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AGE AND GROWTH OF LOGGERHEAD SEA TURTLES (*CARETTA CARETTA*) OF COASTAL GEORGIA: AN ASSESSMENT OF SKELETOCHRONOLOGICAL AGE-ESTIMATES

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ABSTRACT

Loggerhead sea turtles stranded on Cumberland Island (CI), Georgia provide skeletal samples to estimate the ages of individual turtles by skeletochronology. An initial study in 1986 used an average-thickness of humeral cross-section protocol to estimate individual ages and the minimum carapace length (CL) of nesting females to predict the average age at sexual maturity for the CI sample. The original data and two new CI samples are analyzed by average-thickness, correction-factor, and regression-growth protocols to reassess the original age estimates, to test the reliability of the three protocols, and to predict growth rates and age of sexual maturity. All protocols show moderate to high variation in one or more steps of the calculations of the age-estimates. The lowest variation occurs in the correction-factor protocol, and this protocol's assumption for the estimation of the number of resorbed growth layers matches best the observed pattern of bone growth in *Caretta*. The skeletochronological results show growth patterns (von Bertalanffy model) with asymptotes of 96 - 117 cm curved carapace length (CCL) and growth coefficients of 0.040 - 0.106 for the CI samples. These patterns predict sexual maturity occurring from 20 - 63 yr, assuming 92 cm (SCL) as the mean size at sexual maturity. Growth rate estimates range from 30 - 40 mm yr^{-1} for 40 - 49 cm SCL turtles to 10 - 35 mm yr^{-1} for 80 - 89 cm straight carapace length (SCL) turtles.

The age of nesting and adult sea turtles is a critical datum for understanding their demography and developing workable management strategies. The age at which a sea turtle attains sexual maturity directly affects the reproductive potential of that individual and, in composite, the intrinsic growth rate of the population. For sea turtles, the age of maturity and longevity were largely conjectural until about a decade ago when long-term monitoring began to provide estimates of age based on mark-and-recapture studies (Frazer, 1983; Limpus, 1979; Mendonca, 1981) and semi-natural captive studies (Frazer and Schwartz, 1984; Nuitja and Uchida, 1982). These studies revealed that age at maturity was considerably later, commonly >15 yrs and often 25+ yrs, than proposed by anecdotal evidence and captive-hatchling growth rate (6 - 7 yrs for *Caretta*, Caldwell, 1962).

Because many nesting and immature feeding populations of sea turtles occur along the eastern seaboard of North America, these sea turtles are near many biologists and have been studied intensely, resulting in a significant contribution to sea turtle biology, particularly for western Atlantic loggerhead (*Caretta caretta*) populations. The loggerhead population nesting on Cumberland and Little Cumberland Island area (30° 50' N 81° 26' W) has the longest history of continuous monitoring (since 1964; Richardson and Hillstead, 1978) in North America. Two sets of age estimates have been derived from this *Caretta* population. Frazer (1983) estimated that sexual maturity occurred around 22 years, based on mark-and-recapture measurements from females nesting on Little Cumberland. Zug et al. (1986) suggested maturity at about 13 - 15 yrs, based on skeletochronological data from large juveniles and adults stranded on Cumberland Island. The different estimates result, at least in part, from the use of samples of different size ranges, the selection of different carapace sizes for judging the attainment of sexual maturity, and different analyses of the size-age data. The potential of improved accuracy in age estimation with new skeletochronological techniques encouraged us to re-evaluate the Zug et al. (1986) data set and to analyze new data sets, thereby testing the original estimates and possibly providing more robust age data for the coastal Georgia population. This re-evaluation of the data also allows us to examine the reliability of the different age-estimation protocols for sea turtle skeletal data.

MATERIALS AND METHODS

Skeletochronology derives its estimates of ages from cyclic skeletal growth. The resulting periosteal growth layers provide a record of the number of growth cycles. Assuming the production of one layer each year (see Klinger and Musick, 1992, for verification of this assumption), the number of periosteal layers equals the age of the animal. Although analogous to dendrochronology, skeletochronology, particularly in sea turtles, has a major difference — the resorption and remodeling of bone. Once deposited, tree-rings remain unchanged; in contrast, vertebrate bone is a dynamic tissue with a constant reworking of bone. This resorption and redeposition occurs progressively from the core outward, hence earlier growth layers are lost. Data gathering and analysis must address this difficulty.

The humerus and femur show resorption within the core of the shaft (diaphysis) but retain the periosteal layers on the outer periphery, more so than on any other skeletal element (e.g., skull, mandible, carapace, metapodia, phalanges; Zug et al., 1986). The original data set (Zug et al., 1986) derived from loggerheads stranded on Cumberland Island, Georgia in 1979 and subsequently will be referred to as the 79-original sample (n = 69). A second set derives from loggerheads stranding on the same beach mainly in 1980, hence the 80 sample (n = 26); to enlarge the size range of this sample, three Cumberland specimens (< 48 cm CCL, curved carapace length) collected in 1991 and 1993 are included. Because measurement techniques differ somewhat between the 1979 and 1980 data sets owing to differences in bone-section preparation, we re-measured a subset of the 1979 sample slides; these measurements are the 79-new data set (n = 25). In all samples, cross-sections were removed from the diaphysis of the humerus immediately distal to the deltopectoral crest in both data sets. The bone sections (8 - 15 μm) of the 79 samples were prepared by standard paraffin histological techniques, e.g., decalcified and stained (Zug et al., 1986). In contrast, the bone sections (0.5 - 0.8 mm) of the 80 set were cut by an isomet diamond-bladed saw and were examined unstained, immersed in an ethanol-glycerine solution (6:4).

Owing to resorption, growth layers (MSGs, marks of skeletal growth, or periosteal layers) are not of equal presence around the circumference of the humerus and typically persist longer on the dorsal and ventral surfaces (short axis of section) and somewhat lateral to the middle of the section. The MSGs were counted and measured along the short axis, always along the ventral portion of the axis. The short-axis diameters of the resorption core and humerus also were recorded. The 79-original sample was measured with an ocular micrometer (accurate to 0.001 mm), the 79-new and 80 samples with a mechanical stage micrometer (0.1 mm). All calculations used the dimensions of the humerus's radius and MSG thicknesses or widths. For the 79-original sample, the radius was half of the humeral diameter. Because the resorption core is not in the center of the humerus and growth layer thickness is not equal on opposite sides of the humerus, the radius for the 79-new and 1980 samples equals half the diameter of the resorption core plus the sum of the MSGs on the ventral half.

For the 79 data set, the number of layers lost through resorption was estimated originally by an average layer-thickness protocol (Zug et al., 1986). The mean width of the existing layers is divided into the radius of the bone's short axis (minus the radius of a hatchling's humerus), yielding an estimate of the total number of layers, both those present and resorbed ones. This protocol potentially yields an overestimate of the number of layers (= age), because growth rate, thus layer width, declines with increasing age, especially following sexual maturity.

Another approach to the estimate of lost layers derives from a regression protocol regularly used in fisheries biology (dogfish spines, Ketchen, 1975; otoliths, Ralston and Miyamoto, 1983; shark vertebrae, Parsons, 1985). Conceptually, this protocol assumes that growth-layer width declines with age, and the slope of a regression curve for the declining growth rate can be identified by using the radii or diameters (Xbases) of the element at different consecutive ages and the subsequent growth-layer widths (Xdeltas) from each of these radii. The regression equation then serves directly or via a growth model to estimate the total number of layers that would be present in a bony element of a specific radius or diameter. First, we obtain a linear regression Xbase = A + B(Xdelta). Each Xbase represents the radius of the humerus at the beginning of each growth cycle, and Xdelta is the growth layer (MSG) width at the end of that cycle. Since most humeri have several MSGs, each humerus yields several Xbase and Xdelta pairs; the outermost MSG (of all specimens) was excluded because most sea turtles died prior to the complete formation of this final growth layer. The slope and Y-intercept were used to estimate k (intrinsic growth coefficient) and a (asymptote) for the von Bertalanffy growth equation (Allen, 1966):

$$L = a\,\{1 - \exp[-k(t-t_0)]\}$$

with L as humerus radius (mm), t as age in years, and t_0 as age offset, i.e., the intercept of the growth curve with the age axis.

To solve the von Bertalanffy equation, the asymptote and growth coefficient are estimated by substitutions from the linear regression of Xbases and Xdeltas:

$$a = |A/B|$$
$$k = -\ln(1-|B|)$$

Age offset (t_0) is determined by using the radius (X_0) of the hatchling's humerus (age = 0):

$$t_0 = \ln[1-(X_0/a)]/k$$

Determining t_0 leaves only t (age or number of growth layers) as an unknown, and it can be calculated by substitution and rearranging the von Bertalanffy equation:

$$t = t_0 - \ln[1-(L/a)]/k$$
$$t = \ln[(a-X_0)/(a-L)]/k$$

The preceding two age-estimate protocols were used for the 80 and both 79 samples. The 79-new and 80 samples were analyzed also by a third protocol that estimated the number of MSGs lost by resorption. This correction factor is added to the number of MSGs observed to obtain the total number of growth layers. Conceptually, the correction protocol follows a similar protocol developed by Klinger (1988) but differs by estimating the total number of lost layers, instead of only those for individuals greater than 40 cm SCL (straight carapace length). The correction protocol relies on the presence and size of the growth layers in the smaller individuals of the sample. A growth trajectory (X, number of growth layers; Y, radius of the humerus) is determined for each individual by connecting the point (X_i, Y_i) at smallest size to point at death ($X_i + n$, $Y_i + n$). The "average" slope of the trajectories of the smallest individuals is determined by regression analysis (least square) and the Y-intercept is set at the radius of the hatchling's humerus. The number of lost layers is determined by substituting the radius of the resorption core in the regression equation:

$$Y = A + BX$$

or

radius = hatchling radius + [(slope)*(number of lost layers)]

Table 1. A summary of growth model parameters for the 1979-orig Cumberland Island sample (n = 69) of *Caretta caretta.* Column labels: B, growth constant; k, intrinsic growth rate; r^2, adjusted coefficient of determination; MS, residual mean square; Hatchling, predicted CCL based on the preceding growth equation parameters.

Model	Asymptote (mm)	B	k	r^2	MS	Hatchling (mm)
AVERAGE-THICKNESS PROTOCOL						
von Bert	967.6	0.3993	0.0449	0.57	7087	581
Gompertz	966.8	0.4904	0.0507	0.57	7107	592
logistic	965.8	0.6083	0.0567	0.57	7128	601
REGRESSION-GROWTH PROTOCOL						
von Bert	1040.3	0.6901	0.0957	0.72	4046	332
Gompertz	1025.6	0.9855	0.1208	0.72	4015	383
logistic	1015.6	1.4330	0.1465	0.72	3996	417

EQUATIONS

von Bert $CL = Asympt\,(1 - Be^{-kAge})$

Gompertz $CL = Asympt\,(e - Be^{-kAge})$

logistic $CL = Asympt/(1 + Be^{-kAge})$

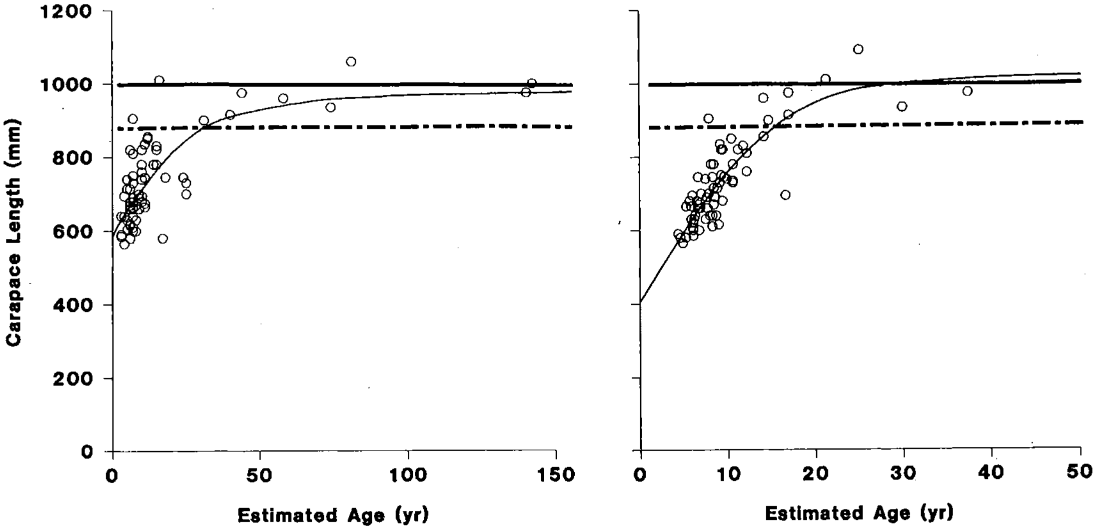

Figure 1. Comparison of age estimates derived from the average growth-layer thickness protocol (left) and the regression-growth protocol (right) for the 1979-original Cumberland Island sample. Carapace length is measured over-the-curve (mm). The horizontal dashed line represents the mean CCL (991 mm) and the horizontal dotted line represents the smallest CCL (874 mm) for females nesting on Cumberland Island (Stoneburner, 1980). A von Bertalanffy curve is shown in the right graph and a logistic curve in the left graph (for equation values, see Table 1).

number of lost layers = (radius - hatchling radius)/slope

The number of lost layers (i.e., correction factor) is added to the number of layers observed and yields an estimate of the age or total number of layers for the individual.

Three growth models (von Bertalanffy, Gompertz, logistic; see Table 1) summarize the association of size and age and provide a depiction of the growth pattern for individuals greater than about 50 cm curved carapace length (CCL), the usual minimum size within our samples.

Table 2. A summary of growth model parameters for the 1979-new Cumberland Island sample (n = 25) of *Caretta caretta*. Column labels are the same as in Table 1.

Model	Asymptote (mm)	B	k	r^2	MS	Hatchling (mm)
AVERAGE-THICKNESS PROTOCOL						
von Bert	1035.3	0.5614	0.0402	0.71	6743	454
Gompertz	1031.8	0.7360	0.0468	0.71	6760	494
logistic	1028.5	0.9802	0.0539	0.71	6884	519
CORRECTION-FACTOR PROTOCOL						
von Bert	1088.2	0.9649	0.0981	0.64	8310	38
Gompertz	1078.3	1.4760	0.1209	0.65	8300	246
logistic	1070.3	2.3269	0.1456	0.64	8301	322
REGRESSION-GROWTH PROTOCOL						
von Bert	1025.5	0.8190	0.0861	0.78	5086	186
Gompertz	1015.2	1.1821	0.1044	0.78	5092	311
logistic	1006.8	1.7401	0.1237	0.78	5108	367

Growth rates are presented for 10 cm growth classes (i.e., -59 cm, 60 - 69 cm CL, etc.) and are derived in two ways. In the first, we selected one age-estimate data set and one growth equation derived from these data; then we calculated growth rates from the equation's predicted size intervals. In the second, we used the growth vector or projection concept described above in the correction-factor protocol; however, instead of a humeral radius to layer vector, we used a carapace length to layer vector. We obtained carapace size at the first visible MSG by the Fraser-Lee back-calculation formula (Everhart et al., 1975). This equation permits the estimation of body size at an earlier age based on the size of a skeletal element at an earlier growth stage and its proportional relationship to the current size of the body and the skeletal element.

$$L' - C = (S'/S)(L - C)$$

where L is CL at death; L' is CL at the time when the first visible MSG formed; S is the radius of the humerus at death; S' is the radius of the humerus to the first visible MSG; C is a correction factor. The correction factor is the X-axis intercept of a power equation of humerus radius (Y) to carapace length (X). CL' at the smallest MSG was determined for each individual in the sample, and the difference from this CL and the CL at the last complete MSG divided by number of complete MSGs yields an average growth rate (mm yr^{-1}) for that individual. Each such growth rate was assigned to the age-class for the individual at CL'.

All turtles salvaged from Cumberland Island had curved carapace length (CCL) recorded when they were first found on the beach. To permit reliable comparison of publications using SCL measurements, we used the conversion formula CCL = 5.24 + 1.02 SCL (Frazer and Ehrhart, 1983). For hatchling size, we used 45.3 mm CL (mean of the means of Atlantic Coast/North America hatchlings, from Dodd, 1988: table 22). All statistical analyses and linear-nonlinear curve modeling (least-squares) were performed using SYSTAT 5.03 (Wilkinson, 1991).

RESULTS

Age and Growth Estimates.— The average-thickness protocol for the 1979-original sample produces age estimates of 3 - 175 yrs (Zug et al., 1986: appendix-part 2). A plot (Fig. 1) of these age estimates with carapace lengths shows a high dispersion of individu-

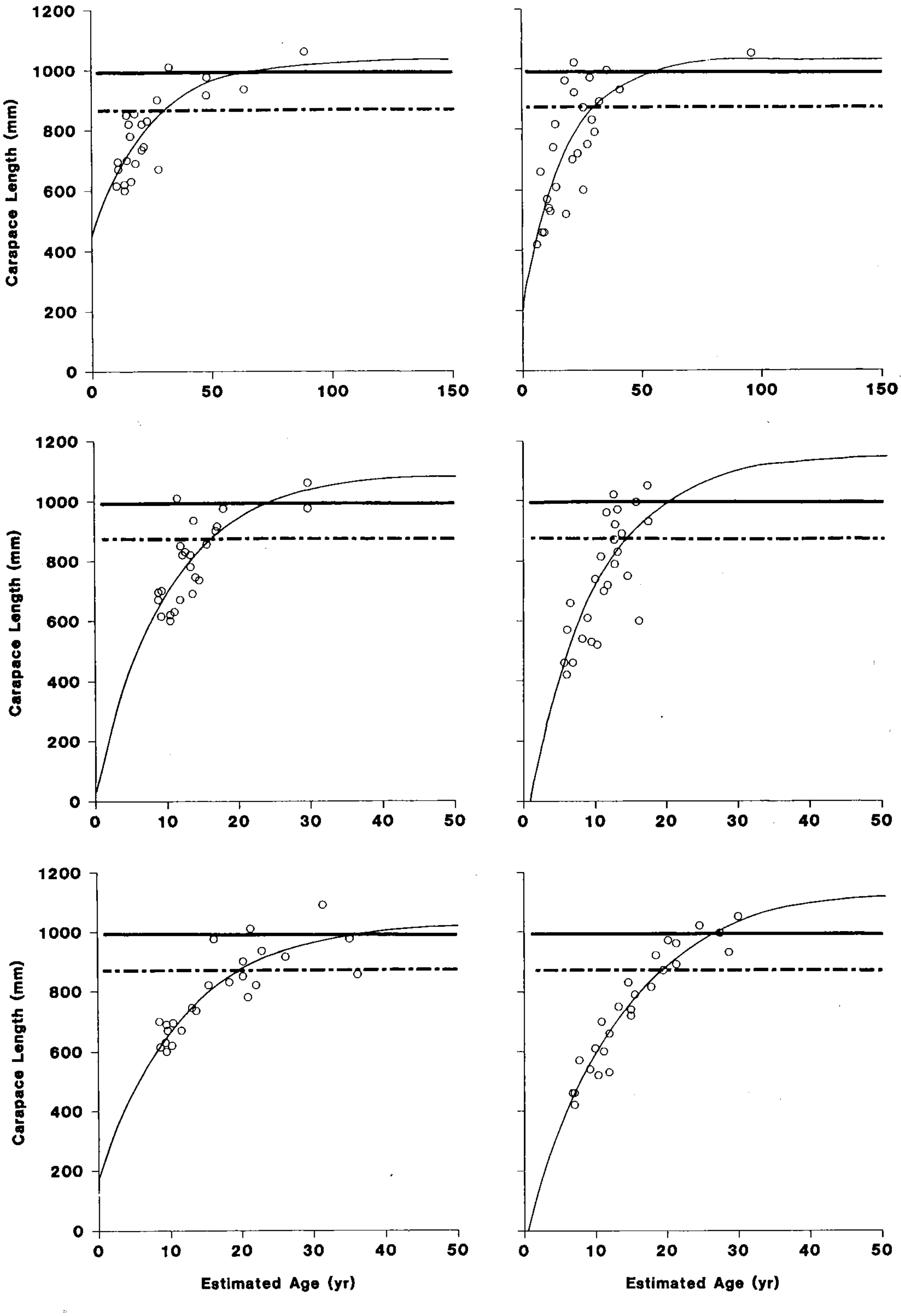

Figure 2. Comparison of the 1979-new (left) and 1980 (right) Cumberland Island samples. The age-estimation protocols from top to bottom are: average-thickness, correction-factor, and regression-growth. A von Bertalanffy growth curve is presented for each data set (Tables 2-3). Labeling information as in Table 1.

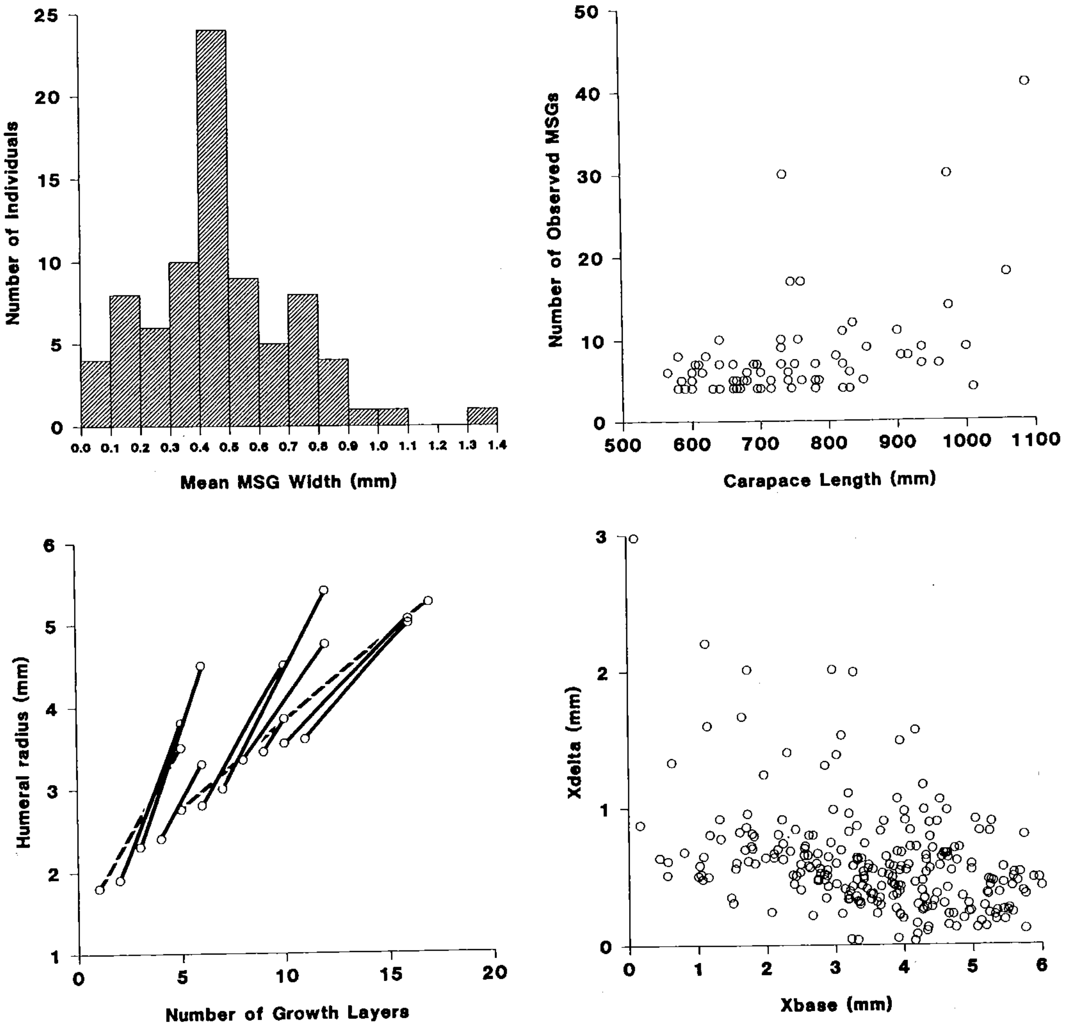

Figure 3. Variation in the data used to estimate sea turtle ages. Frequency distribution (top left) of mean MSG widths and the association (top right) of the number of observed MSGs in individuals to their body size (CCL) in the 1979-original sample. The "average" slope relationship (bottom left) for humerus width and number of growth layers in an 80-subsample; the first layer of each specimens is assigned sequentially to growth layers 1-13 based on increasing humeral radii; each line (solid or broken) connects an individual's innermost and penultimate layer number. The relationship among Xdelta-Xbase pairs (bottom right) for the 79-original sample.

als, in which four individuals can be recognized as distinct outliers owing to their high age estimates (> 100 yrs). The dispersion or variation of the cluster is reflected by a 57% coefficient of determination (corrected r^2) for the growth models (von Bertalanffy, Gompertz, logistic). For the 79-new and 80 samples, age estimates range from 10.3 - 300.0 and 6.2 - 96.0 yrs, respectively. The growth models within each of the three samples possess similar asymptotes; the 79 samples differ little in the dispersion (see mean squares of residuals, Tables 1,2,3) but dispersion is nearly twice as great in the 80 sample. Among the samples, the asymptotes range from 965 to 1033 mm CCL (Tables 1,2,3). Calculations of hatchling size (1 d old) using the growth parameters of the models yield unrealistically large carapace lengths (Tables 1,2,3) for the three samples.

Table 3. A summary of growth model parameters for the 1980 Cumberland Island sample (n = 26) of *Caretta caretta*. Column labels are the same as in Table 1.

Model	Asymptote (mm)	B	k	r^2	MS	Hatchling (mm)
AVERAGE-THICKNESS PROTOCOL						
von Bert	1032.1	0.7699	0.0542	0.61	15790	237
Gompertz	1017.2	1.1558	0.0689	0.61	15952	320
logistic	1006.0	1.7733	0.0842	0.60	16137	362
CORRECTION-FACTOR PROTOCOL						
von Bert	1149.1	1.1021	0.1059	0.60	16043	-117
Gompertz	1052.0	2.2570	0.1744	0.61	15882	110
logistic	1001.7	4.8762	0.2464	0.61	15723	170
REGRESSION-GROWTH PROTOCOL						
von Bert	1165.6	1.0267	0.0739	0.92	3345	-31
Gompertz	1092.5	1.9647	0.1154	0.92	3199	153
logistic	1055.0	3.9240	0.1579	0.92	3097	214

The correction-factor protocol produces age estimates (Fig. 2) of 8.8 - 56.4 and 5.7 - 17.5 years (79-new and 80, respectively). These estimates show moderate dispersion (r^2 = 0.84 - 0.85 and 0.87 - 0.88, respectively). The three growth models have similar asymptotes within the 79-new but not the 80 sample, and mean squares of residuals are similar within each sample (Tables 2,3). Hatchling sizes (CL) derived from these growth-model parameters again are usually unrealistic (Tables 2,3).

The regression-growth protocol produces age estimates of 4.4 - 37.4 (Fig. 1), 8.5 - 65.1, and 6.7 - 30.0 years (79-original, 79-new and 80, respectively). These estimates show moderate dispersion (r^2 = 0.70, 0.78 and 0.92, respectively). The three growth models have similar asymptotes within and among the three samples, and mean squares of residuals are similar within samples (Tables 1,2,3). Hatchling sizes (CL) derived from these growth-model parameters are also unrealistic (Tables 1,2,3).

The average-thickness protocol uses the mean thickness derived from the MSG widths within an individual to estimate the age of that individual. Individuals of identical CL size but with different average thicknesses will obtain different age estimates, potentially and actually producing a greater variation of age estimates. Variation of the mean layer-width ranges from 0.03 - 1.14 mm (x = 0.48±0.26 SD), 0.03 - 0.55 mm (x = 0.32±0.16 SD), and 0.10 - 0.73 mm (x = 0.35±0.14) for 79- original, 79-new, and 80 samples, respectively. The mean width is also representative of the modal and median widths, and the distribution appears normal (Fig. 3). Number of layers present ranges from 4 - 41 (Fig. 3), 3 - 47, and 2 - 13, respectively. The correlation between the size (CL) of an individual and the number of remaining MSGs is weak ($r = 0.52$, $p < 0.001$; $r = 0.54$, $p = 0.005$; $r = 0.03$, $p = 0.87$; respectively). In contrast, the association of the resorption core and body size is high ($r = 0.66$, $p < 0.001$; $r = 0.86$, $p < 0.001$; $r = 0.94$, $p < 0.001$; respectively).

The correction-factor protocol provides age estimates based on the number of MSGs actually observed in an individual and on an estimate (correction factor) of MSGs resorbed. The regression to estimate the number of lost (resorbed) MSGs derives from a subsample (n = 13) of small individuals (i.e., those with resorption core radii less than the mean core- radius [$\bar{x}$= 4.7] for the 80 sample), purposefully excluding the larger indi-

Table 4. Growth rates (mm yr^{-1}) for the three Cumberland Island Caretta samples. The rates for each sample derive from the von Bertalanffy equation and the specific age-estimation protocols for that sample.

CCL Class	1979-orig	1979-new	1980
Average-Thickness			
400-499 mm	-	-	31.8
500-599	-	19.7	26.3
600-699	14.3	15.6	20.9
700-799	9.9	11.6	15.4
800-899	5.2	7.5	9.9
900-999	3.7	3.3	4.3
1000-1099	-	-	-
Correction-Factor			
400-499	-	63.0	74.4
500-599	-	53.2	63.8
600-699	-	43.3	53.2
700-799	-	33.5	42.6
800-899	-	23.6	32.0
900-999	-	13.6	21.3
1000-1099	-	-	10.3
Regression-Growth			
400-499	-	50.0	52.9
500-599	-	40.9	45.0
600-699	14.3	32.1	37.5
700-799	9.9	23.7	31.0
800-899	5.2	15.3	23.1
900-999	3.7	6.2	16.1
1000-1099	-	-	8.5

viduals with narrower MSGs to better match MSG thickness when turtles are smaller and younger. These selection criteria result in a subsample including all individuals with CCL ≤ 700 mm, a 720 and a 750 mm specimen. The resulting regression $Y = 0.407 + 0.75X$ (where Y is radius of humerus and X is number of layers), rearranges to $X = (Y - 0.407)/0.75$, and the substitution of the resorption core radius for Y yields X, i.e, the number of lost layers. The average slope is 0.407 ± 0.157 SD, range 0.208 - 0.733 (Fig. 3).

Variation of the correction-factor age estimates results from (1) differences in radii of resorption core and (2) number of MSGs present. The relation of age to size shows moderate dispersion (Fig. 2), more similar to the level of variation in the regression-growth estimates than to the average-thickness estimates.

The regression-growth protocol derives its estimate of the declining growth rate of the humerus diameter from all individuals within each sample. The resulting age estimate depends entirely on the radius of the humerus at death and ignores the number of MSGs still present, having used the widths of extant MSGs in the initial regression estimate of slope and Y-intercept. The regressions of Xdeltas(Y) and Xbars(X) are: $Y = 0.975 - 0.109X$, $r = 0.52$, $p < 0.001$, $n = 299$ (Fig. 3); $Y = 0.726 - 0.074X$, $r = 0.67$, $p < 0.001$, $n = 222$; $Y = 0.538 - 0.041X$, $r = 0.47$, $p < 0.001$, $n = 119$; 79-original, 79-new and 80,

Table 5. Growth rates (mm yr^{-1}) for two Cumberland Island *Caretta* samples. The rates derive from the back-calculation of carapace lengths for each individual in the samples. For the first two columns, the growth rate for each individual is from the interval (time and distance) between the minimum and maximum back-calculated CCL, and for the third column from the distance between pairs of adjacent back-calculated CCLs (see text for details). The data include mean ± 1 SD, range, and sample size (number of intervals).

CCL Class	1979-new	1980-I	1980-II
200-299		43.7±8.5	45.6±1.9
		37.7-49.7	44.3-47.0
		2	2
300-399	35.4±4.1	41.1±19.0	48.1±15.7
	31.8-40.1	18.9-71.5	26.6-87.7
	4	5	11
400-499	41.3±9.2	28.7±9.0	31.5±16.4
	29.5-53.7	22.3-35.1	15.9-78.0
	7	2	17
500-599	35.3±13.5	38.1±12.0	31.1±18.1
	20.3-51.2	23.5-53.2	9.0-77.0
	4	6	19
600-699	39.2±11.0	22.4	27.4±9.9
	30.9-51.7		10.6-48.3
	3	1	16
700-799	18.4±0.4	27.0±6.6	26.9±10.9
	18.1-18.7	19.8-37.0	10.2-48.3
	2	5	15
800-899	17.3±9.4	34.1±11.7	25.5±13.2
	10.5-28.1	24.9-47.3	8.7-63.0
	3	3	15
900-999	3.5±0.1	25.7±22.6	22.6±11.7
	3.4-3.6	9.7-41.6	9.7-41.6
	2	2	9

respectively. Dispersion of the estimates (Figs. 1,2) for this protocol are always less than for the other two protocols.

Growth rates are determined in two ways: (1) from the growth curve/equation; (2) from back-calculation of carapace length. The first method reflects an "average" growth rate for the sample, and the second yields growth rates for individuals from which central tendency can be estimated for each sample. In both cases, we arbitrarily examine growth rates within 10 cm size classes, i.e., 50 - 59 mm CL, and present rates only for those classes represented in the samples.

The von Bertalanffy equation is used for the first set of growth rate estimates (Table 4), because the von Bertalanffy model regularly has the best fit to age-CL data for sea turtles (Frazer and Ehrhart, 1985, and our data, Tables 1,2,3). Variation in the growth rate-estimates is moderate among samples for the average-thickness protocol (Table 4) and somewhat higher among samples for the correction-factor and the regression protocols.

Because the rates derive from a decaying exponential curve, they show a smooth decline in rate with increasing size and age.

The growth rates from back-calculation of carapace length (Table 5) also show declining rates with increasing size, although the trend is not as smooth as in the preceding sets (Table 4). We determined the average class growth rate in two ways. In the first (Table 5, 1979-new and 1980-I), the change in length from the smallest back-calculated CCL (using the innermost MSG) to the largest back-calculated CCL (using the last complete MSG prior to death) is divided by the number of growth layers between these two MSGs. This single rate for each individual is assigned to the class containing the smallest back-calculated CCL, and when all rates are assigned, the rates are summed and averaged. In the second way (Table 5, 1980-II), the CCLs for all MSGs in each individual for the entire sample are back-calculated. The interval or distance between each pair of neighboring CCLs yields the growth rate, since each interval represents one year of growth. The growth rates are assigned to class based on the CCL at the beginning of the growth interval and then summed and averaged for each class. The 1979-new and 1980-I rate-estimates are very dissimilar, even though they use the same computational technique. The two 1980 sets are similar in means and standard deviation, although their computation differed.

Sex Maturity of Population.— Various parameters of adult body size in a population have been used to indicate the attainment of sexual maturity. In sea turtles, all maturity estimates derive from nesting females, because nesting females are unquestionably mature and carapace length (CL) is a standard item recorded by most researchers studying nesting ecology. Frazer and Ehrhart (1985) showed that the mean CL of nesting populations provides the best index for predicting the "average" age at sexual maturity for a population. The loggerhead populations of the Atlantic coast of North America have means for nesting females ranging from 92 - 94 cm SCL (Stoneburner, 1980; Bjorndal et al., 1983; Henwood, 1984), 92 cm SCL (99 cm CCL) occurs most frequently and is used here. For the Cumberland Island nesting population (Stoneburner, 1980), the range is 80.5 - 107.0 cm SCL (x = 92.4) or 87.4 - 114.4 cm CCL (99.1 cm).

Our three samples, three age-estimate protocols, and three growth-model analyses provide multiple choices in selecting ages for the attainment of sexual maturity. We emphasize the results from the correction-factor protocols (reasons for this choice addressed in the discussion section) and the summary of the age-estimates by the von Bertalanffy model. This model generally yields the best fit for turtle growth data (Dunham and Gibbons, 1990; Frazer et al., 1990). Also this model usually has the lowest residual mean square (a potential evaluator of curve predictability; proposed by Dunham, 1978) for our data.

The average-thickness data yield age-at-maturity estimates of 63, 63, and 54 yrs (79-original, 79-new, 80 samples, respectively) for turtles at 99 cm CCL. The regression data give estimates of 28, 37, and 26 yrs and the correction-factor data yield estimates of 24 and 19 yrs (79-new, 80) for sexual maturity.

DISCUSSION

All loggerheads in this study died off the southeast coast of Georgia and stranded on the 29 km-long beach of Cumberland Island in 1979 and 1980 (except for three small individuals stranding in 1990-91). Owing to the local nature of the strandings, all individuals in the three samples are from a single population in a statistical sense, although not likely from the local biological population, i.e., from the population nesting on Cumberland and adjacent islands. Our samples are composites of individuals, presumably from populations spanning the entire Atlantic seaboard of North America. Recent genetic analyses (Bowen et al., 1993; Sears, 1994) reveal that two distinct genetic populations of loggerheads exist on the Atlantic seaboard, i.e., a Georgia/South Carolina and a Florida one. Further, Sears' samples from three sites in coastal Georgia contain nearly equal numbers of Florida and Georgia/South Carolina turtles. These proportions are probably representative of our CI stranding samples. Because individuals killed in coastal Georgia waters were summer residents there or residents of more northern waters (killed during their northward or southward migration through this area) and likely shared the same "habitat" during their earlier pelagic phase, we assume that they share similar growth rates and ages of maturity, and thus the CI samples are representative of growth rates for loggerheads of coastal Georgia.

Age Estimates.— Age estimates of the individual loggerheads vary among protocols within a sample, for example (79-new) 10.3 - 300, 8.8 - 56.4, and 8.5 - 65.1 yrs for average-thickness, correction-factor, and regression protocols, respectively. Similar variation among protocols occurs for the other samples. Within a protocol (e.g., regression-growth), age- estimate ranges are somewhat more similar (4.4 - 37.4, 8.5 - 65.1, 6.7 - 30.0 yrs, respectively for 79-original, 79-new, 80).

Which protocol provides the most accurate age estimates? This question cannot be answered directly without wild, known-aged specimens in a sample. Such a sample does not exist. We offer a partial answer by examining the amount of variation within the steps of each protocol and within the resulting age-size distributions.

Each protocol used the same basic data of MSG number and widths and humeral radii, so the differences in the age estimates arise from the differences in the assumptions and computations of each protocol. At a basic level, average-thickness protocol uses the mensural data of an individual to estimate the age of that individual. The regression protocol pools the relationships of each individual's size-change for entire sample; the resulting common values serve as constants to estimate the age of each individual. The correction-factor protocol combines the use of a populational constant and the number of observed layers of an individual to estimate the age of that individual.

The average-thickness protocol yields the widest range of age estimates for each sample. The wide range encompasses moderate variation in the association of size with age (r^2 = 0.57, 0.71, 0.61; Tables 1-3) and has unrealistic outliers at both ends of the range, e.g., 3 - 4 year old large juveniles or 150 - 300 yr old adults. These extremes result from a few broad MSGs or numerous narrow MSGs in a bone section that, respectively, underestimate or overestimate age.

The correction-factor protocol produces the narrowest range of age-estimates and the highest association of size and age ($r^2 > 0.85$). Variation in this protocol arises from variation in number of observed MSGs and in the computation of lost MSGs, which is dependent upon the size (radius) of the resorption core and a constant (mean slope of the growth trajectory; Fig. 3, bottom-left) representing the proportional change in bone radius and MSG width with increasing age. The constant has a coefficient of variation of 39%. Resorption- core radius is moderately to highly correlated (positive) with body and humerus size.

Table 6. A survey of growth rates in wild *Caretta*. All growth rates are in mm yr^{-1} and derived from SCL measurements; mean rate are given when range was not published. Locality abbreviations*: CB, Chesapeake Bay, Virginia; CI, Cumberland Island, Georgia; MB, Melbourne Beach, Florida; ML, Mosquito Lagoon, Florida; BA, Great Inagua, Bahamas; EA, eastern Atlantic; NP, northern Pacific; AU, Queensland, Australia.

Class SCL	CBr	CBs	CI	MB	ML	BA	EA	NP	AU
200-299			34-43			148-172	37	45	
300-399			29-37				35	41	
400-499		53	35-36						
500-599	30	53	28-38		74				
600-699	15	53	27-31		60				
700-799	3	44	16-24		50	46-58			
800-899	12	31	9-35	0-9					7-10
900-999	19	29							1-2
>999		7							

* Sources: CBr, CBs, CB recapture and stranding data, Klinger and Musick, 1995; CI, Parham and Zug; MB, Bjorndal et al., 1983; ML, Mendonca, 1981; BA, Bjorndal and Bolten, 1988; EA, Azores-Mediterranean, Bolten et al., 1992, Canaries, Bjorndal et al. 1994 ; NP, northern Pacific, Zug et al., 1995; AU, Limpus 1992, 1994aandb.

The regression protocol has a narrow range of age estimates. This low variation suggests high reliability of estimates but demonstrates only the narrow range of humeral widths used in the age computation. The age estimate for each individual depends upon the size of the individual's humerus at two different steps. The first is in the estimation of two constants, i.e. age = ln[(a - hatchling humerus)/(a - specimen's humerus)]/k (see detailed equation in M & M), and the second is in the actual age estimation. High variation is present in the first during the calculation of the constants a and k from the Xdeltas (MSG widths) and Xbases (humeral radii at successive growth cycles). The Xdelta-Xbase linear regressions to estimate a and k are significant for all samples($P < 0.001$) with $r =$ 0.52, 0.67, 0.47 (79-original, 79-new, 80); however, the regressions explain only 27%, 45%, and 22% of the variation or dispersion within the Xdelta-Xbase distributions (Fig. 3). These levels of variation indicate only a weak association between humerus size and number of growth cycles. Such an interpretation appears correct because the actual number of observed MSGs has no effect on the age estimate. Humerus diameter alone determines the age-estimates in the final step of calculation.

All three samples are handicapped by the absence of small juveniles (< 560 mm CCL for 79, < 420 mm for 80). Although Frazer et al. (1990) showed that the absence of smaller or younger individuals had only a minor effect on the estimation of the von Bertalanffy growth curve, we suspect that such absence is less benign in estimating the number of resorbed growth layers. In general, the larger an individual the greater is the resorption of the earlier bony growth layers and the narrower are the widths of the remaining growth layers. These two factors affect the age estimates, producing potential overestimates for the larger juveniles and adults with all three protocols, likely greatest with the average-thickness protocol; however owing to the broad variation of layer thickness, the effect on smaller individuals is less predictable. As in all age-growth studies, the

Table 7. Estimates of age of sexual maturity in loggerhead seaturtle populations from the Atlantic coast of North America. Carapace length (SCL) is the size selected to recognize the attainment of sexual maturity.

Age (yr)	Carapace Length (mm)	Latitude (° W)	Method	Source
22	925	37	skeletochro	Klinger and Musick, 1995
22	?	31	mark-recapt	Frazer, 1983
13-15	792	31	skeletochro	Zug et al., 1986
20-24	924	31	skeletochro	present study
10-15	750	29	mark-recapt	Mendonç a, 1981
12-30	740-920	29	mark-recapt	Frazer and Ehrhart, 1985

most reliable results obtain in skeletochronology when a full range of sizes (ages) are present in the sample (Zug, 1990).

A final factor potentially affects variation in age estimates among the samples. The 79 data come from histological prepared sections, the 80 data from "raw," unstained sections. The latter are much thicker, and in at least the larger turtles, this thickness might obscure the number of MSGs observed on the outer edge (periosteal) of the bone section. This conclusion is supported by the maximum number of observed MSGs, 41 and 47 in the 79-original and 79- new samples compared to 13 in the 80 sample. This observational bias directly affects the age-estimates of the average-thickness and correction-factor protocols, because the number of observed MSGs in each individual is used in the estimation of that individual's age. The effect would be less in the regression protocol because the unobserved MSGs represent only a fraction of the MSG widths (Xdeltas and Xbases) used to determine the protocol constants.

This brief review of variation among samples recommends ignoring the results from the 1980 age-estimates. The review of protocols indicates that the correction-factor has the lowest variation in the data used to estimate the number of MSGs lost by resorption. The use of observed MSG number also more accurately reflects the number of growth cycles of the individual.

Growth.— The estimated growth rates (Tables 4,5) show the same form and level of variation as the age-estimates. The preceding comments on protocols and samples focus our attention to the growth-rate estimates of the correction-factor 79-new sample (Table 4) and all three sets of back- calculated CL rates (Table 5). The von Bertalanffy model (79- new) produces a steady 10 mm yr^{-1} decline in rates between size classes beginning with 63 mm yr^{-1} in the 40 - 49 cm CL class. Back-calculated growth rates decline irregularly, not unexpected for growth in wild-living turtles. Assuming high accuracy in back-calculated CL, these growth rates should reflect more accurately actual growth rates and their natural variability. Some variation, however, results from computation in the 79-new and 80-I samples. Their growth rates for the smaller age classes (< 70 cm CL) commonly derive from growth intervals that span two age classes; thus, the reported rates are slight underestimates for the size-class at the beginning of the growth interval (and where the rate is reported, Table 5). In the 80 samples, the larger classes (>70 cm CL) are likely overestimates, because the outer MSGs might not have been observed and two or more growth cycles are reported as a single growth cycle.

The preceding observations suggest rates between 35 - 48, 29 - 41, 31 - 35, 22 - 39, 18 - 27, 10 - 22, and 3 - 4 mm yr^{-1} (30 - 39 cm ... 90 - 99 cm CCL classes, respectively; see Table 6 for SCL class growth rates) as reasonable estimates of the growth pattern for the Cumberland Island sample. These rates generally match those of other *Caretta* populations of the warm-temperate and subtropic Atlantic and Pacific (Table 6). The mismatches are the Chesapeake Bay-stranding and Mosquito Lagoon-recapture samples. The growth rate of the former is artificially high because Klinger's age-estimates do not include the number of lost growth layers prior to a turtle reaching 40 cm SCL, i.e., functionally the sea turtle at 40 cm CL is treated as a 1 yr old. The growth rate of recaptured CB loggerheads match those estimated for CI loggerheads. The ML rates portray natural growth and are roughly double the CI rate-estimates and likely equivalent to the one from the Bahamas. The ML and Bahama rates indicate more equitable growing conditions — more food, better quality food, and longer growing seasons. These factors enhance growth in turtles (Avery et al., 1993; Dunham and Gibbons, 1990; Nuitja and Uchida, 1982; Swingle et al., 1993). Local variation in growth rates further emphasizes the danger of extrapolating the growth pattern of one population to another and especially of the use of growth rates of captive turtles to predict growth in wild sea turtle populations.

Tracking growth in captive loggerheads reveals the potential for rapid growth in hatchlings and juveniles, as well as the high variation of growth rates in individuals of the same cohort when subjected to the same captive environment [see reviews by Frazer (1982) and its update by Swingle et al. (1993)]. Hatchlings in captivity can double their size (CL) in ten weeks (Swingle et al., 1993), although 16 - 24 wks seems more common (Witham and Futch, 1977), and growth can be even slower (Frazer, 1982).

Sexual maturity.— Because the variation in age-estimates yields different growth patterns, the estimates of sexual maturity are equally as variable no matter which growth model (von Bertalanffy, Gompertz, or logistic) is used to summarize the age-size relationships. Our choice of the von Bertalanffy model gives age-estimates of maturity ranging from 54-64 yrs (average-thickness), 20 - 24 yrs (correction-factor), and 26 - 27 yrs (regression). Our preference for the correction-factor protocol selects the youngest age set for maturity, and this age range accords well with the conclusions (Table 7) of Frazer and Ehrhart (1985) and Klinger and Musick (1995) using 92 cm SCL for the "average" size at maturity. We also concur with Frazer and Ehrhart's (1985) hypothesis that sexual maturity is probably closer to 30 years for many loggerheads of eastern North America.

The growth rates derived from back-calculated CL advocate such an interpretation. Using the maximal or fastest rate of the Cumberland Island samples for each of the growth-classes (Table 6), a loggerhead requires a minimum of 18 yrs to grow from 30 cm to 90 cm SCL. At the minimum growth rate, 29 yrs are required. Neither of these estimates include the time from hatching to 30 cm CL.

Selection of the minimum size of nesting females for determining age at sexual maturity would significantly lower the age estimates derived from either growth models or average growth rates. Minimum size, however, is biologically unjustified. Evidence continues to mount that the turtles maturing at the smaller sizes are not the youngest maturing individuals but some of the oldest ones. These data derive not from sea turtle populations but from mark-recapture studies of freshwater and terrestrial turtles, and despite the differences in size and habitat, much of the basic biology of the latter is applicable to the former. For example, female Blanding's turtles (*Emydoidea blandingii*) in a southern Michigan population reach maturity in 14 - 20 yrs and between 157 - 210 mm

CL. The smallest primiparous female was 20 yrs and the next smallest was 19 yrs (Congdon and von Loben Sels, 1991, 1993). Such observations support the hypothesis that variable growth rates prior to maturity are a major cause of the size variation in adult turtles. Carr and Goodman (1970) recognized this phenomenon in sea turtles, "some green turtle mature at small, others at large sizes; and that once they are mature...their growth becomes negligible, as compared with individual variation in maturity-size" but were unable to associate age with size at maturity.

Precise-techniques.— For sea turtles in which growth has slowed (i.e., large juveniles and adult), unstained bone sections do not show all the peripheral growth layers revealed by histological preparations. Tests are required to determine whether this is strictly a size (CL) dependent phenomenon or whether accuracy of MSG counts requires staining of bone sections in small as well as large individuals.

Presently three quantitative protocols are available for estimating age or the total number (resorbed + remaining) of MSGs in each bone section. None is totally reliable for all size classes of sea turtles. The average-thickness protocol yields increasingly greater overestimates as MSG width narrow and number of MSGs increases. The regression-growth protocols assume a regular decline in MSG widths with increasing size and an equivalent proportional change in all individuals in the population. MSG widths are highly variable in and between individuals, and in larger juveniles and adults, widths increase and decrease erratically over many growth cycles. The correction-factor protocol also assumes a regular decline in MSG widths, although only estimating the actual number of resorbed MSGs. Because the data set for age-estimate is the same for all three protocols, the level of variation of the data elements for each protocol can be assessed to determine which protocol yields age-estimates with the fewest violations of the assumptions.

The three growth models (von Bertalanffy, Gompertz, logistic) yield similar asymptotic carapace lengths within each data set. The skeletochronological age-estimates are too variable to allow our evaluation of which model best fits the growth pattern of CI *Caretta.*

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