

AGE AT MATURATION AND GROWTH RATES OF GREEN SEA TURTLES (*CHELONIA MYDAS*) ALONG THE SOUTHEASTERN U.S. ATLANTIC COAST ESTIMATED USING SKELETOCHRONOLOGY

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A Thesis Submitted to the
University of North Carolina Wilmington in Partial Fulfillment
of the Requirements for the Degree of
Master of Science

Department of Biology and Marine Biology

University of North Carolina Wilmington

2009

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JOURNAL PAGE

This thesis has been prepared in the style and format of the journal

Marine Biology

TABLE OF CONTENTS

ABSTRACT	v
ACKNOWLEDGMENTS	vi
LIST OF TABLES	vii
LIST OF FIGURES	viii
INTRODUCTION	1
MATERIALS AND METHODS.....	5
Sample Preparation	7
Analyses	11
Relationship between Bone Growth and Total Body Growth	12
Frequency of Growth Mark Deposition – Tagged Turtles	13
Frequency of Growth Mark Deposition – Marginal Increment Analysis.....	14
Correction Factor	15
Growth Rates and Estimates of Age at Maturation	16
RESULTS	18
Relationship between Bone Growth and Total Body Growth	18
Frequency of Growth Mark Deposition – Tagged Turtles.....	21
Frequency of Growth Mark Deposition – Marginal Increment Analysis	25
Correction Factor	28
Growth Rates and Estimates of Age at Maturation	34
DISCUSSION.....	49
Frequency of LAG Deposition.....	55
Oceanic Stage Length	57

Growth Rates	58
Age at Maturation	60
IMPLICATIONS FOR CONSERVATION	64
LITERATURE CITED	65

ABSTRACT

In the present study, the oceanic stage duration, growth rates of all size classes, and sex-specific ages at maturation for green turtles that use the coastal waters of the southeastern U.S. as developmental habitat are estimated using skeletochronology. Three main issues that typically confound skeletochronological analyses of age and growth are addressed: 1) annual deposition of lines of arrested growth (LAGs) is indirectly verified, 2) the relationship between bone and somatic growth is characterized, and 3) a correction factor is established to account for the number of growth marks lost to bone remodeling. Oceanic stage length is estimated at 1 to 7 years, with a mean of 3 years, for newly recruited neritic juvenile green turtles along the southeastern coast of the U.S. A non-monotonic pattern in mean growth rates is demonstrated, with mean growth rates peaking in the 60.0-69.9 cm straight carapace length (SCL) and 80.0-89.9 cm SCL size classes. Age at maturation is estimated at 44 years for the Florida population and 42.5 for the Costa Rican population, based on the length-at-age data and the mean size of nesting females of each population as 101.5 and 100.1 cm SCL, respectively. Analyses indicate that 30 to 31 years are required to reach the minimum size at maturation of 83.2 cm SCL for both populations of nesting females. Males ranging from 84.8 to 94.9 cm SCL are estimated to be 35.5 to 50 years, based on growth models fit to the length-at-age data. The results of this study are significant in that samples were available from all sizes of green turtles, ranging from hatchlings to adults, and genetic composition of the population from which samples for age estimation were obtained was known. This then allows estimation of age at maturation for turtles that use the coast of the southeastern U.S. as developmental habitat, but contribute to the Florida and Costa Rican nesting populations.

ACKNOWLEDGMENTS

I am grateful to the Sea Turtle Stranding and Salvage Network for collecting samples for this study. Special thanks to L Belskis, W Cluse, and W Teas for providing stranding data, J Wyneken, M Bogardus, and Cape Lookout National Seashore for collecting dead hatchlings, M Bresette, D Bagley, K Durham, and P Eliazar for providing tagging histories and measurements for the tagged turtles, and L Avens and F Scharf for assistance with the analyses. I would like to thank my advisor, A Southwood, and my committee members, L Avens, F Scharf, and T Lankford. NOAA Fisheries supported this research, and I would especially like to express my gratitude to L Avens for the constant support and guidance she provided. L Hansen, and A Hohn at the NOAA Fisheries Beaufort Laboratory have been understanding and supportive of the schedule I have kept over the past three years as a student, for which I am grateful. Thanks to the UNCW Graduate School and A Southwood for providing travel funding to present this research. Thanks also to JHT Inc. and Alpha Solutions Inc. for providing academic fee monies. Research was conducted under NMFS Scientific Research Permit # 1260 and USFWS Permit # TE-676379-2 issued to the NMFS SERO.

LIST OF TABLES

Table	Page
1. Sample Sizes for each 10 cm Size Class.....	8
2. Back-calculated SCLs from LAG Diameters of Tagged Green Turtles Compared to SCLs Measured at Tagging.....	26
3. Size-Specific Growth Rates Obtained from Back-Calculated SCLs of the Final 2 LAG Diameters	37
4. Size-Specific Growth Rates from Back-Calculated SCLs of all Measureable LAG Diameters	38
5. Ages and Mean SCLs (cm).....	44
6. Fitting Criteria of Growth Functions Applied to Length-at-Age Data	46
7. Growth Function Parameter Estimates	47
8. Fitting Criteria of Growth Functions Applied to Sex-Specific Length-at-Age Data	50
9. Sex-Specific Growth Function Parameter Estimates.....	51
10. Ages Estimated Based on the Models that Best Fit the Length-at-Age Data from Males	54

LIST OF FIGURES

Figure	Page
1. Linear Regression of vs. Straight Carapace Length (SCL) vs. Curved Carapace Length (CCL)	6
2. Size Distribution of Samples by Sex	9
3. Size Distribution of Samples	10
4. Allometric Relationship between SCL (cm) and Medial Width (mm).....	19
5. SCL vs. Estimated Age Relationship and Humerus Diameter vs. Estimated Age Relationship.....	20
6. Positive Correlation between Residuals Associated with SCL vs. Estimated Age Relationship and Residuals Associated with Humerus Diameter vs. Estimated Age Relationship.....	22
7. Stained Humerus Cross-section of Tagged Green Turtle WMC 051110-02	23
8. Stained Humerus Cross-section of Tagged Green Turtle BJA 000904-01	24
9. Growth External to Last LAG (mm) Plotted Against Julian Stranding Date	27
10. Marginal Increment Analysis for Turtles from 19.2 to 39.9 cm SCL.....	29
11. Marginal Increment Analysis for Turtles Stranding in Florida	30
12. Marginal Increment Analysis for Turtles Stranding in North Carolina And Virginia	32
13. Relationship between LAG Diameter (mm) and LAG Number	35
14. Fabens Modified von Bertalanffy Growth Function Applied to Growth Increment Data.....	40
15. Fabens Modified von Bertalanffy Growth Function Applied to Sex-Specific Growth Increment Data	41
16. Estimated Ages of 19.2 - 29.5 cm SCL Green Turtles	43

17.	Growth Models Applied to Length-at-Age Data	48
18.	Growth Models Applied to Length-at-Age Data from Females	52
19	Growth Models Applied to Length-at-Age Data from Males.....	53
20.	Fabens Modified von Bertalanffy Growth Interval Equation Applied to the Growth Increment Data with Length-at-Age Data Plotted for Comparison.....	61

INTRODUCTION

Green turtles are circumglobal, inhabiting tropical and subtropical waters and their life history is similar to that of other sea turtle species. In the North Atlantic, 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. This shift in habitats is accompanied by a shift from omnivory to herbivory, as stable isotope analyses have confirmed in the Pacific (Arthur et al. 2008). Adult green turtles migrate between foraging and nesting grounds (Troëng et al. 2005), with females nesting at an average size of 101.5 cm straight carapace length (SCL) in Florida (Witherington and Ehrhart 1989) and 100.1 cm SCL in Tortuguero, Costa Rica (Carr and Ogren 1960).

The breeding populations of green turtles in Florida and along the Pacific coast of Mexico are listed as endangered; all other green turtles are listed as threatened under the U.S. Endangered Species Act. The World Conservation Union (IUCN) considers green turtles to be globally endangered (Baillie et al. 2004). The recent 5-year review released by the National Marine Fisheries Service and the U.S. Fish and Wildlife Service (2007) identifies growth and age at maturation as aspects of green turtle biology for which information is lacking, yet needed for population modeling. Despite the need for age and growth data, this information 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 characteristics such as a long life-span, slow growth, and delayed maturity (Chaloupka and Musick 1997).

Age at maturation based on the mean size of nesting green turtles in the Atlantic is estimated at 27 (Frazer and Ehrhart 1985) to 30 years (Mendonça 1981) in Florida, and 26, 33,

35, and 36 years in Costa Rica, U.S Virgin Islands, Ascension Island, and Surinam (Frazer and Ladner 1986), respectively, using mark-recapture methods. Although mark-recapture studies have provided growth rate data on the size ranges of greens inhabiting foraging grounds, small sample sizes and the lack of turtles spanning the entire size range from hatchlings to adults in these aggregations have hindered estimates of age at maturation (Bjorndal and Bolten 1988; Chaloupka and Musick 1997). To date, on the Atlantic coast of the U.S., one skeletochronological study has been conducted on green turtles in Florida (Zug and Glor 1998). However, the geographic scope of the study was restricted to one inshore body of water and samples were lacking from reproductively mature turtles, which allowed growth rate estimates of the size ranges present, but prevented estimation of age at maturation (Zug and Glor 1998). Also, in this study, it was not possible to determine the frequency with which growth marks were deposited in green turtle bones, to validate the assumption that each mark represents an annual cycle.

In the Pacific, mark-recapture studies of green turtles have resulted in estimates of 25 to greater than 50 years at maturation (30 yrs., Limpus and Walter 1980; 40 yrs., Limpus and Chaloupka 1997; 35 to greater than 50 yrs., Balazs and Chaloupka 2004; 25, 30, 40 and at least 50 yrs., Chaloupka et al. 2004). Ages of Hawaiian green turtles ranging in size from 28.7 to 96.0 cm SCL estimated using skeletochronology ranged from 4 to 34 years or 3 to 49 years old, depending on the method used to account for growth marks that were lost to bone remodeling (Zug et al. 2002). The authors estimate the age at maturation for this population to be greater than 30 years (Zug et al. 2002). However, growth rates have been shown to differ for the same species in different ocean basins; therefore age at maturation for greens in the Pacific is not necessarily equivalent to that of green turtles in the Atlantic Ocean (Bjorndal et al. 2000).

Skeletochronology, which involves analyzing growth marks contained in bones, has been used as a means of ascertaining life history information for sea turtles that is otherwise difficult to obtain using traditional mark-recapture methods (Zug et al. 1986). Skeletal growth marks appear in cross-sections of bones of some animals as wide zones of rapid bone growth followed by darker, narrow lines of arrested growth (LAGs) (Castanet et al. 1993). Endogenous rhythms reinforced by seasonal cycles are thought to result in annual LAG deposition, although non-annual LAGs can also occur due to factors such as hatching, physiological stress, disease, starvation, reproductive cycles, and a growth cycle that is interrupted more than once during the year (reviewed by Castanet et al. 1993). The earliest growth is at the center of the bone, with most recent growth occurring along the outer circumference. The center of the bone contains highly vascularized cancellous bone, which does not retain growth marks. Cortical bone encircles the core of cancellous bone and has been shown to contain growth marks (Zug et al. 1986); however early growth marks are destroyed by resorption, or remodeling of the bone as the turtle grows and the core of cancellous bone expands. The humerus bone is typically used in hard-shelled 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).

Before skeletochronology is used as an age estimation tool for sea turtles 1) the frequency of growth mark deposition should be verified, 2) a relationship must exist between bone growth and total body growth to allow for the back-calculation of carapace lengths from growth mark diameters, and 3) a correction factor must be established to account for the number of growth marks lost to bone remodeling (i.e. see Chaloupka and Musick 1997). The annual nature of growth marks has been validated directly in the humeri of known-age loggerheads (*Caretta caretta*) and Kemp's ridleys (*Lepidochelys kempii*) (Snover and Hohn 2004), and in loggerheads

injected with oxytetracycline as a bone marker (Klinger and Musick 1992; Coles et al. 2001). Marginal increment analysis, as applied to Kemp's ridleys (Snover and Hohn 2004) has allowed for the indirect validation of the frequency of growth mark deposition by determining the time of year that growth marks are deposited. The second issue has been addressed in several species in which a correlation was found between humerus diameter and straight carapace length (SCL) (Zug and Glor 1998; Zug et al. 2002; Zug et al. 2006; Snover and Hohn 2004). Furthermore, in marked and recaptured loggerheads, Snover et al. (2007) confirmed that LAG diameters correspond with carapace length, which allows for growth rates of individual turtles to be back-calculated through conversion of successive LAG diameters to estimates of carapace lengths. The correction-factor protocol is one method of accounting for the number of layers lost to resorption (Parham and Zug 1997). This protocol requires samples from individuals in which the first year mark has not been lost to resorption, allowing accurate LAG counts to be made over the lifespan of the animal.

Genetic studies indicate that juvenile greens inhabiting the coastal waters of Florida and North Carolina are primarily from Costa Rican, U.S., and Mexican nesting stocks (Bass and Witzell 2000, Bass et al. 2006) and there is evidence that the females return to the region where they hatched to nest as adults (Meylan et al. 1990). Because the genetic composition of the assemblages on the North Carolina and Florida foraging grounds is known and the size range of females nesting in both Florida and Costa Rica is well documented (see Hirth 1997 for review), the age at maturation will be estimated for females of both populations that use the coast of the southeastern U.S. as developmental habitat.

The current study addresses the issues with skeletochronology to estimate age at maturation, growth rates, and stage durations of green turtles inhabiting temperate to sub-tropical

waters along the U.S. Atlantic coast, for which little data currently exist. To compare estimates of age at maturation yielded by skeletochronology to those from mark-recapture studies, age at maturation was estimated by applying the Fabens' modified von Bertalanffy growth interval equation (Fabens 1965) to growth increment data obtained from stained sections of humeri. Using the same turtles, age at maturation was also estimated by fitting growth models to length-at-age data.

MATERIALS AND METHODS

The left front flipper was removed from green sea turtles that stranded dead along the U.S. Atlantic coast from Virginia to Florida, not including the Gulf of Mexico, 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 110 samples were collected from turtles that ranged in size from a 4.6 cm (SCL) hatchling to a 103.6 cm SCL adult (mean = 43.2, standard deviation = 25.6). SCL was measured from the nuchal notch to the posterior tip of the carapace to the nearest 0.1 cm with forester's calipers (Haglöf Sweden AB, Långsele, Sweden) for all turtles except hatchlings, which were measured with digital calipers (Fowler Co., Inc., Newton, Massachusetts, USA). Hatchlings that had fully emerged from eggs but were discovered dead upon excavation of five nests laid in North Carolina and Florida were collected. The following regression equation was used to convert curved carapace length (CCL) to SCL for the 14 turtles for which only CCL was recorded ($r^2 = 0.99$; $p < 0.001$).

$$\text{SCL} = 0.9426 * (\text{CCL}) - 0.0515 \quad (1)$$

This equation was derived from 310 green turtles that stranded dead from New Jersey to the Atlantic coast of Florida ranging in size from 4.6 to 102.0 cm SCL, for which both SCL and CCL were measured (Fig. 1). Samples were divided into 10 cm size classes for analyses (Table

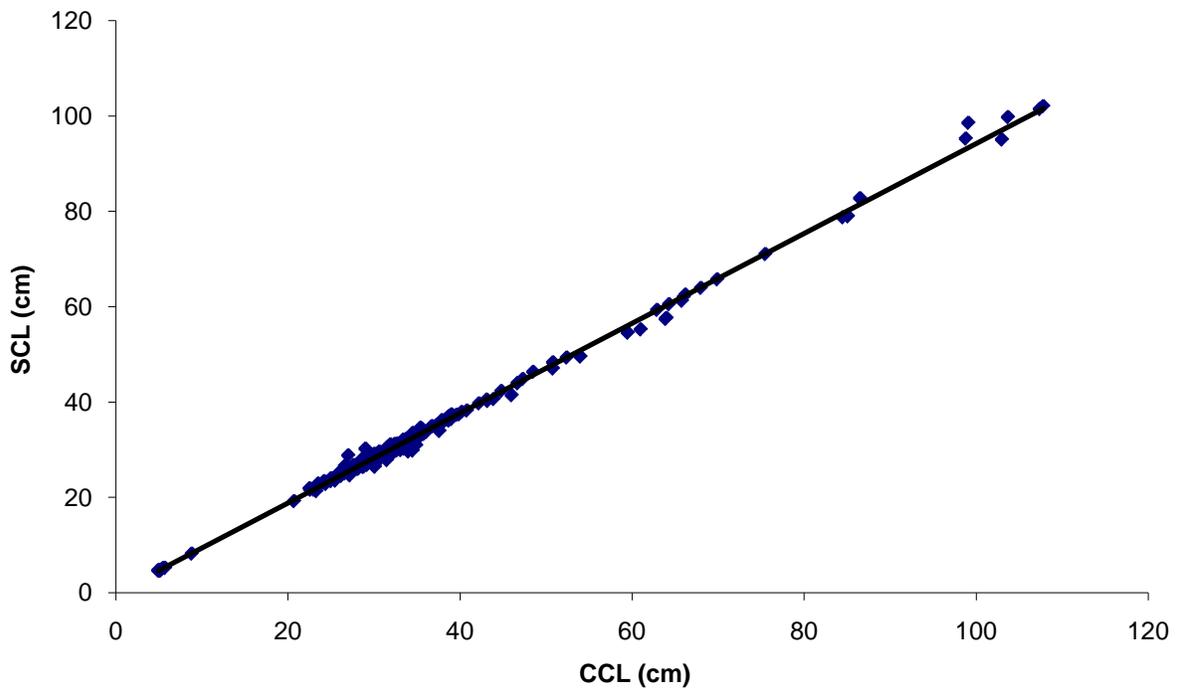


Figure 1. Linear regression of straight carapace length (SCL) vs. curved carapace length (CCL) ($r^2 = 0.99$, $n = 310$).

- 1). The samples in this study included 21 males and 41 females as determined by necropsy, and 48 of unknown sex, either due to decomposition or because the turtles were not necropsied (Fig. 2).
- 2). Six turtles, all from Florida, were noted as having fibropapilloma tumors (Fig. 3).

Sample Preparation:

The following methodology as adapted from Snover and Hohn (2004) and Snover (2002) was used to prepare the samples. Humeri were dissected from flippers, flensed of tissue, boiled, and then allowed to dry in the sun for approximately two weeks. Using digital calipers (Fowler Co., Inc., Newton, Massachusetts, USA), 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. A Buehler low-speed isomet saw (Lake Bluff, Illinois, USA) was used to take a 1-3 mm thick cross-section for histological processing at a standardized location for all humeri, just distal to the deltopectoral muscle insertion scar. Cross-sections were fixed in 10% neutral buffered formalin (Fisher Scientific, Fairlawn, New Jersey, USA) for 3 hours, rinsed with tap water, then allowed to soak in RDO (Apex Engineering Products Corp., Aurora, Illinois, USA), a commercial decalcifier, for between 6 and 36 hours depending on the size of the bone. A Leica freezing stage microtome (Leica Microsystems, Inc., Bannockburn, Illinois, USA) was used to take 25 μ m thin sections, which were placed in histocassettes and allowed to soak in water overnight to remove any decalcifier remaining in the tissue that might interfere with staining. Sections were stained using Ehrlich's hematoxylin (Klevezal 1996), diluted 1:1 with water filtered by reverse osmosis and were allowed to 'blue' by soaking in tap water for 20 minutes. They were then transferred to a solution of 1:1 glycerin-reverse osmosis water for 20 minutes, after which they were transferred to 100% glycerin for 20 minutes. Stained thin sections were mounted on slides in 100% glycerin and a cover slip was sealed in

Table 1. Sample sizes for each 10 cm size class.

Size class	<i>n</i>	Size class	<i>n</i>
hatchlings	12	50.0-59.9	7
post-hatchlings	1	60.0-69.9	7
≤ 19.9	1	70.0-79.9	5
20.0-29.9	22	80.0-89.9	2
30.0-39.9	22	90.0-99.9	7
40.0-49.9	21	100.0-103.6	3

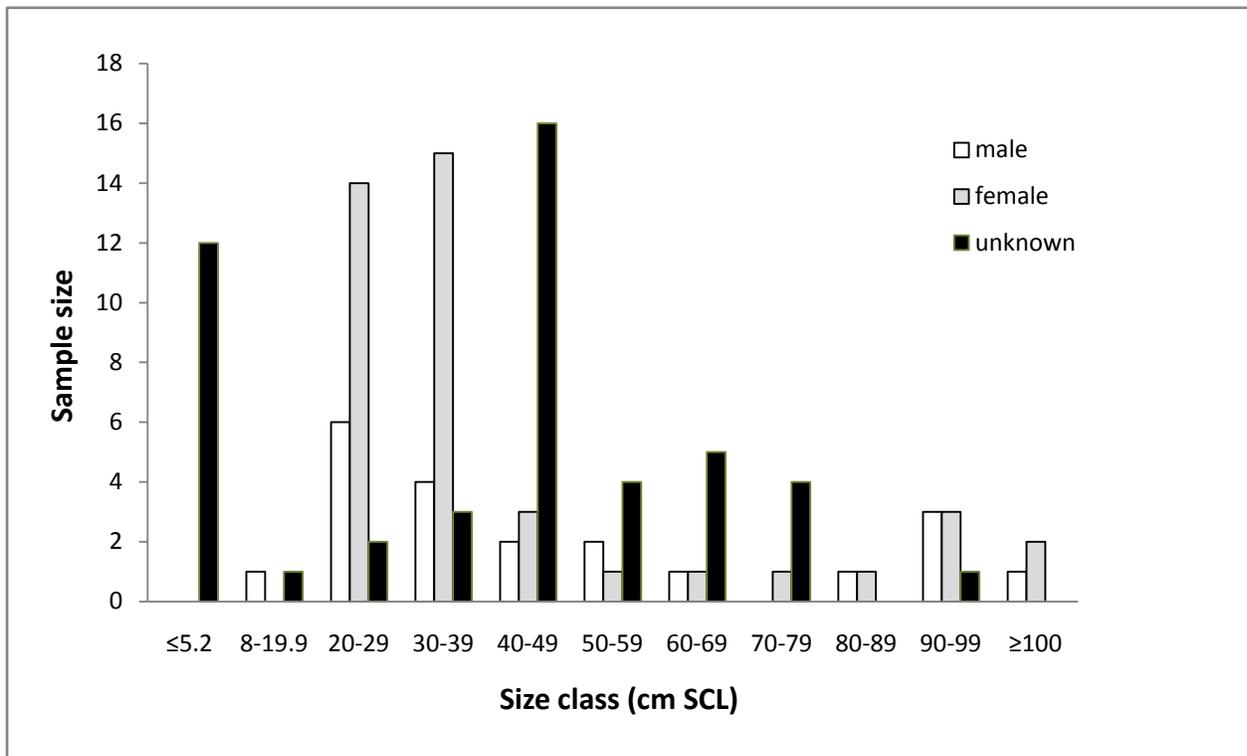


Figure 2. Size distribution of samples by sex.

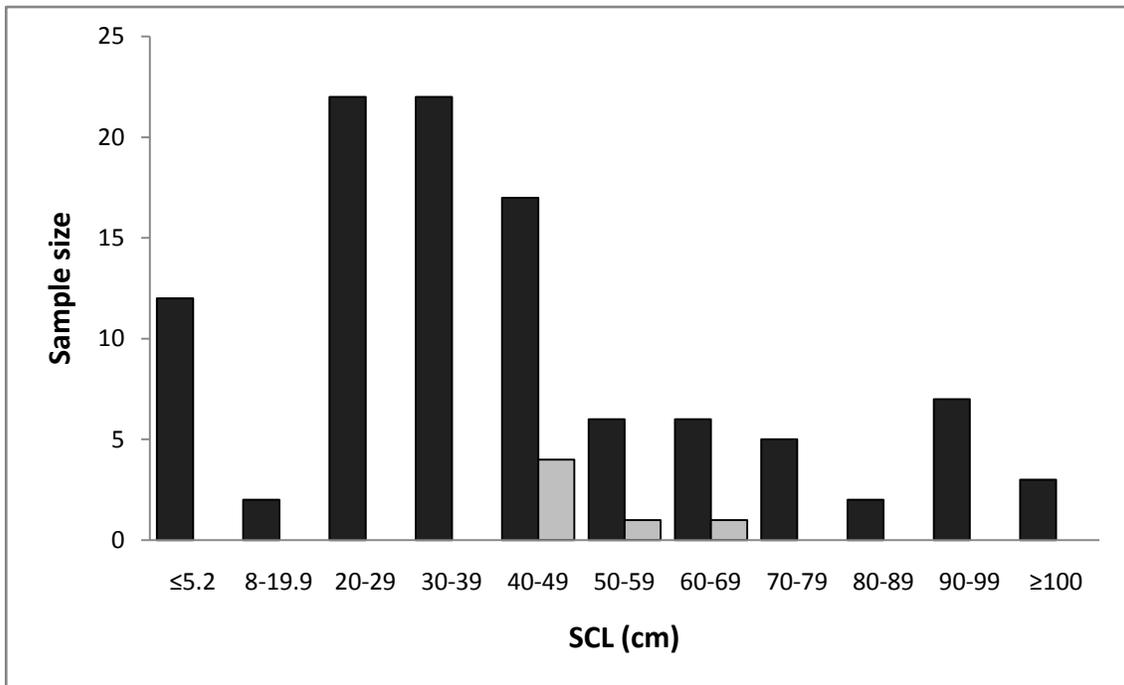


Figure 3. Size distribution of samples. Grey bars indicate turtles with fibropapilloma tumors. Black bars indicate turtles without tumors.

place with Cytoseal 280 (Richard-Allan Scientific, Kalamazoo, Michigan, USA) to allow for viewing and archiving.

Analyses:

As a more permanent method of storage and to enable measurements to be taken using a digital image and image analysis software, sequential portions of stained cross-sections were photographed at x4 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). These sequential images were stitched using Adobe Photoshop (Adobe Systems Inc., San Jose, California, USA) to obtain a high resolution composite digital image for each cross-section. Random numbers were assigned to each image and 10 duplicate images were generated before the lines of arrested growth (LAGs) were counted and marked independently by two readers (LA, LRG). Average percent error was calculated using the 10 duplicates to determine 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). Consensus was reached by both observers when the number or placement of LAGs differed.

Measurements of the LAG, resorption core, and total humerus diameters were taken along an axis parallel to the dorsal edge of the composite digital image of each cross-section using Olympus Microsuite Basic Image Analysis software (Olympus America Inc., Melville, New York, USA). Samples that sectioned poorly, those turtles with fibropapilloma, and those with estimated carapace lengths were excluded from some 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 that of healthy individuals when

tumor severity is advanced (Chaloupka and Balazs 2005). Including individuals with FP could bias estimates toward slower growth which may not be representative of the overall population.

Relationship between Bone Growth and Total Body Growth

A positive relationship must exist between bone and somatic growth if prior carapace lengths are to be estimated from LAG diameters (Chaloupka & Musick 1997). Medial width (mm) was measured as the lateral diameter of the bone at the sectioning site and was taken prior to cross-sectioning and histological processing. Paired medial width and SCL measurements were available for 107 turtles ranging in size from 4.6 to 103.6 cm SCL (mean = 42.3, standard deviation = 25.7). Although turtles with fibropapilloma tumors were included in this analysis, those turtles for which SCL was not measured and could not be estimated using Eq. (1) due to approximated CCLs were not. The relationship between medial width and SCL was modeled using the following allometric equation, as applied to loggerhead sea turtles by Snover et al. (2007):

$$L = L_{op} + b(D - D_{op})^c \quad (2)$$

where L is the estimated SCL (cm), L_{op} is the minimum hatchling SCL (cm), D is the medial width of the humerus (mm), D_{op} is the minimum hatchling humerus diameter (mm), b is the slope of the relationship, and c is the proportionality coefficient.

While the above analysis was used to determine if there was a relationship between bone and somatic measures, it was still necessary to determine if a relationship existed between bone growth and carapace growth over time. Humerus diameter was measured on the composite digital images of the sections after histological processing as the lateral diameter of the cross-section taken on an axis parallel to the dorsal edge of the bone. Ages were estimated using the methods described below. The relationship between SCL and estimated age, as well as humerus

diameter and estimated age was modeled and the functions that best characterized these data were determined. The residuals associated with each were plotted against each other to determine if a trend existed.

Frequency of Growth Mark Deposition - Tagged Turtles

In the absence of known-age turtles or those that had been injected with a bone marker prior to stranding dead, humeri from four turtles that had been tagged, released, and stranded dead at least one year after being tagged were used to indirectly validate the frequency of growth mark deposition. All were free-ranging, wild turtles that had been tagged and released the same day with the exception of one turtle that stranded in poor condition in New York and spent approximately one year in captivity for rehabilitation. Two were tagged after being captured in the intake canal of the St. Lucie Power Plant in Florida. One turtle was tagged after nesting in the Archie Carr National Wildlife Refuge in Florida and was measured during four subsequent nesting events; twice in 2000 and 2007. Turtles ranged in size from 26.9 to 99.9 cm SCL at initial tagging.

Each LAG was assigned a year starting with the LAG closest to the outside edge of the bone working in, under the hypothesis that one LAG was deposited per year in the spring as was found in Kemp's ridleys (*Lepidochelys kempii*, Snover and Hohn 2004). The SCL was back-calculated from the LAG hypothesized to have been deposited closest to the time of tagging and compared to the actual SCL measured at the time the turtle was tagged or re-sighted using the Wilcoxon paired-sample test. Since the assumption was made that LAGs were deposited in the spring, the SCLs measured during the earliest nesting events in 2000 and 2007 were used for the adult female that had been re-sighted.

A correlation between bone and somatic growth, as tested for in the above analysis, allowed LAG diameters to be substituted into Eq. (2) in place of medial width, thus allowing SCLs to be back-calculated. The body proportional hypothesis (Francis 1990), as applied to sea turtles (Snover et al. 2007), was applied to the back-calculated SCLs. To apply the body proportional hypothesis, it was first necessary to use Eq. (2) to estimate the SCL at stranding using the humerus diameter, and the SCL at capture using the LAG diameter hypothesized to have been deposited closest to the capture date. The observed SCL at stranding was divided by the estimated SCL at stranding and the resulting value was multiplied by the estimate of the SCL at capture to yield a proportional estimate of the SCL at capture.

Frequency of Growth Mark Deposition - Marginal Increment Analysis

A correlation between the amount of bone deposited external to the outermost LAG and the date of death has been used to indirectly validate the frequency of LAG deposition in Kemp's ridley sea turtles (Snover and Hohn 2004). A positive correlation between growth increment width and time of year indicates a period of active bone deposition; no change in increment width can indicate a slowing or cessation of growth during the corresponding time of year. Detection of a cyclic pattern of growth and no growth can be used to indirectly validate the frequency with which marks are laid down. This is referred to as marginal increment analysis in the fisheries literature (i.e. Williams and Bedford 1974). To test for such a correlation in green turtles, the humerus diameter and outermost LAG diameter were measured as previously described. The amount of bone deposited external to the outermost LAG was calculated by subtracting the outermost LAG diameter from the humerus diameter and the resulting growth increment was plotted against the Julian stranding date. The data were visually inspected for trends of increasing or no change in growth increment width to which linear regressions were fit.

Due to difficulties sectioning, humerus diameter was not measureable for all samples and in these cases, it was desirable to substitute medial width for humerus diameter, which was measured before the cross-section was taken. To validate this substitution, a t-test was used to test for a difference between medial width and humerus diameter pairs (Zar 1996). Marginal increment analysis was applied to 79 green turtles. The following samples were not included in the marginal increment analysis: turtles with fibropapilloma, the tagged turtle that spent time in captivity during its last year of growth and therefore was not subject to seasonal variation in environmental conditions, and those which sectioned poorly resulting in the inability to obtain reliable humerus and LAG diameter measurements.

Correction Factor

Prior to assigning ages to those turtles whose humeri exhibited resorption of early growth marks, it was necessary to establish a correction factor to account for the number of lost marks. In this study, the correction factor introduced by Parham and Zug (1997) was used, which requires samples containing a first year mark, or annulus, as well as a known frequency of LAG deposition. 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 parametric methods were used to determine which type of relationship best characterized the data. LAG number was equal to age for turtles retaining an annulus based on the indirect validation of annual LAGs from the analysis of tagged turtles (see results- frequency of growth mark deposition – tagged turtles). Turtles with fibropapilloma were not used in establishing the correction factor because their bone growth increments might not be representative of healthy individuals.

For turtles that did not retain an annulus, either the diameter of the resorption core or that of the first LAG outside of the resorption core was measured and substituted for LAG diameter in the equation yielded by the relationship between LAG diameter and LAG number, which resulted in an estimate of the number of LAGs missing within that diameter. The estimate of the number of lost LAGs yielded by the correction factor equation was added to the number of LAGs retained in the section to produce age estimates for each turtle.

For turtles with resorption cores greater than the largest LAG diameter measured in turtles retaining an annulus, additional correction factors were developed using data from those turtles aged using the original correction factor. Methods were the same as those described for the original correction factor. First, for those turtles aged using the original correction factor, the estimated number of LAGs lost to resorption was determined for each sample. This allowed each LAG outside the resorption core to be assigned a number and each of those LAG diameters was then measured, if possible. LAG diameter and LAG number pairs were added to those of turtles that retained an annulus and the relationship was modeled using parametric methods, resulting in a correction factor that could be applied to turtles with resorption core diameters not exceeding the largest LAG diameter measured.

Growth Rates and Estimates of Age at Maturation

For each sample, the diameters of the two outermost LAGs were measured, SCLs were back-calculated using Eq. (2), and the body proportional hypothesis was then applied. A growth increment was calculated for each turtle by subtracting the back-calculated SCL associated with the second to last LAG from that associated with the outermost LAG. Turtles were divided into size classes based on the mean SCL (cm) of the back-calculated SCL pairs and the mean growth rate and standard deviation were calculated for each 10 cm size class. For comparison, the mean

growth rate and standard deviation were also calculated for all measureable LAG diameters present in bone sections for which SCLs were back-calculated. This allowed for an increased sample size of each size class.

The Fabens' modified von Bertalanffy growth interval equation (Fabens 1965) as applied to sea turtle mark-recapture data (Frazer and Ehrhart 1985) is:

$$L_r = a - (a - L_c)e^{-kd} \quad (3)$$

and was applied to the growth increment data from the final two LAGs converted to SCLs as an alternate means of estimating age at maturation. L_r is the length at recapture, L_c is the length at initial capture, a 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 :

$$k = -\text{Ln}[-(L_{\text{final}} - L_{\text{inf}}) / (L_{\text{inf}} - L_{\text{initial}})] / t \quad (4)$$

The back-calculated SCL of the outermost LAG was termed L_{final} and that of the second to last LAG was termed L_{initial} . L_{inf} was set at 121 cm SCL, as this was the largest green turtle reported in the Atlantic (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 age at maturation:

$$\text{SCL at age} = L_{\text{inf}} - (L_{\text{inf}} - L_{\text{hatch}})e^{(-\text{avg } k * \text{age})} \quad (5)$$

where the parameters are as defined for Eq. (4), with L_{hatch} set as 5.0 cm SCL based on the mean hatchling size reported by van Buskirk and Crowder (1994), and age is that in years.

Frazer and Ehrhart (1985) suggested that the mean size of nesting females provided the best estimate of the average age at maturation. The mean size of nesting females has been reported as 101.5 cm straight carapace length (SCL) in Florida ($n = 90$, Witherington and Ehrhart 1989) and 100.1 cm SCL in Tortuguero, Costa Rica ($n = 1146$, Carr and Ogren 1960); therefore these sizes were used in estimating the average age at maturation.

As an alternative means of estimating age at maturation, ages were estimated for each turtle using the correction factor described above. SCL (cm) was measured when turtles stranded dead or was calculated using the CCL (cm) and Eq. (1). The von Bertalanffy, logistic, Gompertz, and power function growth models were fit to the length-at-age data using STATA statistical software (StataCorp.). AIC scores and weight of evidence were used to determine which models best fit the data.

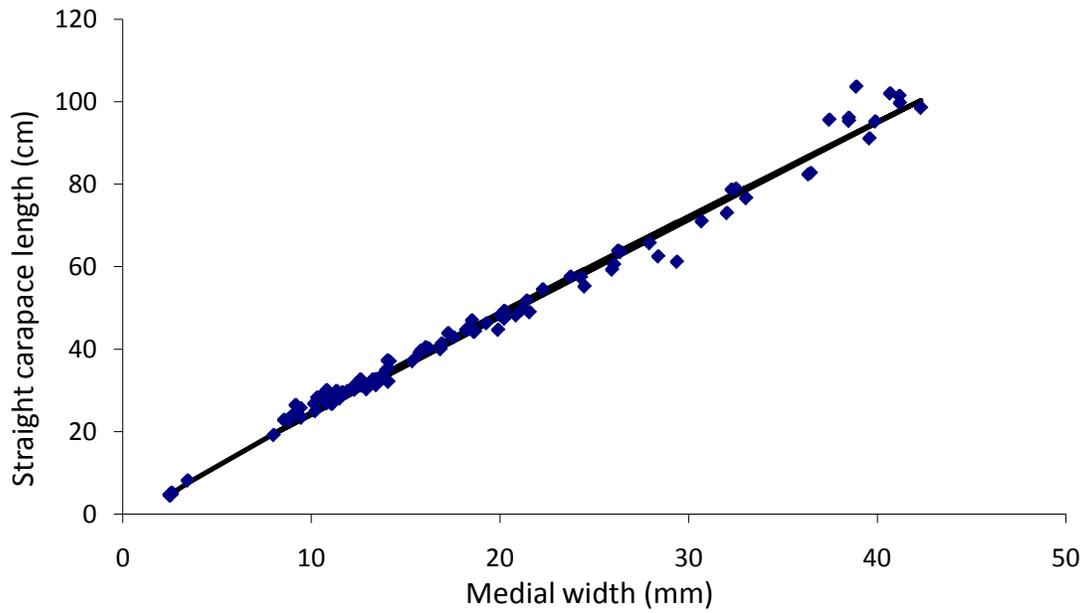
RESULTS

A total of 110 samples were obtained with ages estimated for 109, as one sample was damaged during histological processing. The average percent error of LAG counts for each reader was 13.5% and 5.0%. There was no significant difference in LAG counts between readers ($p = 0.1443$, Wilcoxon paired-sample test, $n = 108$). It was necessary to examine the entire circumference of the cross-section for LAGs as they were not equally visible across the section.

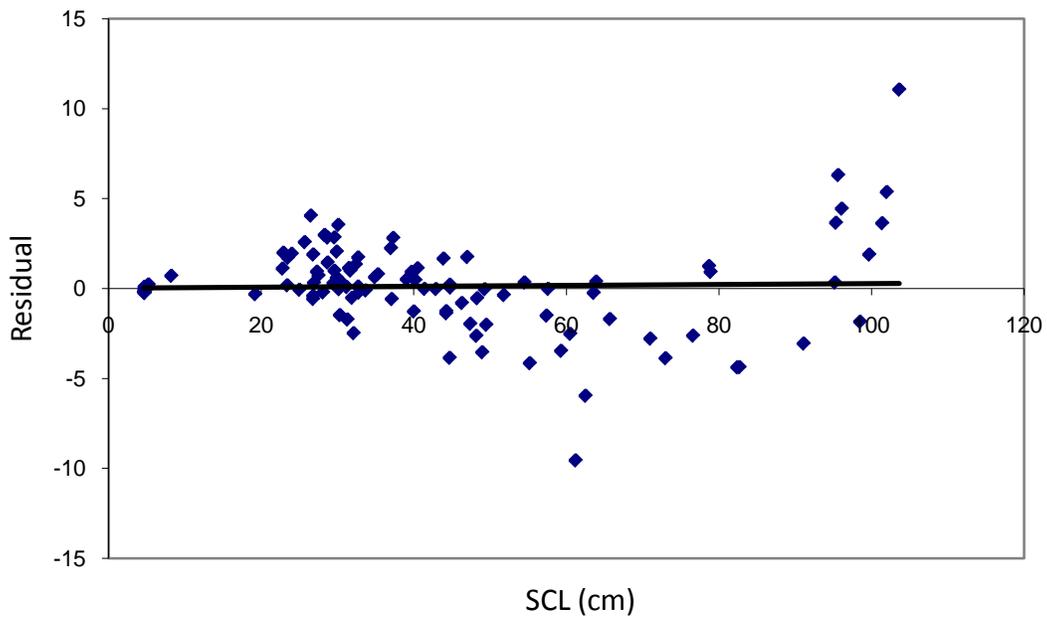
Relationship between Bone Growth and Total Body Growth

There is an allometric relationship between medial width and SCL as described by Eq. (2) (Fig. 4a; $n = 107$). The minimum hatchling SCL was 4.6 cm and the minimum hatchling humerus diameter was 2.47 mm, as determined from the 12 hatchlings in this study. The parameter estimates b and c were 2.981274 and 0.941451, respectively. The residuals showed no significant trend between SCL and residual value (Fig. 4b; $r^2 = 0.0006$, $p > 0.50$, $n = 107$).

Third order polynomials provided the best fit for both SCL versus estimated age, and humerus diameter versus estimated age data (Fig. 5a, SCL vs. estimated age: $r^2 = 0.91$, $n = 99$; Fig. 5b, humerus diameter vs. estimated age: $r^2 = 0.92$, $n = 99$). The residuals associated with both had a positive slope when plotted against each other, indicating that a positive relationship



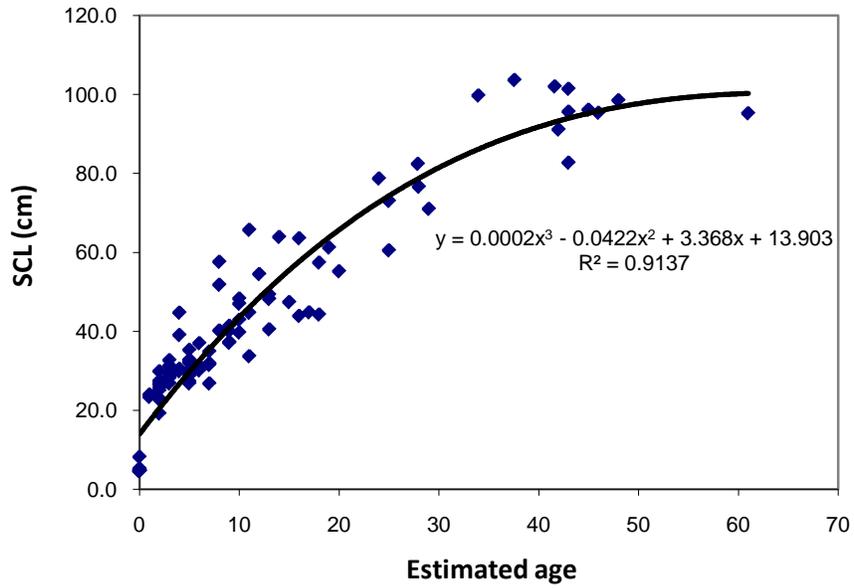
a.



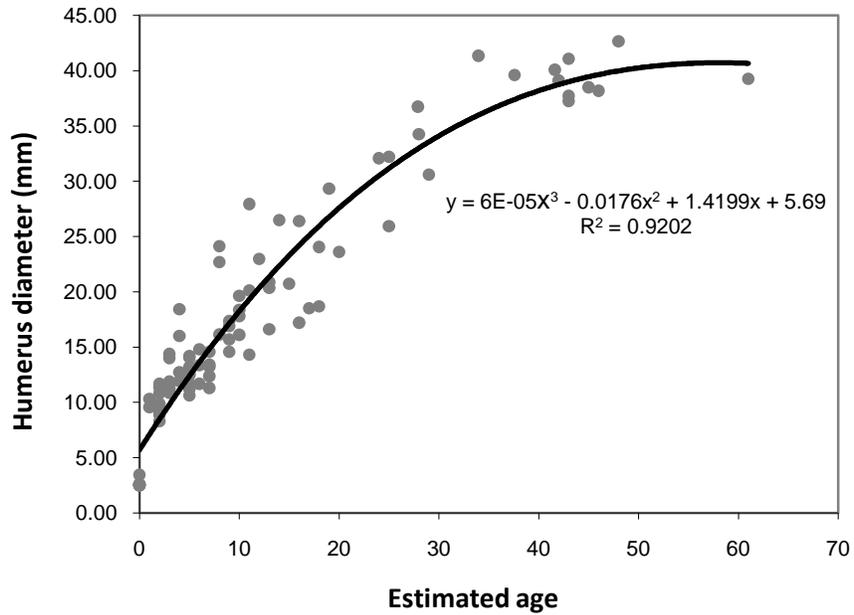
b.

Figure 4. a) Allometric relationship between SCL (cm) and medial width (mm) described by the equation: $\text{Estimated SCL} = 4.6 + 2.981274 * (\text{medial width} - 2.47)^{0.941451}$.

b) Residuals for the allometric model.



a.



b.

Figure 5. a) Relationship between SCL (cm) and estimated age 3rd order polynomial best fit SCL vs. age data ($r^2 = 0.91$).
 b) 3rd order polynomial best fit humerus diameter (mm) vs. estimated age data ($r^2 = 0.92$).

exists between bone and carapace growth, thus allowing the back-calculation of carapace lengths from LAG diameters (Fig. 6, $r^2 = 0.86$, $n = 99$).

Frequency of Growth Mark Deposition - Tagged Turtles

The correlation between bone and somatic growth allowed SCLs to be back-calculated from LAG diameters using Eq. (2). The body proportional hypothesis (Francis 1990) was applied to the back-calculated SCLs. The smallest tagged turtle (WMC 051110-02) was 26.9 cm SCL at initial tagging in October 2004 and 37.0 cm SCL when it stranded dead in November 2005. The hypothesis that one LAG was deposited per year resulted in a larger than expected back-calculated SCL. Upon examination of the history of this turtle, it was discovered that it had spent just over one year in captivity to be rehabilitated and had been released approximately one month prior to stranding dead. Given the diffuse nature of the three outermost LAGs and the history of this turtle, LAGs were re-evaluated and the two outermost LAGs were re-interpreted as supplemental LAGs deposited due to stress. This resulted in back-calculated SCLs of 25.9 cm for the distinct LAG representing spring 2004, which was deposited prior to stranding alive, and 30.1 cm for diffuse spring 2005 LAG deposited while the turtle was in captivity (Fig. 7). There was a 1.0 cm difference between observed and estimated SCLs. BJA 000904-01 was 36.2 cm SCL when captured in March 1999 and 40.0 cm SCL when it stranded dead in September 2000. The LAG hypothesized to have been deposited in spring 1999 was back-calculated to be 38.0 cm SCL, which was larger than expected. LAGs were re-examined and based on their appearance, two were determined not to be true LAGs (Fig. 8). The edges of features within cortical bone at times stains darker than the surrounding tissue and it is possible that this effect was mistaken as additional LAGs. Exclusion of false LAGs resulted in a back-calculated spring 1999 LAG of 35.1 cm SCL, a difference of 1.1 cm from the measured SCL. WGT 000105-01 measured 47 cm

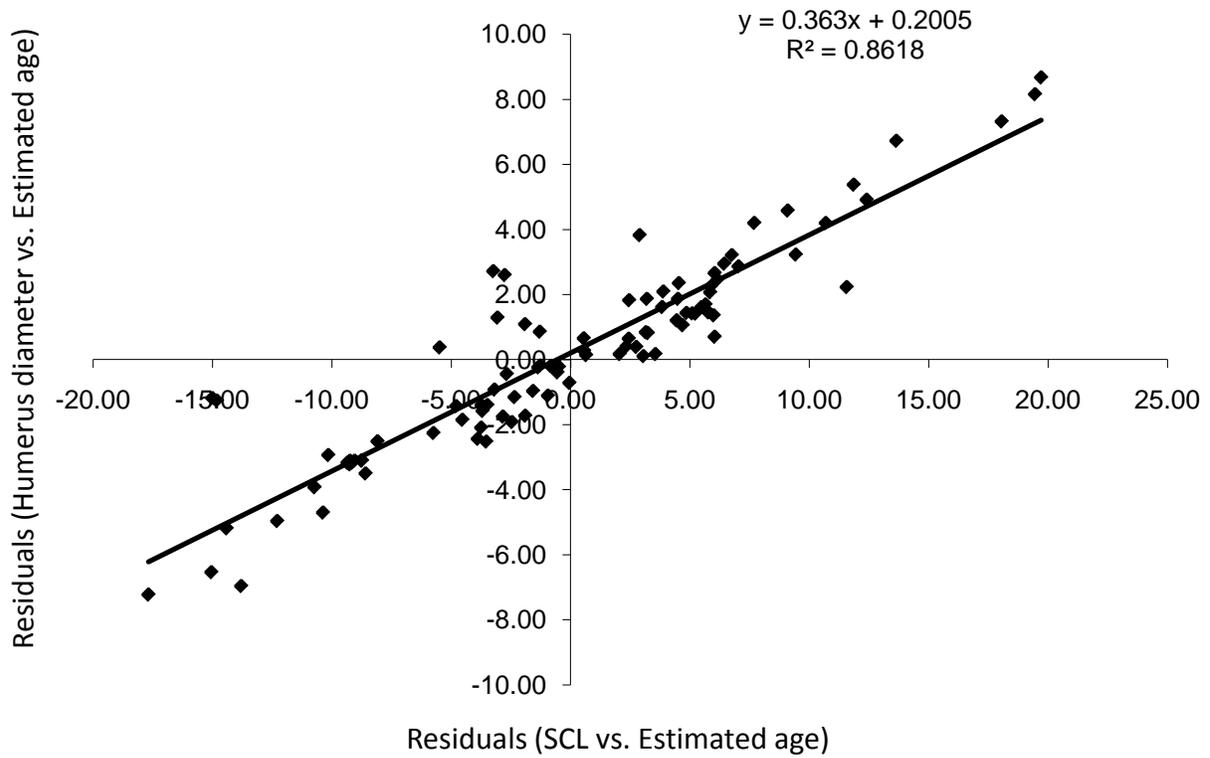


Figure 6. Positive correlation between residuals associated with SCL vs. estimated age relationship and residuals associated with humerus diameter vs. estimated age relationship ($r^2 = 0.86$).

Figure 7. Stained humerus cross-section of tagged turtle WMC 051110-02, SCL = 37.0 cm at dead stranding on November 10, 2005. LAGs are denoted by arrows. Diffuse marks hypothesized as deposited due to stress are indicated with asterisks. Diameter of LAG identified as spring 2004 resulted in a back-calculated SCL of 25.9 cm. Turtle measured 26.9 cm SCL when it stranded alive and was tagged on October 2, 2004. Spring 2005 LAG and two non-annual diffuse marks, hypothesized as due to stress, were deposited while turtle was in captivity. Black bar = 1 mm.

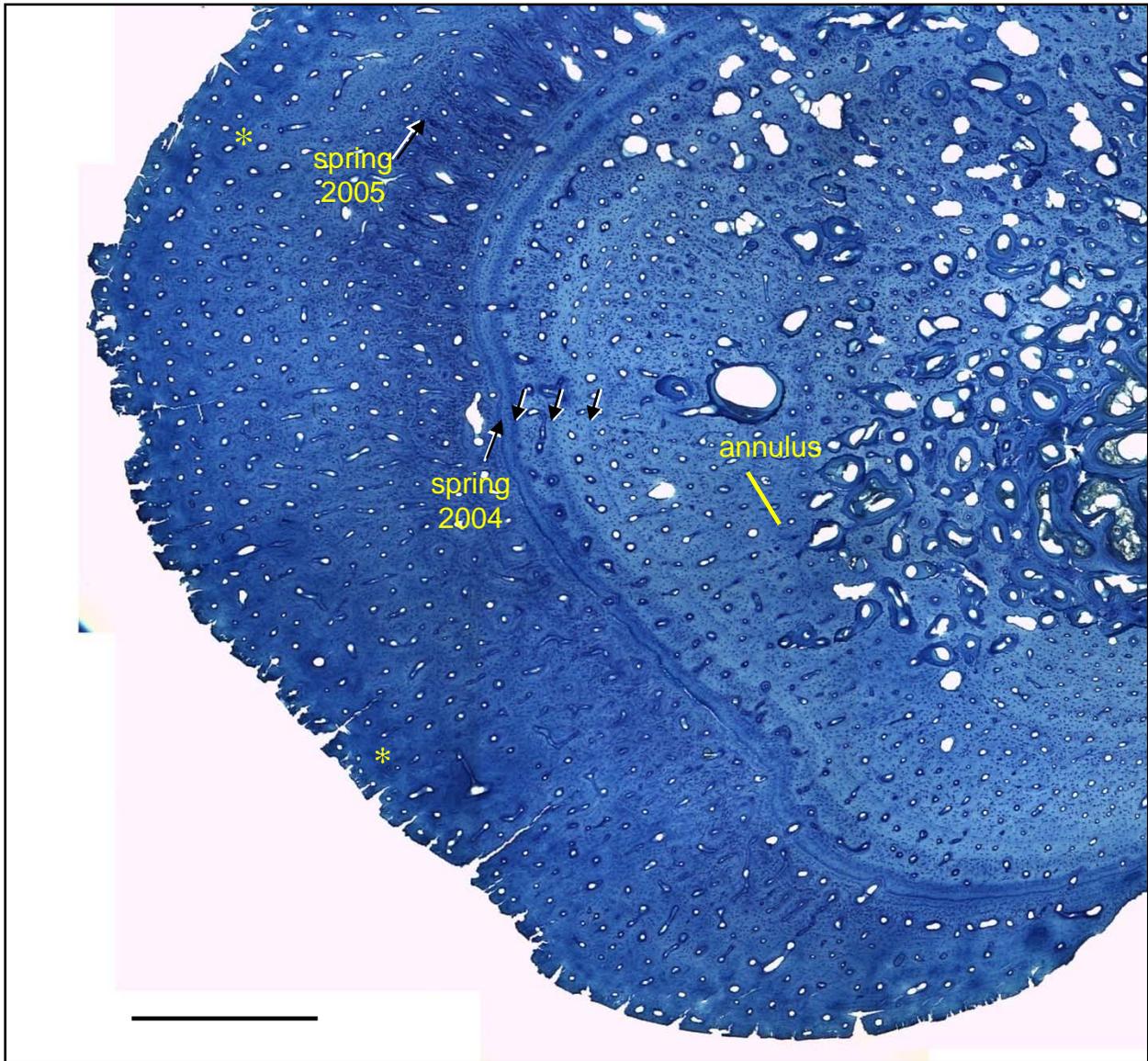
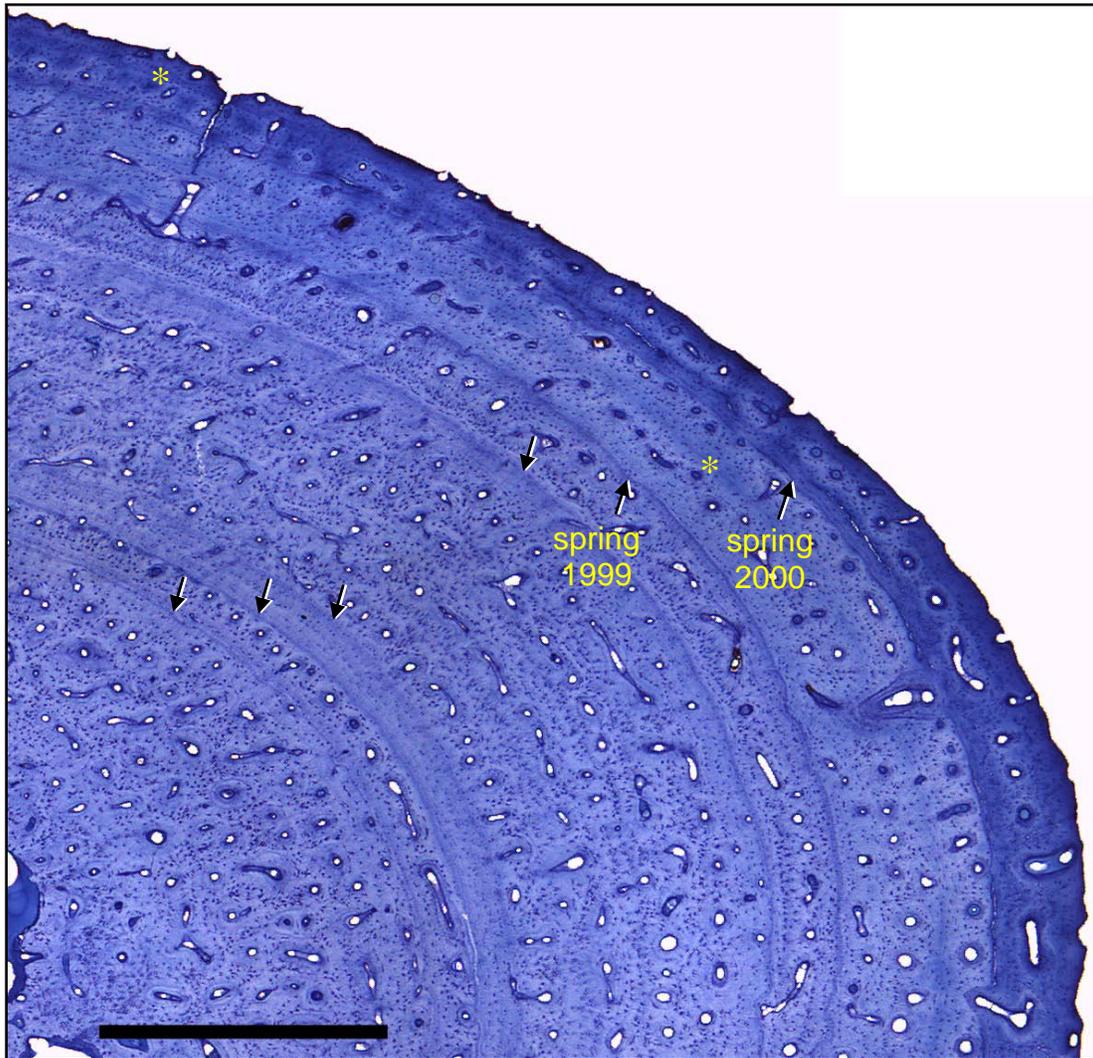


Figure 8. Stained cross-section of the humerus of tagged green turtle BJA 000904-01 measuring 40.0 cm SCL at dead stranding, September 4, 2000. LAGs are denoted by arrows. LAGs re-evaluated as not 'true' LAGs are denoted by asterisks. Diameter of LAG identified as spring 1999 resulted in a back-calculated SCL of 35.1 cm. Turtle measured 36.2 cm SCL when it stranded alive and was tagged on March 3, 1999. Black bar = 1 mm.



SCL when tagged in October 1995. This turtle was 59.3 cm SCL when it stranded dead in January 2000 with fibropapilloma tumors. Both the spring 1995 and spring 1996 back-calculated SCLs were smaller than the measured SCL at tagging. There was a difference of 2.7 cm between the measured and back-calculated SCLs at tagging. The fourth tagged turtle was an adult female tagged in July 1998 at 99.9 cm SCL. The LAG hypothesized to represent spring 1998 was larger than expected. The differences between the observed and back-calculated SCLs for spring 2000 and 2007 were 0.2 cm and 0.8 cm, respectively. SCL at the first re-sighting in 2007 was estimated using Eq. (1) and the reported CCL.

Back-calculated carapace lengths of tagged turtles were not significantly different from the carapace lengths measured at tagging, validating the body proportional hypothesis (Table 2, $p > 0.20$, Wilcoxon paired-sample test, $n = 6$). There was a mean difference of 1.36 cm between observed and estimated SCLs at tagging.

Frequency of Growth Mark Deposition - Marginal Increment Analysis

Medial width was not significantly different than humerus diameter, so this value was substituted in place of humerus diameter when necessary ($p > 0.20$, Student's t-test, $n = 84$). Although no significant difference was found between the two measures, humerus diameter and medial width did not result in exactly the same value, which is important given that the outermost LAG diameter was subtracted from this value with the goal of detecting any growth that occurred prior to stranding dead. For this reason, humerus diameter was the preferred measurement. Marginal increment analysis was possible for 79 samples from green turtles that stranded dead from 1996-2008 during all months of the year. No pattern emerged when growth outside of the last LAG was plotted against Julian stranding date for all samples (Fig. 9, $n = 79$). When turtles larger than 39.9 cm SCL were excluded from the analysis and data were separated

Turtle ID	Stranding SCL (cm)	Date tagged	Observed SCL (cm) at tagging	Estimated SCL (cm) at tagging	Difference (cm)
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	44.3	2.7
WGT 080522-01	103.6	7/28/1998	99.9	102.3	-2.4
WGT 080522-01	103.6	7/14/2000*	102.6	102.4	0.2
WGT 080522-01	103.6	7/20/2007*	104.3	103.5	0.8

Table 2. Back-calculated SCLs from LAG diameters of tagged green turtles compared to SCLs measured at tagging. 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. WGT 080522-01 was re-sighted twice with measurements taken, as marked by asterisks.

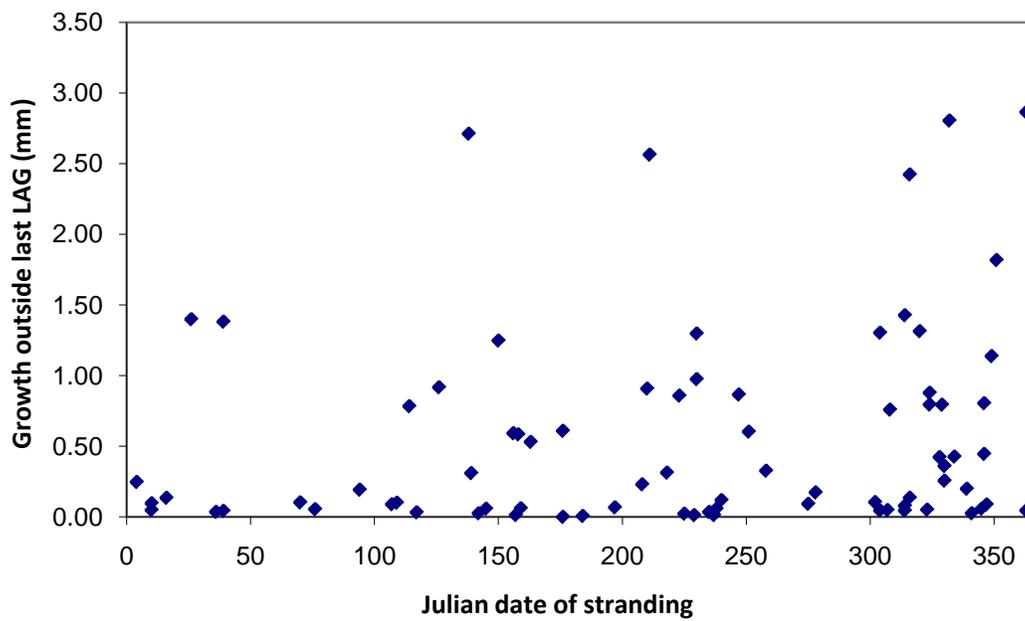


Figure 9. Growth external to last LAG (mm) plotted against Julian stranding date (n = 79).

by season, from June to November and December to May, no pattern emerged (Fig. 10, n = 39). Samples from turtles of all sizes were separated by the region in which they stranded and there was no detectable pattern (Florida strandings, Fig. 11, n = 39; North Carolina & Virginia strandings, Fig. 12, n = 40).

Correction Factor

Forty-six sections retained a diffuse, poorly defined annulus similar in appearance to that described in known-age Kemp's ridleys and validated as representing the first annual growth mark in that species (Snover and Hohn 2004). The assumption was made that an annulus also represented a first year mark in green turtles. This resulted in 211 measureable LAGs in sections from turtles that retained 1 to 17 LAGs. A power function with the following equation best fit the relationship between LAG diameter and LAG number (Fig. 13a, $r^2 = 0.76$, n = 211):

$$\text{LAG diameter (mm)} = 7.3826 * (\text{LAG number})^{0.3147} \quad (6)$$

and was rearranged to solve for LAG number:

$$\text{LAG number} = (\text{LAG diameter (mm)} / 7.3826)^{3.1776} \quad (7)$$

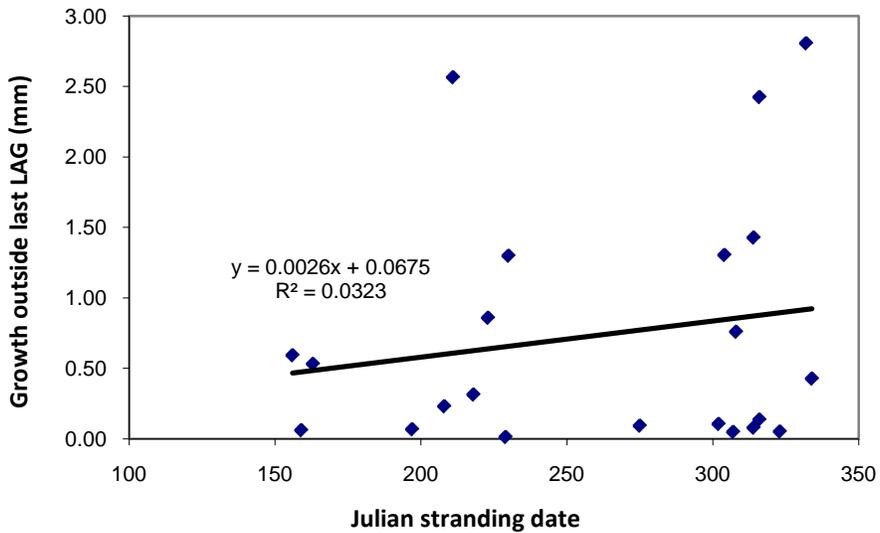
The diameter of the resorption core or that of the first measureable LAG external to the resorption core was substituted for LAG diameter in this equation to estimate the number of LAGs lost to resorption. LAG number indicates the estimated number of resorbed LAGs. This correction factor was applied to 26 turtles with resorption cores measuring less than 18.46 mm, as this was the largest LAG diameter measured in turtles that retained an annulus.

The 26 turtles aged using the power function contained 197 measureable LAGs, which were combined with those used in the power function to extend the correction factor to be used for those with resorption cores measuring 31.09 mm or less. A linear regression best described

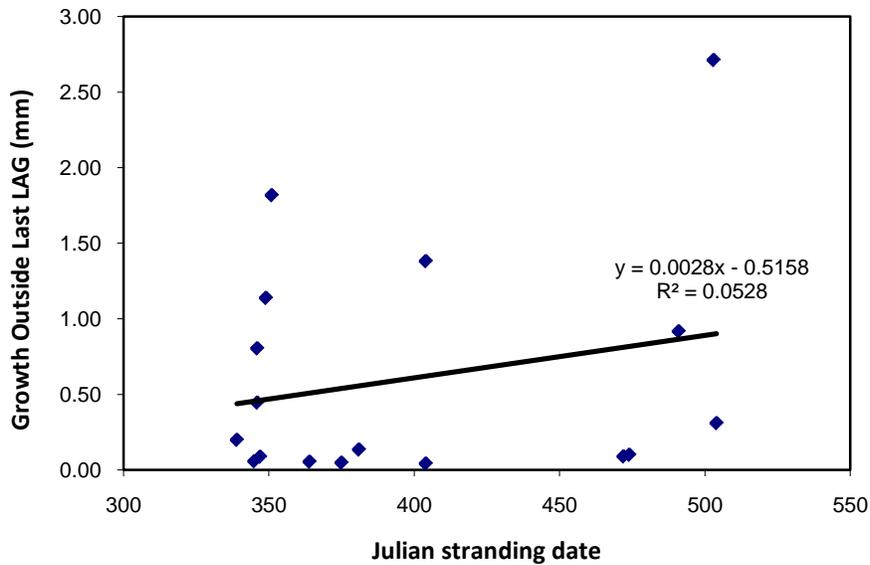
Figure 10.

a) Marginal increment analysis for turtles from 19.2 to 39.9 cm SCL. Growth external to the last LAG plotted against stranding date for turtles that stranded from June to November (n = 39).

b) Marginal increment analysis for turtles from 19.2 to 39.9 cm SCL. Growth external to the last LAG plotted against stranding date for turtles that stranded from December to May (n = 39). Julian stranding dates greater than 365 are 365 + Julian stranding date.

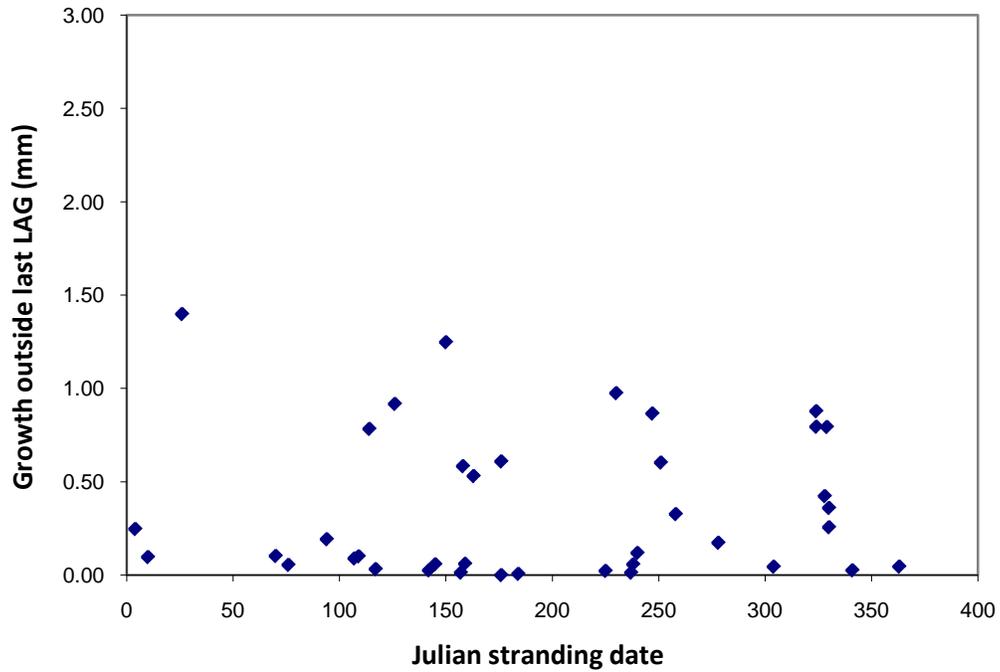


a.

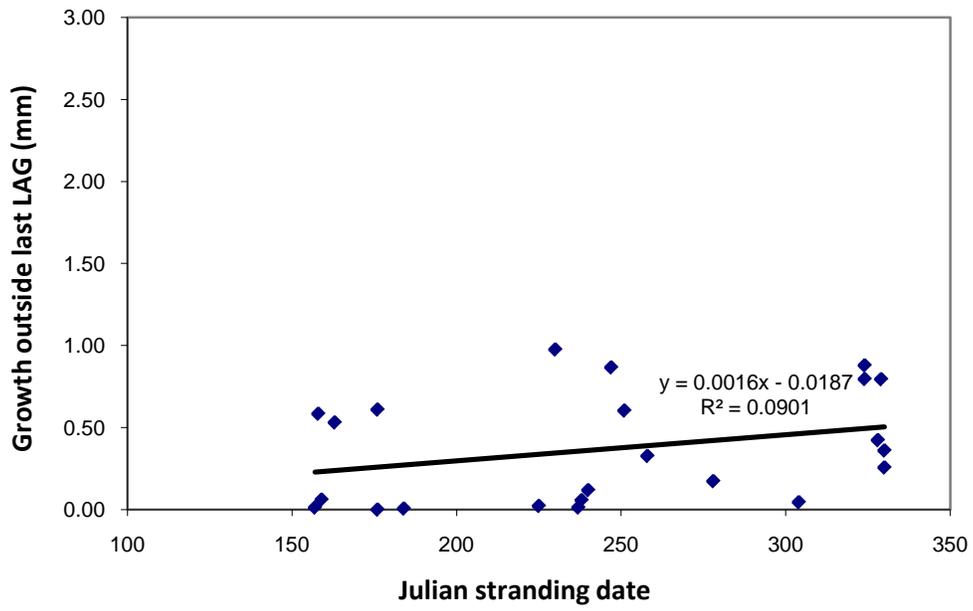


b.

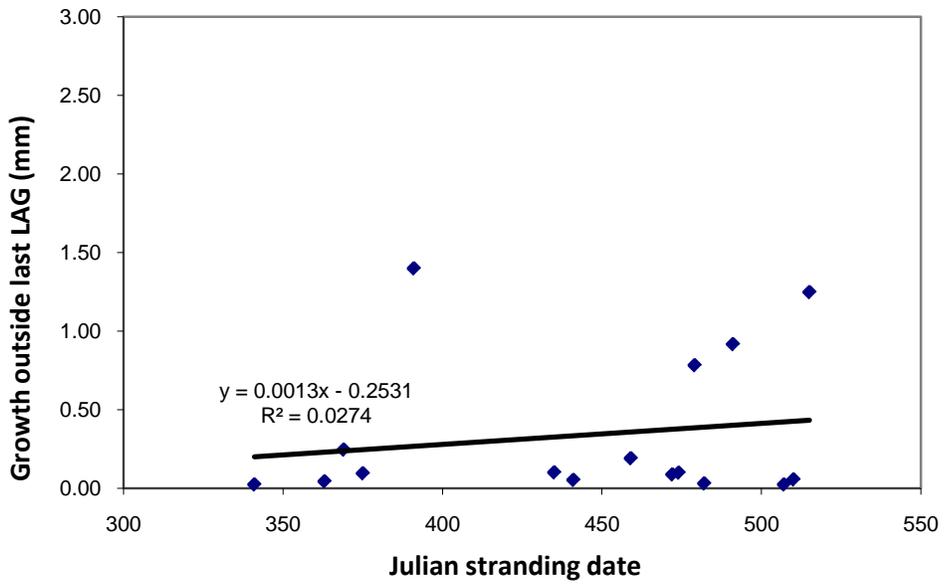
- Figure 11. a) Marginal increment analysis for turtles stranding in Florida during all months of the year.
- b) Marginal increment analysis for turtles stranding in Florida from June – November.
- c) Marginal increment analysis for turtles stranding in Florida from December – May.



a.

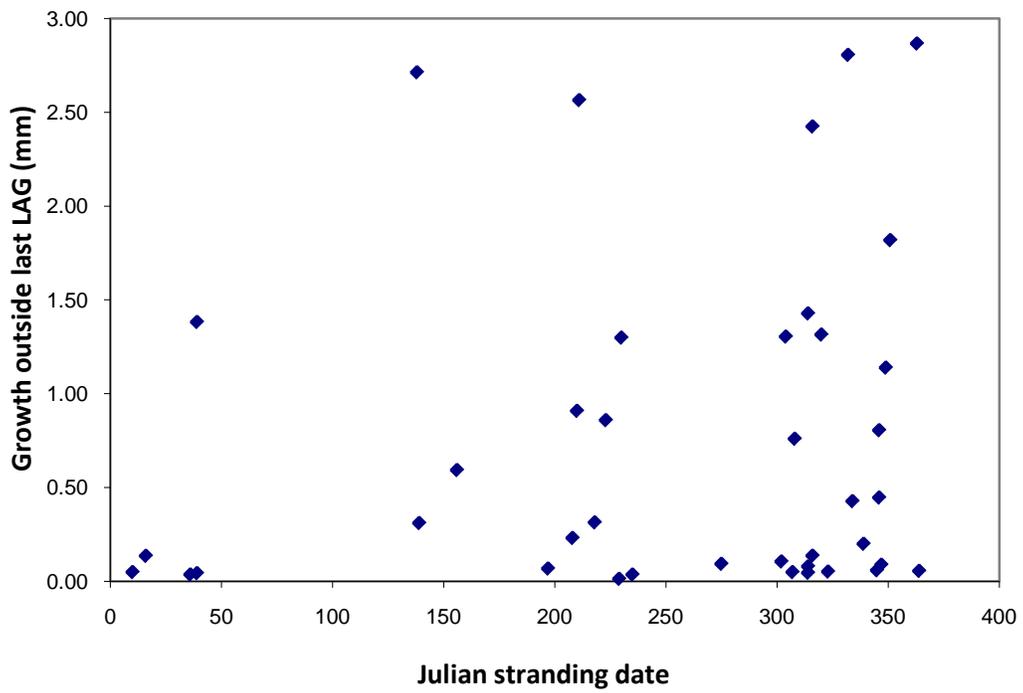


b.

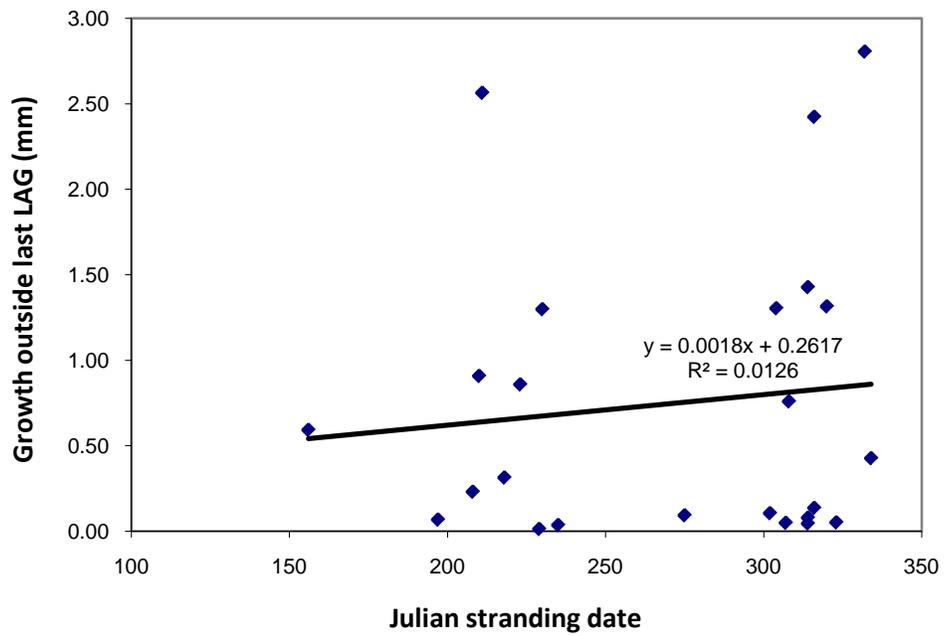


c.

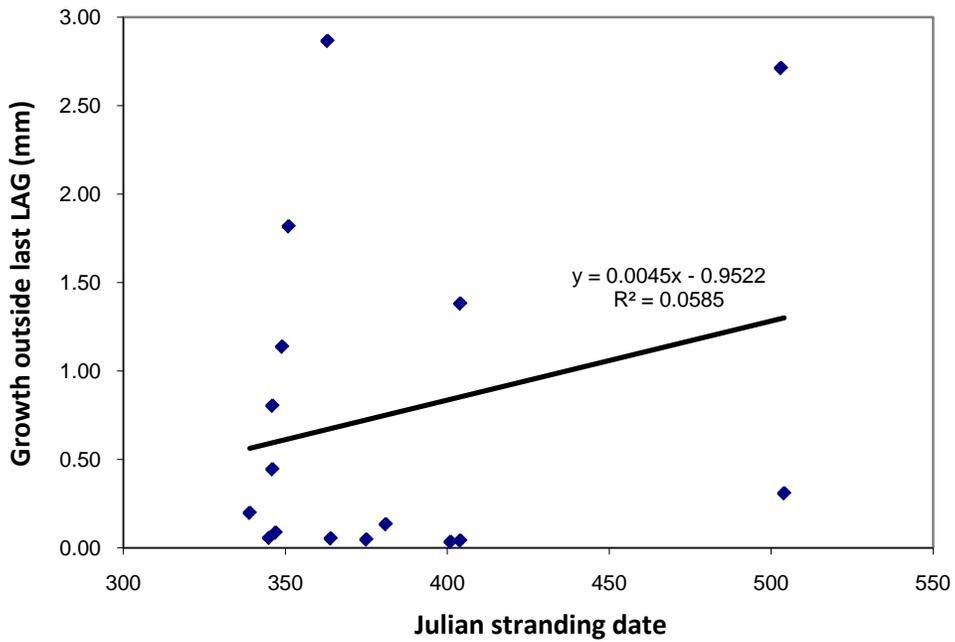
- Figure 12. a) Marginal increment analysis for turtles stranding in North Carolina and Virginia during all months of the year.
- b) Marginal increment analysis for turtles stranding in North Carolina and Virginia from June – November.
- c) Marginal increment analysis for turtles stranding in North Carolina and Virginia from December – May.



a.



b.



c.

the relationship between LAG diameter and LAG number, which yielded the following equation (Fig. 13b, $r^2 = 0.81$, $n = 408$):

$$\text{LAG diameter (mm)} = 0.7776 * (\text{LAG number}) + 8.0689 \quad (8)$$

that was rearranged to solve for LAG number:

$$\text{LAG number} = (\text{LAG diameter (mm)} - 8.0689) / 0.7776 \quad (9)$$

Four turtles had resorption core diameters greater than 31.09 mm. To estimate the number of LAGs lost for these turtles, the relationship between 513 LAG diameter and LAG number pairs was modeled. A linear regression with the following equation best described the relationship (Fig. 13c, $r^2 = 0.90$, $n = 513$):

$$\text{LAG diameter (mm)} = 0.7918 * (\text{LAG number}) + 8.0367 \quad (10)$$

and was rearranged to solve for LAG number:

$$\text{LAG number} = (\text{LAG diameter (mm)} - 8.0367) / 0.7918 \quad (11)$$

A power function provided the best fit to the data from turtles retaining an annulus, and linear regressions best fit the relationship between LAG diameter and LAG number for larger turtles with resorption cores. There was no significant difference in ages estimated using the power function (Eq. 7) or linear regression (Eq. 9) correction factors for turtles ranging in size from 37.1 to 78.7 cm SCL ($p > 0.50$, Student's t-test, $n = 26$).

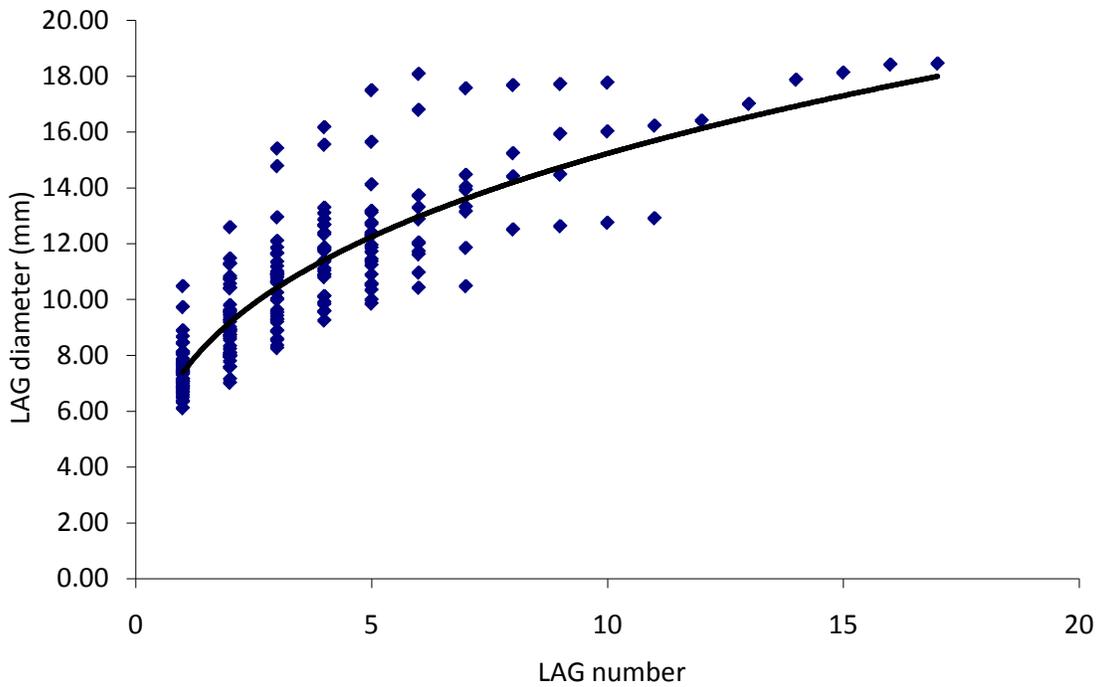
Growth Rates and Estimates of Age at Maturation

The mean growth rate and standard deviation for each 10 cm size class based on the back-calculated SCLs of the final 2 LAG diameters are presented in Table 3 ($n = 79$). These data are included in that obtained from the back-calculated SCLs of all measureable LAG diameters (Table 4, $n = 406$). The mean growth rates were lower for the 30.0-39.9 cm SCL size class than the two smaller size classes. From the 40-49.9 cm SCL size class, mean growth rates increased,

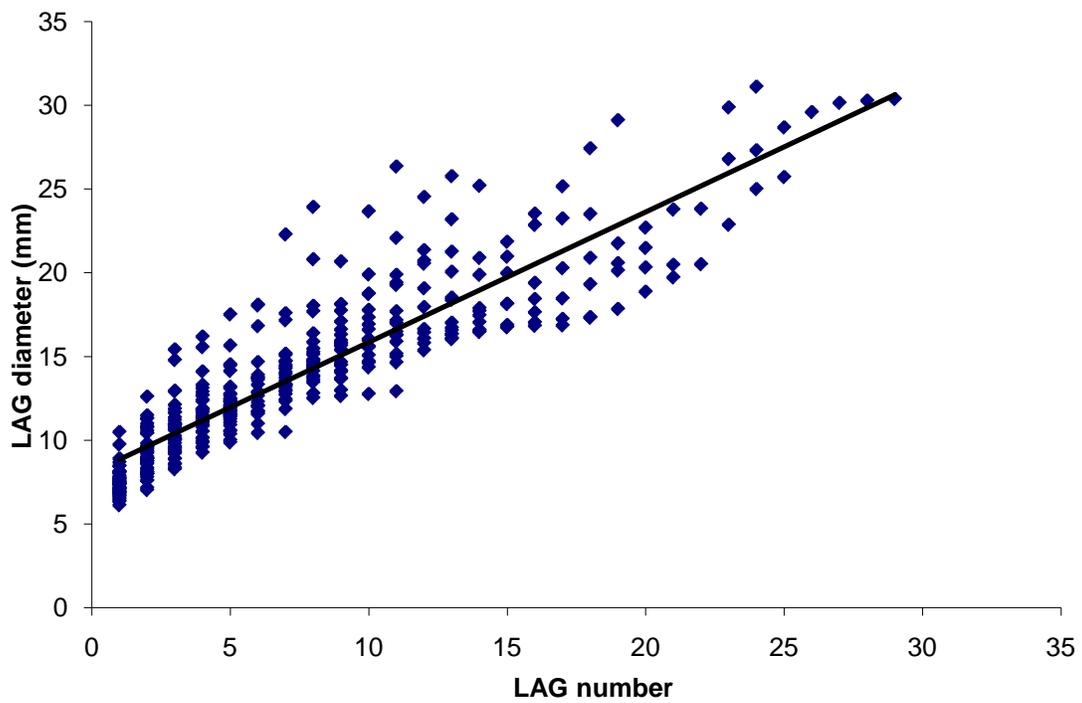
Figure 13. a) Relationship between LAG diameter (mm) and LAG number. A power function best described the relationship and was used to estimate the number of LAGs lost to resorption for those turtles that did not retain an annulus but had a resorption core that measured less than 18.46 mm ($r^2 = 0.76$, $n = 211$).

b) Relationship between LAG diameter (mm) and LAG number. A linear regression best described the relationship and was used to estimate the number of LAGs lost to resorption for those turtles that did not retain an annulus but had a resorption core that measured > 18.46 mm, but < 31.09 mm ($r^2 = 0.81$, $n = 408$).

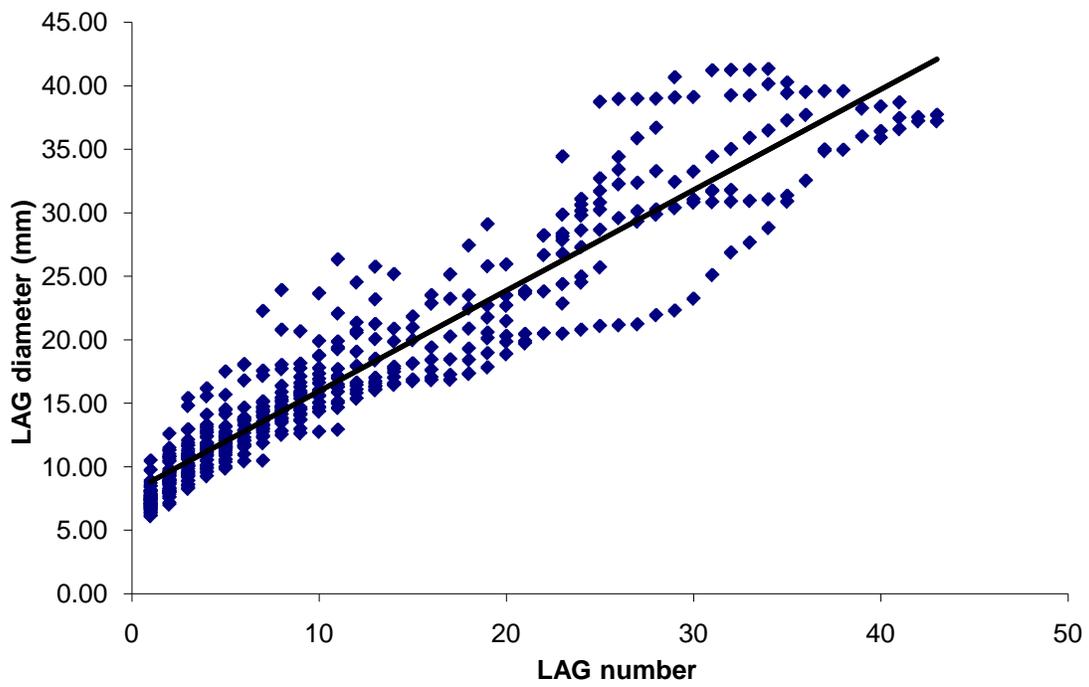
c) Relationship between LAG diameter (mm) and LAG number. A linear regression best described the relationship and was used to estimate the number of LAGs lost to resorption for those turtles that did not retain an annulus but had a resorption core that measured > 31.09 mm ($r^2 = 0.90$, $n = 513$).



a.



b.



c.

Table 3. Size-specific growth rates obtained from back-calculated SCLs of the final 2 LAG diameters (n = 79).

Size class (cm SCL)	Mean Growth Rate (cm/yr)	SD	Growth Rate Range (cm/yr)	<i>n</i>
16.5 - 19.9	4.1	0.74	3.4 - 5.0	4
20.0 - 29.9	3.8	2.64	0.1 - 8.8	23
30.0 - 39.9	1.6	1.10	0.2 - 4.0	16
40.0 - 49.9	2.4	2.47	0.1 - 8.1	14
50.0 - 59.9	2.3	1.09	0.6 - 3.5	6
60.0 - 69.9	2.4	0.47	2.0 - 2.7	2
70.0 - 79.9	2.6	1.92	0.3 - 4.2	4
80.0 - 89.9	0.4	-----	-----	1
90.0 - 99.9	0.1	0.06	0.0 - 0.2	6
100.0 -103.6	0.1	0.18	0.0 - 0.3	3

Table 4. Size-specific growth rates from back-calculated SCLs of all measurable LAG diameters (n = 406). Turtles were divided into size classes based on the mean SCL of the back-calculated SCL pairs.

Size class (cm SCL)	Mean Growth Rate (cm/yr)	SD	Growth Rate Range (cm/yr)	<i>n</i>
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

peaking at 60.0-69.9 and again at 80.0-89.9, then decreased through the remaining size classes. The growth rates from the back-calculated SCLs of all measurable LAG diameters (Table 4) for each 10 cm size class result in estimates of 34 years to grow from 20 to 100 cm SCL and 39 years to grow from 20 to 101.5 cm SCL.

The Fabens' modified von Bertalanffy growth interval equation as applied to the growth increment data from the back-calculated SCLs of the final 2 LAG diameters (presented in Table 3) resulted in an estimated 59 years to maturation based on an average size at maturation of 101.5 cm SCL for the Florida population and 57 years to reach 100.1 cm SCL for Costa Rica (Fig. 14, $n = 79$). The minimum size reported at nesting in both Costa Rica (Carr and Hirth 1962) and Florida (Witherington and Ehrhart 1989) is 83.2 cm SCL. The equation estimated 37.5 years to reach the minimum size at maturation for females. The average k was 0.03005.

Sex-specific growth increment data estimated the age of females as 67 and 64.5 years at 101.5 and 100.1 cm SCL, respectively; males were estimated at 52.5 and 50.5 years at the same sizes (Fig. 15, females, $n = 34$; males, $n = 17$). To reach the minimum size at maturation for females, the equation estimated 42 years were required. Individual males reported stranded dead on or captured alive near nesting beaches have measured 84.8 cm SCL, 94.9 cm SCL (Ross and Lagueux 1993), 97.4 cm CCL, and 103.6 cm CCL (Troëng 2000). The CCLs were converted to SCLs using Eq. (1) and corresponding age estimates were 34 to 44 years. The average k was 0.026657 for females and 0.033993 for males.

A diffuse annulus, as found to represent the first year mark in wild, known-age Kemp's ridleys (Snover and Hohn 2004), was identified in 46 green turtle humerus cross-sections and, based on the findings for Kemp's ridleys, was interpreted as the first year mark. Results suggest that the pelagic stage can be as short as 1 year based on the 23.4 and 24.0 cm SCL turtles that

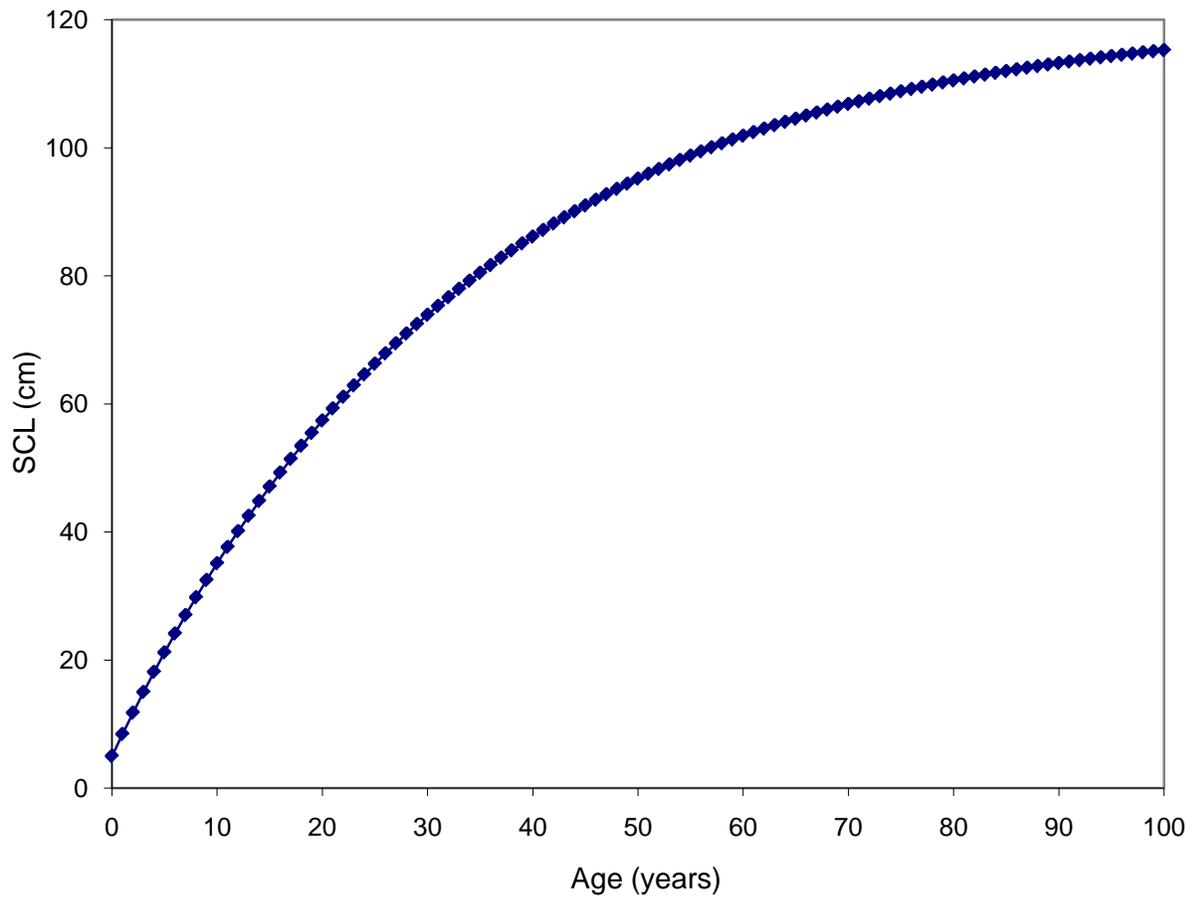


Figure 14. Von Bertalanffy growth function applied to growth increment data from all turtles to estimate age at maturity (n = 79).

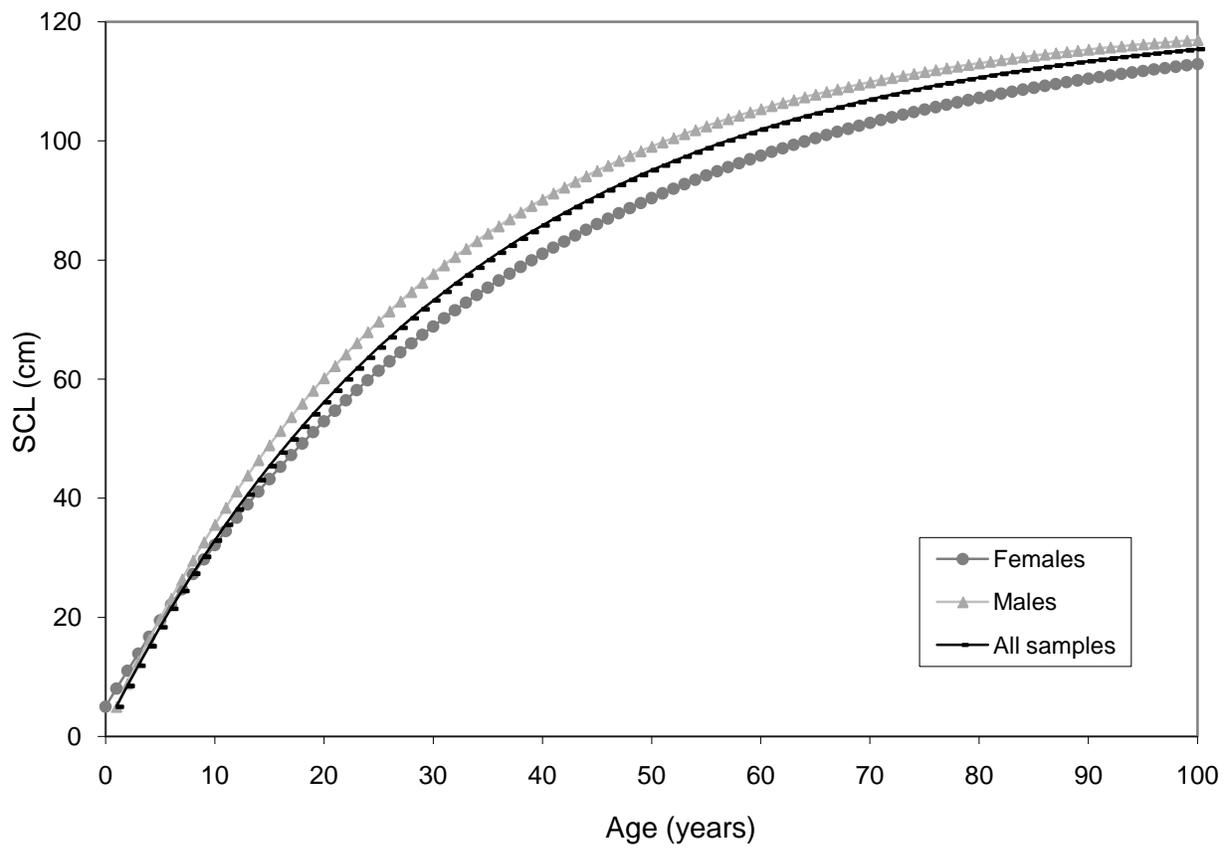


Figure 15. Fabens modified von Bertalanffy growth function applied to sex-specific growth increment data to estimate age at maturity (females: $n = 34$; males: $n = 17$).

retained an annulus but did not have a second year mark. Green turtles first appear along the coast of the southeastern U.S. at approximately 24 cm CCL in North Carolina (Epperly et al. 1995) and at 21 to 29.5 cm SCL in Florida (as reviewed by Hirth 1997). Age estimates for turtles within the size range of 19.2 to 29.5 cm SCL are 1 to 7 years (Fig. 16, mean = 2.9 yrs., SD = 1.56, n = 19).

The mean SCL-at-age data are reported in Table 5. The length-at-age data are those for which ages were estimated and the mean SCLs were those measured at stranding (n = 85). Including the SCL-at-age data from SCLs back-calculated using LAG diameters allowed for larger sample sizes and for mean SCLs to be calculated for each age (n = 520). For the youngest turtles, the mean SCLs from the length-at-age data were greater than those obtained through back-calculation of SCLs-at-age from LAG diameters. This could be expected because turtles less than 20 cm SCL rarely strand dead in the southeast U.S. and thus would not be accounted for, and because partial ages were not assigned. For example, for an annulus or LAG to be visible in the bones, there must be growth external to it; therefore a turtle aged at 1 year may be greater than 1 but less than 2 years old, as exhibited by growth outside the annulus.

In estimating age at maturation from the length-at-age data not including the hatchlings or 8.2 cm SCL post-hatchling, the logistic and Gompertz growth functions were best supported, followed by the von Bertalanffy and power functions (Table 6, n = 85). Parameter estimates are reported in Table 7. The age at maturation was estimated at 57.5 and 53 years based on 101.5 cm SCL for Florida and 53 and 51 years to reach 100.1 cm SCL for Costa Rica based on the logistic and Gompertz growth models, respectively (Fig. 17, n = 85). For the minimum size reported at nesting of 83.2 cm SCL, the logistic and Gompertz growth models predicted ages of 31.5 and 32.5, respectively.

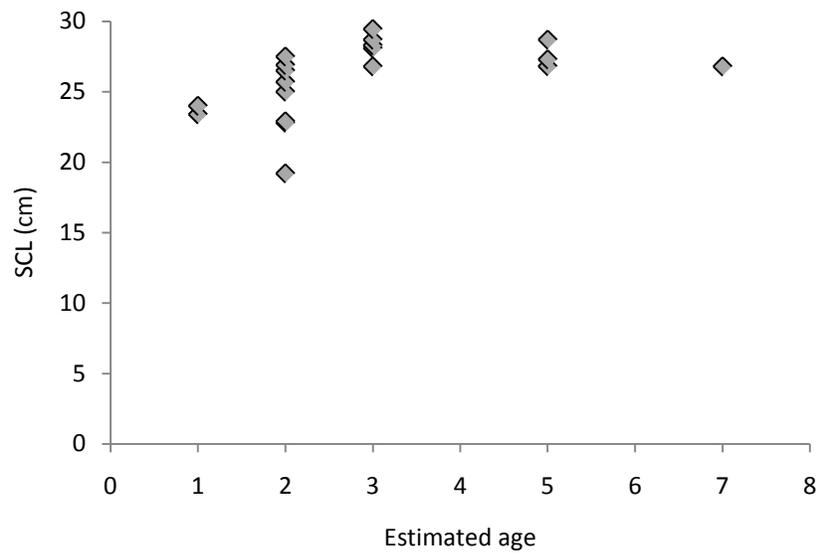


Figure 16. Estimated ages of 19.2-29.5 cm SCL green turtles (n = 19).

Table 5. Ages and mean SCLs (cm). Mean SCL for the length-at-age data is the average SCL at dead stranding (n = 85). For the length-at-age data from back-calculated SCLs, the mean SCL reported is the average SCL of the back-calculated SCL pairs (n = 520).

Length-at-age					Length-at-age from back-calculated SCLs			
Age (yrs)	Mean SCL (cm)	SD	SCL Range (cm)	<i>n</i>	Mean SCL (cm)	SD	SCL Range (cm)	<i>n</i>
1	23.7	0.42	23.4 - 24.0	2	18.2	2.26	14.0 - 25.1	46
2	25.2	3.15	19.9 - 29.9	9	22.4	3.08	17.6 - 30.1	45
3	29.4	1.88	26.8 - 32.7	8	25.8	3.66	19.4 - 37.6	40
4	36.0	7.14	29.9 - 44.7	4	28.3	3.75	21.9 - 38.6	34
5	30.7	2.58	26.8 - 35.3	11	29.7	3.75	23.4 - 41.7	34
6	30.7	0.78	30.1 - 31.2	2	32.2	5.05	24.7 - 43.4	22
7	31.4	2.90	26.8 - 34.9	5	34.1	5.69	24.9 - 53.3	23
8	49.9	8.20	40.2 - 57.6	3	36.9	5.97	29.5 - 57.2	22
9	39.0	2.10	37.1 - 41.4	4	36.8	3.74	29.8 - 42.7	19
10	44.5	3.93	39.7 - 48.3	4	39.3	4.71	30.1 - 48.3	16
11	48.0	16.26	33.7 - 65.7	3	40.7	5.65	30.5 - 53.5	14
12	54.5	----	----	1	44.4	7.13	36.3 - 59.2	11
13	46.0	4.79	40.5 - 49.3	3	44.3	7.65	37.5 - 62.1	13
14	63.9	----	----	1	43.8	6.52	39.1 - 60.9	10
15	47.4	----	----	1	43.9	3.96	39.6 - 52.3	8
16	53.7	13.91	43.9 - 63.6	2	45.6	5.04	39.7 - 54.6	7
17	44.8	----	----	1	46.9	6.34	39.8 - 55.5	6
18	50.8	9.30	44.3 - 57.4	2	49.0	6.34	40.9 - 57.4	8
19	61.2	----	----	1	51.8	5.94	42.0 - 60.7	8
20	55.2	----	----	1	52.2	4.77	44.4 - 58.6	7
21					54.2	6.60	46.4 - 63.7	6
22					60.7	9.90	48.2 - 74.9	5
23					65.3	11.50	53.5 - 90.7	9
24	78.7	----	----	1	65.1	7.44	54.6 - 76.4	9
25	66.8	8.84	60.5 - 73	2	71.6	14.15	55.3 - 101.5	8
26					76.2	15.65	55.4 - 102.0	6
27					76.1	16.19	55.6 - 102.0	6
28	79.5	4.10	76.6 - 82.4	2	74.9	12.47	57.5 - 94.3	6
29	71.0	----	----	1	81.1	18.68	58.4 - 102.3	5
30					79.3	14.89	60.7 - 102.4	5
31					80.3	9.97	65.4 - 99.4	7
32					86.0	11.86	69.9 - 102.7	7
33					88.3	11.18	71.9 - 102.7	7
34	99.7	----	----	1	88.6	9.72	74.7 - 99.7	7
35					90.6	9.23	78.9 - 103.2	7
36					92.6	7.35	84.0 - 103.4	5
37					94.6	6.46	87.7 - 103.6	5
38	103.6	----	----	1	96.8	9.60	90.0 - 103.6	2
39					89.6	0.76	89.1 - 90.2	2
40					93.2	4.56	89.5 - 99.8	4
41					94.8	4.79	90.2 - 101.6	4
42	96.5	7.71	91.1 - 102.0	2	97.1	4.23	93.8 - 101.9	3
43	93.2	9.57	82.7 - 101.4	3	94.9	0.90	94.2 - 95.5	2
45	96.1	----	----	1				
46	95.3	----	----	1				
48	98.5	----	----	1				
61	95.2	----	----	1				

Model	<i>K</i>	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

Table 6. Fitting criteria of growth functions applied to length-at-age data without hatchlings or post-hatchling ($n = 85$). K = number of parameters estimated, RSS = residual sum of squares, Δ AIC = AIC_c of model – lowest AIC_c. The models with the lowest RSS and greatest weight of evidence best fit the data.

Parameter	von Bertalanffy	Logistic	Gompertz	Power
a	141.2558	104.6748	113.071	15.22592
b	0.0217141	0.814536	0.0510606	5.972076
c	-7.055407	14.96835	9.467045	0.6838236

Table 7. Growth function parameter estimates. Hatchlings and post-hatchling were not included (n = 85).

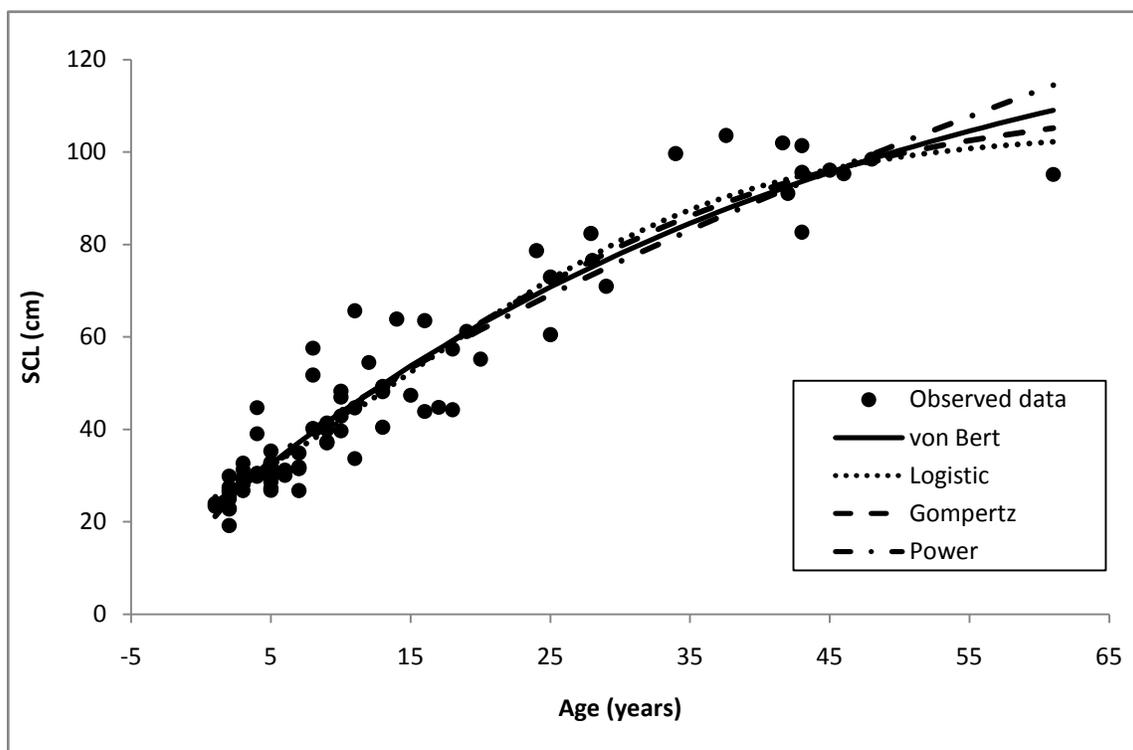


Figure 17. Growth models applied to length-at-age data from all turtles except the hatchlings and post-hatchling (n = 85).

When the length-at-age data were separated by sex and the hatchlings were excluded, results best supported the logistic and Gompertz growth models for the females and the von Bertalanffy followed by the Gompertz growth models for males (Table 8, females n = 39; males n = 20). Sex-specific parameter estimates are presented in Table 9. Both the logistic and Gompertz growth models estimated 44 years to maturation for females based on 101.5 cm SCL and 42.5 years to maturation based on 100.1 cm SCL (Fig. 18, n = 39). The logistic and Gompertz growth models estimated 30 to 31 years to reach the minimum reported size at maturation of 83.2 cm SCL for nesting females. For males ranging from 84.8 to 94.9 cm SCL age estimates were 35.5 to 50 years based on the von Bertalanffy and Gompertz growth models (Fig. 19, Table 10, n = 20). At 100.1 cm SCL, males were estimated to be 59.5 years based on the von Bertalanffy growth model. The age of males at an equivalent size as that of the average-sized female nesting in Florida was not possible as it would have required extrapolating beyond the available data.

DISCUSSION

The results of this study are significant in that annual LAGs were indirectly verified, allowing estimation of growth rates and the mean carapace length-at-age for green turtles inhabiting coastal waters of the southeastern U.S. Samples were available from all sizes, ranging from hatchlings to adults, and genetic composition of the population from which samples for age estimation were obtained was known. This then allowed estimation of age at maturation for turtles that use the coast of the southeastern U.S. as developmental habitat but contribute to the Florida and Costa Rican nesting populations.

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

Table 8. Fitting criteria of growth functions applied to sex-specific length-at-age data without hatchlings or post-hatchling (females, n = 39; males, n = 20). *K* = number of parameters estimated, RSS = residual sum of squares, Δ AIC = AIC of model – lowest AIC.

Parameter	von Bertalanffy	Logistic	Gompertz	Power
females				
a	261.5791	114.366	132.6128	21.16667
b	0.0093648	0.0777604	0.0433663	2.488453
c	-8.974158	17.46834	13.28275	0.9239629
males				
a	114.9258	99.86983	103.5581	6.188334
b	0.031422	0.082442	0.0576755	12.04094
c	-5.630912	13.99777	7.67636	0.5111021

Table 9. Sex-specific growth function parameter estimates. Hatchlings and post-hatchling were not included (females, n = 39; males, n = 20).

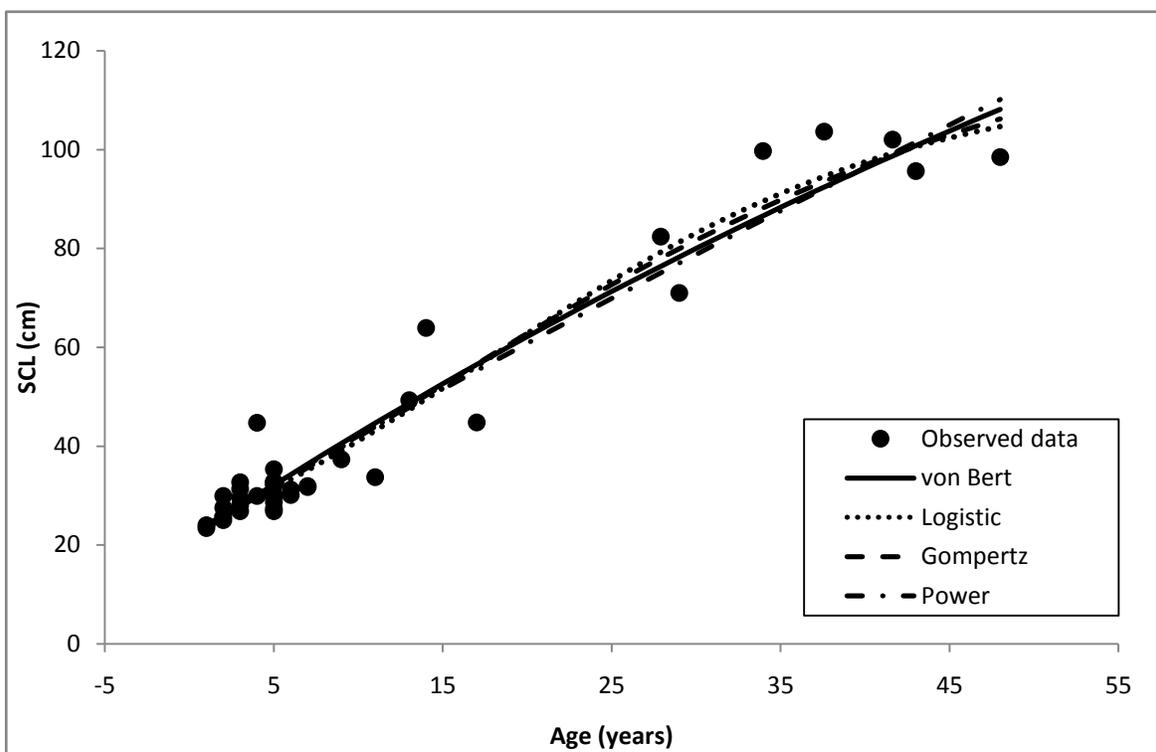


Figure 18. Growth models applied to length-at-age data from females without hatchlings or post-hatchling (n = 39).

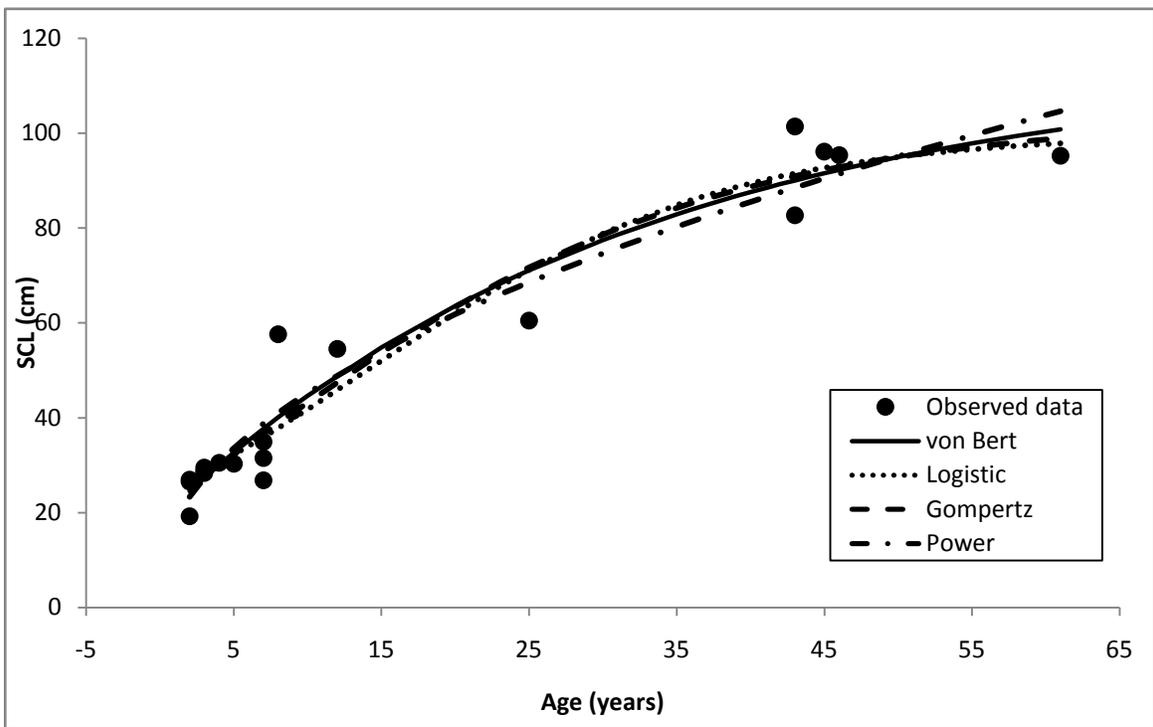


Figure 19. Growth models applied to length-at-age data from males without hatchlings or post-hatchling (n = 20).

Table 10. Ages estimated based on the models that best fit the length-at-age data from males for sizes of males in nesting areas as reported in the literature.

Age	Size reported	References
37 yrs von Bertalanffy 35.5 yrs Gompertz	84.8 cm SCL	Ross & Lagueux 1993
41 yrs von Bertalanffy 40 yrs Gompertz	88.5 cm SCL (*reported as CCL)	Troëng 2000
45 yrs von Bertalanffy 44 yrs Gompertz	91.8 cm SCL (*reported as CCL)	Troëng 2000
50 yrs von Bertalanffy 50 yrs Gompertz	94.9 cm SCL	Ross & Lagueux 1993

Frequency of LAG Deposition

The re-evaluations of the two smallest tagged turtles (WMC 051110-02 and BJA 000904-01) supported the hypothesis of annual LAG deposition. 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 the tagged turtle in this study that was in captivity prior to release (WMC 051110-02) also deposited non-annual LAGs. The SCL at tagging was greater than that back-calculated from the LAG. This supported the hypothesis that LAGs are deposited in the spring, given that the turtle was likely to have grown during the summer months before being tagged and measured in the fall. One diffuse LAG deposited between the LAG representing 2004 and the outer edge of the bone supported annual deposition of LAGs. Upon re-evaluation of BJA 000904-01, it was determined that two LAGs originally interpreted to be annual likely were non-annual features that had stained darker than the surrounding bone. The re-evaluation resulted in a back-calculated 1999 SCL that was smaller than that measured in March when the turtle was captured, also supporting spring deposition of LAGs. One distinct LAG was present between the 1999 LAG and the outer edge of the bone, indirectly validating annual deposition of LAGs.

Four LAGs were present between the hypothesized 1995 LAG and the outer edge of the bone for WGT 000105-01, which supported annual LAG deposition. However, both the 1995 and 1996 back-calculated SCLs were smaller than that observed at tagging in October 1995. This turtle experienced 11 cm of growth in SCL between the LAGs hypothesized as representing 1996 and 1998. One diffuse LAG (1997) was identified between these LAGs and it is possible that an additional diffuse LAG was present, but not discernible, resulting in placing the

hypothesized spring 1995 LAG too far to the interior. Results from this turtle confirm that no greater than one LAG per year was deposited.

Back-calculated SCLs for the reproductively mature adult female (WGT 080522-01) indicated that greater than 1, but less than 2 LAGs were deposited per year between the original tagging date and when the turtle stranded dead. The LAGs identified as spring 2000 and 2007 resulted in back-calculated SCLs 0.2 cm and 0.8 cm less than those recorded during nesting events those years. The differences could be due to growth or measurement error, as results indicate that 0.3 cm/yr. is the mean growth rate of turtles in this size class and SCL measurement error is reported as 0.20 cm (Bresette & Gorham 2001). The spring 1998 back-calculated SCL and three back-calculated SCLs internal to it were larger than the observed SCL at tagging that year under the assumption of annual LAG deposition. This turtle was a mature nesting female when tagged, so it is possible that cessation of growth due to migrations or the allocation of resources toward reproduction resulted in the deposition of non-annual LAGs, which would place the actual 1998 LAG more internal. Based on the results, annual marks in adult green turtles could not be confirmed. Bone marking is recommended as a means of verifying the periodicity of growth marks for green turtles of this size.

There is a mean difference of 1.4 cm SCL between observed and back-calculated SCLs in this study, which is greater than the 0.6 cm mean difference reported for loggerheads (Snover et al. 2007). Some difference can be expected given that LAGs are likely deposited during a different time of the year (i.e. spring) than when most of the turtles were tagged and measured. SCL or LAG diameter measurement error could also account for the difference.

Marginal increment analysis was attempted as an alternate method of indirectly verifying the frequency of LAG deposition, however there was no pattern of periods of the year in which

growth occurs or ceases. Some individuals exhibited little to no growth throughout the year, preventing the detection of trends in growth. Low and negligible yearly growth rates have been documented in marked and recaptured loggerheads inhabiting the inshore waters of North Carolina (Braun-McNeill et al. 2008). In the current study, low or negligible yearly growth rates of some individuals is also documented, given the range of growth rates within each size class (Fig. 4). Turtles representing smaller size classes were analyzed separately to prevent the potentially slower-growing, larger turtles from confounding attempts to detect a seasonal pattern in growth. However, no pattern emerged, as some small turtles also exhibited little to no growth throughout the year. Although Florida and North Carolina/Virginia turtles were also examined separately, to account for the possibility that the two groups exhibited different growing seasons, individuals displaying little or no growth throughout the year prevented detection of any seasonal patterns in growth. A low or negligible amount of growth in any given year could have resulted from the temperatures experienced (reviewed by Mrosovsky 1980), availability of food (Bjorndal et al. 2000), or the quality of food (captive green turtles, Wood and Wood 1981). Others have suggested that low growth rates may be attributed to energy demands such as migrations (Klinger and Musick 1995; Braun-McNeill et al. 2008), which green turtles inhabiting the inshore waters of North Carolina may undergo on a seasonal basis as has been found for loggerheads (McClellan and Read 2007). It is possible that monthly growth varies from year to year and thus combining months from different years may have confounded the analyses. Marginal increment analysis should be revisited when a large number of samples are available from green turtles that stranded in all months of the same year.

Oceanic Stage Length

The oceanic stage, in which juveniles occupy the open ocean before transitioning to the neritic zone (Bolten 2003), has been estimated at 3 to 6 years (Zug and Glor 1998) and 3 to 5 years (Reich et al. 2007) for green turtles 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 to 10 years old at 35 to 37 cm SCL (Zug et al. 2002). By contrast, the results of this study indicate that green turtles of settlement size along the southeastern U.S. coast range from 1 to 7 years old, suggesting an oceanic stage length of the same duration if the turtles within this size range are assumed to be new recruits. This is also assuming a discrete ontogenetic shift from oceanic to neritic habitats, which is not the case in loggerheads in the southeastern U.S. (McClellan and Read 2007). The lower end of this new estimate suggests that for some individuals, the oceanic stage duration may approach that proposed by Carr et al. (1978) of 7 to 14 months, which is shorter than previous studies have found (Zug and Glor 1998; Zug et al. 2002; Reich et al. 2007). The average age of 3 years for turtles of settlement size falls within the oceanic stage duration range that others have found in the Atlantic (Zug and Glor 1998; Reich et al. 2007) and is shorter than that estimated in the Pacific (Zug et al. 2002). Studies are underway using stable isotope analysis of individual growth layers within cross-sections of bones from turtles in which ages were estimated using skeletochronology to further investigate oceanic stage duration.

Growth Rates

Modeling of Florida green turtle growth rates has yielded both a monotonic declining pattern in growth rates as carapace length increases (Mendonça 1981) and non-monotonic growth rate patterns (Zug and Glor 1998; Kubis 2003). In the current study, a non-monotonic pattern in mean growth rates was detected with mean growth rates peaking in the 60.0-69.9 cm

SCL and 80.0-89.9 cm SCL size classes. A peak in mean growth rates in the 50.0-59.9 cm SCL size class is reported for greens in the inshore waters of the Indian River Lagoon in Florida using both skeletochronology (Zug and Glor 1998) and mark-recapture (Kubis 2003), with both studies reporting higher mean growth rates overall compared to those found in this study. The lower mean growth rates of the smaller size classes in this study compared to those of Florida turtles of the same sizes inhabiting inshore waters may indicate foraging ground differences in growth rates, as North Carolina and Virginia green turtles comprised the majority of samples in the 20 to 40 cm size range. Variability in growth rates among foraging grounds is found in green turtles in Hawaii (Balazs and Chaloupka 2004) and within the southern Great Barrier Reef genetic stock (Chaloupka et al. 2004). The differences in growth rates may be due 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. Studies are needed to evaluate the influence of these factors on growth rates. The mean growth rates of green turtles between 30 and 60 cm SCL captured in nearshore waters in Florida (Bresette and Gorham 2001, Kubis 2003) are similar to those reported in the current study.

Skeletochronology has allowed the detection of a second peak in mean growth rates for green turtles from 80.0-89.9 cm SCL, a size class that is rarely seen in mark-recapture studies on the foraging grounds. Although it has been suggested that green turtles leave developmental foraging grounds at a size of 70 to 80 cm SCL to inhabit sub-adult foraging grounds (Bjorndal et al. 2000), studies are needed to elucidate the locations of such foraging grounds and thus the growth rates of green turtles in the upper size classes prior to reaching maturation are largely unknown. An increase in growth rates followed by a decline corresponds with an ontogenetic

shift in loggerheads (Snover 2002). The second growth spurt detected in green turtles may indicate the suspected ontogenetic shift in habitats before growth rates slow with the onset of reproductive maturity.

Differences were observed when the growth rates yielded by this study were compared to those of other geographic regions. A monotonic declining growth rate is reported for green turtles in the Bahamas with higher mean growth rates than those of the current study for turtles between 30 and 60 cm SCL (Bjorndal and Bolten 1988). Growth rates in the U.S. Virgin Islands and Puerto Rico are higher than those of the current study for turtles between 20 and 60 cm SCL (U.S.V.I., Boulon and Frazer 1990; Puerto Rico, Collazo et al. 1992). Compared to green turtles in the Pacific, mean growth rates reported in the current study are lower between 20 and 40 cm SCL but higher from 40 to 100 cm SCL than those reported in Hawaii (Zug et al. 2002). The mean growth rates of green turtles in Australia (Limpus and Walter 1980), the Galápagos (Green 1993), and the Gulf of California (Seminoff et al. 2002) were lower than those found for green turtles of the same size classes in the current study.

Age at Maturation

Application of a growth interval equation to growth data yielded by mark-recapture studies is often used to estimate age at maturation. The growth increment data obtained in the current study by converting the final two LAGs to SCLs is not unlike the type of data obtained in mark-recapture studies, except in the case of skeletochronology, the interval between LAGs is assumed to be exactly 1 year. The ages at maturation estimated using the Fabens modified von Bertalanffy growth interval equation applied to the growth increment data and the length-at-age data from all samples are similar, with the growth increment data yielding higher age estimates (Fig. 20). The estimates of age at maturation using the former method were sensitive to the

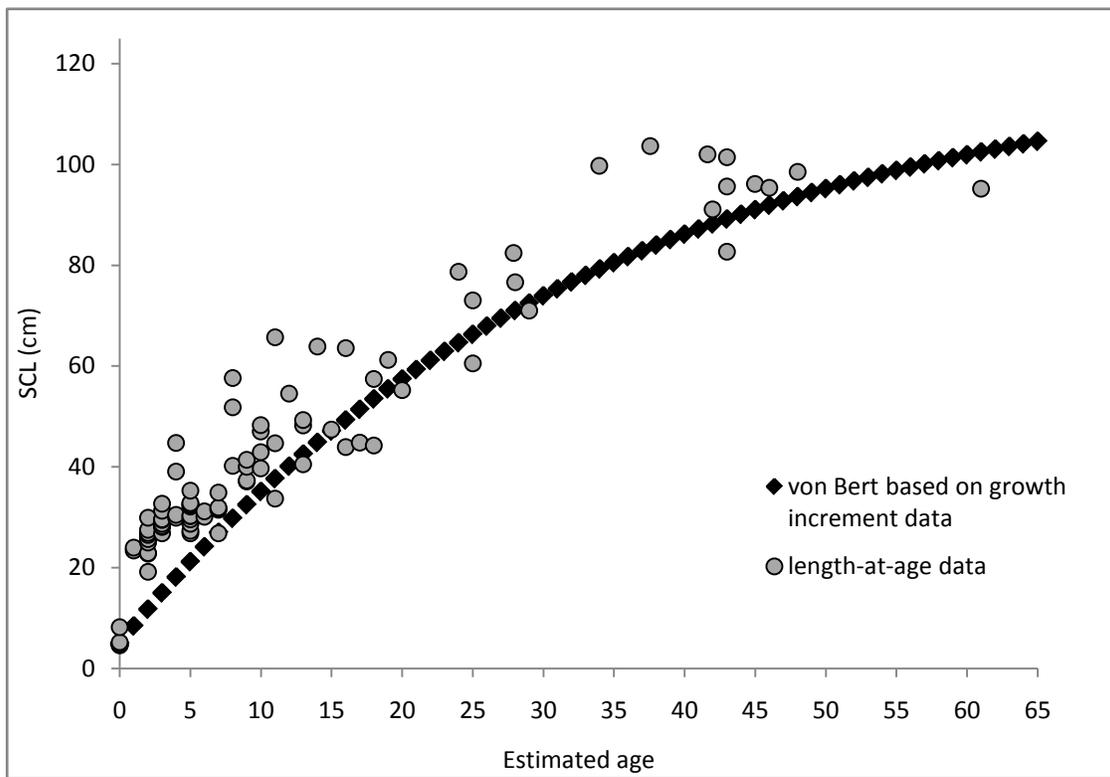


Figure 20. Fabens modified von Bertalanffy growth interval equation applied to the growth increment data of all turtles with length-at-age data from all turtles plotted for comparison. Hatchlings and 8.2 cm SCL post-hatchling are plotted with the length-at-age data.

value at which L_{inf} was set; lower values resulted in higher age estimates. L_{inf} was set at 121 cm SCL, as this was the largest green turtle that I was aware of as reported in the literature (Bjorndal et al. 1983).

The difference in age estimates could be due to the application of one type of growth curve to the growth increment data while several were applied to the length-at-age data to determine which was best supported. While the results indicate that juvenile green turtles deposit annual growth marks, due to remaining uncertainty regarding the precise frequency of mark deposition for adults, it is possible that ages within this life stage are overestimated. As skeletochronological age estimates hinge on the proper interpretation of LAGs, future studies could address the issue of the nature of LAGs in adult green turtles through bone marking, continued analysis of tagged adults should samples become available, or through the analysis of known-age individuals. Despite these issues with both methods, based on the carapace lengths of nesting females in different regions, the age at maturation using all samples is estimated at 53 to 59 years for the average size nesting female in Florida, and 51 to 57 years in Costa Rica for turtles that use the waters of the southeastern U.S. as developmental habitat. These estimates are higher than previous estimates of 26 to 36 years for green turtles in the Atlantic (Mendonça 1981, Frazer and Ehrhart 1985, Frazer and Ladner 1986), although others have noted that previous estimates have been based on small sample sizes and size ranges of turtles were limited (Bjorndal and Bolten 1988; Chaloupka and Musick 1997). Estimates are closer to the upper end of the range predicted for green turtles in the Pacific (25 to 50 yrs., Great Barrier Reef, Chaloupka et al. 2004; 35 to > 50 years, Hawaiian Archipelago, Balazs and Chaloupka 2004).

When the objective is to estimate the age at maturation of females, results indicate that it is most appropriate to use sex-specific length-at-age data. Age at maturation estimates using

only the length-at-age data from females indicate that females mature at a younger age (44 yrs. Florida, 42.5 yrs. Costa Rica) than that predicted by the length-at-age data using all samples. These estimates remain higher than previous estimates in the Atlantic, but are within the range reported in the Pacific. Size-at-maturation for males in the Atlantic remains largely unknown. Given that males were estimated as much older at a size equivalent to that of mature females, it is possible that males reach maturation at a smaller size and after attaining such a size, growth rates decrease considerably. A negligible growth rate upon reaching maturation has been documented for both sexes (females, Carr and Goodman 1970; males, Limpus 1979; males and females, Limpus and Chaloupka 1997). Results indicate that the age at maturation of males and females may be similar; however the inclusion of males (and turtles of unknown sex) can result in overestimates of age at maturation for females based on their average size at maturation.

When separated by sex, the utility of the growth increment data for sex-specific age at maturation estimates was limited by the lack of turtles of known sex within the size range of 50 to 90 cm SCL for both males and females. It is possible that the lack of known sex samples from this size range resulted in age estimates that were very different than those estimated using the sex-specific length-at-age data. This data should be revisited in the future if samples from turtles of known sex within this size range become available.

Age at maturity can also be estimated based on the mean growth rate of each size class without utilizing growth models. Adding the mean oceanic stage duration of 3 years to the estimated length of time needed to grow from 20 cm SCL to the mean size at maturation yields estimates of 42 years to maturation for the Florida population and 37 years for the Costa Rican population. These estimates approach those estimated for females using the length-at-age data

and fall within the range of age at maturation of 30 to 44 years for the Florida population and 30 to 42.5 years for the Costa Rican population.

IMPLICATIONS FOR CONSERVATION

The age at maturation is likely quite variable within breeding populations, depending largely on the growth rates during the juvenile neritic stage in developmental habitats. 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 previous studies indicate (Mendonça 1981; Frazer and Ehrhart 1985). This implies that nesting populations of green turtles in the Atlantic comprised primarily of individuals utilizing these foraging grounds may take longer to recover than previously estimated. In addition, elasticity analyses indicate that the survival of individuals in the stage with the longest duration has the greatest impact on the population growth rate (Heppell et al. 1999). Given that the duration is considerably longer than that of the oceanic stage, it may be most important to protect green turtles in the neritic stage during which boat strikes, interactions with coastal fishing activities, and ingestion of or entanglement in marine debris threaten their survival (Lutcavage et al. 1997). The results from this study should be considered for use in population models to assess the status and recovery of this species.

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