstrapping growth increments to fit Faben's modified von Bertalanffy growth curve yielded mean values for *k* of 0.045 and 0.043 for females and males, respectively, and estimates of $L_{inf}$ in cm SCL ranged from 110.2 to 110.9 for females (mean = 110.7) and 113.7–114.1 (mean = 114.0) for males. Estimates of age at maturation yielded by this approach for the minimum and mean SSMs predicted from rapprochement were 25 and 38 years for females and 28 and 42 years for males. For the entire range of proposed SSMs drawn from the literature, ASM estimates ranged from 24 to 39 years for females and 27–42 years for males (Table 2).

Humeri of 59 loggerheads (76.0–108.2 cm SCL at stranding; mean = 97.5 ± 6.7 cm SD) exhibited an abrupt decrease in LAG spacing consistent with rapprochement (e.g., Fig. 1). Of that subset, it was possible to estimate

SCL at rapprochement for 38; resorption interfered with accurate total diameter measurements for the remainder (Table 4). SCL at rapprochement ranged from 75.0 to 103.8 cm, with male values tending to be slightly higher than those for females (Table 4). Resorption core size allowed estimation of age at rapprochement for 46 turtles using the third-order correction factor and estimates ranged from 22.75 to 50.75 years for females (mean = 36.1) and 26.75–50.75 years for males (mean = 37.1) (Tables 2, 4). Post-rapprochement longevity, i.e., adult-stage duration, ranged from 4 to 46 years with an overall mean of 19 years (Fig. 6a), but with estimates for females being slightly greater than those for males (Table 4).

For another subset of 18 turtles whose humeri exhibited rapprochement, it was possible to calculate a series of annual growth increments prior and subsequent to

**Fig. 4** Graphical comparison of size class-specific growth rates back-calculated using skeletochronology (*black bars*; current study, Avens et al. 2013) and measured through mark recapture (*white bars*; Bjorndal et al. 2013b) for US Atlantic loggerhead sea turtles. *Horizontal line* through *each bar* represents the mean and extent of *bar* to *either side* represents range within one standard deviation. Whiskers encompass total range of growth rates, and sample size for each group is shown above top whisker
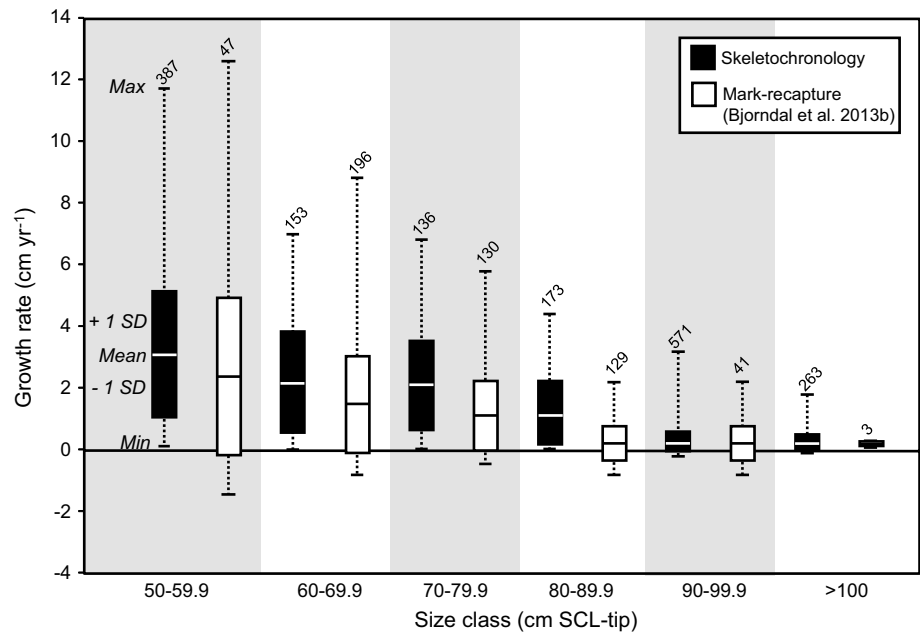


the rapprochement LAG. Post-rapprochement growth was significantly slower than pre-rapprochement growth for both individuals ($p < 0.001$; Paired $t$ test) and overall ($p < 0.001$; Mann–Whitney rank-sum test) (Fig. 6b). No relationship was found between estimated SCL at rapprochement and mean growth rates averaged over all measurable pre- (Spearman, $r_s = 0.174$, $p = 0.482$, $n = 18$) and post- (Spearman, $r_s = -0.181$, $p = 0.466$, $n = 18$) rapprochement increments, as well as 4 years pre- (Spearman, $r_s = -0.370$, $p = 0.127$, $n = 18$) and 4 years post- (Spearman, $r_s = -0.150$, $p = 0.546$, $n = 18$) rapprochement. However, a significant negative correlation was found between mean annual growth rate calculated over the life of each turtle prior to rapprochement and estimated age at rapprochement (ASM; Spearman, $r_s = -0.918$, $p < 0.001$, $n = 18$; Fig. 7a) and was found to account for the majority of the variation (linear regression; $p < 0.001$, $R^2 = 0.916$). A negative correlation between estimated lifetime mean annual growth rate and the size at rapprochement was also found (SSM; Spearman, $r_s = -0.575$, $p = 0.013$, $n = 18$; Fig. 7b), although this relationship was not as strong and only accounted for a small amount of the observed variation (linear regression; $p = 0.02$, $R^2 = 0.304$). Mean lifetime annual growth rates were estimated to range from 1.79 to 3.23 cm SCL years$^{-1}$ (mean = 2.62, SD = 0.37, CV = 0.14). A significant, positive correlation was found between estimated ASM and SSM (Spearman, $r_s = 0.822$, $p < 0.001$, $n = 18$; Fig. 7c), accounting for roughly half of the variation observed in the relationship (linear regression; $p < 0.001$; $R^2 = 0.530$).

## Discussion

Age at maturation has frequently been identified as a critical demographic parameter for improving population models to facilitate management and conservation of threatened and endangered sea turtle populations (Heppell et al. 2003; NRC 2010). However, obtaining these data can be challenging due to the generally slow somatic growth, delayed maturation, and highly migratory behavior characteristic of sea turtle species, which make it difficult to follow individuals throughout development and maturation (Avens and Snover 2013). In addition, adult sea turtle population data are necessarily biased toward females that can be more readily studied when they come ashore to nest, while data collection for males is more opportunistic and infrequent, as they remain relatively inaccessible in the marine environment throughout their lives (Arendt et al. 2012). Furthermore, although point estimates of ASM offer some insight into this demographic parameter and its potential influence on population dynamics, accurate characterization requires information regarding not only mean values, but also variability, temporal trends, and potential sex-specific differences (NRC 2010).

To gain a broader understanding of characteristics associated with maturation for loggerhead sea turtles in the western North Atlantic, we applied skeletochronological analysis to humerus bones collected from dead, stranded turtles ranging from oceanic-stage juveniles to mature adults. This approach allowed estimation of annual, somatic growth rates for different life stages over decadal time frames, as well as size-at-age relationships

**Table 3** Comparison of loggerhead size class-specific growth rates [cm year$^{-1}$; straightline carapace length (SCL)] back-calculated using skeletochronology in the current study to those yielded by mark-recapture studies along the Atlantic US coast

| Mean SCL | Growth rates (cm year$^{-1}$) | | |
|---|---|---|---|
| | Skeletochronology | Mark recapture | |
| | Current study and Avens et al. (2013) | Bjorndal et al. (2013b) | Braun-McNeill et al. (2008) |
| 4.6–9.9 | 8.8 ± 0.1 (8.7 and 8.9) n = 2 | | |
| 10–19.9 | 6.6 ± 4.8 (1.3–13.7) n = 9 | | |
| 20–29.9 | 2.6 ± 1.1 (0.7–4.7) n = 99 | | |
| 30–39.9 | 2.6 ± 1.4 (0.1–7.3) n = 493 | 5.9 (2.9 and 8.9) n = 2 | – |
| 40–49.9 | 2.8 ± 1.6 (0.1–14.9) n = 635 | – | – |
| 50–59.9 | 3.1 ± 2.0 (0.1–11.7) n = 387 | 2.4 ± 2.5 (−1.4 to 12.6) n = 47 | 1.58 (−1.0 to 5.7) n = 44 |
| 60–69.9 | 2.2 ± 1.6 (0.0–7.0) n = 153 | 1.5 ± 1.5 (−0.8 to 8.8) n = 196 | 1.82 (−0.2 to 6.1) n = 122 |
| 70–79.9 | 2.1 ± 1.4 (0.0–6.8) n = 136 | 1.1 ± 1.1 (−0.5 to 5.8) n = 130 | 1.63 (0.1 to 7.3) n = 43 |
| 80–89.9 | 1.0 ± 1.1 (0.0–4.4) n = 173 | 0.2 ± 0.4 (−0.7 to 2.5) n = 129 | – |
| 90–99.9 | 0.2 ± 0.4 (0.0–3.2) n = 571 | 0.2 ± 0.5 (−0.8 to 2.2) n = 41 | – |
| >100 | 0.2 ± 0.3 (0.0–1.8) n = 263 | 0.2 ± 0.1 (0.1 to 0.3) n = 3 | – |

and maturation trajectories for both males and females. Results of the current analyses reinforced the high somatic growth rate variability and temporal trends characterized through previous mark-recapture studies. Sex-specific differences in subadult growth patterns and maturation attributes were observed, and estimates of ages and sizes at maturation, as well as adult-stage durations, spanned a wide range.

The variability observed in the current study is perhaps not surprising, as freshwater turtle population studies have revealed sex-specific, temporally varying growth patterns and maturation schedules, in addition to differences between geographically adjacent populations that diverge only somewhat in habitat and forage type (Gibbons 1967; Gibbons et al. 1981; Frazer et al. 1991a, b; Snover et al. 2015). In comparison, movements and habitat use for the loggerhead sea turtle population considered in the current study encompass much of the North Atlantic Ocean basin (Bolten 2003; Ceriani et al. 2014). Within this large region, dichotomies in migration and foraging strategies have been observed for both juveniles (McClellan and Read 2007; Mansfield et al. 2009) and adults (Reich et al. 2009) and individuals appear to exhibit a degree of consistency in resource use at different life stages (Avens et al. 2003; McClellan et al. 2010; Vander Zanden et al. 2010). Available data suggest that in some cases, differences in
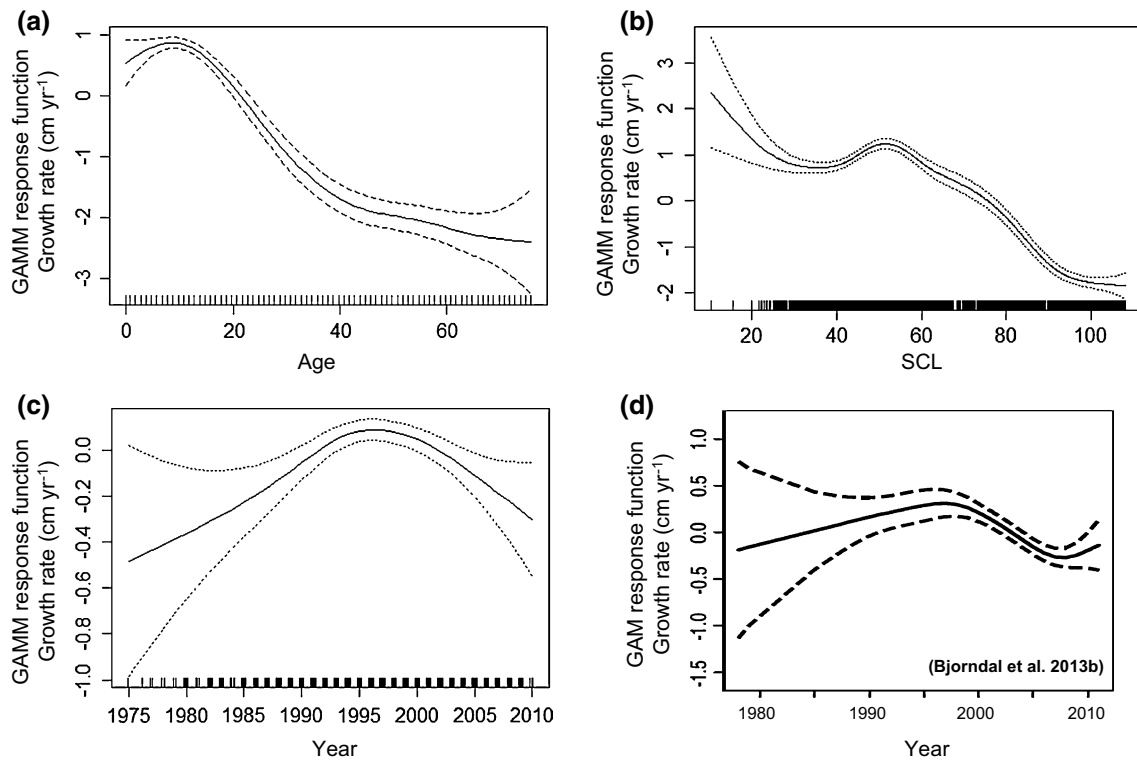
**Fig. 5** Graphical summary of covariates exhibiting a significant influence on growth response for generalized additive mixed models (GAMMs) incorporating back-calculated growth rates for juvenile and adult loggerhead sea turtles. Within the models, age and year are the age estimate and calendar year associated with the line of arrested growth (LAG) marking the beginning of the growth interval; SCL is the mean straightline carapace length for the back-calculated growth interval. **a** GAMM$_{All\_Age}$; **b**, **c** GAMM$_{All\_SCL}$ (see Table 1 for statistical output). **d** Graphical output of growth response by year for GAM incorporating mark-recapture growth rate data collected along the US Atlantic coast (Bjorndal et al. 2013b) for comparison with (**c**). For each factor plotted, the *solid line* represents the mean growth response (on a response scale centered around 0) for the covariate conditioned on other covariates included in the model and the *dashed lines* represent the extent of the 95 % Bayesian credible interval. The "rugs" or short, vertical lines above the *horizontal axes* represent the numbers and/or distributions of covariate values

**Table 4** Summary of estimates of size at sexual maturation (SSM), age at sexual maturation (ASM), and adult-stage duration (i.e., longevity following maturation) for US Atlantic loggerheads as inferred from the rapprochement line of arrested growth (LAG) (e.g., Fig. 1)

| Loggerhead attributes related to reproductive maturation estimated from rapprochement | | | | | | | | Kemp's ridleys[a] | | Kemp's ridleys (captive)[b] | | Green sea turtles (captive)[c] | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $n$ | Mean | SD | Min | Max | Median | CV | $n$ | CV | $n$ | CV | $n$ | CV |
| *SSM (cm; SCL notch to tip)* | | | | | | | | | | | | | |
| All | 59 | 92.9 | 6.6 | 75 | 103.8 | 93 | 0.07 | – | – | – | – | – | – |
| Females | 32 | 90.5 | 5.8 | 75 | 101.3 | 91.3 | 0.06 | 49 | 0.03 | 14 | 0.07 | 47 | 0.07 |
| Males | 27 | 95.8 | 6.5 | 80.6 | 103.8 | 96.2 | 0.07 | – | – | – | – | – | – |
| *ASM (years)* | | | | | | | | | | | | | |
| All | 59 | 36.6 | 7.9 | 22.75 | 50.75 | 35.75 | 0.22 | – | – | – | – | – | – |
| Females | 32 | 36.1 | 9.2 | 22.75 | 50.75 | 34.75 | 0.25 | 49 | 0.24 | 14 | 0.25 | 47 | 0.11 |
| Males | 27 | 37.1 | 6.5 | 26.75 | 50.75 | 36.75 | 0.18 | – | – | – | – | – | – |
| *Adult-stage duration (years)* | | | | | | | | | | | | | |
| All | 59 | 19 | 11 | 4 | 46 | 19 | 0.58 | – | – | – | – | – | – |
| Females | 32 | 20 | 13 | 4 | 46 | 18.5 | 0.65 | – | – | – | – | – | – |
| Males | 27 | 18 | 9 | 4 | 42 | 19 | 0.5 | – | – | – | – | – | – |

[a] Caillouet et al. (2011); [b] Bjorndal et al. (2014); [c] Bjorndal et al. (2013a)
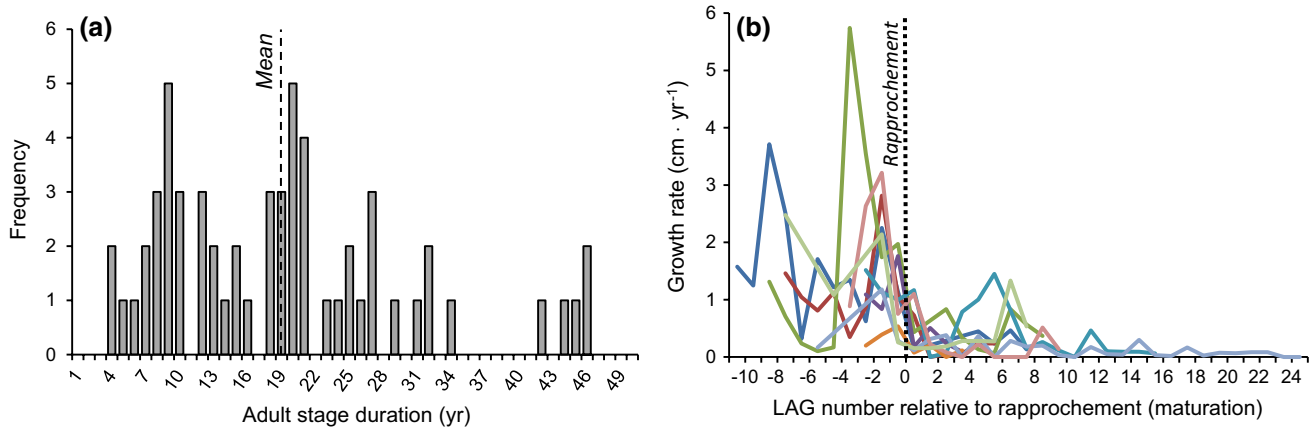
**Fig. 6 a** Frequency distribution of longevity after reaching reproductive maturity (i.e., adult-stage duration for all loggerheads whose humeri exhibited rapprochement, or the abrupt decrease in line of arrested growth (LAG) spacing associated with maturation (e.g., Fig. 1). **b** Back-calculated growth rates relative to the rapprochement LAG, designated here as LAG 0; *negative numbers* correspond with pre-rapprochement LAGs and *positive numbers* with post-rapprochement LAGs. Growth was significantly higher pre-rapprochement than post-rapprochement for both individuals and the entire group ($p < 0.001$ in both cases; see text for details of analysis)
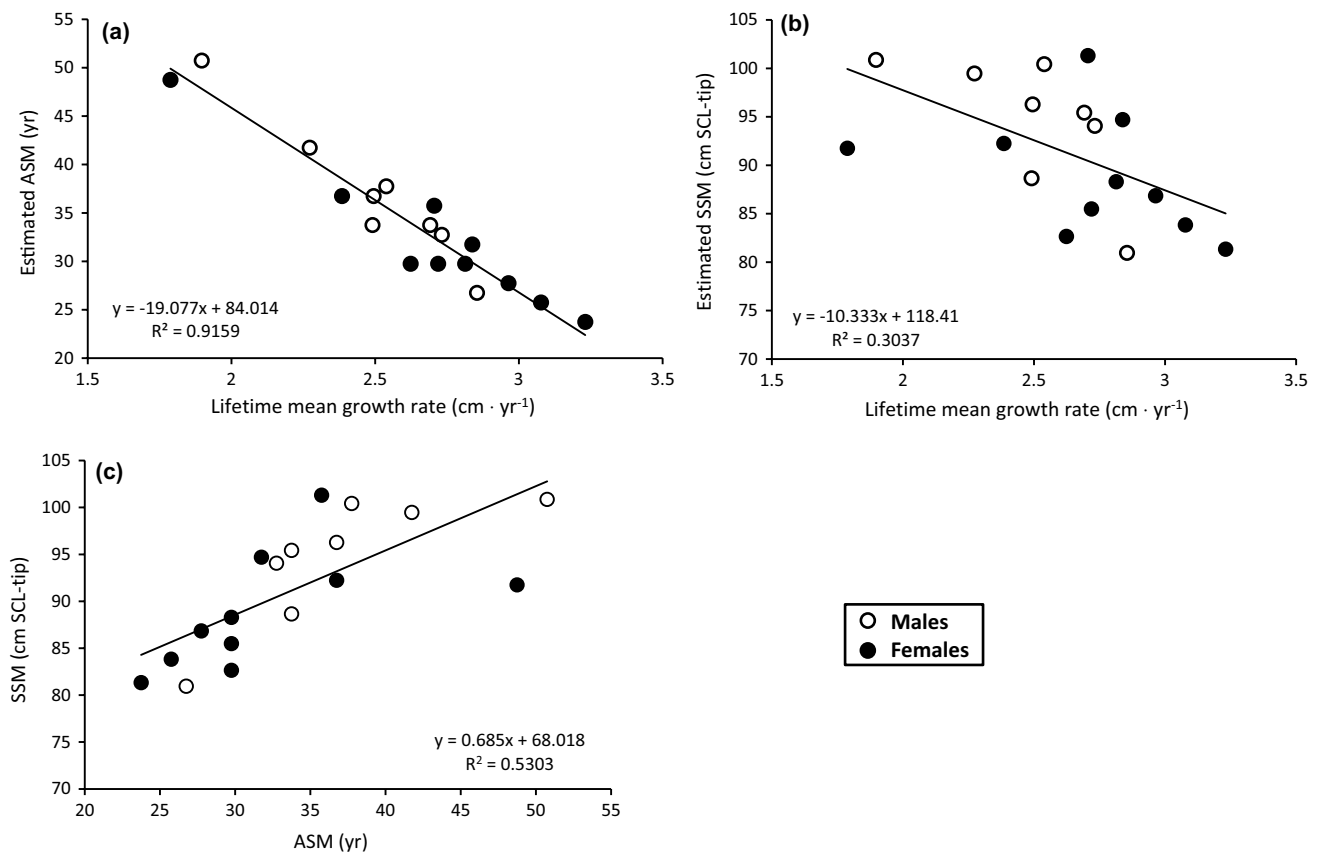






**Fig. 7** Relationships between lifetime mean growth rate and **a** age at sexual maturation (ASM) and **b** size at sexual maturation (SSM). **c** Relationship between ASM and SSM (see text for details of analysis and Spearman's correlation statistics). *Open circles* denote males; *solid circles* denote females

foraging habitat may not influence reproductive parameters (Hawkes et al. 2007), while in others effects have been observed (Vander Zanden et al. 2014). Future advances in

the skeletochronological approaches detailed in this study combined with annual skeletal growth increment-specific stable isotope (e.g., Avens et al. 2013) and trace element

(e.g., López-Castro et al. 2014) analyses have the potential to facilitate investigation of associations between habitat use, growth, and reproductive attributes.

## Age and size at sexual maturation (ASM and SSM)

In the current study, three different approaches involving skeletochronological data were applied to investigate ASM for loggerhead sea turtles in the western North Atlantic: (1) inference from the skeletal growth mark associated with maturation (i.e., the rapprochement LAG), (2) fitting nonparametric curves to SCL-at-age estimates, and (3) fitting parametric, von Bertalanffy growth curves to SCL-at-age relationships inferred from annual growth rate estimates. These approaches allowed evaluation of ASM for both males and females and sex-specific differences were yielded by each type of analysis. The total range of potential ASMs for both males and females was quite broad (Tables 2, 4), indicating the absence of a knife-edge maturation threshold for this population, similar to what has been reported in other studies (Limpus and Limpus 2003; Caillouet et al. 2011; Bjorndal et al. 2013a, 2014). The lower ends of the ranges of age estimates for proposed, minimum SSMs offer insight into potential for relatively early maturation (Table 2, total age range). However, caution should be taken with respect to interpreting age estimates toward the upper end of the total age range for larger SCLs as actual ASM estimates (Table 2); while these ages represent possible maxima for a given SCL, individuals at these SCLs might already have matured at a smaller size and earlier age. Mean ASM estimates yielded by the three different approaches converged closely, with highest estimates resulting from the von Bertalanffy growth curve fits (Table 2). Overall, central predictions of minimum and mean ASM from all analyses were 22.5–25 and 36–38 years for females and 26–28 and 37–42 years for males. Although the minimum and mean ASM estimates yielded by the current study are within the range previously proposed for female loggerhead sea turtles in this geographic region (Table 2), these results represent the first such data for males.

Convergence among mean ASM estimates yielded by the different approaches indicates that analysis of rapprochement skeletal growth marks may be an effective tool for studying aspects of reproductive maturation for sea turtles, as has been demonstrated for some amphibians and reptiles (Francillon-Viellot et al. 1990; El Mouden et al. 1997; Guarino et al. 2008). No humeri from females with a known first nesting year were available for analysis to allow validation of correspondence between rapprochement and onset of reproductive activity. However, for those adult females in the sample with known nesting events ($n = 10$ individuals), all LAGs assigned to years that corresponded

with nesting years were deposited subsequent to the rapprochement LAG. Despite potential association between rapprochement and onset of maturation, it is important to note that this anatomic feature might not correspond with age at first reproductive contribution to the population (e.g., for female sea turtles age at first nesting (AFN); Caillouet et al. 2011). For example, in captive, female green turtles and Kemp's ridleys some individuals were observed to reproduce immediately after attaining SSM, while others delayed reproduction for several years (Bjorndal et al. 2013a, 2014). In the current study, patterns of LAG deposition following rapprochement along the ventral aspect of humerus sections for adult female loggerheads were suggestive of periodicity that could correspond with reproductive cycles (i.e., recurring clusters of several closely spaced LAGs followed by single intervals of broader spacing between clusters). Analysis of these patterns and/or isotope or elemental composition of individual skeletal growth marks in humeri of females with complete nesting histories would be informative for elucidating both onset of reproduction (nesting) as well as reproductive frequency.

SSMs calculated through conversion of rapprochement LAG diameters to estimates of SCL in the current study spanned a wide range, with 75–101.3 cm SCL for females and 80.6–103.8 cm SCL for males (Table 4). For males, while minimum estimated SSM is comparable to that previously proposed (Table 2; NMFS and USFWS 2008), other mean male SSM data were not available for comparison with results from the current study. Although for females, both minimum and mean SSM estimates fall within the range of previously proposed values, the mean is lower than the majority of earlier estimates (Table 2; Bjorndal and Meylan 1983). It is possible that this discrepancy reflects differences in sample size and time frames among studies. However, it could also be due to the fact that the mean SSM estimate in the current study incorporates only SCL estimated at initial maturation, while many other reported values (e.g., references in Table 2) have necessarily represented the mean size of all mature females observed for a given nesting population, potentially increasing SSM estimates. In a recent study, although neophyte nester status could not be demonstrated, mean size of only those female loggerheads observed on the beach for the first time at a nesting location along the US Atlantic coast was 91.2 cm SCL (Ehrhart et al. 2014), more similar to the result reported herein (90.5 cm SCL). When estimating ASM, effects of even these minor differences can become magnified, as the slow growth rates documented for loggerheads >90 cm SCL (e.g., Table 3) translate into the need for long periods of time to grow very small increments.

Recent studies of captive-reared female green sea turtles (*C. mydas*; Bjorndal et al. 2013a) and head-started and captive female Kemp's ridley sea turtles that have nested

(*L. kempii*; Caillouet et al. 2011; Bjorndal et al. 2014) have provided information regarding possible ranges of ASM and SSM for sea turtles. Comparison of the coefficients of variation (CV) for ASM and SSM yielded by these studies with the estimates for female loggerheads presented herein offers interesting insights into potential variability surrounding these traits for the different species (Table 4). Loggerhead CV for SSM was comparable to that calculated for the captive green turtles and head-started Kemp's ridleys, but much greater than that described for the wild Kemp's ridleys. Perhaps one factor contributing to this difference is that mean SSM for loggerheads (90–92.2 cm SCL; summarized in Table 2) and greens (99.5–101.5 cm SCL; reviewed by Goshe et al. 2010) is far greater than that for Kemp's ridleys (60–65 cm SCL; Heppell et al. 2005), potentially allowing for greater variability around optimal SSM while still maximizing reproductive output (van Buskirk and Crowder 1994). Although the captive Kemp's ridley CV for SSM was unexpectedly comparable to that for the wild loggerheads and captive greens, it is possible that this increased variability relative to head-started Kemp's ridleys resulted from the unusually small minimum and mean SSM observed for the species under captive conditions (i.e., 47.0 and 55.2 cm CCL, respectively; Bjorndal et al. 2014). By comparison, the captive green turtles did not exhibit a similar lowering of minimum and mean SSMs (i.e., 87.6 and 101.8 cm CCL; Bjorndal et al. 2013a) relative to their wild counterparts (i.e., 83.2 and 99.5–101.5 cm SCL; reviewed by Goshe et al. 2010). In contrast to the SSM results, loggerhead CV for ASM was comparable to those for both the wild and captive Kemp's ridleys, but more than twice as large as that for the green turtles (Table 4). In part, this result might be expected, as the variability for the captive green turtles would predominantly reflect genetic effects, while for the wild loggerheads and head-started Kemp's ridleys myriad external factors, both internal (genetic) and external (e.g., forage availability, migratory behavior, environmental conditions, mortality pressures) would all exert different influences on individuals, resulting in different developmental and maturation trajectories (Bernardo 1993). The high CV for ASM in the captive Kemp's ridleys may relate to the increased CV for SSM described above.

Comparison of results from the current study with ASM and SSM estimates for loggerheads in the Mediterranean Sea may offer additional insights into the potential influence of different factors on growth and maturation. Piovano et al. (2011) fit growth models to somatic growth rates back-calculated using skeletochronology for loggerhead sea turtles stranded in the Mediterranean that were determined to be either of western North Atlantic or Mediterranean genetic origin. Results indicated that loggerheads of Atlantic origin grew more slowly in the Mediterranean and

would take longer to reach maturity, particularly given that nesting female loggerheads in the Mediterranean are much smaller than those in the western North Atlantic (Piovano et al. 2011). Growth rates for juveniles in the two groups were comparable until approximately 50 cm CCL, at which point growth rates for juveniles of Atlantic origin declined. A portion of juvenile loggerheads in the western North Atlantic exhibits a shift from oceanic to neritic habitat at this size, which appears to correspond with an increase in growth potential (Snover et al. 2010; Avens et al. 2013). Therefore, it is possible that juvenile loggerheads of Atlantic genetic origin might simply not be able to express optimal phenotypes in Mediterranean developmental areas as a result of environmental differences (Metcalfe and Monaghan 2001). In contrast to the declining growth rates for Atlantic origin loggerheads in the Mediterranean, those for the juveniles of Mediterranean origin increased above 50 cm CCL and remained high beyond minimum and mean adult carapace lengths for this population. This result is of particular interest, as somatic growth typically declines and becomes negligible as sea turtles reach maturity (Frazer 1983a), suggesting differences in maturation trajectories for the Mediterranean and Atlantic populations. However, comparison of size-at-age relationships for Atlantic loggerheads in the current study to those of Mediterranean origin inhabiting Mediterranean foraging areas (Piovano et al. 2011) indicates that although the slopes of the trajectories might periodically differ, the final outcome is comparable. ASMs for minimum, mean, and maximum nesting female SSMs in the Mediterranean of 66.4, 69, and 84.7 cm CCL have been estimated at 15–28 years based on Mediterranean growth studies (Casale et al. 2009, 2011a, b; Piovano et al. 2011), and the size-at-age relationships from the current study infer similar ASMs of 16–24 years at those same CCLs. This result suggests that Mediterranean loggerheads might not be growing faster than those in the western North Atlantic to reach smaller SSMs at earlier ASMs, but only that SSM and ASM have shifted downward along the growth trajectory for the Mediterranean population. Given the positive relationship between carapace length and clutch size, decreasing SSM for the Mediterranean loggerhead population may seem to run counter to maximization of reproductive output, but perhaps could reflect the outcome of prolonged, high mortality pressures, as seen in heavily exploited fish populations (Trippel 1995).

Life-history theory predicts that the ASM and SSM achieved by an individual represent a balance between delaying maturation sufficiently to attain SSM that will optimize lifetime reproductive success, while minimizing the probability of mortality prior to maturation (Gadgil and Bossert 1970). Furthermore, growth rates during development should be negatively correlated with ASM so that organisms experiencing rapid juvenile growth

will generally mature earlier (Stearns and Koella 1986; Day and Rowe 2002). In some cases, lower ASMs may also correspond with larger SSMs, where individuals exhibiting the fastest growth reach larger sizes more quickly, while conversely individuals with the slowest growth may exhibit the highest ASMs and yet the smallest SSMs, as they mature at minimum reproductively viable sizes (Day and Rowe 2002). Although the sample size from the current study appropriate for investigating relationships between growth, ASM, and SSM was small ($n = 18$), these data provided a means to begin to investigate these concepts for wild loggerhead sea turtles. Similar to observations made for Blanding's turtles (*Emydoidea blandingii*; Congdon and van Loben Sels 1993), captive green sea turtles and Kemp's ridleys (Bjorndal et al. 2013a, 2014), and head-started Kemp's ridley sea turtles (Caillouet et al. 2011), loggerheads were estimated to reach reproductive maturation over a wide range of SSMs. Taken together with negligible estimated growth rates following maturation (Fig. 6b) and a positive relationship between ASM and SSM (Fig. 7c), these results suggest that the turtles do not exhibit a population-wide SSM or "physical" threshold (Plaistow et al. 2004) and that SSM is instead influenced by individual growth trajectories and/or ASMs (Congdon and van Loben Sels 1993). Consistent with life-history theory predictions and results of previous turtle studies (Congdon and van Loben Sels 1993; Bjorndal et al. 2013a), in the current study, higher mean annual lifetime growth rates for loggerheads corresponded strongly with lower ASMs (Fig. 7a). In contrast to these prior studies, as well as predictions of larger size at maturation with faster developmental growth, higher mean annual lifetime growth rate estimates also corresponded negatively with SSM (Fig. 7b). However, this relationship was less robust than that observed between growth and ASM, suggesting that other factors (e.g., mass growth trajectories; Bjorndal et al. 2013a) might exert greater influence in determining the size at which resources are diverted from SCL growth to reproductive effort, consistent with the existence of an "overhead threshold" for maturation for the species (Plaistow et al. 2004).

## Growth

Means and statistical distributions for growth rates back-calculated by applying validated conversion of skeletal growth mark diameters to SCL estimates were quite comparable to growth rates measured during mark-recapture studies in this region (Fig. 4; Table 3). The largest discrepancy between means of 1.0 cm year$^{-1}$ was observed for the 70–79.9 size class. Because the number of turtles in each group is comparable for the two data sources, it is unlikely that

the difference is the result of sample size and instead may reflect temporal and/or geographic influences. Despite some variation, the overall observed convergence demonstrates that the annual growth rates generated using this approach are representative of loggerheads inhabiting areas along the US Atlantic coast and highlights the utility of skeletochronology for obtaining long-term growth rate data, both for individuals and for populations. However, because growth rates have been found to vary in the northwestern Atlantic, increasing significantly at lower latitudes (Bjorndal et al. 2013b), the growth and size-at-age relationships described herein are specific to the US Atlantic coast and should not be applied outside the geographic scope of the study. Additional skeletochronological analysis of loggerhead samples from other geographic areas (e.g., the Gulf of Mexico and Caribbean) is needed to allow regional comparison of growth patterns and resulting estimates of ASM.

Prior analyses of small oceanic and neritic juvenile loggerheads in the northwestern Atlantic indicated no sex-specific differences in growth rates for juvenile loggerheads <80 cm SCL (Fig. 3b; Avens et al. 2013). However, analysis of humeri from large juvenile and adult loggerheads demonstrated that for turtles >80 cm SCL, males exhibited faster growth rates than females (Fig. 3b; Table 1; Supplementary material, Fig. 1c, f), resulting in divergent SCL-at-age relationships that necessitated sex-specific estimates of ASM. This difference is also reflected in the larger SSM estimates associated with the rapprochement LAG for males than for females (Table 4). The finding that adult male loggerheads might grow faster and mature at larger sizes than females is in contrast to previous studies of other species, where the opposite pattern has been found for green turtles (Hirth 1997; Limpus and Chaloupka 1997) and hawksbills (*Eretmochelys imbricata*; Chaloupka and Limpus 1997). Furthermore, in freshwater turtle populations, females are commonly found to exhibit greater SSMs and corresponding ASMs than males, which is thought to reflect the greater reproductive advantage (i.e., increased clutch size) conferred for females by delaying maturation to reach larger body size (Gibbons et al. 1981; Snover et al. 2015). Nevertheless, this result from the current study is consistent with available data indicating that mature male loggerhead carapace lengths are greater than those of females in this population (Dodd Jr 1988; Kamezaki 2003). Bimaturism where male ASM and SSM are greater than that of females can occur in animal populations where males compete with one another for mating opportunities (Stearns 1992). Although information regarding loggerhead sea turtle courtship and mating behavior is scarce, observations indicate that male–male combat and interference with mating pairs by attendant males occur (Scholfield et al. 2006), which could influence manifestation of bimaturism in loggerhead populations.

Generalized additive mixed models (GAMMs) incorporating growth data from neritic turtles stranded along the US Atlantic coast demonstrated that, overall, growth response declined significantly with age and SCL (Fig. 5a, b; Table 1), as observed in other studies of this population (summarized in Bjorndal et al. 2013b). However, for SCL, a transient increase in growth response was observed around the size at which juvenile turtles are expected to transition from oceanic to neritic habitat (Avens et al. 2013). A significant relationship was observed between growth response and calendar year, with an increase from 1990 to 1996/1997 and a subsequent decrease through 2010 (Fig. 5c; Table 1). This temporal trend was consistent with the pattern yielded by a GAM applied to mark-recapture data collected in the same geographic region over a comparable time frame (Fig. 5d; Bjorndal et al. 2013b), again demonstrating close correspondence between the two data sources. When examination of temporal trends in growth rates was restricted to loggerheads >80 cm SCL, relationships were linear and decreased significantly over the entire study period (1975–2010; Supplementary material, Fig. 2), raising potential concerns regarding the condition and stability of size classes with high reproductive value that are impacted by numerous threats (NMFS and USFWS 2008; Wallace et al. 2008). This decades-long decrease in growth rates for subadult and adult loggerheads may relate to density-dependent effects and/or environmental conditions (Bjorndal et al. 2013b). Positive correspondence between temperature and growth appears to be typical for ectotherms, including turtles (Snover et al. 2015), and long-term increases in somatic growth corresponding with increasing temperatures at mid- and shallow water depths due to climate change have been documented for a number of fish populations in the southwest Pacific (Thresher et al. 2007). However, in the northern Atlantic, long-term decreases in juvenile fish growth have been associated with increases in sea surface temperature and are thought to result from decreased prey availability (Todd et al. 2008). Episodic increases in bottom water temperature in the Mid-Atlantic Bight (MAB) during the time period from 1958 to 2007 were recently found to correspond with significantly reduced growth and increased mortality for the surfclam (*Spisula solidissima*) population, particularly on the inner shelf (Narváez et al. 2015). Given that the MAB provides important foraging habitat for large neritic juvenile and adult loggerhead sea turtles (Arendt et al. 2012; Griffin et al. 2013; Ceriani et al. 2014), the potential for linkages between temperature changes, benthic productivity, and loggerhead growth dynamics merits further investigation.

**Adult-stage duration and life span**

Previous studies of nesting female loggerheads along the US Atlantic coast have suggested that longevity subsequent to maturation might span several decades (Frazer 1983a; Dahlen et al. 2000; Ehrhart et al. 2014). Herein, we present empirically derived estimates of mean and range for both male and female adult-stage duration, varying widely from a minimum of 4 years to a maximum of 46 years (Table 4). Because these samples were obtained from stranded turtles whose cause of death generally could not be determined, it is not possible to associate adult-stage durations with natural versus anthropogenic sources of mortality to assess what should be typical for the population. However, these data offer some insight into the possible scope of reproductive longevity and contribute to a framework in which to consider adult survival and likelihood of reproductive success under an iteroparous reproductive strategy and numerous mortality pressures (NMFS and USFWS 2008).

In addition, results of these analyses provide data to help address the often-asked question of how long sea turtles might live. Wide-ranging assertions in the popular media of sea turtle longevity ranging anywhere from 50 to 400 years notwithstanding, the age estimates yielded by the current study suggest that loggerhead sea turtles along the US Atlantic coast may live to be as old as 70–77 years. Similarly, adding the overall mean ages to maturation yielded by the three analytical approaches applied in the current study (37 years for females and 39.5 years for males) to the mean and maximum adult-stage duration estimates (20 and 46 years for females; 18 and 42 years for males) yields mean and maximum theoretical age estimates of 57 and 83 years for females and 57.5 and 81.5 years for males. These mean longevity estimates are comparable to the mean 47- to 62-year life span suggested by Frazer (1983a), and the maximum estimates correspond with those of longer-lived aquatic and terrestrial turtles, which range anywhere from 60 to 110 years (reviewed by Litzgus 2006).

**Conclusions**

Taken together, results of the current study provide new insights into growth patterns, size-at-age relationships, and life-stage durations for loggerhead sea turtles inhabiting areas along the US Atlantic coast. Convergence between results yielded by skeletochronological approaches and mark-recapture studies reinforces the potential utility of skeletal growth mark analysis as a tool to look back in time to evaluate long-term trends in size-at-age relationships and growth patterns, for individuals as well as populations. Future studies applying and expanding these approaches will provide additional information regarding potential spatial and temporal variability in these characteristics and how they might influence population dynamics of threatened and endangered sea turtle populations.

**Compliance with ethical standards**

**Conflict of interest** The authors declare that they have no conflict of interest.

**Human and animal rights** This article does not contain any studies with human participants or live animals performed by any of the authors.

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