

Estimates of age and growth in a population of green sea turtles (*Chelonia mydas*) from the Indian River lagoon system, Florida: a skeletochronological analysis¹

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Abstract: The Indian River lagoon system harbors a dynamic population of juvenile green sea turtles (*Chelonia mydas*). This foraging or developmental population occupies the lagoon year-round and periodically experiences cold-stunning events that kill a portion of the population. A sample of 59 *C. mydas* (28–74 cm straight carapace length) from the December 1989 cold-stunning event was aged by skeletochronology, yielding age estimates of 3–14 years. Mean growth-rate estimates range from 30 to 52 mm/year for most age and size classes, with means for the 6- to 11-year age classes (44–49 mm/year) not significantly different but greater than those of the youngest and oldest classes (3–5 and 12 years old, respectively) (32–38 mm/year). Because of the lack of adults and near-adults in the sample, growth models (e.g., Gompertz) do not yield biologically realistic asymptotes, hence they do not provide accurate estimates of age at sexual maturity. The age estimates suggest that the western Atlantic *C. mydas* change from a pelagic to a neritic life predominantly as 5- to 6-year-olds and, in central Florida, juveniles may live in a developmental habitat for 6 or more years.

Résumé : Le système de lagunes de la rivière Indian abrite une population dynamique de juvéniles de la Chélonée franche, *Chelonia mydas*. La population en quête de nourriture ou en développement occupe la lagune toute l'année et doit parfois faire face à des chutes importantes de température qui tuent une partie de la population. L'âge des tortues d'un échantillon de 59 chélonées (longueur de la carapace en ligne droite, 28–74 mm) a été déterminé par squeletochronologie au cours d'une telle chute de température en décembre 1989, ce qui a donné des estimations de l'âge de 3 à 14 ans. Les taux moyens de croissance ont été estimés à 30–51 mm/année chez la plupart des classes d'âge et de taille avec une moyenne de 44–49 mm/année chez les classes d'âge de 6–11 ans, une valeur non significativement différente, mais plus élevée que celles enregistrées chez les classes d'âge les plus jeunes et les plus âgées (32–38 mm/année chez les classes de 3–5 ans et de 12 ans, respectivement). À cause de l'absence d'adultes et d'individus presque adultes dans l'échantillon, les modèles de croissance (e.g., Gompertz) n'ont pas donné d'asymptotes biologiquement réalistes et n'ont donc pas permis d'obtenir des estimations précises de l'âge à la maturité sexuelle. Les estimations de l'âge semblent indiquer que les tortues de l'Atlantique de l'ouest passent d'une forme pélagique à une forme néritique surtout vers l'âge de 5–6 ans, alors que, dans le centre de la Floride, les juvéniles peuvent vivre dans un milieu de développement pour 6 ans ou plus.

[Traduit par la Rédaction]

Introduction

The green sea turtle (*Chelonia mydas*) occurs along the Atlantic coast of North America from New England southward (Márquez 1990; Ernst et al. 1994). However, year-round residency, mainly of juveniles, seems to be restricted to nearshore and estuarine habitats of central Florida and

southward. No regular nesting occurs north of Florida (Carr et al. 1982; Dodd 1982; Ernst et al. 1994).

Although small relative to many tropical nesting populations, the central Florida population is the largest in North America (Ehrhart and Witherington 1992; Meylan et al. 1994). These nesting females represent a unique genetic assemblage, their closest affinities being with the Caribbean populations (Bowen et al. 1992); however, the genetic composition of the various juvenile feeding populations found along coastal Florida is unknown. In spite of potential genetic differences, a similar growth pattern can be expected from conspecific turtles feeding in the same area and on the same foods and experiencing the same environmental conditions.

For this reason, studying a foraging population offers an opportunity to gather longitudinal growth data on the association of size and age. One such foraging population that has been intensively studied occupies the Indian River lagoon system on the east coast of Florida (Mendonça and Ehrhart

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1982; Ehrhart 1983; Mendonça 1983; Frazer and Ehrhart 1985; Henwood and Ogren 1987; Witherington and Ehrhart 1989a; Guseman and Ehrhart 1990; Schroeder et al. 1990). This estuary, created by a barrier of sand-dune islands, has been labeled a developmental habitat (Carr et al. 1978; Mendonça 1981; Mendonça and Ehrhart 1982) and contains a population of juvenile green sea turtles ranging in size from 246 to 754 mm straight carapace length (SCL) (Mendonça 1981; Mendonça and Ehrhart 1982; Frazer and Ehrhart 1985), as well as juvenile loggerhead (*Caretta caretta*) and Kemp's ridley (*Lepidochelys kempii*) turtles. In the past, the sea turtles of this region were harvested by a small fishing industry (Brice 1896; Wilcox 1896; Ehrhart 1983). However, commercial capture has been minimal since the late 1800s, when a combination of overharvesting and an intense cold-kill decimated the lagoon's sea turtle population and halted its commercial exploitation. Nevertheless, some harvesting continued on a small scale until the early 1970s (Ehrhart 1983).

Though hunting by humans is no longer a major mortality factor for the Indian River sea turtles, the shallow and enclosed nature of this lagoon system subjects resident sea turtles to episodic cold-stunning events, when the water temperature drops below approximately 8°C (Witherington and Ehrhart 1989a; Schroeder et al. 1990). Such recurring "natural disasters" kill large numbers of sea turtles and provide an opportunity to salvage whole specimens for scientific study.

Skeletochronology requires limb bones to obtain age estimates, a critical demographic parameter for individual turtles. The age data then allow the modeling of growth patterns of individuals in the population and yield life-history information. Such data are essential for the development of accurate ecological models as well as for effective conservation management of this endangered species. Even though growth and age data can be gathered in a direct fashion for many individual organisms, this luxury is presently not available for most sea turtle populations, owing to the turtles' long lives and extended unavailability for direct observations.

Our goal was to obtain skeletochronological age estimates for a sample of cold-stunned *C. mydas* and to use these estimates to examine a variety of age- and growth-related phenomena in the Indian River foraging population. We also interpret these data relative to the life-cycle of coastal Florida green sea turtles.

Materials and methods

Our skeletochronological sample derives from 59 *C. mydas* salvaged from the Indian River lagoon system (Indian River and Mosquito Lagoon) in Brevard and Volusia counties, Florida, between December 26 and 28, 1989 (Schroeder et al. 1990). The rescued green sea turtles ranged in size from 266 to 770 mm SCL ($\bar{x} = 523$, $n = 246$). During necropsy of these cold-killed individuals, the right humerus was removed from each animal, macerated to remove muscle and connective tissue, rinsed in water, and stored in 70% ethanol. Subsequently, cross sections (0.5–0.8 mm thick) were removed from the middle of the diaphysis for skeletochronological analysis (for details of bone preparation and data collection see Parham and Zug 1997).

Our data consist of carapace length (straight (SCL)), maximum humerus length, diameters (long axis of humeral cross section, i.e.,

abaxial to adaxial axis) of the outside of the humerus, each growth layer, and the resorption core, and the number of growth layers (bone growth marks, GM). Each GM is defined by a line of arrested growth (LAG) and (or) an annulus on the GM's outer edge. These data permit us to calculate a number of parameters to estimate age, body size at different ages, and growth rate. A single specimen (609 mm SCL) was excluded because it had no LAGs or annuli.

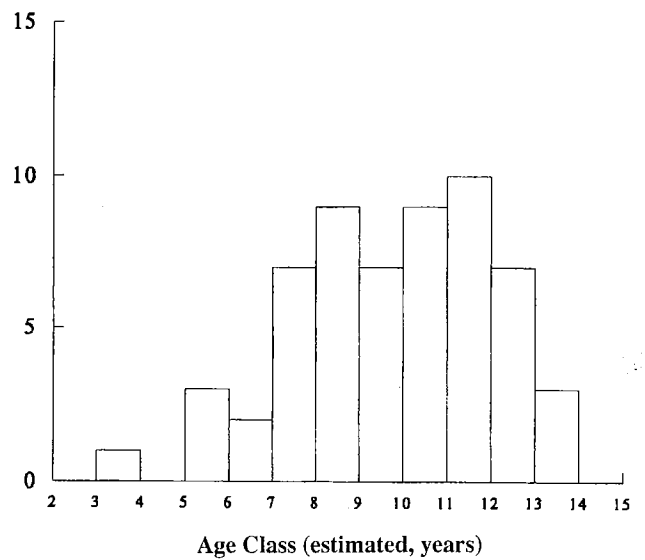
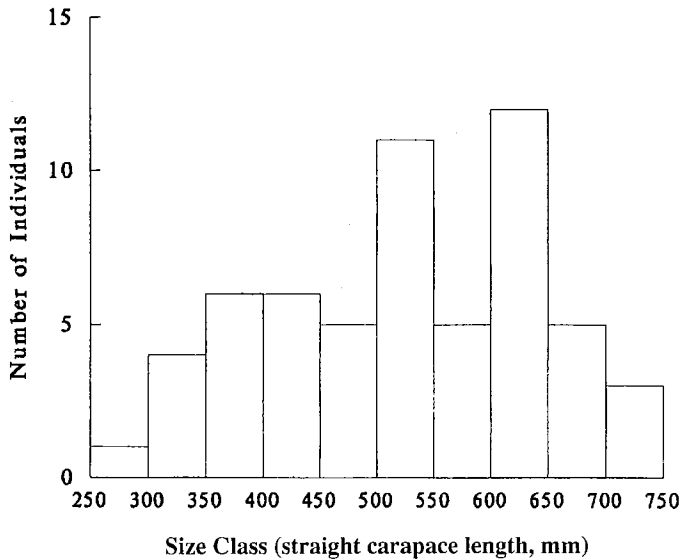
Although the humerus retains more growth layers than most other bones (Zug et al. 1986), it is still profoundly influenced by skeletal remodeling. This remodeling works from the inside of the bone outward and confounds skeletochronological analysis by obscuring or destroying the innermost (i.e., oldest or earliest) growth layers. Large turtles, such as sea turtles, undergo a relatively high rate of remodeling compared with other extant ectothermic vertebrates (Castanet 1982). Because the inner GMs are inevitably lost, a protocol must be used to estimate the number of lost GMs in order to obtain an age estimate. For the current analysis we use the correction-factor protocol (Parham and Zug 1997). The age estimate from this protocol is the sum of the observed GMs and the estimated resorbed GMs. The number of lost layers is estimated on the basis of the diameters of visible GMs in the smallest members of the sample. For the Indian River sample, 25 individuals with resorption core width <14.00 mm and (or) SCL <560 mm were used to calculate the correction factor to estimate the lost layer number (for a detailed explanation of the technique see Parham and Zug 1997).

Growth-pattern analysis

For analysis of the growth pattern of the Indian River population, two techniques are used. The first is mathematical models that examine growth directly from the age estimates and SCL data using the Gompertz and logistic equations. Previous studies have indicated that the von Bertalanffy model often provides the best fit for freshwater turtle (Dunham and Gibbons 1990) and sea turtle growth (Frazer and Ehrhart 1985; Bjorndal and Bolten 1988); however, Chaloupka and Musick (1996), Day and Taylor (1997), and others have argued that the von Bertalanffy model is not a reliable model for size-based growth. We also use a smoothing function (LOWESS, tension 0.35) to explore changes in growth vectors.

To determine growth rates at specific times in individuals' lives, we estimate the body size of individuals at the end of each growth interval via the Fraser-Lee size back-calculation equation (Everhart et al. 1975). This equation estimates body length on the basis of the proportional relationship of the known length or diameter of a body structure and the body length at the present time and uses the known length of that structure at an earlier time to calculate the body length at the earlier time (a fuller explanation of technique is given in Parham and Zug 1997; Zug et al. 1997). Our proportional values are humerus diameters (at each GM and at death) and SCL at death to estimate SCL at the end of each growth interval, i.e., at the time of the formation of an annulus or LAG. Using these size estimates for each growth interval and accepting the assumption that each growth layer or LAG represents 1 year, this technique provides multiple SCL estimates at 1-year intervals for each turtle. From these estimates we obtain multiple annual growth rates for each individual based on the difference between adjacent SCLs. For population-level evaluation, we assign each growth rate to the size class of the individual at the middle of a growth interval. Because most previous sea turtle growth studies have examined rates in 10-cm size classes, we use the same dimensions for our comparisons. Further, we can examine growth at different ages by using these differences and subtracting the appropriate number of GMs from the skeletochronological age estimate and then ranking the growth rates in age-classes. Unlike mark-recapture data, our data cannot reveal negative or zero growth rates.

Fig. 1. Size and age class distributions for the Indian River green sea turtle sample.



Statistical analyses and nonlinear equation modeling were performed with SYSTAT 5.03 and 6.01. SYSTAT's least squares nonlinear curve fitting module uses a quasi-Newton iterative algorithm.

Results

Age estimates and size

The cold-killed sample included individuals ranging in SCL from 281 to 742 mm (Fig. 1). Most (86%) individuals were in the 350- to 700-mm range. Correction-factor age estimates for this sample range from 3.3 to 13.6 years, with most (84%) turtles in the 7- to 12-year classes (Fig. 1). The smallest turtle (281 mm) was also the youngest (3.3 years) (Fig. 2). The largest turtle (742 mm, 11.1 years) was not the oldest; instead, a individual of 711 mm SCL was the oldest at 13.6 years (Fig. 2).

There is a general association of age estimates and size (linear: $r^2 = 0.65$, $p < 0.001$, $n = 58$). This association yields a linear regression of $Y = 134.2 + 40.3X$ (Y is in millimetres SCL; X is in years (females: $n = 39$, $a = 159.3$, $b = 36.57$, $r^2 = 0.58$; males: $n = 19$, $a = 58.8$, $b = 49.37$, $r^2 = 0.81$; slopes not significantly different, $F = 2.81$, $p = 0.10$). The mean estimated age and size of the females are not significantly different from those of the males ($t = 0.41$ and 0.32 , $p = 0.68$ and 0.75 , respectively). The association between humeral diameter (Y) and size (X) is strong ($r^2 = 0.95$, $p < 0.001$, $n = 58$) and linear ($Y = -1.06 + 40.045X$). The sample sex ratio (39:19) is marginally significantly different from 1:1 ($\chi^2 = 3.554$, $0.90 > p > 0.95$).

Growth pattern

As noted above, the age estimates and SCLs have a moderate linear association (Fig. 2). Our attempts to fit this linearity to exponential growth models (Gompertz, logistic) produced unnatural asymptotes (Table 1). This is not an unexpected result, owing to the absence of large juveniles, subadults, and adults from our sample. The shape of the LOWESS curves (Fig. 2) indicates a growth plateau among some of the older individuals. The smaller sample of males

Table 1. Growth-model parameters for the Indian River *Chelonia mydas* sample, based on skeletochronological age estimates (years) and straight-line carapace lengths (mm).

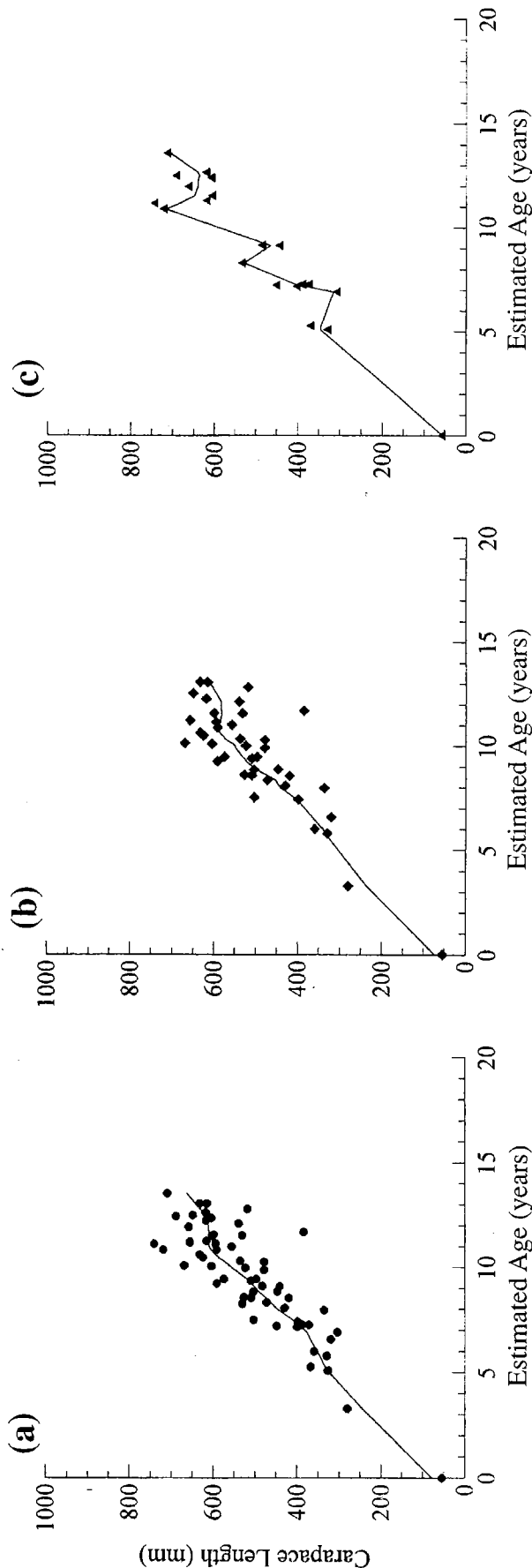
	Asymptote	<i>b</i>	<i>k</i>
Gompertz			
Total	831.5±139.2	2.402±0.448	0.172±0.056
Females	729.2±136.5	2.263±0.826	0.198±0.094
Males	1065.0±626.0	2.533±0.634	0.137±0.117
Logistic			
Total	725.9±71.7	6.545±2.181	0.299±0.071
Females	666.9±75.8	5.712±3.151	0.316±0.110
Males	862.8±245.0	6.944±3.030	0.257±0.127

Note: The parameters are for the total sample (59), females (39), males (19), and one hatchling. Parametric estimates and standard errors are given; the asymptote is expressed in millimetres SCL; *b* is a growth constant and *k* is the intrinsic growth rate.

creates an impression of greater variability in the age-size association for individuals 10 years of age and older; this variation is also reflected in the greater standard error for males in both growth model estimates of *k*, the intrinsic growth rate, and the asymptote (Table 1). The *k* values for the growth models show a somewhat steeper slope for males, although not significantly different ($t = 0.06$ and 0.14 for the Gompertz and the logistic equation, respectively).

The age estimate and size data permit us to examine growth rates in several ways. Growth rates from the models show uniform declining rates, e.g., 55.6 mm/year for the 300- to 350-mm class to 13.2 mm/year for the 650- to 700-mm class, based on the logistic equation; the Gompertz model yields similar rates because the curves of the two models are nearly the same within the 300- to 600-mm range. Estimated growth rates for year classes (Table 2) and size classes (Table 2) derived from back-calculated SCLs show high variance in all classes. The age-class data yield more uniform growth rates (44–49 mm/year) throughout the juvenile classes of 6–11 years, and rates for the youngest (3, 4, and 5 years) and oldest (12–13 years) classes are slower (28–37 mm/year in samples with $n > 5$) than for the interme-

Fig. 2. Association of size and age estimates for the Indian River green sea turtle sample. The curve in the each scatterplot is the best fit line using the LOWESS smoothing function (tension = 0.35). (a) Total sample. (b) Females. (c) Males.



diate classes. The fastest rate is for the youngest specimen, a 2-year-old. The mean growth rates of the age-classes (excluding the 2- and 13-year-olds) are not, however, significantly different from one another ($F_{[9,201]} = 1.70$, $p = 0.09$); variance is high in all age classes but homogeneous among them.

The growth rates among the size classes increase progressively from 30.9 mm/year in the 200- to 299-mm SCL class to 52.9 mm/year in the 500- to 599-mm SCL class, then decline (Table 2). Rates among size classes (excluding the 700-mm class) are significantly different ($F_{[4,207]} = 4.4$, $p = 0.002$). This differences results from a slower rate in the 200-mm class, e.g., it and the 300-mm class are significantly different ($F_{[1,91]} = 6.09$, $p = 0.34$). In contrast, the rates for the 300- through 500-mm classes are not significantly different ($F_{[3,185]} = 1.70$, $p = 0.17$). Variance is heterogeneous ($p = 0.04$) among the size classes. As an aside, we found no significant differences in the mean growth rates for size classes whether individuals were assigned to a class according to their size at the beginning or middle of the growth interval (e.g., for 300- to 399-mm class, $n = 60$ and 70 , $t = 1.52$).

Although the slope of the relationship between age and size is slightly steeper for males than for females ($b = 49.3$ and 36.6 , respectively), the slopes are not significantly different. Nonetheless, in the larger individuals, males are usually larger than females of the same estimated age (Fig. 2). Growth rates also support the impression of faster growth in males, potentially indicating a growth surge. There are no significant differences between females and males through the 500-mm class, although the 500-mm class approaches significance (females: 49.1 ± 18.6 mm, $n = 27$; males: 60.7 ± 18.3 , $n = 13$, $t = 1.86$, $p = 0.07$). In the 600-mm class, males' growth rates (50.3 ± 19.4 , $n = 8$) are significantly greater ($t = 3.09$, $p = 0.01$) than females' (14.4 ± 3.4 mm, $n = 3$), but the variances are unequal and sample sizes are small.

Discussion

Our age estimates suggest that the green sea turtles of the Indian River system range in age from 3 to 14 years, and that these juveniles have growth rates ranging from 8 to 113 mm/year, although the mean rates for most size and age classes are usually 30–50 mm/year. These data, in association with those from the numerous other studies of east-coast Florida *C. mydas*, allow us to examine some aspects of postpelagic life in this species.

Growth

In 1916, Schmidt reported growth rates of 12–82 mm/year for wild juvenile *C. mydas* in the Virgin Islands. Another 50 years were to pass before mark-recapture studies (Carr and Caldwell 1956; Balazs 1980, 1982; Limpus and Walter 1980; Mendonça 1981) provided additional growth data for free-living juvenile *C. mydas*. These latter studies and those on other sea turtle species called attention to the fact that sea turtles grow more slowly and mature much later, often in excess of 20 years, than was commonly predicted from growth of captive hatchlings.

Such longitudinal studies of growth in the same individuals over several to dozens of years remain the best method

Table 2. Size-specific and age-specific growth rates for the Indian River green sea turtle sample.

Size class (mm SCL)	Growth rate			Age class (years)	Growth rate		
	Mean \pm SD	Range	<i>n</i>		Mean \pm SD	Range	<i>n</i>
200–299	30.9 \pm 14.02	8.3–66.8	23	2	66.8		1
300–399	44.2 \pm 24.54	8.6–113.4	70	3	32.1 \pm 22.03	16.5–47.7	2
400–499	48.1 \pm 20.64	14.2–100.0	68	4	37.8 \pm 18.27	10.8–79.2	11
500–599	52.9 \pm 19.04	14.2–80.8	40	5	33.1 \pm 19.53	8.3–75.3	20
600–699	40.5 \pm 23.42	11.3–101.4	11	6	48.3 \pm 27.02	11.6–113.4	32
700–799	13.4		1	7	48.4 \pm 21.30	14.6–89.0	35
				8	49.0 \pm 22.87	14.2–101.4	39
				9	47.1 \pm 19.30	11.3–85.7	29
				10	44.5 \pm 18.39	13.4–76.9	22
				11	48.0 \pm 24.11	13.8–102.4	15
				12	32.7 \pm 16.10	14.2–51.1	6
				13	27.7		1

Note: All growth rates are presented in millimetres per year. Data are given as the mean \pm 1 standard deviation; the total number of growth increments is 213.

for obtaining growth data from wild populations. Skeletochronology can also provide comparable growth data for individuals and, importantly, adds the age component. However, skeletochronology assumes cyclic bone growth, with each cycle of the same duration. For this population sample, we equate one bone layer to 1 year of growth, a proposition requiring validation through a longitudinal study. Annual growth layers have been confirmed for *C. caretta* (Klinger and Musick 1992) and *L. kempii* (J.A. Musick, personal communication, December 1996) from the Chesapeake Bay area, but for no *C. mydas* population.

Bjorndal et al. (1998) demonstrated that growth layers are not produced on the epicondylar surfaces of the humeri during active growth in juvenile *C. mydas* in a Bahamian developmental habitat. We do not challenge their results, which were derived from a rigorously designed and executed vital-dye experiment; we also agree with their recommendation on the cautious use of skeletochronological data. However, for the Indian River population, several observations support the use of skeletochronological age estimates. First, because Indian River turtles live in a habitat with seasonal fluctuation of temperatures that reduces or halts growth once each year, growth layers were evident in all but one specimen in our sample (98% occurrence). Second, the size of an individual is not a factor in estimating its age, yet the age estimates have a positive correlation (linear $r = 0.81$) with body length, even though the number of observed growth layers, which are used to estimate age, have a weak association ($r = 0.34$) with body size. These data support the assumption of an annual deposition of a single growth layer for individuals in the Indian River developmental population. Third, skeletochronologically derived growth rates match those derived from mark-recapture studies of Indian River green sea turtles and are similar to the rates reported from the Bahamian and Caribbean populations. These similarities of rates seem more than coincidental. Exceptions notwithstanding, we advocate the usefulness of skeletochronological age and growth estimates for examining aspects of sea turtle life history, while agreeing with Bjorndal et al. (1998) on the limitations of these data (see also Zug et al. 1986; Zug 1990;

Parham and Zug 1997). We also note the concern expressed (Bjorndal and Bolten 1988; Chaloupka and Musick 1996) about comparing growth rates derived from methodologically different studies, although we argue for the validity of such comparisons, owing to the similarity of results from different methodologies used on the same population (e.g., Bjorndal and Bolten 1988, 1995; Bolten et al. 1992).

For the Indian River *C. mydas*, we are able to compare skeletochronological growth rates with those of Mendonça's (1981) mark-recapture study of juvenile Indian River turtles in Mosquito Lagoon. Her turtles were not aged but were assigned to size classes. Mendonça's data (Table 3) portray faster growth for her 300- and 700-mm size classes and slower growth for her 500- and 600-mm classes; nonetheless, Mendonça's mean rates are within the ranges of our skeletochronologically based rates for each size class. We attribute the differences mainly to differences in sample size: the standard deviations of her and our means for Indian River turtles are similar.

These standard deviations demonstrate large variation within each size class. The similar levels of variance in our and Mendonça's data (Table 3) suggest that this is a natural phenomenon. This level is generally seen in the other studies, although the variance is lower for the Pacific samples, particularly the Galápagos sample (note the standard deviation for the 600-mm class). The difference in variance can be attributed in part to smaller samples and slower growth rates. Variance in each population has two major components: (1) actual growth variation among individual turtles; and (2) measurement error/variation by the data collector. Bjorndal and Bolten (1988) examined the latter cause of variation in their Bahamian sample and took precautions to reduce measurement error, yet their variance for size classes with comparable numbers of individuals is only slightly less than the variance for the other mark-recapture rates and the skeletochronological ones. Nonetheless, it is likely that both recorder error and our back-calculated size estimates increased the variance in our rates. Further, the absence of zero growth in our data may produce somewhat higher rates in each size and age class.

Table 3. Summary of green sea turtle growth rates.

SCL (mm)	Florida						Texas (Mansfield Channel) ^d	Bahamas ^e (Great Inagua)		
	Indian River ^d		Indian River ^b		Broward Co. ^c					
	Mean ± SD	n	Mean ± SD	n	Mean ± SD	n				
200–299	30.9±14.0	23	—	—	—	—	90±32	4	—	—
300–399	44.2±24.5	70	53.2±27.8	4	36.0	?	89±27	13	88±10.0	10
400–499	48.1±20.6	68	—	—	44.4	?	—	—	49±20.0	40
500–599	52.9±19.4	40	31.4±18.3	2	20.4 ^k	?	66	1	31±16.0	67
600–699	40.5±23.4	11	28.1±12.3	3	—	—	—	—	18±14.0	22
700–799	13.4	1	21.5±11.0	3	—	—	—	—	12±09.0	9
800–899										

Note: All growth rates are presented in millimetres per year; where necessary, these data have been transformed from the original source to match our age classes or scale. The data are given as the mean ± 1 standard deviation.

^aOur skeletochronological data.

^bFrom Mendonça (1981, Table 1 (Mosquito Lagoon, Florida)).

^cFrom Wershoven and Wershoven (1992); no sample sizes are given (Broward County, Florida).

^dFrom Shaver (1994, Table 1); all rates derive from intervals of less than 1 year (South Padre Island, Texas).

^eFrom Bjorndal and Bolten (1988, Table 4 (Union Creek, Great Inagua)).

^fFrom Collazo et al. (1992, Table 3 (Isla de Culebra)).

^gFrom Boulon and Frazer (1990, Table 1 (St. Croix, St. John, and St. Thomas)).

^hFrom Balazs et al. (1998, Fig. 2 (Kihola, Hawai'i Island)) and Balazs (1982, Table 1 (Necker Island and French Frigate Shoals)); these may be overestimates because zero growth increments were excluded from the original data (fide Bjorndal and Bolten 1988, p. 562).

ⁱFrom Green (1993, Table 1 (Isabel, Fernandina, and Santa Cruz islands)).

^jFrom Limpus and Walter (1980, Table 1, CCL measurements (Heron Island and Wistari Reefs)).

^kRate for turtles >50 cm SCL.

Growth rates from nearby localities (Table 3) are not greatly dissimilar, considering differences in sample sizes and methodologies. Wershoven and Wershoven's data (1992) for a more southerly Florida population match for the 300- and 400-mm classes, but their >500-mm class grows at half the rate of either the Indian River turtles' 500- or 600-mm classes. They did not provide sample sizes, and their sea turtles were captured in coastal waters lacking seagrass beds. Juveniles from lagoonlike bays in the southern Bahamas (Bjorndal and Bolten 1988) show a progressive decline in growth rates, with a rate nearly double that of the Indian River turtles in the 300-mm class to a rate less than half that in the 600-mm class. The rates for a Puerto Rican sample (Collazo et al. 1992) are generally comparable to the Indian River ones. The U.S. Virgin Islands sample (Boulon and Frazer 1990) shows a declining rate with increasing size but shares similar rates for the 300- and 400-mm classes with our Indian River sample. The Texan sample shows the highest rates and variance. We agree with Shaver's interpretation (1994) that these fast rates probably result from the calculation of yearly growth from recapture intervals of significantly less than 1 year.

Although western Atlantic populations display differences in growth among localities, their growth is, in our opinion, more similar than different. Boulon and Frazer (1990) also noted this similarity between Floridian and Caribbean populations as well as similar rates between samples from 1912–1913 and 1981–1986. Observed differences may result in part from the manner of assigning growth rates to size class. Our rates and those of Bjorndal and Bolten (1988, 1995) and Shaver (1994) are assigned to classes on the basis of an individual's size in the middle of the growth interval; the manner of assignment is not specified for the other studies. One general pattern emerges from all studies of western Atlantic

juveniles. They share average growth rates of 30–50 mm/year following their entry into developmental (neritic) habitats.

Generally, growth rates for Pacific *C. mydas* are strikingly slower, with most rates ranging between 5 and 15 mm/year for the 300- to 600-mm classes. Site-specific differences are also evident in the Pacific, with the lowest rates in the Galápagos. Overall, growth rates for Pacific populations are about 20–25% those of the Indian River and the other western Atlantic samples. Some differences between Atlantic and Pacific populations might be attributed to the diversity of techniques used for studying them and to the limited size of most Pacific samples, but the same slow growth pattern is also evident in Pacific *C. caretta* (Zug et al. 1995). Furthermore, the Hawaiian data derive from a single researcher and his associates. Earlier, Balazs (1982) had reported strikingly higher rates for the southern Hawaiian populations; these rates were nearly equivalent to those for the western Atlantic. However, rates based on larger samples (Balazs et al. 1994, 1998) are more similar to growth data from other Pacific populations, but the difference between the northern and southern populations remains. He (Balazs 1982) noted that the various Hawaiian populations feed on different algae and suggested diet as the main factor in determining the growth rates, although he also noted that the cooler water habitat of the northwestern populations might slow growth. It is noteworthy that Bjorndal and Bolten (1988) observed differences in growth rates within their Bahamian study site of approximately 29 km²; The causes (e.g., season, location) have not yet been identified, although sex does not appear to be a factor (Bolten et al. 1992). Balazs' (1998) conclusion that the slower rates are associated with poorer food resources for Pacific sea turtles is likely correct. We also agree with him that for northern Hawaiian turtles, the lower water

Table 3 (concluded).

Puerto Rico ^f (Culebra)		Hawai'i ^h				French Frigate Shoals		Galápagos ⁱ		Australia ^j (Heron Reef)	
Mean ± SD	n	Mean ± SD	n	Mean ± SD	n	Mean ± SD	n	Mean ± SD	n	Mean ± SD	n
36±04	4	69.3±29.2	4	—	—	—	—	—	—	—	—
51±13	6	49.6±17.2	26	13	49	09.8±2.33	6	—	—	—	—
60±06	9	46.7±30.4	12	18	261	09.4±5.34	11	04.0±0	2	07.5±06.3	4
38±05	4	34.8±18.3	5	18	159	10.0±3.67	3	04.5±5.4	11	09.5	1
39±20	3	18.7	2	13	104	—	—	01.5±1.9	25	14.3±19.6	14
—	—	—	—	4	6	—	—	01.2	34	14.6±06.5	9
—	—	—	—	—	—	—	—	01.1	18	11.0±10.7	11

temperatures are a factor. Water temperature may also be a factor in the slow growth rates of the Galápagos green turtles; we further speculate that they live in a marginal habitat for green sea turtles and are incapable of gathering and assimilating adequate plant/energy resources to produce rapid or even moderate growth.

For comparison, age-specific growth rates are available only for the southern Great Barrier Reef population (Chaloupka and Limpus 1996). There, the age of each individual is determined from when it arrives in the neritic habitat; thus, the implicit assumption is that all individuals become neritic inhabitants at the same age. This large sample yields robust age-specific growth rates for both sexes. The growth rate increases through the 10th neritic year for the females and through the 12th year for males, and then declines. In contrast, the Indian River sample shows increasing rates from the 3rd through the 6th year, then shows relative constancy in 7- to 10-year-olds and declines thereafter. Considering that Pacific epipelagic *C. mydas* probably grow more slowly and may not enter the coastal developmental habitats until their 10th year, the growth patterns of these two populations are strikingly different. We speculate only that the differences are nutritional rather than genetic.

Even with the moderate association of estimated age and SCL ($r^2 = 0.65$), we hesitate to assign ages, even age ranges, to the size classes in our sample. It is even more speculative to assign ages to other, nearby populations. At best, we can guess, on the basis of the similar size-specific growth patterns, that the 5- to 12-year-olds in other western Atlantic-Caribbean populations have either slowly decreasing or uniform rates until their 10th to 12th years and sharply declining rates thereafter.

Because the estimated ages of most Indian River turtles are 5–13 years, our data suggest that each turtle has a 7- to 8-year residence in this developmental habitat. A growth rate of approximately 40 mm/year for 8 years would allow a 320 mm SCL turtle to grow to 640 mm at 13 years of age, and this rate is the approximate average of our age-specific growth rates (Table 2). Bjorndal and Bolten (1988) predict that Bahamian turtles will require 17 years to grow from 300 to 700 mm SCL, and about 8 years to grow from 320 to 640 mm. The growth data of Boulon and Frazer (1990) and Collazo et al. (1992) yield similar time estimates for this growth interval. What is not resolved by these data is whether an individual turtle remains in same developmental habitat for the entire 8-year interval.

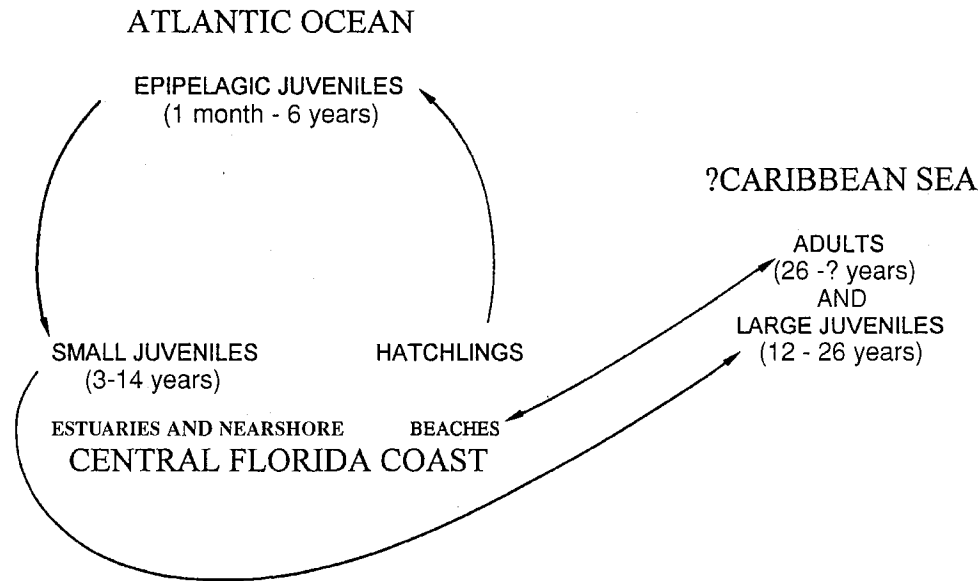
The association of age estimate and size (Fig. 2) suggests that males grow faster than females, because estimates for males produce a steeper LOWESS slope, and at equivalent ages, males tend to be larger. However, our male samples for most size and age classes are inadequate to confirm or deny the seeming sexual differences. Limpus and Chaloupka (1997) report significant differences in growth, with females growing faster than males (Australia); Bolten et al. (1992) observed no differences in male and female growth rates (Bahamas). In both sexes, the LOWESS curves (Fig. 2) suggest that growth slows at 10–11 years of age (SCL > 600 mm), matching the trend shown in Bahamian and Virgin Island populations (Table 3) but not seen in our estimated growth rates.

A striking aspect of sea turtle growth is the high variation among individuals within age and size classes. Our skeletochronological data reinforce the highly individualistic growth patterns of green sea turtles (see also Davenport and Scott 1993a, 1993b). The annual variation in growth rates within individuals is evident in the variable widths of GMs in humeri. Even though the general trend is a reduction of width in subsequent growth seasons, many individuals have narrow layers followed by one or more wider layers, demonstrating faster growth when the animal is older. Clearly, each individual's growth is influenced by numerous biotic and abiotic factors, and this aspect is underestimated in many age and growth studies.

Growth studies on captive individuals, such as those carried out at the Cayman Turtle Farm Ltd. (Wood and Wood 1980), show that *C. mydas* has the potential for extremely rapid growth, i.e., growing from hatchling to egg-laying female in 8–10 years. But this growth potential is likely seldom attained in wild turtles. Nevertheless, this potential for rapid growth and the general reptilian ability to slow or stop growth under poor conditions (Andrews 1982) are major causes of the large variation in growth rates within sea turtle populations. Several studies on freshwater turtles have also demonstrated the effect of incubation conditions on hatchling size and subsequent growth (e.g., Packard et al. 1991; Bohn and Brooks 1994). Genetic factors likely affect growth as well.

In spite of the actual variation in growth and the variation due to technique, we see more similarities than differences among the foraging populations within a region. This regional uniformity likely derives from similarities in diet and annual consumption of food. Where there is a sharp break in

Fig. 3. Hypothetical life-cycle diagram for green sea turtles of the central Florida Atlantic coast. The integers in parentheses represent the estimated ages of the turtles during the different life phases.



the type and (or) availability of food, there is also a distinct change in growth rates, as in Hawaiian Islands turtles (Balazs 1982).

Maturity

The sizes of female *C. mydas* nesting on the Atlantic beaches of Florida have been reported by numerous authors, with mature females ranging from 832 to 1210 mm SCL (Gallagher et al. 1972; Ehrhart and Yoder 1978; Bjorndal et al. 1983; Ehrhart and Witherington 1987; Witherington and Ehrhart 1989b). The average size of those nesting in central Florida is 1015 mm SCL (832–1167 mm, $s = 58.3$, $n = 90$; Witherington and Ehrhart 1989b).

Because of the limited size and age range of our sample, the use of a growth model to predict age at maturity is inappropriate. Even extrapolating growth of individuals beyond 700 mm SCL is speculative; however, because the age of maturity is such a critical life-history parameter, we offer the following conjecture. Using the Indian River growth rate (13.4 mm/year) for the 700-mm class and a postulated age of 14 years for the 750-mm class, turtles require another 20 years to reach average mature size (1015 mm), suggesting maturity, on the "average," at 34 years from hatching. Using the growth rate of Mendonça's 700-mm class, an additional 12 years of growth is required, with maturity at 26 years. This 26- to 34-year range of age at maturity matches previous estimates for green sea turtles of the western Atlantic and Caribbean (19–23 years, Ehrhardt and Witham 1992; 18–27 years, Frazer and Ehrhart 1985; 27–33 years, Frazer and Ladner 1986, also see their Table 1 for other Atlantic populations; 25–30 years, Mendonça 1981) and is typically less than the estimated age at maturity for Pacific populations (>30 years, Limpus and Walter 1980; 9–59 years, Balazs 1982; >50 years, Green 1993; >35 years, Limpus and Chaloupka 1997).

Postpelagic life history and age estimates

While sea turtle biologists were long aware of the seasonal occurrence of juvenile sea turtles in estuaries and

nearshore waters of eastern North America, they were unaware of the importance of this phenomenon. Carr and associates recognized that these juveniles formed feeding assemblages whose composition was size-specific, hence likely also age-specific. Owing to the persistence of these assemblages in the same locality, they introduced the concept of developmental habitat in a diagrammatic depiction of the life cycle of *C. mydas* (Fig. 2 in Carr et al. 1978). Both the life-cycle diagram and the developmental-habitat concept were rapidly adopted (e.g., Balazs 1980) and have provided an interpretative framework for examining sea turtle biology.

Developmental habitat refers to the residence (seasonal or year-round) of juvenile sea turtles of a specific size range, commonly a mixed-species assemblage, in a specific area. The Indian River lagoon system contains one of many juvenile foraging groups along the Atlantic seaboard of North America. Our skeletochronological age estimates create the first opportunity to assign data-based age estimates to green sea turtles in a developmental habitat (Fig. 3). We hypothesize that (i) *C. mydas* of the Indian River foraging assemblage complete their Atlantic "lost year" or pelagic phase as 3- to 6-year-olds. The pelagic phase ends for some individuals at about 250 mm SCL, although the dominance of the 300-mm class indicates that most individuals return to coastal waters when >300 mm; (ii) the coastal developmental phase lasts from 6 to 8 years (300- through 600-mm classes), with 7- to 12-year-olds in the majority. These turtles maintain a relatively high growth rate even though they have shifted to a totally herbivorous diet (Balazs 1982; Guseman and Ehrhart 1990); (iii) the age and size of juveniles leaving the developmental habitats are variable and begin with 500 mm class individuals (roughly 10–14 years old), and none remain beyond the 700-mm class; (iv) most juvenile *C. mydas* in central Florida developmental habitats and southward are probably year-round residents.

This hypothesized life cycle of the Indian River green sea turtles (Fig. 3) represents only a part of the complexity of the life cycle of Florida *C. mydas*. For example, some

Florida turtles may never enter estuarine waters and may migrate southward at smaller sizes (possibly at younger ages), but our hypothesis does highlight the importance of developmental habitats for the survival of green sea turtle populations. Developmental habitats require the same intensity of protection as nesting beaches. If we fail to protect these habitats and their juvenile turtle residents, there will be no need to preserve nesting beaches.

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