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Regional comparison of leatherback sea turtle maturation attributes and reproductive longevity

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Abstract

Data characterizing somatic growth patterns and the ages and sizes at which organisms mature are fundamental to understanding population dynamics. However, obtaining this information for endangered leatherback sea turtles (*Dermochelys coriacea*) is particularly challenging due to unusual physiology and prevalence of remote oceanic habitat use, which limit direct observation. While inference has been made through indirect approaches such as captive, genetic, and/or skeletal growth mark (skeletochronology) studies, these diverse methods have yielded similarly varied results, limiting usefulness of available information for management and conservation. To address this data gap, we conducted refined skeletochronological analysis of Atlantic and Pacific leatherback scleral ossicle bones, allowing estimation of carapace length-at-age relationships throughout individual turtles' lives, including the juvenile life stage. In addition, this improved approach made it possible to estimate mean and range for age and size at sexual maturation (ASM and SSM, respectively), as well as post-maturation longevity. Updated mean ASM estimates from the current study of 17–19 years were lower than those previously proposed using skeletochronology and more similar to predictions from captive growth and genetic data. Maximum estimates of reproductive longevity (18–22 years) were consistent with the 16–19 years reported previously from mark–recapture of nesting females. Together, these results indicate that the application of the refined analytical approach described in the current study may offer opportunities to increase understanding of leatherback age and growth.

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Introduction

Despite their status as a species of global conservation concern and having been the focus of decades of monitoring and research efforts, many details of the lives of leatherback sea turtles, *Dermochelys coriacea*, remain enigmatic (Pritchard 2015; Scott et al. 2017). Study of sea turtles in the marine environment is generally challenging, as their ontogenetic transitions together with foraging and reproductive migratory movements can span entire ocean basins and cross numerous geopolitical boundaries (Musick and Limpus 1997; Plotkin 2003). Furthermore, their large size relative to most other turtle species makes them difficult to capture and handle, yet does not necessarily facilitate locating individuals at sea due to infrequent surfacing (Lutcavage and Lutz 1997), typically solitary occurrence, and lack of vocalizations that can be detected from a distance (in the manner of cetaceans, e.g., Gillespie et al. 2013). These challenges are amplified in leatherbacks, as they attain very large adult sizes (carapace lengths up to ~2 m), undertake particularly long migrations, and predominantly inhabit remote, open-ocean areas (Pritchard 2015).

Characterization of somatic growth patterns, as well as the ages and sizes at which leatherbacks mature is of particular interest, as this information is fundamental to understanding population dynamics and anticipating time frames over which potential effects of management actions might manifest (Sarti Martínez et al. 2007; TEWG 2007). The need for increased understanding of leatherback life history is particularly acute in light of nesting population collapses in the western Pacific in Malaysia (Chan and Liew 1996; Benson et al. 2015) and eastern Pacific in Mexico (Sarti Martínez et al. 2007) and Costa Rica (Steyermark et al. 1996). Furthermore, decreases in the western North Atlantic have been observed, where until recently, numbers were thought to be stable or increasing (TEWG 2007; Northwest Atlantic Leatherback Working Group 2018).

In the absence of capacity for direct, long-term observation of leatherbacks in the wild, inference through indirect approaches for study of age and growth has been explored, yielding diverse results. Early estimates of 2–6 years to maturation from short-term captive growth studies combined with anatomical observations (Deraniyagala 1952; Birkenmeier 1971; Rhodin 1985; Bels et al. 1988) contrast with estimates of 12–20 years yielded by recent, longer term captive growth observations and genetic inference of generation times (Dutton et al. 2005; Jones et al. 2011). Initial skeletal growth mark analysis (skeletochronology) of lateral edges of scleral ossicle bones from the eyes of leatherbacks that died prior to 1996 in the eastern Pacific yielded mean estimates of 13–14 years to reach adult sizes (Zug and Parham 1996). However, later skeletochronological analysis of western North Atlantic scleral ossicles collected from 2001 to 2008 found greater growth mark retention and clarity at ossicle section tips (Avens et al. 2009). Analysis of marks from this alternate location yielded age ranges associated with mean minimum size and mean size of nesting females in this region as 16–22 and 24.5–29 years (Avens et al. 2009).

As leatherback age and growth data generated to date are limited in scope and estimates range widely, usefulness of available information to guide management and conservation is constrained. Variability in reported estimates is likely due in part to properties specific to the different approaches used; for example, results of early captive growth extrapolation vary depending on whether models fit to data are linear or incorporate exponential decay (Jones et al. 2011). In addition, while prior skeletochronology studies could offer insight into how old adult-sized leatherback sea turtles might be at the time they died, data describing mid-sized juvenile patterns as well as ages and sizes specifically at the time of maturation were lacking (Wallace and Jones 2015). In addition to these considerations, recent hard-shelled sea turtle captive, mark–recapture, and skeletochronology age and growth studies of green (*Chelonia mydas*), Kemp's ridley (*Lepidochelys kempii*), and loggerhead (*Caretta caretta*) sea

turtles indicate that wide ranges of ages and sizes at maturation are possible within populations, reflecting diverse growth trajectories influenced by genetic origins and environmental influences (Caillouet et al. 2011; Bjorndal et al. 2013, 2014; Avens et al. 2015, 2017). Furthermore, mean nesting female size varies among leatherback populations (Stewart et al. 2007; Eckert et al. 2012), which could also correspond with differences in age at maturation. For example, nesting females in the eastern Pacific population are smaller than those in the western North Atlantic and have longer remigration intervals, potentially due to differences in oceanographic regimes and forage quality (Wallace and Saba 2009).

To address persisting leatherback age and growth data gaps, in the current study, we applied recent refinements in sea turtle skeletochronological analysis to characterize longitudinal somatic growth and size-at-age relationships, which allowed evaluation of growth patterns for the juvenile life stage. In addition, we evaluated growth mark deposition patterns in scleral ossicles to identify characteristics associated with maturation, such as age and size at sexual maturation (ASM and SSM, respectively), and estimate reproductive longevity. Finally, applying these standardized analytical approaches to samples collected from both Pacific and Atlantic Ocean populations allowed us to conduct regional comparison of age and growth attributes.

Methods

Sample collection and processing

Leatherback scleral ossicles from the Atlantic Ocean were obtained as part of a previous study (Avens et al. 2009), from dead juvenile and adult turtles stranded along the US Atlantic and Gulf of Mexico coasts between 2001 and 2008 [$n = 27$, mean curved carapace length (CCL) = 138.2 cm, range = 16.6–173 cm CCL]. Of these Atlantic turtles, nine were female, 10 were male, and eight were of unknown sex. Ossicles from the Pacific Ocean originated from a total of 25 individuals and three different sources. The majority were collected for a prior study from large juvenile and adult leatherbacks discarded in a Peruvian fishing dump in the eastern Pacific prior to 1996 and sex was unknown for all of these turtles (Zug and Parham 1996; ($n = 19$, CCL mean = 142.5 cm, range = 126–160 cm CCL). Additional samples from the Pacific were obtained from juveniles bycaught dead in longline fisheries based on Hawaii and American Samoa in 1993, 2006, 2010, and 2011 ($n = 5$, CCL mean = 65.3 cm, range = 42–87.3 cm CCL); of these, one was female, two were male, and two were of unknown

sex. Finally, ossicles from one adult female leatherback (CCL = 161.5 cm) that stranded dead along the US California coast in 2012 were also included in the analysis. Although it is preferable to conduct sex- and stock-specific analyses to evaluate growth patterns and maturation attributes, due to the small sample size of known-sex turtles, we combined analysis of all available ossicles for each ocean basin. Furthermore, while all Atlantic samples originated from one regional population segment, in the Pacific sample size constraints necessitated combining information from two different population segments, i.e., eastern Pacific turtles from Peru vs. the bycaught juveniles and California-stranded adult that would have originated from the western Pacific nesting population (Dutton et al. 1999).

Archived, calibrated digital images of the Atlantic leatherback ossicles evaluated in Avens et al. (2009) were used for the current study, and Pacific ossicles were prepared for analysis using the methods outlined in Avens et al. (2009) as well. Briefly, ossicle rings were dissected from freshly collected eyes, after which individual ossicles were separated and allowed to air dry. Entire ossicles were then fixed in 10% formalin, rinsed thoroughly with water, decalcified using a dilute hydrochloric acid preparation (RDO; Apex Engineering), and cut using a freezing stage microtome (Leica microsystems) to obtain 25 μm-thick sections from the center. Sections were stained using modified Mayer's hematoxylin and mounted in 100% glycerin using glass microscope slides and coverslips. Sequential, partial, digital images of each stained ossicle section were taken at 10× magnification using a compound microscope (Olympus BX41) in conjunction with a digital video camera and image capture software that also allowed calibrated measurement (Colorcube-12 Color CCD with Microsuite Basic). Partial images were then stitched together using image-editing software (Adobe Photoshop) to yield a calibrated, complete digital image of each section.

Age estimation

Lines of arrested growth (LAGs) that border skeletal growth increments in leatherback bones vary in appearance; regular deposition patterns consist of one or more lighter, diffuse LAGs followed by a dark, distinct LAG, with each group thought to represent an annual cycle (Avens et al. 2009). As a result, in the current study, we only counted the darker, distinct LAGs demarcating the outer edges of LAG groups to estimate age and performed counts at the wider tip of ossicle sections, where the greatest number of LAGs is retained (Avens et al. 2009). An individual reader (L. Avens) carried out LAG counts at 5-day intervals or longer without

information from prior reads and a consensus count was used for further analysis (Avens et al. 2009).

Because some ossicles exhibited resorption, i.e., loss of early LAGs toward the core during growth, it was necessary to estimate the number of missing LAGs to evaluate age. For Atlantic leatherbacks, Avens et al. (2009) developed a "correction factor" for this purpose using those ossicles with no resorption (i.e., that retained all or part of the core mark denoting hatching) to model the relationship between LAG number and LAG radius, starting with LAG year^{-1}. Substituting resorption core radius for LAG radius in the relationship provided an estimate of the number of resorbed LAGs, which was then added to the number of observed LAGs to yield a total age estimate. The same approach was applied in the current study to generate a correction factor and age estimates for Pacific leatherbacks and allow comparison with Atlantic data. The data sets yielded by the current analyses can be made available by the corresponding author upon reasonable request.

Maturation attributes

In contrast to leatherbacks, whose skeletal structures are generally very porous, the humerus bone of hard-shelled sea turtle species retains the greatest number of LAGs and is, therefore, the structure used most often for skeletochronological analysis (Avens and Snover 2013). As a result, prior efforts to relate somatic and bone measures for hard-shelled sea turtles have relied on the close, allometric relationship between humerus diameter and carapace length, which allows estimation of one measure from the other. Accuracy of predicting carapace length from humerus LAG diameters, i.e., back calculation, has been validated for loggerheads (Snover et al. 2007; Avens et al. 2013, 2015), green turtles (Avens et al. 2012; Goshe et al. 2010, 2016), and Kemp's ridleys (Avens et al. 2017). While Avens et al. (2009) reported a significant, positive relationship between leatherback CCL and ossicle lengths, it was thought that relatively greater variability in that relationship caused by the broad range of ossicle lengths within individual eyes might preclude back-calculation for the species. To surmount this issue, in the current study, we performed proportional back-calculation by relating individual-specific (vs. a sample-wide mean) ossicle radius and CCL, based on the previously described, linear relationship (Avens et al. 2009). The proportion of the total radius of an individual ossicle represented by each measurable LAG radius was first calculated and then multiplied by total CCL to yield an estimated CCL associated with each LAG. For example, for a hypothetical leatherback with CCL of 140 cm and ossicle radius of 4 mm, an LAG within that ossicle measuring 3 mm radius (0.75 total ossicle radius) would correspond with CCL of 105 cm CCL.

Upon reaching reproductive maturation, reptiles and amphibians significantly decrease somatic growth, which for some species has been validated to correspond with markedly decreased bone growth and LAG spacing, a phenomenon termed "rapprochement" (Francillon-Viellot et al. 1990; El Mouden et al. 1997; Guarino et al. 2008). In loggerhead (Avens et al. 2015) and Kemp's ridley (Avens et al. 2017) humeri, decreased LAG spacing consistent with rapprochement has been observed for individuals potentially of adult size, allowing age estimates and back-calculated sizes associated with LAGs demarcating the transition to serve as proxies for ASM and SSM. Similarly, for leatherbacks, an abrupt decrease in LAG spacing was observed in ossicles collected from turtles that were approaching or had attained what are characterized as possible adult-sized CCLs at the time that they stranded (Fig. 1). Applying the approach developed with hard-shelled sea turtle species, Atlantic and Pacific leatherback ASM and SSM were estimated using ages and back-calculated CCLs corresponding to rapprochement LAGs for individuals in each population. In addition, counting the number of LAGs deposited following rapprochement yielded estimates of population-specific reproductive longevity.

Back-calculation of CCL associated with every measurable LAG in each ossicle made it possible to model the complete size-at-age relationship from hatchling to adult, filling in data gaps for mid-sized juveniles. First-year growth rates for wild leatherbacks were calculated by taking the difference between approximate CCL at hatching (6 cm; Avens et al. 2009) and CCL estimated from the first-year LAG radius and then compared with captive first-year growth data (Jones et al. 2011). Generalized additive mixed models (GAMMs) that could account for the multiple CCL-at-age data points from individual turtles generated through back-calculation were used to fit smoothing splines and 95% credible intervals to the Atlantic and Pacific CCL-at-age data. GAMMs were implemented using the packages *mgcv* and *nlme* in the statistical program R version 3.4.1 (Wood 2006; R Core Team 2017) and incorporated CCL as the continuous response variable, age as the fixed covariate, turtle ID as a random, individual-specific effect, and a robust quasi-likelihood error function. Atlantic and Pacific leatherback ASM were then estimated from population-specific model predictions of age corresponding to CCLs of adult nesting females published in the literature, as well as SSM estimated from rapprochement in the current study (above).

Results

The correction factor developed previously for Atlantic leatherbacks to account for resorbed LAGs and allow age estimation was best described as a logarithmic relationship, where y represents LAG radius and x represents LAG number (Avens et al. 2009):

$$y = 1.028 \ln(x) + 1.5167 \; (R^2 = 0.862). \qquad (1)$$

However, for the Pacific leatherback sample that (unlike the Atlantic sample) included five mid-sized juveniles, we found that a third-order polynomial curve best described this relationship, yielding the following correction factor:

$$y = -0.0022x^3 + 0.0377x^2 + 0.0695x + 1.2369 \; (R^2 = 0.849). \qquad (2)$$

Somatic growth rates during the first year of life in wild juvenile leatherbacks were estimated to be very rapid in the Atlantic, with a mean of 39.3 cm CCL year^{-1} (range 18.3–50.2 cm CCL year^{-1}). These estimates were comparable to first-year growth rates of 20–50+ cm straightline carapace length (SCL) year^{-1} reported for captive Atlantic-origin juvenile leatherbacks (Wallace and Jones 2015). Significantly lower first-year growth rates were estimated for Pacific juveniles during their first year, with a mean of 18.6 cm CCL year^{-1} (range 12.5–30.2 cm CCL year^{-1} ($p < 0.001$, paired t test).

Ossicles from 25 Atlantic (mean stranding CCL = 147.5 cm, range 122–173 cm CCL) and 19 Pacific leatherbacks (mean stranding CCL = 143.1 cm, range 126–161.5 cm CCL) displayed sharp decreases in LAG spacing toward section tips, consistent with rapprochement.

Fig. 1 Example of line of arrested growth (LAG) rapprochement in a leatherback scleral ossicle bone section (marked with a row of five white dots); this term refers to abrupt decreases in LAG spacing, corresponding to a decrease in somatic growth. Ossicle section was obtained from a Leatherback Sea Turtle stranded dead in the western North Atlantic on 29 May 2003, with CCL = 148 cm

0.20 mm
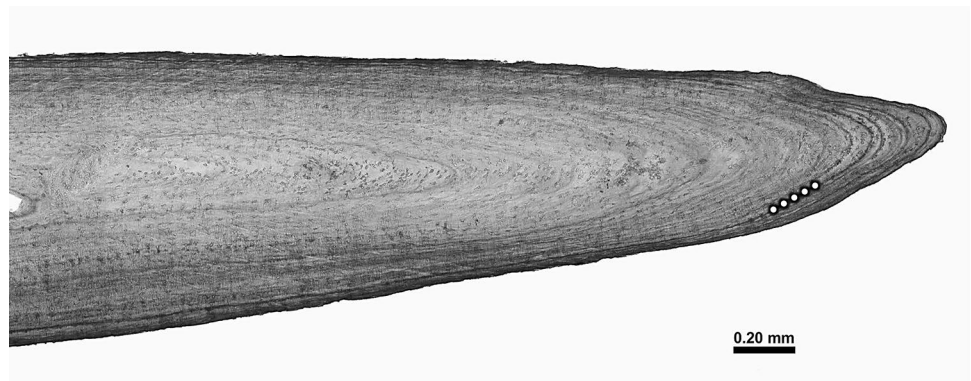
For Atlantic leatherbacks, the LAG at which the transition to rapprochement occurred was estimated to correspond with maturation at a mean CCL of 129.2 cm (range 112.8–153.8 cm CCL) and mean age of 19 years (range 13–28 years) (Table 1). Similarly, for Pacific leatherbacks, mean maturation CCL back-calculated for the transition LAG was 129.3 cm (range 110.7–152.3 cm CCL) and mean age was 17 years (range 12–28 years) (Table 1).

GAMM spline fits to CCL-at-age data (Fig. 2) were significant for both the Atlantic ($p < 0.001$, adjusted $R^2 = 0.91$) and Pacific ($p < 0.001$, adjusted $R^2 = 0.83$) and individual, random effects were also found to be significant for both populations ($p < 0.001$, log-likelihood ratio tests). Comparison of the Atlantic GAMM spline fit with a von Bertalanffy (VB) growth curve previously fit to early captive Atlantic juvenile growth data supplemented with adult size and age estimates (Jones et al. 2011) demonstrated close correspondence in early growth trajectories for small juveniles. However, the curves diverged with respect to the sizes and ages at which inflections occurred, with the spline initially diverging from the VB curve around 80 cm CCL (Fig. 3).

GAMM spline fits and 95% credible intervals were first used to predict ASM for Atlantic and Pacific populations based on minimum and mean CCLs estimated from rapprochement. For Atlantic samples, minimum maturation CCL of 112.8 cm corresponded with ages of 12–13 years (95% CI 10.5–13.5 years) and mean maturation CCL of 129.2 cm was associated with age estimates of 19–19.5 years (95% CI 17–21.5 years). For the Pacific population, rapprochement was associated with minimum maturation CCL and ages of 110.7 cm and 11.5–12 years (95% CI 10–14 years) and mean maturation CCL and ages of 129.7 cm and 17–20 years (95% CI 17–24 years). Given that mean CCL of all nesting females in a population is likely greater than mean CCL at maturation/first nesting, additional estimates of age at maturation were predicted using the spline fits for other minimum CCLs reported in the published literature (Table 2). The full span of ASM predictions from the spline 95% credible
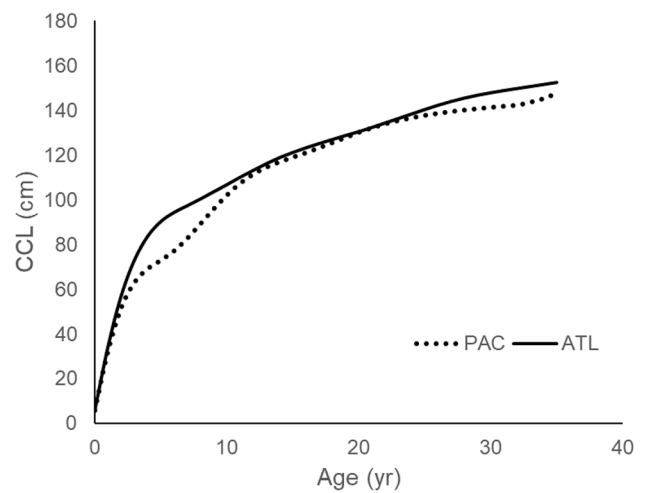

Fig. 2 Mean smoothing splines fit to back-calculated curved carapace length (CCL)-at-age data for Atlantic (solid line; $n = 700$, $R^2 = 0.91$, $p < 0.001$) and Pacific (dashed line; $n = 431$, $R^2 = 0.83$, $p < 0.001$) Leatherback Sea Turtles using generalized additive mixed models (GAMMs) to accommodate individual, longitudinal data

intervals was broad, spanning 8–26 years in the Atlantic and 10–24 years in the Pacific. Although a slightly positive relationship between ASM and SSM was found for Atlantic leatherbacks (Spearman, $r_s = 0.404$, $p = 0.05$, $n = 25$), no relationship was observed in the Pacific (Spearman, $r_s = -0.166$, $p = 0.49$, $n = 19$) leatherbacks.

Reproductive longevity calculated using the number of LAGs deposited following rapprochement was comparable between populations, ranging from 3 to 22 years for Atlantic leatherbacks and 3–18 years for Pacific turtles (Table 1).

Discussion

To facilitate understanding the drivers of and implications for leatherback sea turtle population oscillations and anticipate future trends for this protected species, improved estimates

Table 1 Summary statistics for Atlantic and Pacific Leatherback Sea Turtle size and age at sexual maturation (SSM and ASM, respectively) and longevity following maturation (adult stage duration) calculated using the rapprochement line of arrested growth (LAG) in scleral ossicles denoting an abrupt decrease in somatic growth associated with maturation

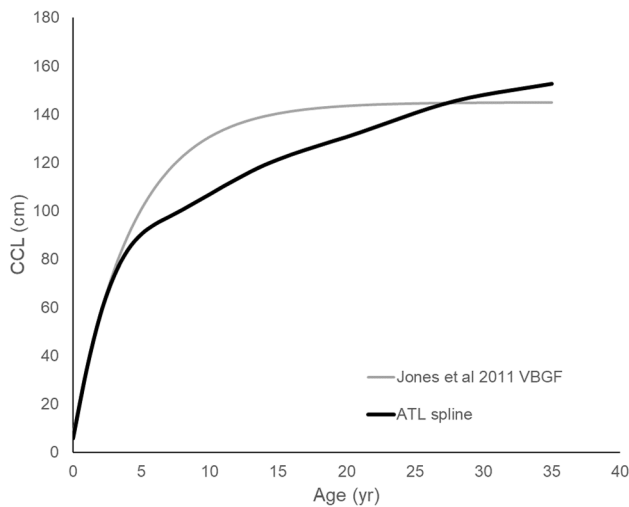| Rapprochement-related estimates of attributes related to reproductive maturation							
	Mean	SD	CV	Min	Max	Median	n
SSM (cm; CCL)							
PAC	129.3	9.9	0.08	110.7	152.3	129.7	19
ATL	129.2	9.3	0.07	112.8	153.8	127.2	25
ASM (year)							
PAC	17	10	0.60	12	28	16	19
ATL	19	5	0.24	13	28	17	25
Adult stage duration (year)							
PAC	8	4	0.55	3	18	6	19
ATL	11	6	0.54	3	22	10	25

Fig. 3 Comparison of smoothing spline fit to back-calculated curved carapace length (CCL)-at-age data for western North Atlantic Leatherback Sea Turtles in the current study (Fig. 2) with most recent published von Bertalanffy growth curve incorporating captive juvenile age and growth data (Jones et al. 2011)

of leatherback life-stage durations and maturation attributes are needed. Both inferred and observed leatherback sea turtle population dynamics seem particularly volatile relative to other sea turtle species and causes remain ambiguous (TEWG 2007). Genetic data indicate that divergence of leatherbacks from hard-shelled sea turtles occurred > 65 million years ago, yet genetic differentiation among current leatherback populations worldwide is much more recent (Dutton et al. 1999). Global comparison of leatherback genetic lineages suggest that as late as < 900,000 years ago, their distribution constricted to the Indo-Pacific during a

population bottleneck, followed by expansion and worldwide re-colonization (Dutton et al. 1999). Such extensive, past fluctuations are reflected on smaller scales in recent, sporadic upsurges of leatherback nesting numbers in areas, where decades past few were known to occur (Girondot and Fretey 1996; TEWG 2007; Stewart et al. 2011). Conversely, large nesting aggregations have suddenly exhibited abrupt, steep declines, and lack of subsequent recovery despite long-term conservation efforts (e.g., Chan and Liew 1996; Steyermark et al. 1996; Sarti Martínez et al. 2007; Tomillo et al. 2007; Tapilatu et al. 2013).

Leatherbacks worldwide are exposed to diverse sources of injury and mortality that could potentially result in population decreases, with threats differing in their exact nature but of significant magnitude occurring in all regions, yet population responses are not always intuitive (TEWG 2007; NMFS and USFWS 2013). For example, Trinidad hosts one of the largest nesting aggregations in the western North Atlantic, but high levels of poaching have occurred in the past prior to mitigation by more recent grassroots conservation efforts (Forestry Division 2010). Furthermore, gillnet fisheries with extensive bycatch (e.g., 3000 adults year^{-1} with 30% mortality) are active near nesting beaches during reproductive seasons (Lee Lum 2006; Northwest Atlantic Leatherback Working Group 2018). Remarkably, despite long-term, seemingly unsustainable adult mortality, nesting population status for this location was until relatively recently evaluated as stable or even increasing (TEWG 2007, Wallace et al. 2013). However, taking into consideration the relative suddenness with which leatherback population trajectories can shift, this situation had been compared to a "time bomb" (Wallace and Saba 2009). In fact, the latest assessment indicates an overall and concerning decrease

Table 2 Summary of estimates of curved carapace length (CCL) thought to correspond with maturation (size at sexual maturation or SSM) and ages at sexual maturation (ASM) reported in the published literature, as well as estimated in the current study using the rapprochement line of arrested growth (LAG) associated with maturation and predicted from models fit to back-calculated CCL-at-age data. *FL* Florida, USA

Source for CCL at maturation (SSM)	CCL (cm)	ASM estimates (year)	Rapprochement ASM (year)	Spline mean ASM (year)	Spline 95% CI ASM (year)
Atlantic					
NW Atlantic min (Stewart et al. 2007)	105			9.5	8–11
Current study min	112.8		13	12	10.5–13.5
VB curve (Jones et al. 2011)	121	16.1		15	13.5–16.5
FL and Trinidad Min (Stewart et al. 2007)	125	16–20.5		17.5	15.5–19.5
Current study mean	129.2		19	19.5	17–21.5
FL min (lower 95% CI for Mean; Stewart et al. 2007)	138.5			24	22–26
Pacific					
Current study min	110.7		12	11.5	10–14
VB curve (Jones et al. 2011)	121	16.1		16	13–19
East Pacific min (Stewart et al. 2007)	123			17	13.5–19.5
Current study mean	129.7		17	20	17–24

in leatherback nesting populations throughout the western North Atlantic region, including Trinidad (Northwest Atlantic Leatherback Working Group 2018). As a result, the goal of the current study was to address leatherback sea turtle age and growth data gaps and provide updated information that can be applied to help address these unresolved population dynamics questions.

Juvenile life stage

A primary focus of the analyses described herein was to generate data for the particularly cryptic juvenile leatherback life stage, for which almost all knowledge to date has been limited to hard-won captive observations (e.g., Jones et al. 2011) and sporadic strandings or incidental captures (Eckert 2002; Huang 2015). First-year growth rates back-calculated for wild juvenile leatherbacks were estimated to be high overall and in the western North Atlantic were much more rapid than those reported for hard-shelled species in this region [×3.5 that of loggerheads (Avens et al. 2015) and ×2.4 that of Kemp's ridleys (Avens et al. 2017)]. Interestingly, the Atlantic back-calculated first-year juvenile leatherback growth rates corresponded closely with captive data from individuals from the same source population (Jones et al. 2011; Fig. 3). In addition, earlier growth models incorporating these captive growth data predicted 2.8 years at ~70 cm SCL (~72 cm CCL after applying the conversion equation from Tucker and Frazer 1991), similar to the 3 years of age estimated for juveniles 73 cm CCL in the current study. Atlantic juvenile growth data yielded by the current study were also consistent with size-at-age estimates inferred from active dispersal model predictions for this population (Lalire and Gaspar 2019). For the most part, the back-calculated Pacific early juvenile leatherback growth rates were slower than those estimated for the Atlantic, but consistent with size-at-age predictions from North Pacific dispersal scenarios (Gaspar et al. 2012). Using models of passive drift incorporating seasonal migrations, Gaspar et al. (2012) estimated that leatherbacks between 50 and 87.5 cm CCL would be 2–4 years; similarly, the spline fit for back-calculated Pacific CCL-at-age data in the current study predicted turtles of those CCLs to be 2–7.5 years of age.

Given the divergence observed between captive and wild growth rates for hard-shelled sea turtle species (reviewed by Avens and Snover 2013), finding consistency between the two for leatherbacks seems unexpected. However, Jones et al. (2011) reported no significant difference between length and mass relationships of captive-reared and wild stranded or bycaught leatherbacks, despite presumed discrepancies in both environment and diet (squid vs. gelatinous zooplankton, respectively). Although detailed information regarding small juvenile leatherback distribution and foraging ecology is lacking, available data

indicate that during this life stage, individuals remain in high-productivity equatorial regions, where water temperatures are warm (>26 °C, Eckert 2002; Huang 2015; Scott et al. 2017). Limiting distribution to areas with particularly favorable developmental conditions together with anticipated high-energy assimilation efficiency of prey consisting primarily of gelatinous zooplankton is likely to maximize growth potential (Jones et al. 2011). This, in turn, would allow for higher growth rates than those exhibited by hard-shelled sea turtle populations, whose juveniles are often found at higher latitudes (Musick and Limpus 1997).

It has previously been proposed that because leatherbacks inhabit oceanic–pelagic habitat throughout their lives, their ontogenetic transitions are not likely to be as distinct as those for hard-shelled sea turtles (Jones et al. 2011). However, following the early juvenile stage, where individuals inhabit lower latitudes, differential distribution of mid-sized to large juveniles (<100 cm carapace length) and sub-adult and adult leatherbacks does appear to occur (Eckert 2002; Dodge et al. 2011; Jones et al. 2011). The spline fits for both Atlantic and Pacific back-calculated CCL-at-age data exhibit inflections associated with CCLs between 60 and 100 cm, supporting occurrence of a shift in habitat use and/or foraging behavior during this life stage that is of sufficient significance to cause changes in somatic growth. One possibility is that decreased growth could result from energetic costs of migration and thermoregulation incurred by larger leatherbacks, as they begin to use seasonal foraging grounds at higher latitudes and occupy colder water temperatures (Bostrom et al. 2010). Furthermore, as large juveniles approach adult size, additional inflections in the relationship between size and age will reflect a shift in allocation of energetic resources from somatic growth to reproductive maturation (Bjorndal et al. 2013, 2014).

SSM, ASM, and variability

Whereas earlier leatherback skeletochronology studies were limited to estimating ages for adult-sized turtles at the time that they stranded (Zug and Parham 1996, Avens et al. 2009), in the current analyses, we attempted to gain insight into CCL and age specifically at the time of maturation (SSM and ASM, respectively). It should be noted that ASM can differ from age at first reproduction (AFR); although sea turtles can attain reproductive maturity and initiate reproductive activity within the same calendar year, it is also possible for these life history events to be separated by longer, individual-specific time intervals (Caillouet et al. 2011; Bjorndal et al. 2013, 2014). As a result, for some leatherbacks in the current study, it is possible that the ASM data presented herein underestimate individual AFR by an unknown time period.

Although it is preferable to conduct sex-specific analyses to account for potential differences in growth patterns, as well as ASM and SSM, between females and males, limitations on available samples and associated data necessitated combining all ossicles available for each ocean basin during this study. Furthermore, it is important to note that constraints on sample availability in the Pacific necessitated combining information for leatherbacks from western and eastern nesting populations, which exhibit disparity in mean size of nesting females (Eckert et al. 2012) and potentially different environmental conditions and prey quality in foraging areas (Saba et al. 2008). However, based on the currently available data, we found that minimum back-calculated SSMs for rapprochement LAGs (~ 111–113 cm CCL) fell between the previous reports of nesting female minima from Atlantic (105 cm CCL) and Pacific (123 cm) populations (Stewart et al. 2007), supporting the use of rapprochement as an indicator of maturation. Mean SSMs predicted from rapprochement LAGs were similar for both ocean basins, yielding 129.2 cm CCL for Atlantic leatherbacks and 129.3 cm CCL for Pacific turtles, with both estimates smaller than the mean CCLs reported for all nesting females from the two study populations (Eckert et al. 2012). However, because overall mean size for a population will naturally be greater than the size at which maturation first occurs, this outcome is not unexpected. Furthermore, the result provides support for the recommendation to use minimum size as a proxy for initial reproductive size and average size as a maximum (Frazer and Ehrhart 1985; Stewart et al. 2007).

In the current study, both the age estimates associated with rapprochement SSMs and the spline fit and 95% CI for the CCL-at-age data yielded a wide range of possible ASMs corresponding to the different SSMs. In the Atlantic, age estimates ranged from a minimum of 8 years to maximum of 26 years, with minimum and maximum of 10 years and 24 years in the Pacific, respectively. Similar to the congruence observed for captive and wild juvenile growth rates (above), these updated wild ASM estimates are lower than those previously proposed (Avens et al. 2009) and more comparable to those predicted from growth curves incorporating long-term captive juvenile growth data (13–20 years, Wallace and Jones 2015). This similarity may result from incorporation of previously unavailable estimates of wild juvenile leatherback growth data yielded by the current study.

The similarities in SSM and ASM for Atlantic and Pacific leatherbacks observed in the current study are counter to previously proposed differences in ASM between populations based on smaller reported SSM in the eastern Pacific, where the majority of adult Pacific samples originated, than in the western North Atlantic (Eckert et al. 2012). Given the greater first-year growth rates for the Atlantic sample, the finding of slightly earlier (but not significantly different)

minimum ASM for the Pacific sample might seem counterintuitive. However, an upward inflection in growth trajectory for juvenile Pacific leatherbacks ~ 70 cm CCL resulted in convergence of the two growth curves at CCLs just under the minimum proposed SSMs (~ 110 cm). In addition, the lack of difference between populations could relate to incorporation of samples from juveniles and one adult from the western Pacific, where mean nesting female size is greater, resulting in an integrated, intermediate growth trajectory for the ocean basin. Furthermore, results might have been influenced by disparity in the time frames during which the sample sets were collected (Pacific primarily pre-1996 vs. Atlantic early 2000s), and although comparable size-at-age might be possible in the two regions, this might not necessarily be the case at the current time. For example, recent data indicate that two loggerhead sub-populations in the western North Atlantic and Mediterranean exhibit the same growth trajectory, but those in the Mediterranean mature at an earlier point along that trajectory, at a smaller size and younger age (Avens et al. 2015). Given relatively recent differentiation among leatherback populations worldwide [e.g., division between the Atlantic and Pacific Ocean basins occurring approximately 0.17 million years ago (Duchene et al. 2012)], it may be reasonable for overall growth trajectories to remain similar, but for population-specific maturation attributes to shift depending on regional influences (Wallace and Saba 2009).

The broad scope of possible maturation outcomes for leatherback ASM and SSM is consistent with recent data for hard-shelled sea turtle species, suggesting analogous development within common constraints for the clade despite divergence between extant families > 65 million years ago (Dutton et al. 1999; van Buskirk and Crowder 1994). Data from multiple sources (captive-rearing, mark–recapture, and skeletochronology) indicate that a wide range of ASM and SSM are possible both for captive and wild hard-shelled sea turtles, reflecting variable growth trajectories relative to a mean, as determined by genetic and environmental factors (Caillouet et al. 2011; Bjorndal et al. 2013, 2014; Avens et al. 2015, 2017). Given that the substantially greater size change leatherbacks undergo transitioning from hatchling to adult relative to other sea turtle species (van Buskirk and Crowder 1994), it might seem that potential for an even greater scope of outcomes could exist, despite presumed dietary consistency throughout different life stages (Jones et al. 2011). Interestingly, the coefficient of variation (CV) for leatherback SSM in both study populations (0.07–0.08, Table 1) is similar to that reported for loggerheads in the western North Atlantic (CV = 0.07; Avens et al. 2015) and Kemp's ridleys in the Gulf of Mexico (CV = 0.05; Avens et al. 2017). However, while Atlantic leatherback ASM CV (0.24) was also comparable to that of western North Atlantic loggerheads (CV = 0.22; Avens et al. 2015) and

Gulf of Mexico Kemp's ridleys (CV = 0.29; Avens et al. 2017), Pacific leatherback ASM CV was more than twice as large (0.60). Perhaps, this difference for the Pacific ASM CV relates to relatively small sample size and the need to combine samples from both western and eastern Pacific populations. However, it might also correspond to decreased forage quality in the eastern Pacific due to differences in oceanographic regimes and trophic transfer efficiency, as well as reduced geographic scope of foraging areas (Wallace et al. 2006).

Adult stage duration and longevity

Estimates of leatherback reproductive longevity presented here averaged 8–10 years, with a total possible range of 3–22 years, and are consistent with intervals observed from tagging studies on nesting beaches. Although few mark–recapture records are available, survival for 19 years following tagging was documented for a female leatherback in the western North Atlantic and females in the southwest Indian Ocean have returned to nest over maximum spans of 10–18 years (reviewed by Eckert et al. 2012). Recent observations of three turtles from the nesting leatherback population on St. Croix, USVI, have demonstrated that reproductive longevity of 31 years is possible (K. Stewart and C. Lombard, pers. comm.), suggesting that our results might underestimate maximum possible intervals for the Atlantic population. However, the adult stage duration estimates of two-to-three decades for leatherbacks are less than the 38 years (greens; mark–recapture, Humburg and Balazs 2014) and 46 years (loggerheads; skeletochronology, Avens et al. 2015) reported for larger hard-shelled sea turtle species, but approximately, two-to-three times 10 years found for Kemp's ridleys (skeletochronology, Avens et al. 2017).

Whereas previously, no empirically derived estimates of total longevity have been available for leatherback sea turtles (Eckert et al. 2012), taking together mean age at maturation and mean reproductive stage duration from rapprochement in the current study yields mean lifespan estimates of 30 years for the Atlantic sample and 23 years for the Pacific group. Using maximum maturation age and adult stage duration estimates from rapprochement results in maximum lifespan estimates of 50 years and 46 years for the Atlantic and Pacific, respectively. Given that the cause of death for the stranded turtles in the Atlantic from which samples were collected for this study was unknown and in the Pacific, most ossicles were taken from turtles that died as a result of human activities, these values are likely underestimates of possible total lifespan. However, comparison with western North Atlantic leatherback age and growth data generated using the same analytical approaches for loggerhead (Avens et al. 2015) and Kemp's ridley (Avens et al. 2017) sea turtles in the same region offers interesting insights into relative growth trajectories (and, therefore, life-history strategies) for the different species within this taxonomic grouping (Fig. 4).

Conclusions

While the study of leatherback sea turtles presents significant challenges, the results of the current study indicate that the application of the refined skeletochronological analyses described here offers opportunities to increase understanding of leatherback age and growth. Given that the number of ossicles available for the current study was limited, future efforts should focus on increasing sex-specific sample sizes to improve the characterization of age and growth parameters and to obtain ossicles from other geographic areas to allow global comparison. Unfortunately, the small size of ossicles (mean adult radius ~ 5 mm, e.g., Fig. 1 for scale) is likely to prohibit collection of sufficient quantities of bone tissue to conduct the recently developed skeletal growth increment-specific stable isotope analyses of sea turtle humeri that are providing valuable, long-term habitat use and trophic ecology data (e.g., Ramirez et al. 2015, 2017; Turner Tomaszewicz et al. 2017, 2018). However, trace-element analyses that sample bone growth increments on a finer scale using laser ablation inductively coupled plasma mass spectrometry (ICPMS; Ramirez et al. 2019) hold potential to be useful in a similar capacity for smaller skeletal structures.
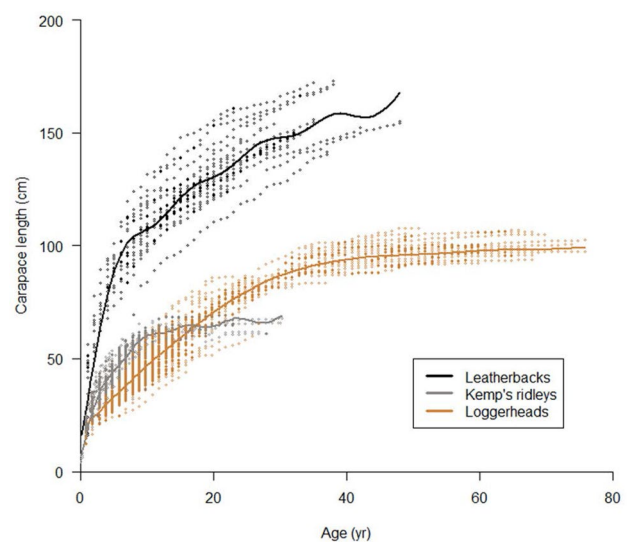

Fig. 4 Comparison of mean smoothing splines (lines) and carapace length-at-age data (points) generated using the same skeletochronological analysis methods for Leatherback (current study) and Loggerhead (Avens et al. 2015) Sea Turtles stranded along the US Atlantic coast and Kemp's Ridley Sea Turtles stranded in the Gulf of Mexico (Avens et al. 2017). Carapace length is curved carapace length (CCL) for Leatherback Sea Turtles and straightline carapace length (SCL) for Loggerhead and Kemp's Ridley Sea Turtles

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Human and animal rights statement All procedures performed in the current study were approved and permitted by the United States Fish and Wildlife Service (permit no. TE-67379 issued to the National Marine Fisheries Service Southeast Fisheries Science Center).

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