Mar Biol (2010) 157:1725–1740
DOI 10.1007/s00227-010-1446-0

ORIGINAL PAPER

Estimation of age at maturation and growth of Atlantic green turtles (*Chelonia mydas*) using skeletochronology

Lisa R. Goshe · Larisa Avens · Frederick S. Scharf · Amanda L. Southwood

Received: 8 January 2010 / Accepted: 6 April 2010 / Published online: 20 April 2010

Abstract Despite the vast amount of research on threatened and endangered green turtle populations, some uncertainty regarding stage durations, growth rates, and age at maturation remains. We used skeletochronology to address this gap in knowledge for green turtle populations in the North Atlantic Ocean that use coastal waters along the southeastern U.S. as developmental habitat. Oceanic stage duration was estimated at 1–7 years ($\overline{X} = 3$ years). Several growth models, including von Bertalanffy, logistic, Gompertz, and power functions were evaluated for describing sex-specific length-at-age data. Ages at maturation estimated using mean size at nesting for females from each genetic sub-population contributing juveniles to this neritic foraging area were 44 years (Florida), 42.5 years (Costa Rica), and 42 years (Mexico), which were higher than previously reported ages. This implies that nesting populations comprising primarily individuals utilizing foraging grounds in the southeastern U.S. may take longer to recover than previously estimated.

Communicated by R. Lewison.

L. R. Goshe (✉) · L. Avens
NOAA Fisheries, Southeast Fisheries Science Center,
Beaufort Laboratory, 101 Pivers Island Road,
Beaufort, NC 28516, USA
e-mail: Lisa.Goshe@noaa.gov

F. S. Scharf · A. L. Southwood
Department of Biology and Marine Biology,
University of North Carolina Wilmington,
601 S. College Road, Wilmington, NC 28403, USA

Introduction

Age at maturation and growth rates have been identified as aspects of green turtle (*Chelonia mydas*) biology for which sufficient information is lacking yet needed for effective modeling of population growth trajectories (NMFS and USFWS 2007). Management decisions intended to bring about the recovery of green turtles rely on the accuracy of such models. Unfortunately, age and growth data can be challenging to obtain given the oceanic and highly migratory nature of juveniles (Musick and Limpus 1997) and adults (Plotkin 2003; Troëng et al. 2005), combined with life history traits that include a long life-span, slow growth, and delayed maturity (Chaloupka and Musick 1997).

Green turtles are circumglobal, inhabiting tropical, subtropical, and temperate waters. Their life history is similar to that of other sea turtle species in that after hatching on nesting beaches, they swim offshore and inhabit the oceanic zone for the first years of their lives where they are rarely encountered by researchers (Carr 1987). As small juveniles, they recruit to the neritic zone in tropical and temperate waters to forage, shifting from omnivory to herbivory (Arthur et al. 2008). Adult green turtles migrate between foraging habitats and nesting grounds (Troëng et al. 2005), with females nesting at an average size of 99.1 cm straight carapace length (SCL) (van Buskirk and Crowder 1994).

Age at maturation is usually estimated using growth functions and the size of nesting females unless turtles of a known-age are observed nesting, in which case the size and age of individual turtles can be directly ascertained. In the North Atlantic, of the known-age green turtles released from captivity as hatchlings, a single male was observed mating after 19 years at large, and a single female was observed nesting at 17 years old (Bell et al. 2005). However, the small sample size of known-age turtles limits the value of these data. Early estimates of 18–33 years to maturation using mark-recapture data from wild green turtles in Florida (Mendonça 1981; Frazer and Ehrhart 1985) and the Caribbean (Frazer and Ladner 1986) are based on small sample sizes of green turtles that are not representative of the entire size range (Bjorndal and Bolten 1988; Chaloupka and Musick 1997). Although mark-recapture studies have continued to provide growth rate data for green turtles inhabiting foraging grounds in the North Atlantic (Mendonça 1981; Bjorndal and Bolten 1988; Boulon and Frazer 1990; Collazo et al. 1992; Bresette and Gorham 2001; McMichael et al. 2008; Kubis et al. 2009), the lack of data from turtles spanning the entire size range from hatchlings to adults in these aggregations has hindered estimation of age at maturation.

Skeletochronology, which involves analyzing growth marks retained in bones, is an alternative means of obtaining growth rate data and age at maturation estimates similar to those obtained in mark-recapture studies (Snover et al. 2007b). However, skeletochronology differs from mark-recapture in that it allows growth rates from multiple years to be obtained, provided that each growth mark represents an annual cycle. To date, only one skeletochronological study has been conducted on Atlantic green turtles, from a Florida inshore lagoon (Zug and Glor 1998). The geographic scope of the study was limited and aging samples were lacking from reproductively mature turtles and, therefore, while it was possible to estimate growth rates for the size ranges present, age at maturation could not be estimated with confidence (Zug and Glor 1998). Nor was it possible to validate the assumption that each growth mark represents an annual cycle (Zug and Glor 1998). Although skeletochronology has been used to estimate the age at maturation of green turtles as 30 years or greater in the Pacific (Zug et al. 2002), given that growth rates for the same species can differ among different ocean basins (Bjorndal et al. 2000), these age estimates are not necessarily applicable to green turtles in the Atlantic.

The humerus bone is typically used in cheloniid sea turtle skeletochronological studies because it possesses the greatest ratio of cortical to cancellous bone, and thus should retain the most growth marks (Zug et al. 1986). As humeri were available from green turtles ranging from hatchlings to adults, the aim of the current study was to estimate the age at maturation for green turtles in the North Atlantic using sex-specific age- and growth rate data obtained through skeletochronology. The annual nature of growth marks has been validated directly in the humeri of known-age loggerheads (*Caretta caretta*) and Kemp's ridleys (*Lepidochelyskempii*) (Snover and Hohn 2004), in loggerheads injected with oxytetracycline as a bone marker (Klinger and Musick 1992; Coles et al. 2001), and in recaptured tagged loggerheads (Bjorndal et al. 2003), but has yet to be validated in the humeri of Atlantic green turtles. We verified this assumption using growth marks retained in a known-age turtle and in wild tagged turtles. To calculate prior growth rates, we characterized the relationship between total body growth and bone growth, which allowed previous carapace lengths to be back-calculated from growth mark diameters. For age estimates, early growth marks destroyed by resorption or remodeling of bone were accounted for using a correction factor to estimate the number of missing growth marks. The current study addresses the main assumptions that typically confound skeletochronological analyses of age and growth, allowing growth rates and the oceanic stage duration to be estimated for green turtles using the coastal waters of the southeastern U.S. as developmental habitat. Because the genetic composition of the assemblages on the North Carolina and Florida foraging grounds is known (Bass and Witzell 2000; Bass et al. 2006), and females have been demonstrated to return to the region from which they hatched to nest as adults (Meylan et al. 1990), we present estimates of sex-specific ages at maturation for green turtles that use the southeastern U.S. as developmental habitat and contribute to the Florida, Costa Rican, and Mexican nesting populations.

Materials and methods

Sample collection and preparation

The left front flipper was removed from green sea turtles (*Chelonia mydas*) that stranded dead along the U.S. Atlantic coast from Virginia through the Atlantic coast of Florida by members of the Sea Turtle Stranding and Salvage Network. If it was not possible to collect the left front flipper, the right was removed and processed instead. A total of 111 humeri were collected from turtles that ranged in size from a 4.6 cm SCL hatchling to a 103.6 cm SCL adult ($\overline{X} = 43.2 \pm 25.6$ SD). SCL was measured from the nuchal notch to the posterior tip of the carapace to the nearest 0.1 cm using forester's calipers (Haglöf Sweden AB, Långsele, Sweden) for all turtles except hatchlings, which were measured using digital calipers (Fowler Co., Inc., Newton, Massachusetts, USA). Hatchlings that had fully emerged from eggs but were discovered dead upon excavation were collected from five nests in North Carolina and Florida. The remaining turtles included 21 males and 41 females, as determined by necropsy, and 49 of unknown sex, either due to decomposition or because the turtles were not necropsied. Six turtles, all from Florida, were noted as having fibropapilloma tumors.

The humerus bone was dissected from each flipper, flensed of tissue, boiled, and then allowed to dry in the sun for approximately 2 weeks. Using digital calipers, the medial width, or the lateral diameter at the sectioning site (Zug et al. 1986), was measured to the nearest 0.01 mm prior to removing cross-sections for histological processing. The methodology of Snover and Hohn (2004) was used to histologically prepare the cross-sections. As a more permanent method of archiving and to enable measurements to be taken using a digital image and image analysis software, sequential portions of stained cross-sections were photographed at 4× magnification using an Olympus Colorcube-12 Color CCD digital camera fitted to an Olympus BX41 trinocular compound microscope (Olympus America Inc., Melville, New York, USA). For each turtle, the sequential images were stitched together using Adobe Photoshop (Adobe Systems Inc., San Jose, California, USA) to obtain a high resolution composite digital image of each cross-section. In the decalcified and stained sections, skeletal growth marks appeared as wide zones that stained light, followed by darker lines of arrested growth (LAGs). The appearance of LAGs varied from distinct to diffuse. Random numbers were assigned to the digital image of each cross-section before LAGs were marked and counted by two independent readers (LRG and LA). We attempted to increase the precision of our reads through the use of consistent aging criteria among independent reads. For example, marks were evaluated by tracing them around the entire circumference of the section. A wide lightly stained growth zone followed by two consistently closely spaced LAGs along the entire circumference was interpreted as a double LAG representing 1 year, whereas two closely spaced marks with variable spacing when traced around the section were each interpreted as annual LAGs. For LAGs that appeared as one dark LAG but split into multiple LAGs when traced around the section, each of the multiple LAGs was interpreted as an annual mark. The interpretation of the double and splitting LAGs was based on the previous evaluation of similar marks by Castanet et al. (1993) and Snover and Hohn (2004), as well as the character of LAGs in the known-age and tagged turtles in this study. Average percent error was calculated using 10 duplicate images that were included to estimate the precision of LAG counts for each reader (Beamish and Fournier 1981). The Wilcoxon paired-sample test was used to compare LAG counts between readers (Zar 1996). When the number or placement of LAGs differed, both readers viewed the images together to arrive at consensus. Measurements of the LAG, resorption core, and total humerus diameters were taken along an axis parallel to the dorsal edge of the section using the composite digital images and Olympus Microsuite Basic Image Analysis software (Olympus America Inc., Melville, New York, USA).

Verification of annual growth marks

Humeri from one known-age green turtle and four green turtles that had been tagged, released, and stranded dead at least 1 year after being tagged were used to indirectly validate the frequency of growth mark deposition. The known-age turtle had been raised in captivity for 9.5 years prior to release into the wild, spending 6.5 years at large before stranding dead. The four tagged turtles were free-ranging wild turtles, three of which were tagged and released on the same day, while one spent approximately 1 year in captivity for rehabilitation before release. Turtles ranged in size from 26.9 to 99.9 cm SCL at initial tagging. Without prior knowledge of the tagging history of each turtle, all LAGs were identified, measured, and converted to previous SCLs (see "Results"), to which the body proportional hypothesis (Francis 1990), as modified for application to sea turtles (Snover et al. 2007a), was applied. Each LAG was assigned a year starting with the LAG closest to the outside edge of the bone and working toward the center, under the assumption that one LAG was deposited per year, as was determined for Kemp's ridleys inhabiting the same region (Snover and Hohn 2004). The Wilcoxon paired-sample test (Zar 1996) was used to compare the actual SCL measured at the time of tagging to the back-calculated SCL based on the LAG hypothesized to have been deposited closest to the time of tagging.

Age estimates

The earliest growth marks in sea turtles are deposited toward the center of the bone, while the most recent occur along the outer circumference (Zug et al. 1986). Because a diffuse annulus has been validated as the first year mark in known-age Kemp's ridleys (Snover and Hohn 2004), we assumed an annulus represented the first year mark in green turtles. For turtles retaining an annulus, the total LAG count was equal to age.

Not all turtles retained an annulus because early growth marks are destroyed by resorption, or remodeling of the bone as the turtle grows. To estimate age for such turtles, the number of LAGs lost to resorption was estimated using a correction factor protocol (Parham and Zug 1998). Turtles retaining an annulus were used to develop a correction factor to estimate the number of missing LAGs for the remaining green turtles in this study. LAG diameters were measured in all cross-sections that retained an annulus and LAGs were numbered from the interior to the outside edge of the section. LAG diameter was plotted against LAG number and several regression models were assessed to determine the relationship which best described the data. The best-fitting model was determined based on r^2 values and examination of residual patterns.

To estimate the number of missing LAGs using this correction factor, the resorption core diameter was measured. In cross-sections lacking a clear, definable resorption core, the most interior LAG with a measureable diameter was measured to represent the diameter of the resorption core. The resorption core diameter was substituted for LAG diameter in the correction factor equation to estimate the number of missing LAGs. For age estimates, the estimated number of missing LAGs was added to the number of LAGs retained in the cross-section.

This correction factor could not be applied to turtles with resorption core diameters exceeding the largest LAG diameter measured in turtles retaining an annulus. For this reason, additional correction factors were developed. All LAG diameter and LAG number data from turtles aged using the correction factor were combined with the data from turtles retaining an annulus. The relationship between LAG diameter and LAG number was modeled using regressions with the best fit determined by r^2 values and examination of the residual patterns, which resulted in an additional correction factor. Turtles with fibropapilloma were not used in establishing the correction factors because their bone growth increments may not be representative of healthy individuals.

Estimation of oceanic stage duration

Based on the size range of the smallest green turtles along the U.S. Atlantic coast reported in the literature, we calculated the minimum, maximum, and mean age of green turtles with SCLs within that range. Turtles within this size range were assumed to be new recruits from the oceanic zone.

Calculation of growth rates

In marked and recaptured loggerheads, Snover et al. (2007a) confirmed that LAG diameters corresponded with carapace length, which allowed for growth rates of individual turtles to be back-calculated through conversion of successive LAG diameters to estimates of carapace lengths. To estimate prior carapace lengths from LAG diameters, a positive relationship must exist between bone growth and somatic growth (Chaloupka and Musick 1997). The relationship between green turtle bone medial width and SCL was modeled using the following allometric equation, which was applied to loggerhead sea turtles by Snover et al. (2007a):

$$L = L_{\mathrm{op}} + b(D - D_{\mathrm{op}})^c \qquad (1)$$

where L is the estimated SCL, L_{op} is the minimum hatchling SCL, D is the medial width of the humerus, D_{op} is the minimum hatchling humerus diameter, b is the slope of the relationship, and c is the proportionality coefficient. Although turtles with fibropapilloma tumors ($n = 6$) were included in this analysis, those turtles for which SCL was not measured and could not be estimated using the relationship between SCL and curved carapace length (CCL) were not included.

While the above analysis was used to test for a positive association between bone and somatic measures, such an association does not by itself indicate a positive relationship between bone growth and somatic growth over time. To test for this, the relationships between SCL and estimated age, as well as humerus diameter and estimated age were modeled using best-fitting functions as determined based on the highest r^2 values. The residuals of these size-at-age relationships were plotted against each other to determine if a positive association was present between bone growth and somatic growth.

For each turtle, the diameters of all LAGs were measured, SCLs were back-calculated using Eq. (1), and the body proportional hypothesis (Francis 1990) was applied. Growth rates were calculated by subtracting the back-calculated SCL of the inner LAG from that of the outer LAG for each LAG pair. Growth rates were divided into size classes based on the mean SCL of the back-calculated SCL pairs. The mean growth rate and standard deviation were calculated for each 10 cm size class using the combined data from turtles of known and unknown sex, as well as separately for males and females. Humeri that sectioned poorly, those turtles with fibropapilloma, and those with estimated carapace lengths were excluded from growth rate analyses. Fibropapilloma is a disease characterized by the development of lesions internally as well as on the skin (reviewed by Herbst 1994) and it can result in slower growth rates compared to those of healthy individuals when tumor severity is advanced (Chaloupka and Balazs 2005). Turtles with fibropapilloma were excluded from growth rate calculations because they could bias calculations toward slower growth and may not be representative of the overall population.

Estimation of age at maturation

Because bones retain a record of prior growth rates of turtles, much like mark-recapture data, skeletochronological estimates of age at maturation can be obtained using different approaches. If results from each approach yield similar estimates of age at maturation, confidence in the accuracy of those estimates would be increased. Sex-specific age at maturation was estimated by: (1) fitting growth models to the length-at-age data, (2) applying the Fabens' modified von Bertalanffy growth interval equation to the growth increment data, (3) determining the number of years required to reach maturation size based on mean growth rates through each 10 cm size class, and (4) estimating age at the start of rapprochement, or the compaction of peripheral LAGs. For comparison, we also estimated age at maturation by combining the length-at-age data from turtles of known and unknown sex. In the first three approaches, the age at maturation of females was estimated based on the minimum and mean SCLs reported in the literature for each sub-population. Because similar data were lacking for males, the reported sizes of males near nesting beaches were used in estimating age at maturation.

Estimates of age at maturation were arrived at by evaluating the fit of several growth models, including von Bertalanffy, logistic, Gompertz, and power functions, to the sex-specific length-at-age data using STATA statistical software (StataCorp. 2006, College Station, Texas, USA; Table 1). Akaike's information criterion (AIC) scores were calculated and the relative weight of evidence was used to determine the models that best described the data.

Sex-specific growth increment data were used as an alternative means of estimating age at maturation using the Fabens' modified von Bertalanffy growth interval equation (Fabens 1965) as applied to sea turtle mark-recapture data (Frazer and Ehrhart 1985):

$$L_r = L_\infty - (L_\infty - L_c)e^{-kd} \tag{2}$$

where L_r is the length at recapture, L_c is the length at initial capture, L_∞ is the asymptotic length, k is the intrinsic growth rate, and d is time in years between captures. The following equation was used to calculate the intrinsic growth rate, k:

Table 1 Growth model equations

von Bertalanffy growth model $y = B_0\left(1 - e^{(-B_1(x-B_2))}\right)$	B_0 = Asymptotic length $B_1 = K$ (Brody growth coefficient) $B_2 = t_0$ (Hypothetical age when length = 0)
Logistic growth model $y = B_0\left(1 + e^{(-B_1(x-B_2))}\right)^{-1}$	B_0 = Asymptotic length $B_1 = K$ (relative growth rate parameter) B_2 = Age at the inflection point
Gompertz growth model $y = B_0 e^{(-e^{-B_1(x-B_2)})}$	B_0 = Asymptotic length $B_1 = K$ (the rate of exponential decrease of the relative growth rate with age) B_2 = Age at the inflection point
Power growth model $y = B_0 + B_1 x^{B_2}$	This equation does not estimate asymptotic length; the parameter B_2 determines concavity of the curve

For all models: y = SCL (cm) and x = age (y)

Reference: Katsanevakis and Maravelias (2008)

$$k = -Ln[-(L_{\text{final}} - L_\infty)/(L_\infty - L_{\text{initial}})]/t \tag{3}$$

where the back-calculated SCL of the outer LAG of each pair was termed L_{final} and the inner was termed L_{initial}. The maximum reported length was assumed to equal L_∞; therefore L_∞ was set at 121 cm SCL, as this is the largest green turtle reported among the three sub-populations (Bjorndal et al. 1983). The time in years, t, was equal to 1, assuming annual LAG deposition (see "Results"). The following equation was used to estimate sex-specific length for a given age:

$$\text{SCL at age} = L_\infty - (L_\infty - L_{\text{hatch}})e^{(-\text{avg}\,k * \text{age})} \tag{4}$$

where the parameters are defined as for Eq. (3), with L_{hatch} set as 5.18 cm SCL based on the mean hatchling size as calculated from the SCLs of green turtle hatchlings in the North Atlantic as reviewed by Hirth (1997), and age is in years.

Age at maturation was also estimated based on the sex-specific mean growth rate of each size class without utilizing growth models. Mean growth rates were calculated as previously described and the addition of the mean oceanic stage duration allowed estimation of the number of years required to reach the minimum and mean nesting size for each population.

Rapprochement of LAGs is thought to result from a decrease in growth rate with the onset of reproductive maturity (e.g., Francillon-Vieillot et al. 1990). To estimate age at maturation, the previously described correction factor was used to estimate the number of LAGs lost to resorption and that estimate was added to the number of LAGs retained in the bone prior to the start of rapprochement. For the corresponding size at maturation, the SCL was back-calculated for the LAG marking rapprochement using Eq. (1) and the body proportional hypothesis.

Results

Of the 111 green turtle humeri obtained, age was estimated for 109; one cross-section damaged during histological processing was unusable, and one was a known-age turtle. The average percent error in LAG counts made by two independent readers was 5.0 and 13.5%. There was no significant difference in LAG counts between readers ($P = 0.1443$, Wilcoxon paired-sample test, $n = 108$). Consensus was reached on all occasions when the number or placement of LAGs differed.

Frequency of growth mark deposition

The results from the known-age green turtle (TXH 980626-01) supported the assumption of annual LAG deposition.

Table 2 Back-calculated SCLs from LAG diameters of tagged green turtles compared to SCLs measured at tagging

Turtle ID	Stranding SCL (cm)	Date tagged	Observed SCL (cm) at tagging	Estimated SCL (cm) at tagging	Difference (cm)
TXH 980626-01	64	12/06/1991	49.6	49.8	−0.2
WMC 051110-02	37.0	10/02/2004	26.9	25.9	1.0
BJA 000904-01	40.0	3/03/1999	36.2	35.1	1.1
WGT 000105-01	59.3	10/04/1995	47	45.5	1.5
WGT 080522-01	103.6	7/28/1998	99.9	102.3	−2.4
WGT 080522-01	103.6	7/14/2000[a]	102.6	102.4	0.2
WGT 080522-01	103.6	7/20/2007[a]	104.3	103.5	0.8

Turtle ID is observer initials followed by the date the turtle stranded dead in the form yr_mo_day-turtle number by day. Stranding SCL is that at dead stranding

[a] WGT 080522-01 was re-sighted twice with measurements taken

The back-calculated SCL for the LAG deposited closest to tagging approximated the actual SCL measured when the turtle was tagged and released in December 1991 (Table 2). This LAG appeared light and non-continuous; therefore we interpreted it as a supplemental LAG likely deposited due to release from captivity. The number of marks exterior to that mark corresponded with the number of years the turtle was at large prior to stranding dead in June of 1998 (Fig. 1), with double LAGs deposited in 1996 and 1997. It was not possible to directly age this turtle as the earliest growth marks were lost to expansion of the resorption core.

For the two smallest tagged turtles (WMC 051110-02 and BJA 000904-01), LAGs originally assumed to be annual were re-interpreted because they were diffuse in nature and resulted in larger back-calculated SCLs than those measured at tagging. The history of WMC 051110-02 revealed that this turtle spent 1 year in captivity then stranded dead approximately 1 month post-release. Based on re-examination of the growth marks and the conversion of all LAGs to SCLs, we concluded that the turtle deposited a distinct double LAG in 2004, followed by one diffuse annual mark while in captivity and two diffuse non-annual marks likely deposited due to stress related to release (Fig. 2). Results from the re-examination of LAGs supported the assumption of annual LAG deposition. For BJA 000904-01, all LAGs were re-examined and converted to previous SCLs. When diffuse LAGs were excluded, results supported annual LAG deposition (Fig. 3; Table 2). The majority of discernible LAGs for this turtle were double LAGs (71%), including those LAGs deposited in 1999 and 2000.

Results from the fourth tagged turtle (WGT 000105-01) supported the assumption of annual LAG deposition. This turtle measured 47 cm SCL in October 1995 at tagging. The back-calculated SCL for that year was 45.5 cm, a difference of 1.5 cm (Table 2). Of the four LAGs exterior to the 1995 LAG, one was a double; 43% of the LAGs deposited prior to tagging in 1995 were identified as doubles.

The fifth tagged turtle was a reproductively mature adult female (WGT 080522-01) that was measured after nesting in 1998, 2000, and 2007. While the back-calculated SCLs for 2000 and 2007 were similar to the actual measurements taken after nesting (Table 2), the back-calculated SCLs for the LAG assumed to have been deposited in 1998 and three LAGs interior to that mark were larger than the actual SCL measured at tagging in 1998. These observations indicate the potential for the deposition of more than one LAG per year in adult female green turtles.

Back-calculated carapace lengths of tagged turtles were not significantly different from those measured at tagging, supporting the body proportional hypothesis (Table 2, $P > 0.20$, Wilcoxon paired-sample test, $n = 7$). There was a mean difference of 1.0 cm between observed and estimated SCLs at tagging.

Age estimates

A diffuse, poorly defined annulus was detected in 47 sections (SCL range = 19.2–44.8 cm) and assumed to be the first year mark, as has been validated in known-age Kemp's ridleys (Snover and Hohn 2004). Turtles with an annulus retained between 1 and 17 LAGs, with age being equal to the number of LAGs. The following power function was fitted to the relationship between LAG diameter and LAG number for the turtles with first year marks:

$$\text{LAG diameter (mm)} = 7.3826 * (\text{LAG number})^{0.3147} \qquad (5)$$

and $r^2 = 0.76$, $n = 211$ LAGs, mean 95% CI ±2.3 years. Equation 5 was rearranged to solve for LAG number and applied to 26 humeri missing the first year mark, but with resorption cores smaller than 18.46 mm. Adding the estimated number of lost LAGs to the number of

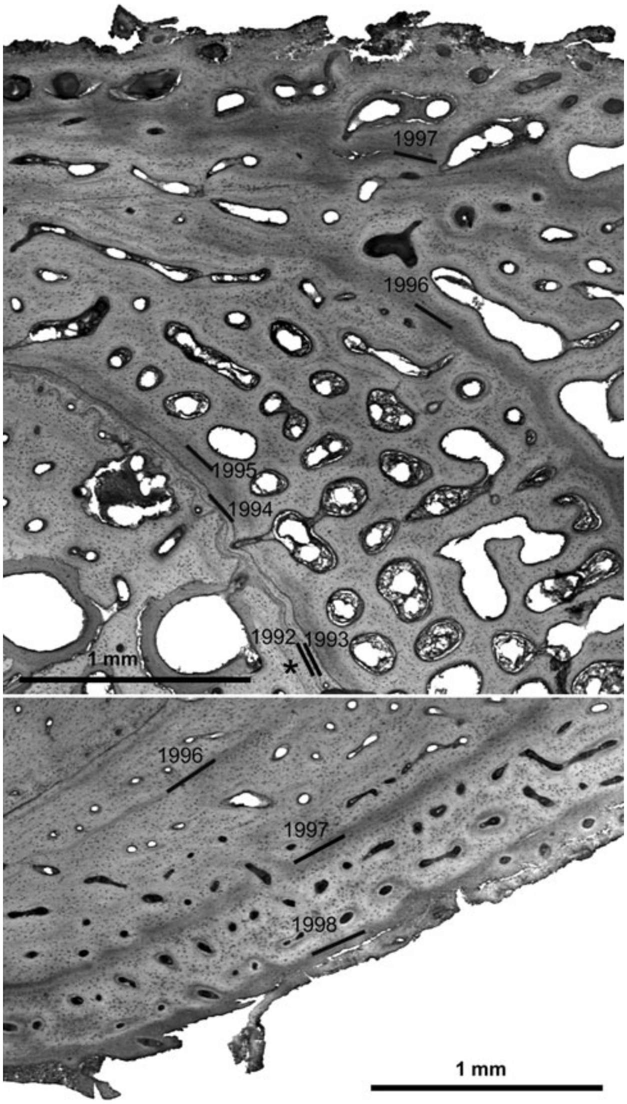

Fig. 1 Stained humerus cross-section of known-age green turtle TXH 980626-01. *Black lines* indicate LAGs. *Asterisk* indicates supplemental LAG likely deposited at release from captivity. Resulting back-calculated SCL was 49.8 cm, 0.2 cm greater than SCL measured at release in December 1991. Three compressed LAGs follow, indicating very little growth in the years following release from captivity. Seven LAGs are visible exterior to the supplemental LAG, validating annual LAG deposition

observed LAGs for those turtles yielded age estimates ranging from 8 to 29 years. The LAGs remaining in these humeri were numbered according to the estimated number of resorbed LAGs, e.g., if 5 LAGs were estimated to have been lost, the first LAG outside the resorption core was counted as LAG 6, and so on. These humeri retained a total of 197 measureable LAGs and their LAG numbers and diameters were combined with the LAG numbers and diameters from the turtles with first year marks to yield the following linear relationship:

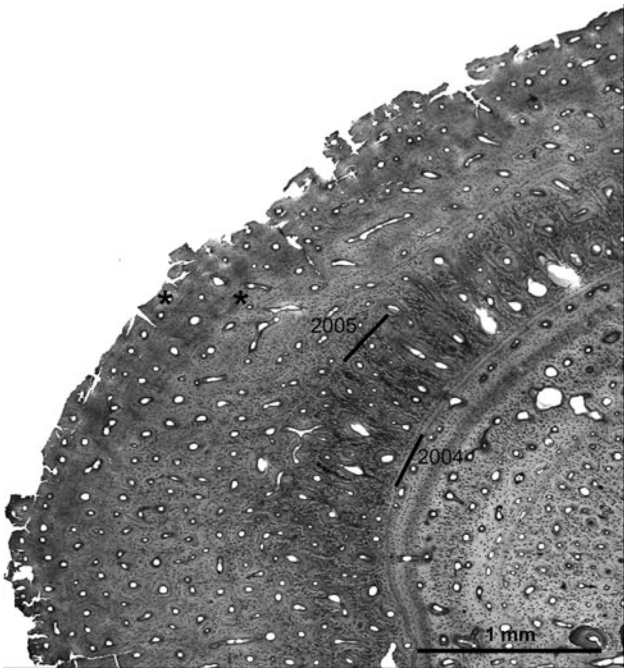

Fig. 2 Stained humerus cross-section of tagged green turtle WMC 051110-02. *Black lines* indicate LAGs. Diameter of the LAG labeled 2004 resulted in a back-calculated SCL of 25.9 cm, 1.0 cm less than the actual SCL of 26.9 cm measured at live stranding on October 2, 2004. *Asterisks* indicate two non-annual diffuse marks that follow the diffuse 2005 LAG that was deposited while in captivity

Fig. 3 Stained humerus cross-section of tagged green turtle BJA 000904-01 measuring 40.0 cm SCL at dead stranding, September 4, 2000. *Black lines* indicate LAGs. *Asterisks* indicate false LAGs. Diameter of the LAG identified as 1999 resulted in a back-calculated SCL of 35.1, 1.1 cm less than that measured at tagging on March 3, 1999

$$\text{LAG diameter (mm)} = 0.7776 * (\text{LAG number}) + 8.0689 \tag{6}$$

and $r^2 = 0.81$, $n = 408$ LAGs, mean 95% CI ±5.7 years. Equation 6 was then rearranged to solve for LAG number, which allowed the number of missing LAGs to be estimated for humeri with resorption cores between 18.46 and 31.09 mm diameter. Lastly, by combining all previously arrived at LAG number and diameter pairs a third correction relationship was developed, which was used to estimate the number of missing LAGs in the four turtles with resorption cores greater than 31.09 mm diameter:

$$\text{LAG diameter (mm)} = 0.7918 * (\text{LAG number}) + 8.0367 \tag{7}$$

and $r^2 = 0.90$, $n = 513$ LAGs, mean 95% CI ±7.3 years. For each of the three steps in this correction process, the equation that best fit the relationship between LAG number and diameter for each group was determined based on r^2 values and the examination of residual patterns. Using these criteria, the linear function described the data for the larger juvenile turtles better than the power function. Although the r^2 values were similar for both linear and power functions, the residuals for the linear function were more uniformly distributed about zero, while the power function produced several large negative residuals at higher LAG numbers for both the second and third correction factors, revealing a tendency for the rearranged power function to overestimate the number of LAGs lost for larger resorption core diameters.

Oceanic stage duration

The smallest green turtles reported along the U.S. Atlantic coast ranged from 19.2 (this study) to 29.5 cm SCL (Mendonça 1981). For green turtles within this size range, oceanic stage duration was estimated at 1–7 years ($\overline{X} = 3$ years ± 1.6 SD, $n = 19$) assuming turtles were new recruits from the oceanic zone.

Growth rates

The following linear regression equation ($r^2 = 0.99$; $P < 0.001$) was used to convert CCL to SCL for the 14 turtles for which only CCL was recorded.

$$\text{SCL} = 0.9426 * (\text{CCL}) - 0.0515 \tag{8}$$

This relationship was derived using 310 green turtles that had stranded dead from New Jersey to the Atlantic coast of Florida for which both SCL and CCL were measured (size range: 4.6–102.0 cm SCL; $\overline{X} = 32.1 \pm 13.9$ SD).

Paired bone medial width and SCL measurements were available for 107 turtles ranging from 4.6 to 103.6 cm SCL ($\overline{X} = 42.3 \pm 25.7$ SD). The relationship between medial width and SCL was allometric, as described by Eq. (1). The minimum hatchling SCL was 4.6 cm and the minimum hatchling humerus diameter was 2.47 mm, as determined from the 12 hatchlings. The parameter estimates were $b = 2.981274$ and $c = 0.941451$, and the residuals were not related to SCL ($r^2 = 0.0006$, $P > 0.50$, $n = 107$).

When testing for a positive relationship between bone growth and somatic growth over time, we found that third-order polynomials provided the best fit for both the relationship between SCL and estimated age, as well as between humerus diameter and estimated age (Fig. 4a, SCL vs. estimated age: $r^2 = 0.91$, $n = 99$; Fig. 4b, humerus diameter vs. estimated age: $r^2 = 0.92$, $n = 99$). The residuals from each relationship demonstrated a positive slope when plotted against each other (Fig. 4c, $r^2 = 0.86$, $n = 99$); an indication that a positive relationship existed between bone growth and carapace growth, thus allowing the back-calculation of carapace lengths from LAG diameters.

Size-specific mean growth rates and standard deviations were calculated using the combined data from 85 turtles of known and unknown sex (Table 3, $n = 406$ growth rates). Sex-specific growth rates are also presented (Table 3, $n = 19$ males, 73 growth rates; $n = 37$ females, 183 growth rates).

Age at maturation

The sex-specific length-at-age data were best described by the logistic and Gompertz growth models for females and by the von Bertalanffy growth model followed by the Gompertz growth model for males (Table 4, females $n = 39$; males $n = 20$). Estimates of age at maturation based on the mean size of nesting females from the Florida, Costa Rican, and Mexican populations were 44, 42.5, and 42 years, respectively, using the sex-specific length-at-age data. When data from turtles of known and unknown sex were combined, the logistic and Gompertz growth functions were best supported, followed by the von Bertalanffy and power functions (Table 5, $n = 85$). The combined length-at-age data of turtles of known and unknown sex resulted in higher estimates of age at maturation for females (Table 6).

The Fabens' modified von Bertalanffy growth interval equation was applied to 183 growth intervals from the back-calculated SCLs of all measureable LAG diameters from 37 females for which the average k was 0.03991 and to 73 growth intervals from the back-calculated SCLs of 19 males, for which the average k was 0.03142. The Fabens' modified von Bertalanffy growth interval equation applied

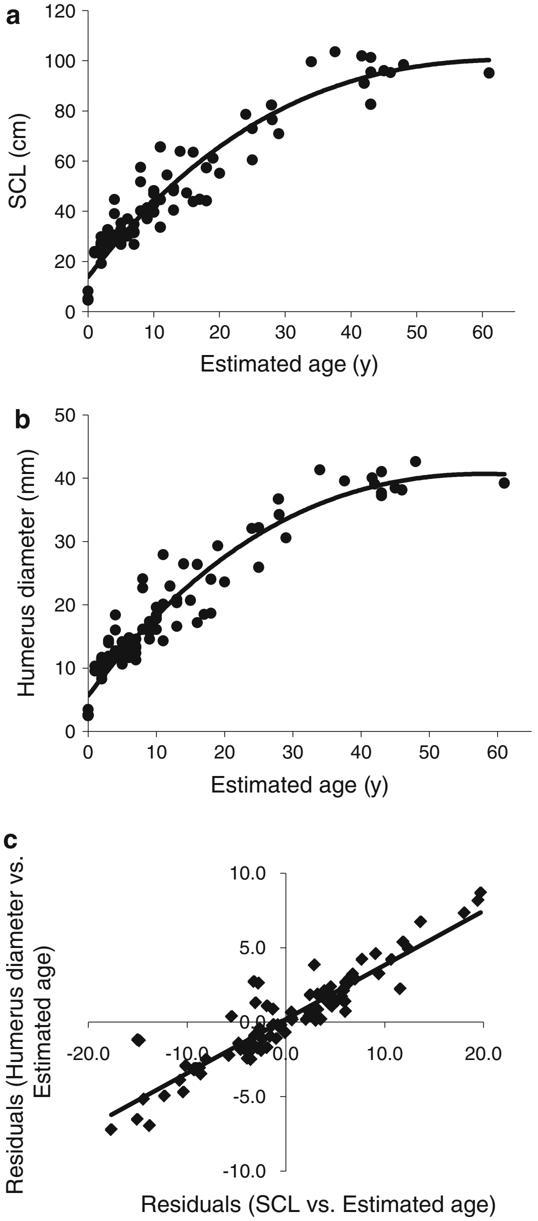

Fig. 4 **a** Relationship between SCL (cm) and estimated age. *Black line* indicates 3rd-order polynomial fit to data ($r^2 = 0.91$). **b** Relationship between humerus diameter (mm) and estimated age. *Black line* indicates 3rd-order polynomial fit to data ($r^2 = 0.92$). **c** Positive correlation between residuals generated from SCL versus estimated age relationship and residuals generated from humerus diameter versus estimated age relationship. *Black line* indicates linear regression fit to data ($r^2 = 0.86$)

to the sex-specific growth increment data and the sex-specific length-at-age data resulted in similar estimates of age at maturation (Table 6; Fig. 5).

Based on the mean growth rate of females through each size class and adding 3 years as the mean oceanic stage duration, it was estimated that 38, 34, and 33 years were required to reach the mean size at maturation for the Florida, Costa Rican, and Mexican populations, respectively. It was estimated that 28 years were required to reach the minimum size at maturation.

The mean age of females at rapprochement was 34 years, ranging from 25 to 41 years (SD = ±7, $n = 4$). Corresponding back-calculated SCLs for the LAG marking the beginning of rapprochement ranged from 89.7 to 101.5 cm SCL ($\overline{X} = 96.7 \pm 5.1$ SD, $n = 4$). The female assumed to have reached maturation at the smallest size was not the youngest.

Discussion

Verification of annual growth marks

Results from the known-age turtle and tagged turtles supported annual LAG deposition in green turtles with the exception of the tagged adult female. Two of the tagged turtles contained supplemental and false LAGs that were originally interpreted as annual LAGs. Non-annual LAG deposition, likely due to stress related to release after time in captivity, has been documented in a loggerhead sea turtle (Snover and Hohn 2004). Therefore, it is plausible that both the known-age and tagged turtle in this study that were in captivity prior to release also deposited non-annual, supplemental LAGs. Diffuse, less distinct LAGs, such as those re-evaluated as false LAGs in the tagged turtle BJA 000904-01 have been characterized by others as non-annual marks (e.g., Trenham et al. 2000; Snover and Hohn 2004; Guarino et al. 2008), which supports our re-interpretation of LAGs in this turtle.

Distinguishing false LAGs from true LAGs is difficult without knowledge of the history of the turtle. To reduce the potential of under- or overestimating age, it has been recommended that a reference collection of known-age individuals be established to identify the aging features within a structure (Campana 2001). However, as there was only one sample from a known-age green turtle available for this study, such a reference collection could not be established. While the results from the tagged turtles in this study can be somewhat informative as to the characteristics of aging features within a bone cross-section, a much larger sample size is needed to establish a reference collection, preferably including turtles of known-age or turtles that had been injected with a bone marker prior to stranding dead and recovery of the humerus bone.

Double LAGs identified in the juvenile known-age and tagged turtles were interpreted as a single annual mark. The number of LAGs exterior to the LAG deposited closest to tagging was equal to the number of years at large for each of the tagged juveniles supporting this interpretation of

Table 3 Size-specific growth rates from back-calculated SCLs of all measurable LAG diameters ($n = 406$ growth intervals) in the humeri of 85 green turtles of known and unknown sex combined and from 19 males ($n = 73$ growth intervals) and 37 females ($n = 183$ growth intervals)

Size class (cm SCL)	All data Mean growth rate (cm year^{-1})	SD	Growth rate range (cm year^{-1})	*n*
16.5–19.9	3.3	1.71	0.34–6.98	25
20.0–29.9	3.0	2.22	0.14–8.90	118
30.0–39.9	2.1	2.05	0.05–9.98	93
40.0–49.9	2.5	2.27	0.09–9.91	54
50.0–59.9	2.7	2.19	0.15–7.62	34
60.0–69.9	3.3	2.63	0.15–11.26	16
70.0–79.9	2.4	2.19	0.08–6.53	21
80.0–89.9	2.6	3.88	0.02–15.75	16
90.0–99.9	1.4	1.86	0.0–7.21	20
100.0 –103.6	0.3	0.56	0.0–1.75	9

Size class (cm SCL)	Males Mean growth rate (cm year^{-1})	SD	*n*	Females Mean growth rate (cm year^{-1})	SD	*n*
16.5–19.9	4.0	1.80	7	3.0	1.69	17
20.0–29.9	3.6	2.68	21	3.1	2.11	73
30.0–39.9	1.6	2.23	17	1.8	2.04	23
40.0–49.9	3.7	3.11	8	2.2	2.18	13
50.0–59.9	3.9	1.65	4	2.0	2.66	13
60.0–69.9	–	–	0	4.1	3.26	8
70.0–79.9	0.5	0.63	6	3.4	2.46	8
80.0–89.9	0.3*	–	1	4.2	5.13	8
90.0–99.9	0.6	0.73	9	2.1	2.26	11
100.0–103.6	–	–	0	0.3	0.56	9

Growth rates were divided into size classes based on the mean SCL of the back-calculated SCL pairs

* Indicates $n = 1$

double LAGs. In this case, double LAGs likely indicated a cessation of growth twice a year as opposed to 2 years of very little growth. Based on our results, this interpretation of double LAGs was applied to all turtles in this study. It is likely that the increased magnification and resolution of the images of the cross-sections in this study allowed for the identification of double LAGs that under lower power may appear as a single LAG. Although the character of the LAGs in the tagged turtles in this study was somewhat informative, validation of this interpretation of double LAGs is still needed and deserves further attention.

Back-calculated SCLs of the reproductively mature adult female (WGT 080522-01) indicated the potential for more than one LAG to have been deposited per year. Reproductive migrations between foraging and breeding grounds or the allocation of resources toward reproduction may have resulted in the deposition of additional LAGs. On the other hand, it is possible that the difference between the observed and estimated carapace lengths could simply be due to measurement error. Because multiple LAGs are compacted near the outer edge of bone cross-sections in reproductively mature adults, even minor measurement error can result in incorrectly including (or excluding) LAGs, thus prohibiting the frequency of LAG deposition from being determined accurately. For example, the SCL measured in May 2008 for the tagged adult female was less than that measured in August of 2007. As negative growth is unlikely, it could be assumed that measurement error occurred in this instance and thus, may also have occurred when other measurements were taken for this turtle, preventing the frequency of LAG deposition from being determined. Future studies should address the frequency of LAGs in adult green turtles, possibly using individuals injected with a bone marker that later strand dead and are recovered.

Overall, the mean difference of 1.0 cm SCL between observed and back-calculated SCLs in this study is greater than the 0.6 cm mean difference reported for loggerheads (Snover et al. 2007a). Some difference can be expected given that LAGs are likely deposited during a different

Table 4 Sex-specific growth function parameter estimates and fitting criteria (females, $n = 39$; males, $n = 20$)

Parameter	von Bertalanffy	Logistic	Gompertz	Power
Females				
B_o	261.5791	114.366	132.6128	21.16667
B_1	0.0093648	0.0777604	0.0433663	2.488453
B_2	−8.974158	17.46834	13.28275	0.9239629
Males				
B_o	114.9258	99.86983	103.5581	6.188334
B_1	0.031422	0.082442	0.0576755	12.04094
B_2	−5.630912	13.99777	7.67636	0.5111021

Model	K	RSS	AIC$_c$	Δ AIC	Weight of evidence
Females					
Logistic	3	1174	139.4606	0	0.742
Gompertz	3	1254	142.0465	2.585909	0.204
von Bertalanffy	3	1372	145.5402	6.079513	0.035
Power	3	1416	146.7835	7.322857	0.019
Males					
von Bertalanffy	3	911	83.87312	0	0.325
Gompertz	3	918	84.01844	0.145313	0.302
Logistic	3	951	84.73062	0.8575	0.211
Power	3	976	85.26247	1.389347	0.162

The parameters are as defined in Table 1 for each model

K number of parameters estimated, *RSS* residual sum of squares, *ΔAIC* AIC$_c$ of model—lowest AIC$_c$. The models with the lowest RSS and greatest weight of evidence best fit the data

Table 5 Growth function parameter estimates and fitting criteria using the combined data from turtles of known and unknown sex ($n = 85$)

Parameter	von Bertalanffy	Logistic	Gompertz	Power
B_o	141.2558	104.6748	113.071	15.22592
B_1	0.0217141	0.814536	0.0510606	5.972076
B_2	−7.055407	14.96835	9.467045	0.6838236

Model	K	RSS	AIC$_c$	Δ AIC	Weight of evidence
Logistic	3	3843	330.2556034	0	0.669
Gompertz	3	3919	331.9320729	1.676469	0.289
von Bertalanffy	3	4106	335.8986597	5.643056	0.040
Power	3	4382	341.4254915	11.16989	0.003

The parameters are as defined in Table 1 for each model

K number of parameters estimated, *RSS* residual sum of squares, *ΔAIC* AIC$_c$ of model—lowest AIC$_c$. The models with the lowest RSS and greatest weight of evidence best fit the data

time of year (i.e., late spring; Snover and Hohn 2004) than when most turtles were tagged and measured (summer and/or fall). SCL and/or LAG diameter measurement error could also partially account for the difference.

Oceanic stage duration

The oceanic stage, during which juvenile green turtles occupy the open ocean before transitioning to the neritic zone (Bolten 2003), has been previously estimated to last between 3 and 6 years (Zug and Glor 1998) and between 3 and 5 years (Reich et al. 2007) in the Atlantic. Green turtles in the Pacific generally recruit from oceanic to neritic habitats at a larger size than their counterparts in the Atlantic and are estimated to be 4–10 years old at 35–37 cm SCL (Zug et al. 2002). In contrast, our observations indicate that green turtles of settlement size along the southeastern U.S. coast can range from 1 to 7 years old,

Table 6 Age at maturation estimated using sex-specific data and the combined data from green turtles of known and unknown sex

	SCL (cm)	Age at maturation (y)			
		Sex-specific Fabens' modified growth interval eq.	Sex-specific length-at-age	All length-at-age	
				Logistic	Gompertz
Females					
Florida	101.5[a]	44.5	44	57.5	53
Costa Rica	100.1[b]	43	42.5	53	51
Mexico	99.5[c]	42	42	51	50
Min. size	83.2[d]	28	30–31	31.5	32.5
Males					
Range	84.8–94.9[e]	37–47.5	35.5–50	33–43	34–43.5

SCL is mean nesting size unless otherwise indicated

[a] Witherington and Ehrhart (1989) ($n = 90$)

[b] Carr and Ogren (1960) ($n = 1146$)

[c] Calculated from the mean SCLs of nesting turtles reviewed by Hirth (1997) ($n = 51$)

[d] Carr and Hirth (1962) (Costa Rica), Witherington and Ehrhart (1989) (Florida)

[e] Ross and Lagueux (1993), Troëng (2000) reported CCLs which fell within this range once converted to SCLs

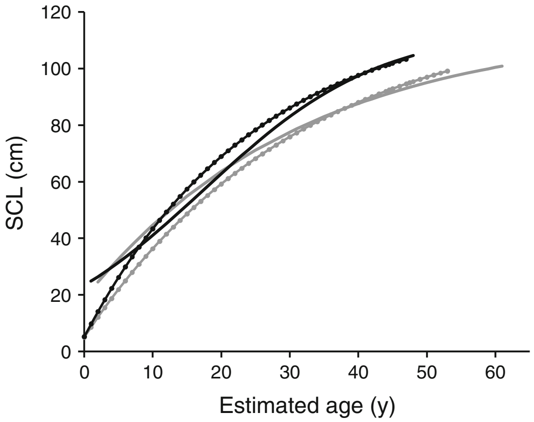

Fig. 5 Length-at-age relationship for Atlantic green turtles. *Black* indicates females; *gray* indicates males. *Connected dotted lines* indicate the Fabens' modified von Bertalanffy growth interval equation applied to the sex-specific growth increment data. *Solid lines* indicate the growth model that best described the sex-specific length-at-age data (females = logistic, males = von Bertalanffy)

suggesting an oceanic stage length of the same duration, assuming the turtles within this size range are new recruits. Our estimate of the oceanic stage duration also assumes a discrete ontogenetic shift from oceanic to neritic habitats, which is not always observed for loggerheads in the southeastern U.S. (McClellan and Read 2007; Mansfield et al. 2009). The lower end of our estimate suggests that for some turtles the oceanic stage duration may be relatively short, aligning with the estimates of 7–14 months made by Carr et al. (1978), which is much shorter than other studies have estimated (Zug and Glor 1998; Zug et al. 2002; Reich et al. 2007). However, our estimate of the average age of 3 years for turtles of settlement size falls well within the ranges of oceanic stage duration that others have proposed for green turtles in the Atlantic (Zug and Glor 1998; Reich et al. 2007).

Growth rates

The growth rates we calculated represent the first reported for the largely inaccessible oceanic stage green turtles, as the growth marks retained in the bones of small turtles allowed the back-calculation of prior carapace lengths. A peak in growth rates appears to occur in the 60.0–69.9 cm SCL size class. Previous modeling of Florida green turtle growth rates has yielded both a monotonic decline in growth rates as carapace length increased (Mendonça 1981) as well as non-monotonic growth rate patterns (Kubis et al. 2009). A peak in mean growth rates also has been reported at a smaller size (50.0–59.9 cm SCL) than that observed here for Florida green turtles in the inshore waters of the Indian River Lagoon using skeletochronology (Zug and Glor 1998). In general, mean growth rates of green turtles in the current study were lower than those reported in inshore waters along the Atlantic coast of Florida (Zug and Glor 1998) and along the Gulf coast of Florida (McMichael et al. 2008), except when compared to early growth rates reported in Florida (Mendonça 1981), in which small sample sizes may have affected those results (Table 7). The lower mean growth rates in this study compared to those turtles of the same size inhabiting inshore and Gulf coast waters of Florida may indicate foraging ground differences in growth rates assuming that green turtles that stranded dead in North Carolina and Virginia utilized the area as a foraging ground prior to

Table 7 Mean growth rates of green turtles as found in this study compared to those in the Atlantic

Size class (cm SCL)	Mean growth rate (cm year^{-1})							
	This study Virginia to Florida[a]	Florida Inshore[b] (Mendonça 1981)	Florida Inshore[a] (Zug and Glor 1998)	Florida Gulf[b] (McMichael et al. 2008)	Florida Nearshore[b] (Bresette and Gorham 2001)	Bahamas[b] (Bjorndal and Bolten 1988)	U.S.V.I.[b] (Boulon and Frazer 1990)	Puerto Rico[b] (Collazo et al. 1992)
16.5–19.9	3.3	–	–	–	–	–	–	–
20.0–29.9	3.0	–	3.1	–	–	–	6.9	3.6
30.0–39.9	2.1	5.3	4.4	4.7	2.3	8.8	5.0	5.1
40.0–49.9	2.5	–	4.8	4.3	2.6	4.9	4.7	6.0
50.0–59.9	2.7	3.1	5.3	4.8	2.7	3.1	3.5	3.8
60.0–69.9	3.3	2.8	4.1	3.8*	–	1.8	1.9	3.9
70.0–79.9	2.4	2.2	1.3*	–	1.8	1.9	3.9	–
80.0–89.9	2.6	–	–	–	–	–	–	–
90.0–99.9	1.4	–	–	–	–	–	–	–
100.0–103.6	0.3	–	–	–	–	–	–	–

* Indicates $n = 1$

[a] Growth rate data acquired through skeletochronology

[b] Growth rate data acquired through mark-recapture

stranding, as the majority (89%) of the turtles in this study between 20 and 40 cm SCL had stranded in those states. Variability in growth rates among foraging grounds has been reported for green turtles in Hawaii (Balazs and Chaloupka 2004), within the southern Great Barrier Reef genetic stock (Chaloupka et al. 2004), and in Florida (Kubis et al. 2009). Differences in growth rates could be related to the availability (Bjorndal et al. 2000) or quality of food (captive green turtles, Wood and Wood 1981), water temperatures (reviewed by Mrosovsky 1980), genetics, length of the growing season, or the energy expense associated with seasonal migrations. More comprehensive studies are needed to evaluate the relative influence of these factors on green turtle growth rates. Green turtles captured in nearshore Florida waters on the Atlantic coast between 30 and 60 cm SCL (Bresette and Gorham 2001) display mean growth rates similar to those reported in the current study (Table 7).

Compared to other geographic locations, green turtles in the current study displayed lower mean growth rates than turtles <60 cm SCL in the Bahamas (Bjorndal and Bolten 1988) and the U.S. Virgin Islands (Boulon and Frazer 1990), as well as those reported in Puerto Rico (Collazo et al. 1992) (Table 7). Compared to green turtles in the Pacific, growth rates reported in this study were higher for all size classes (Limpus and Walter 1980; Green 1993; Seminoff et al. 2002), except those between 20 and 40 cm in Hawaii (Zug et al. 2002) (Table 8).

Age at maturation

When sex-specific data were used, each approach generated a different estimate of age at maturation, but each of the estimates fell between 28 and 44.5 years (Table 6). We recommend using sex-specific data whenever possible to estimate the age at maturation of females because, as found in this study, that age would have been overestimated using the combined length-at-age data from males, females, and turtles of unknown sex. Slower growth by males may tend to bias age at maturation estimates of females upwards. We arrived at similar estimates of age at maturation using the Fabens' modified von Bertalanffy growth interval equation applied to the sex-specific growth increment data and using the sex-specific length-at-age data. These estimates were based on fitted growth models, which could have resulted in the estimates differing from those based on mean growth rates alone. The mean growth rate estimates assume an oceanic stage duration of 3 years, which could vary among turtles, potentially affecting estimates of age at maturation using this approach. The estimated age at maturation based on the mean age of females when rapprochement of LAGs begins was estimated using data from only four females, which limits their value. However, with larger sample sizes, this method could be quite useful for not only estimating age at maturation, but also reproductive longevity, for which little data exist.

The age at maturation of green turtles that use the waters of the southeastern U.S. as developmental habitat likely

Table 8 Comparison of mean growth rates in this study to green turtles in the Pacific

Size class (cm SCL)	Mean growth rate (cm year^{-1})				
	This study Virginia to Florida[a]	Australia[b] (Limpus and Walter 1980)	Galápagos[b] (Green 1993)	Gulf of California[b] (Seminoff et al. 2002)	Hawaii[a] (Zug et al. 2002)
16.5–19.9	3.3	–	–	–	–
20.0–29.9	3.0	–	–	–	4.4
30.0–39.9	2.1	–	–	–	3.5
40.0–49.9	2.5	0.75[c]	0.4	–	2.1
50.0–59.9	2.7	0.95[c,*]	0.5	1.0	2.3
60.0–69.9	3.3	1.43[c]	0.2	1.4	2.2
70.0–79.9	2.4	1.46[c]	0.1	1.2	2.1
80.0–89.9	2.6	1.10[c]	0.1	1.9	1.3
90.0–99.9	1.4	–	–	1.0	0.6
100.0 –103.6	0.3	–	–	–	–

* Indicates $n = 1$

[a] Growth rate data acquired through skeletochronology

[b] Growth rate data acquired through mark-recapture

[c] Indicates growth reported as CCL

ranges from 30 to 44 years based on the minimum and average size of nesting females in the Florida, Costa Rican, and Mexican populations. Frazer and Ehrhart (1985) suggested that the mean size of nesting females may provide the best estimate of the mean age at maturation, as using the smallest documented nesting females might underestimate the mean age at maturation of the population. Furthermore, our rapprochement results indicated that the female that reached maturation at the smallest size was not the youngest, which has also been found for other species of turtles (e.g., Gibbons et al. 1981; Congdon and van Loben Sels 1993); therefore, we advise that the minimum estimate of age at maturation be viewed with caution. Our estimates are higher than previous estimates of 26–36 years for green turtles in the Atlantic (Mendonça 1981; Frazer and Ehrhart 1985; Frazer and Ladner 1986), although these early estimates were based on small sample sizes and a limited size range of turtles (Bjorndal and Bolten 1988; Chaloupka and Musick 1997). Ages at maturation predicted here are similar to those predicted for green turtles in the Pacific of 25–50 years in Australia (Chaloupka et al. 2004) and 35 to >50 years in the Hawaiian Archipelago (Balazs and Chaloupka 2004).

Implications for conservation

Age at maturation of green turtles likely is quite variable within and among breeding populations, depending largely on growth rates realized during the juvenile stage in developmental habitats. For example, the known-age green turtle that was released as a hatchling from the Cayman Turtle Farm and was documented nesting in the Cayman Islands at 17 years old (Bell et al. 2005) likely occupied developmental habitats throughout the Caribbean, which may have allowed for higher growth rates and thus a lower age at maturation when compared to green turtles utilizing the southeastern coast of the United States. The skeletochronological estimates of age at maturation for female green turtles in the Atlantic utilizing developmental habitats of the southeastern U.S. are higher than indicated in previous studies (Mendonça 1981; Frazer and Ehrhart 1985; Frazer and Ladner 1986). Given our estimates of 30–44 years to maturation, it is possible that those turtles that were juveniles when protected by the Endangered Species Act in 1978 may now be contributing to the populations of nesting adults for which a positive trend has recently been detected (Troëng and Rankin 2005; Chaloupka et al. 2008). Higher estimates of age at maturation and lower growth rates imply that nesting populations of green turtles in the Atlantic comprising primarily individuals utilizing foraging grounds in the southeastern U.S. may take longer to recover than previously estimated. In addition, elasticity analyses indicate that variation in survival of individuals during the stage of longest duration has the greatest impact on the population growth rate (Heppell et al. 1999). Given that the neritic stage duration is considerably longer than that of the oceanic stage, it may be more important to protect green turtles in this stage during which boat strikes, interactions with coastal fishing activities, and ingestion of or entanglement in marine debris impact their survival (Lutcavage et al. 1997). Our findings should be considered for use in population models to assess the status and recovery of this species.

Acknowledgments We thank the Sea Turtle Stranding and Salvage Network for collecting the humeri that made this research possible, especially B. Ahern, L. Belskis, Biscayne National Park, Cape Hatteras National Seashore, Cape Lookout National Seashore, E. Hanrahan, North Carolina Wildlife Resources Commission, W. Teas, and the Virginia Aquarium Stranding Center. L. Belskis, W. Cluse, and W. Teas provided stranding data, J. Wyneken, M. Bogardus, and Cape Lookout National Seashore collected the hatchlings, and M. Bresette, D. Bagley, K. Durham, and P. Eliazar provided tagging histories and measurements of the tagged turtles. Special thanks to M. Snover for granting us permission to use the known-age tagged turtle in this study. We are grateful to A. Chester, A. Hohn, P. Marraro, J. McNeill, and three anonymous reviewers for providing comments that improved this manuscript and to T. Lankford for providing valuable feedback during this project. Research was conducted under NMFS Scientific Research Permit # 1260 and USFWS Permit # TE-676379-2 issued to the NMFS SERO. Reference to trade names does not imply endorsement by the authors or their institutions.

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