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Growth Rates of Immature Green Turtles, *Chelonia mydas*, on Feeding Grounds in the Southern Bahamas

KAREN A. BJORN DAL AND ALAN B. BOLTEN

Growth in carapace length, carapace width, plastron length and body mass was measured in 149 growth increments for 122 green turtles, *Chelonia mydas*, at Great Inagua, Bahamas. Initial carapace length of the 149 growth increments ranged from 28.3–75.5 cm. Absolute growth rates for all linear parameters decreased with increasing size, but no significant difference in absolute growth rates for body mass was noted over the size range measured. Equations were developed to convert carapace length or plastron length to mass so that growth in mass could be modeled from data for either linear parameter. Three size-specific growth models—Von Bertalanffy, Gompertz and logistic—were tested for goodness of fit. The Von Bertalanffy model had the best fit for seven body size parameters. With increasing size, there was a significant negative allometric relationship between carapace width and carapace length, but the relationship between plastron length and carapace length was isometric. Growth rates were compared with those of other green turtle populations. In our study area, green turtles grow more slowly than hawksbills, *Eretmochelys imbricata*, or loggerheads, *Caretta caretta*, of similar size.

THE rate at which an animal grows, and how growth rates change with size or age, are important elements in understanding the demography and life history pattern of a species. Comparative growth rates can also be used for interpreting ecological and nutritional quality of habitats and for determining an animal's environmental requirements (Dunham, 1978; Schoener and Schoener, 1978; Van Devender, 1978). In addition, development of rational management and conservation plans for endangered sea turtle species depends on a knowledge of their growth rates.

Growth data for green turtles (*Chelonia mydas*) living under natural conditions are slowly accumulating from study areas around the world (Limpus and Walter, 1980; Mendonca, 1981; Balazs, 1982; Frazer and Ehrhart, 1985). These studies are hampered by both small sample sizes and limited size ranges of turtles measured. We present data for 149 growth increments measured in 122 green turtles ranging in size from 28.3–75.5 cm initial straight-line carapace length collected from 1979–85 at Great Inagua, Bahamas. This size range includes turtles that have just arrived on their benthic feeding grounds from their early, pelagic habitat, to large sub-adult turtles.

Growth can be evaluated at two levels: changes in a single dimension over time and relative changes between two dimensions. To evaluate

growth in green turtles we have analyzed four linear dimensions as well as body mass. Relative changes in shape are evaluated from the allometric relationships between carapace length and carapace width and carapace length and plastron length. We also compare our data with growth rates measured in other populations of green turtles and in other species of marine turtles.

METHODS

Study area.—Union Creek (21°07'N, 73°34'W) is a bay (in the Bahamas, the word "creek" means a salt-water bay) of approx. 20 km² located on the north shore of Great Inagua, the southernmost island in the Bahamas. The area is protected as a wildlife sanctuary by the Bahamas National Trust. Most of the area is covered with dense stands of the seagrass *Thalassia testudinum* and is surrounded by, and interlaced with, mangroves. Union Creek is a natural feeding ground for all sizes of green turtles, loggerheads (*Caretta caretta*), and hawksbills (*Eretmochelys imbricata*) and was traditionally known as the best location to catch turtles on the island (pers. comm. from local inhabitants).

In 1964, Union Creek was fenced off to provide a protected area where marine turtles could be studied on their natural feeding grounds. Today, at least 300 green turtles inhabit the

study area; all of these turtles have entered from the ocean adjacent to Union Creek. Most green turtles are from 25–35 cm straight carapace length when they enter the study area through gaps in the fences. They are attracted to Union Creek by unknown cues—perhaps olfactory cues either from the beds of *Thalassia*, the primary food of green turtles (Mortimer, 1982), or from the other green turtles. The primary role of the fences is to protect the population from hunting by local inhabitants, but the fences also slow the exit of turtles from Union Creek. However, tags put on turtles in Union Creek have been returned from throughout the Caribbean, indicating that turtles do leave Union Creek.

Characteristics of the Union Creek habitat that may be important for determining growth rates in green turtles have been quantified by one of us (KAB), who lived at Union Creek in 1975–76. Water temperatures, nutrient composition of *T. testudinum*, and the intake and digestive efficiencies in four size classes of green turtles (8, 30, 48, and 66 kg) feeding on *Thalassia* were monitored biweekly for 12 mo. Water temperatures in Union Creek varied from 20–34 C during the 12 mo period; 9 C was the greatest variation in temperature for any 2 wk period (Bjorndal, 1980). The energy, cell wall, lignin and nitrogen content of *Thalassia* were constant over the year, as were the intake and digestive efficiencies of the green turtles (Bjorndal, 1980). The *Thalassia* beds in Union Creek show no signs of overgrazing; “grazing plots” where turtles feed in the seagrass flats (Bjorndal, 1980) are difficult to locate. Union Creek, then, offers a good opportunity to study free-living, but protected, green turtles in a natural feeding habitat.

Data collection.—Each year from 1979–85, we spent 1–2 wk catching turtles in Union Creek. We would chase a turtle briefly in a motor boat and then dive from the boat to catch it. The turtle was brought into the boat and transferred to shore where it was tagged, weighed and measured. Four tags were applied to each animal, one on each flipper. Linear measurements collected were straight-line carapace length from anterior point of midline (nuchal notch) to posterior end of posterior marginal (CL), straight-line carapace length from anterior to posterior point of midline (nuchal notch to posterior notch) (CLm), straight-line carapace width at widest point (CW), and straight-line plastron length along midline (PL). Linear measure-

ments were taken to the nearest 0.1 cm with anthropometer calipers (GPM model 101). Every measurement in this study was made by one of us (ABB) and recorded by the other (KAB) to avoid individual differences in measurement technique, a major source of error in growth data. We determined the mean discrepancy for each linear measurement by measuring a group of 26 green turtles and then re-measuring them. Mean discrepancy was calculated as the mean of the absolute difference between the first and second measure of the 26 pairs of measurements.

Turtles were weighed using spring scales. Small turtles were weighed with a 20 kg capacity scale to the nearest 0.1 kg; larger turtles were weighed on a 225 kg capacity scale to the nearest 0.5 kg.

Data analysis.—Recapture intervals that yielded no measurable growth (growth rate equal to zero) were not excluded from the data set, as other authors have done in the past. No negative growth increments were recorded, probably because of the precision of our measurements (see below) and the relatively long recapture intervals.

Absolute growth rates are expressed as a function of the mean of the initial and recapture sizes for each growth interval. Expressing growth rate as a function of initial body size will often underestimate the growth rate for that size because, at least for linear parameters, growth rate decreases with increasing size. If size is defined by initial size, the turtles will spend the entire growth interval at a larger size, and therefore at a slower growth rate. However, if mean size is used, the turtle will usually spend slightly less than half of the time interval at a smaller size (faster growth rate) and slightly more than half at a larger size (slower growth rate). Therefore, mean size is better than initial size for describing body size for each growth interval.

Von Bertalanffy, Gompertz and logistic growth models were compared to determine which model best fit size-specific growth data using the following differential equations of Kaufmann (1981):

$$\begin{aligned} \text{Von Bertalanffy: } & G = (a/S) - b \\ \text{Gompertz: } & G = -a(\ln S) + b \\ \text{Logistic: } & G = -aS + b \end{aligned}$$

where G is size-specific growth rate (growth rate divided by mean size) and S is mean size. The

differential equations were used because linear regression analysis can be used to test for goodness of fit among the models without estimating an asymptotic value or a size of known age as required by non-linear regression analysis to solve for parameters a and b . These values are not available for the Great Inagua population, and, as discussed below, we feel it is inappropriate to estimate these values from our data set.

All regressions presented in this paper met the assumptions of homogeneous variance about the regression line and a normal distribution of the residuals about the line. Significance of regression coefficients was tested according to Sokal and Rohlf (1969).

RESULTS AND DISCUSSION

Growth rates for linear parameters.—From 1979–85, 122 green turtles were recaptured a total of 149 times, yielding 148 CL growth increments for 121 turtles, 107 CLm growth increments for 96 turtles, 141 CW growth increments for 116 turtles, and 146 PL growth increments for 120 turtles. Sample sizes for different parameters vary because if a minor abnormality (e.g., a broken scute) interfered with a measurement, that parameter was not included. Also, we began recording CLm in 1983.

Time intervals between recaptures ranged from 6.5–55.5 mo, with a median interval of 12 mo; 62% of the intervals were between 12–18.5 mo. Excluding short (<1 yr) and long (>2 yr) intervals did not significantly change mean growth rates for any size class (t -tests, $P < 0.01$).

Our study at Union Creek has yielded a large, well-distributed set of growth data in green turtles ranging in size from 28.3–75.5 cm initial CL (Fig. 1). Growth rates for all linear measurements decrease significantly with increasing size (Fig. 2a–d; ANOVA, $P < 0.001$). This trend has already been noted for growth in CL in green turtles (Mendonca, 1981; Frazer and Ehrhart, 1985).

In addition to the 271 captures and recaptures described above, 193 green turtles were captured only once. The 464 sets of measurements on 315 individual turtles ranged in CL from 26.8–84.3 cm with a mean of 51.6 cm and a normal distribution (Shapiro-Wilk test for normality, $P < 0.01$). Correlations of the body size parameters are given in Table 1.

The small mean discrepancies for the four linear measurements (Table 2) result from the

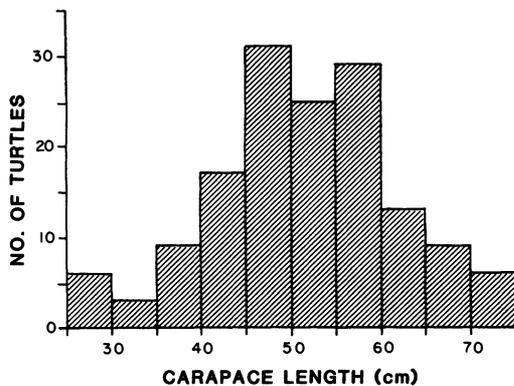


Fig. 1. Initial straight-line carapace lengths for 148 green turtle carapace length growth increments.

use of precise calipers and the fact that all measurements were made by one person. Mean discrepancy for CL is significantly less than that of PL (ANOVA, Student-Newman-Keuls, $P < 0.05$), but the differences among CL, CLm and CW and among CLm, CW and PL are not significant. CW and PL are more difficult to measure than CL or CLm because: 1) both change by a measurable amount when the turtle inhales or exhales, at least in immature turtles; 2) no morphological features mark the points at which CW should be measured, increasing the chance for poor repeatability; and 3) the anterior and posterior ends of the plastron are quite flexible, so PL varies depending on how much pressure is applied to the calipers.

Although a measure of repeatability or precision of measurements is essential for interpreting growth data, no previous study of growth in sea turtles has included such a measure. Determining how much of the measured "growth" increment is attributable to measurement error is particularly critical when working with slow-growing animals. Our precision (Table 2) insures that measurement error does not prevent measuring growth precisely at the levels reported here.

Because of the close relation between the various linear parameters (Table 1) and the similar shape of the growth rate curves (Fig. 2a–d), information on only one linear parameter is necessary to describe linear growth in green turtles. The linear measure with the least variation in growth rates for all size intervals would be the best measure to use. When coefficients of variation (CV) for CL, CW, PL and mass growth rates were calculated for each 5 cm mean

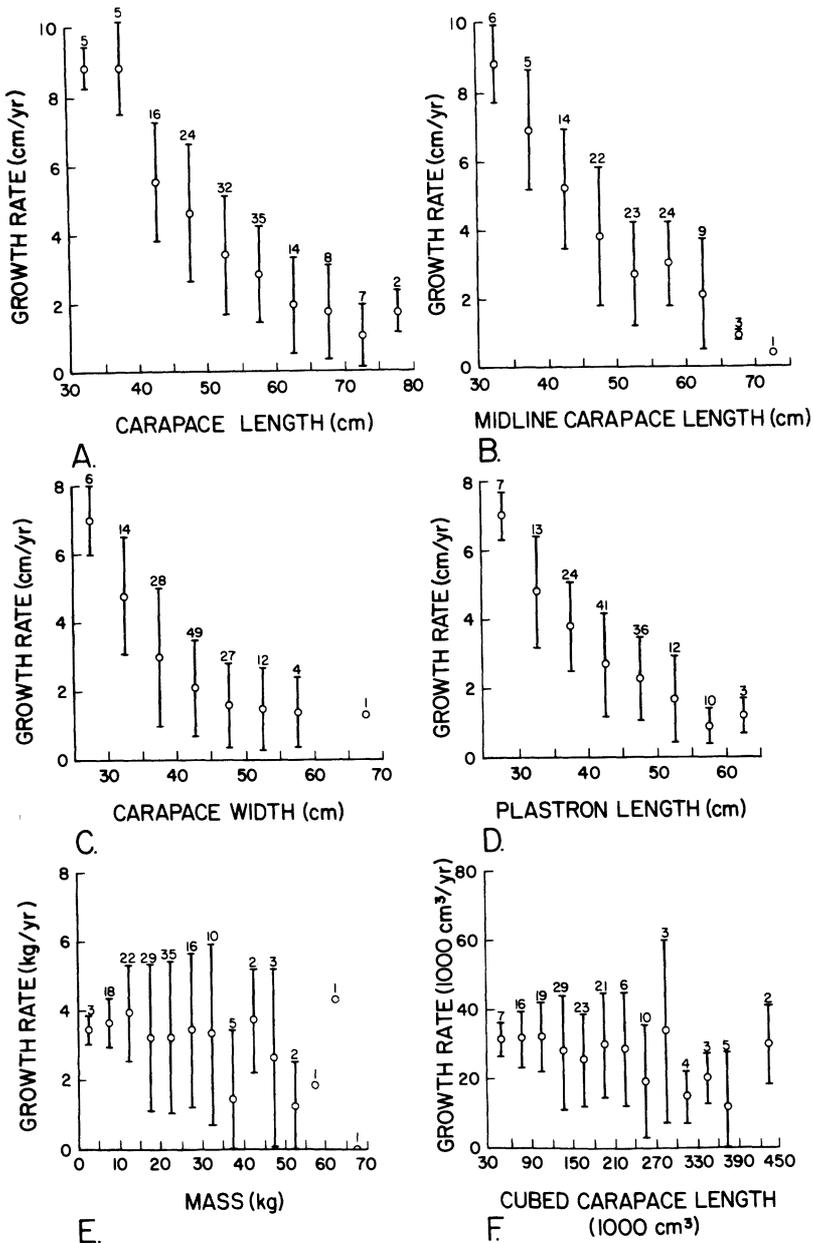


Fig. 2. Growth rates for six body size parameters of green turtles. Body size is mean of initial and recapture values. Circle is mean value; bars show one standard deviation; sample size is above each bar.

CL interval and ranked within each 5 cm interval, the mean ranks for PL, CL, mass and CW were 1.4, 2.1, 2.9, and 3.6, respectively. The ranks were significantly different (Kruskal Wallis, $P < 0.001$). PL growth rates had the lowest ranking and, thus, the least variation. However, the variation in PL growth rates was

not significantly less than that of CL (Mann-Whitney U, $\alpha = 0.05$) but was significantly less than the variation in CW and mass growth rates (Mann-Whitney U, $P < 0.005$). Therefore, because variation in CL growth rates is not significantly different from that of PL growth rates, because more data are available

TABLE 1. PEARSON'S PRODUCT MOMENT CORRELATION COEFFICIENTS FOR BODY SIZE PARAMETERS OF GREEN TURTLES. See text for abbreviations. In all cases $P < 0.001$. Sample size = n .

	CL	CLm	CW	PL	Mass	CL ³
CLm	0.999 $n = 362$					
CW	0.984 $n = 448$	0.981 $n = 363$				
PL	0.995 $n = 449$	0.995 $n = 364$	0.984 $n = 452$			
Mass	0.941 $n = 454$	0.955 $n = 369$	0.928 $n = 456$	0.942 $n = 457$		
CL ³	0.961 $n = 455$	0.968 $n = 362$	0.941 $n = 448$	0.957 $n = 449$	0.989 $n = 454$	
PL ³	0.955 $n = 449$	0.961 $n = 364$	0.939 $n = 452$	0.961 $n = 458$	0.990 $n = 457$	0.993 $n = 449$

for CL than for other parameters, and because CL has a significantly lower discrepancy than PL (Table 2) and thus can apparently be measured with greater precision, CL is probably the best measurement to describe linear growth in green turtles.

Growth rates for body mass.—We measured 148 mass growth increments for 121 turtles. The growth data for body mass (Fig. 2e) give a different pattern than that of the linear measurements. Over the range of body size, absolute rate of gain in mass does not vary significantly with body size (ANOVA, $\alpha = 0.05$). That is, turtles in our size range gain mass at a constant rate regardless of size. There may be a trend towards a decrease in growth rate in the largest size classes (Fig. 2e), but in these categories the sample size is small and the values may be misleading.

Body mass is the most biologically significant measure of body size because physiological and thermoregulatory parameters scale to mass. However, mass is usually not included in growth rate studies because it is more difficult to measure and more variable, due to reproductive state and nutritional status, than linear measurements (Dunham, 1978; Pough, 1980). In his growth studies of green turtles in Hawaii, Balazs (1982) found little value in the use of body mass as a measure of body size. He attributed the problem to variation in gut contents, which can comprise up to 18% of body mass in immature Hawaiian green turtles (Balazs, 1982).

Because we work with subadult turtles, vari-

ation in body mass due to ingestion and egestion, but not reproductive condition, is of concern. The sum of the mass of food consumed and the mass of feces produced per day varies from 1.9–2.5% of body mass (wet mass/live mass) in green turtles of 8–66 kg in Union Creek (Bjorndal, 1979). Under normal conditions, daily variation in body mass due to differences in feeding or defecation would be expected to fall within that percent range. However, if normal patterns of feeding and defecation are disturbed, for example, by the process of catching turtles for data collection, the variation in body mass measurements could be greater. As dis-

TABLE 2. PRECISION OF MEASUREMENTS EXPRESSED AS DISCREPANCY (MEAN \pm STANDARD DEVIATION) BETWEEN REPEATED MEASUREMENTS. See text for calculation and abbreviations. Sample size = n . Range of each body size parameter is given for the turtles measured. Means with different superscripts are significantly different (ANOVA, Student-Newman-Keuls, $P < 0.05$).

	n	Discrepancy (cm)	Range of turtle size (cm)
CL	26	0.046 ^a ± 0.065	29.7–82.3
CLm	26	0.058 ^{a,b} ± 0.058	29.1–81.8
CW	26	0.062 ^{a,b} ± 0.064	23.6–63.4
PL	26	0.100 ^b ± 0.089	23.5–67.6

TABLE 3. GOODNESS OF FIT FOR THREE GROWTH MODELS FOR SEVEN BODY SIZE PARAMETERS. See text for abbreviations. Sample size = n. SSQR/N is the residual error mean square; F statistics are significant at $P < 0.001$.

	n	Von Bertalanffy			Gompertz			Logistic		
		R ²	SSQR/N ×10 ⁻⁶	F	R ²	SSQR/N ×10 ⁻⁶	F	R ²	SSQR/N ×10 ⁻⁶	F
CL	148	0.737	7.44	412.01	0.687	8.85	320.03	0.620	10.8	238.30
CL _m	107	0.744	7.67	305.77	0.700	8.98	243.99	0.640	10.8	186.62
CW	141	0.637	9.82	243.44	0.576	11.5	188.01	0.499	13.6	138.22
PL	146	0.716	7.36	361.55	0.667	8.64	286.91	0.600	10.4	216.32
Mass	148	0.716	64.9	366.62	0.634	83.7	251.93	0.423	132.0	107.59
CL ³	148	0.744	59.2	425.35	0.672	76.0	299.25	0.466	123.6	127.94
PL ³	146	0.723	59.0	374.32	0.651	74.3	269.84	0.446	117.9	116.55

cussed above, the CV values for growth rates in body mass fall within the CV values for the linear measurements. This indicates that, despite the possible sources of variation in mass, growth rates of mass in subadult green turtles are not more variable than growth rates of linear measurements and should not be excluded from studies on the basis of greater potential variation.

In addition, failure to evaluate growth as a function of body mass ignores the parameter that may most closely reflect the controlling mechanism(s) of growth rate. Wilbur (1975) suggested that for freshwater turtles "growth is probably functionally linked more closely to body weight than to age or to plastron length per se."

Because body mass is often difficult to measure in green turtles under field conditions, predicting body mass from a linear parameter would be helpful. Many authors use the cube of body length to model growth in body mass (Dunham, 1978; Schoener and Schoener, 1978). We used our data to test whether growth in CL³ or PL³ provided good models of growth in body mass in green turtles. As with mass, absolute growth rates in CL³ and PL³ do not significantly vary with body size (ANOVA, alpha = 0.05). The growth rates of CL³ and PL³ have a pattern similar to mass growth rates (Fig. 2e-f). In addition, the von Bertalanffy growth model has the best fit for growth data for mass, CL³ and PL³ (see section below and Table 3).

Although these factors indicate that changes in CL³ or PL³ can be used to estimate relative changes in body mass in subadult green turtles, we suggest that researchers use this relationship with caution because CL³ and PL³ do not ac-

curately estimate mass, and thus growth in CL³ and PL³ may not accurately model growth in mass. This can be seen from the following regressions. A regression of log-transformed mass (kg) on log-transformed CL (cm) data gave the equation

$$\text{Mass} = 1.07 \times 10^{-4} \text{CL}^{3.04}$$

with an R² of 0.990 (n = 454). The analogous equation for PL is

$$\text{Mass} = 2.00 \times 10^{-4} \text{PL}^{3.05}$$

with an R² of 0.988 (n = 457). These equations allow us to accurately convert values for CL or PL to mass. However, regression coefficients of these equations (3.04 and 3.05, respectively) are both significantly different from 3 ($P < 0.01$), indicating that the relationships between mass and CL^{3.04} or PL^{3.05} are significantly different than those between mass and CL³ or PL³. Therefore using CL³ or PL³ to model growth in mass may not be accurate.

Fitting growth models.—The Von Bertalanffy model has the best fit for each of the body size parameters (Table 3) when either the smallest residual mean square (SSQR/N) or the largest coefficient of determination (R²) is used as the criterion for the best model (Dunham, 1978; Schoener and Schoener, 1978).

We have not used the Von Bertalanffy model to extrapolate to age of sexual maturity for two reasons. First, we do not know to which breeding population the subadult turtles from Great Inagua belong, and therefore do not know the size at sexual maturity. Even if the identity of the adult population is assumed, the size to use as the size at sexual maturity—smallest adult

size, mean adult size or mean of recruit size—is difficult to determine (Frazer and Ehrhart, 1985).

Second, we are unwilling to extrapolate from our data base to the extent necessary to extend the Von Bertalanffy model from hatchling to breeding adult. After hatching and before arriving at its benthic feeding ground at a CL of approx. 20–25 cm, a green turtle occupies a pelagic habitat for an unknown length of time (Carr, 1980, 1982). There is no reason to assume that these pelagic, omnivorous post-hatchlings follow the same growth pattern as the larger, herbivorous turtles in our study.

However, we can calculate that a green turtle in Union Creek requires approx. 17 yr to grow from 30–75 cm CL, the size range of turtles in our study. This time interval was obtained by summing the number of years needed to grow through each 5 cm carapace length interval at the mean growth rate for that interval (Fig. 2a).

Allometric growth.—As Carr (1984) noted, the systematics of the green turtle is “a taxonomic mess.” We discuss allometric growth not only to characterize growth in green turtles more completely, but also because comparisons of allometric changes among populations can be useful taxonomic tools. Changes in body proportions with increasing size can be analyzed from the well-distributed size range of green turtles at Union Creek. Although the four linear dimensions are strongly correlated (Table 1), a significant negative allometric relationship exists between CW and CL, as expressed by the regression equation:

$$\log CW = 0.0205 + 0.928 \log CL.$$

The slope is significantly different from the isometric condition ($t = -10.39$, $df = 446$, $P < 0.001$). Thus, carapace width increases proportionally less than carapace length. However, the relationship of PL to CL, expressed by the regression equation

$$\log PL = -0.0814 + 0.993 \log CL$$

was not significantly different from the isometric condition ($t = -1.69$, $df = 447$, $\alpha = 0.05$).

Comparisons with other green turtle populations.—Comparisons among green turtle populations are difficult because of limited data. All data of which we are aware for growth rates of CL in green turtles are given in Table 4. Comparisons

TABLE 4. GROWTH RATE (GR) MEANS AND STANDARD DEVIATIONS IN CM/YEAR FOR CARAPACE LENGTH (CL) IN GREEN TURTLES FROM SIX REGIONS. Florida, Hawaii, Australia and West Indies data are from Mendonca (1981), Balazs (1982, unpubl.), Limpus and Walter (1980) and Schmidt (1916), respectively. Sample size = n. All are straight CL except Australia and West Indies are curved CL. Turtles were assigned to size classes by mean of initial and recapture CL.

x CL (cm)	Hawaiian Islands						West Indies					
	Great Inagua		Florida		Central		NW		Australia		West Indies	
	n	GR	n	GR	n	GR	n	GR	n	GR	n	GR
30–40	10	8.8 ± 1.0	4	5.3 ± 2.8	—	—	4	1.1 ± 0.4	—	—	2	7.9 ± 0.6
40–50	40	4.9 ± 2.0	—	—	1	2.5	21	1.0 ± 0.6	—	—	5	4.4 ± 3.1
50–60	67	3.1 ± 1.6	2	3.1 ± 1.8	9	4.5 ± 1.2	7	1.1 ± 0.4	4	0.8 ± 0.6	1	3.4
60–70	22	1.8 ± 1.4	3	2.8 ± 1.2	2	3.6 ± 0.1	1	1.4	14	1.4 ± 2.0	—	—
70–80	9	1.2 ± 0.9	3	2.2 ± 1.1	1	3.0	—	—	15	1.5 ± 0.7	—	—

TABLE 5. GROWTH RATE (GR) MEANS AND STANDARD DEVIATIONS FOR CARAPACE LENGTH (CL) AND BODY MASS IN GREEN TURTLES, HAWKSBILLS AND LOGGERHEADS IN UNION CREEK. Sample size = n. Turtles were assigned to size classes by mean of initial and recapture CL.

♀ CL (cm)	Carapace length (cm/yr)						Body mass (kg/yr)					
	Green		Hawksbill		Loggerhead		Green		Hawksbill		Loggerhead	
	n	GR	n	GR	n	GR	n	GR	n	GR	n	GR
30-35	5	8.8 ± 0.6	1	15.7	—	—	5	3.7 ± 0.4	1	6.7	—	—
40-45	16	5.5 ± 1.7	1	5.9	—	—	16	3.5 ± 1.0	1	4.3	—	—
45-50	24	4.6 ± 2.1	—	—	3	15.7 ± 1.3	24	3.8 ± 2.1	—	—	3	13.4 ± 2.5
60-65	14	1.9 ± 1.4	2	2.4 ± 0.1	—	—	14	2.7 ± 2.3	2	4.3 ± 2.3	—	—
65-70	8	1.7 ± 1.4	1	3.1	—	—	8	3.0 ± 2.7	1	6.3	—	—
70-75	7	1.0 ± 0.9	—	—	1	5.8	6	1.7 ± 1.2	—	—	1	13.4
75-80	2	1.7 ± 0.6	—	—	1	4.6	2	2.2 ± 3.1	—	—	1	15.6

among populations should be made only within the same size class because growth rates change with size.

Conclusions must be drawn with care because of differences among the studies presented in Table 4. Growth rates for Australia (Limpus and Walter, 1980) and the West Indies (Schmidt, 1916) are based on curved CL and are not directly comparable with the data based on straight-line measurements. Also, different methods were used to measure straight-line CL among the different studies; the effect of this variation is not known. In addition, the small sample sizes and large standard deviations for most of the populations indicate that the values given may not accurately estimate the mean growth rates. Growth data from the Hawaiian islands include 39 positive growth increments and omit 34 increments of zero growth (Balazs, 1982). Thus, the Hawaiian data may overestimate growth rates and are not directly comparable to the Great Inagua data, which included zero growth increments.

These disparities preclude testing for statistical differences among the columns in Table 4. However, several important points can be seen in the table. Growth rates within size classes are relatively similar throughout the green turtle's range except for the northwest Hawaiian islands and Australia. Also, the trend for decreasing growth rates with increasing size was recorded for Florida, the West Indies, Great Inagua, and perhaps the central islands of Hawaii. The data from the northwest islands of Hawaii and from Australia show no trend. Larger sample sizes are needed for large Hawaiian turtles and small Australian turtles before conclusions can be drawn on the effect of body size on growth rates in these two populations.

Sources of variation.—Even within relatively narrow size classes in a single population, growth rates of green turtles are highly variable (Fig. 2, Table 4). No attempt has yet been made to identify to what degree different sources of variation influence growth rate. Genotype, sex, habitat quality, water temperature and diet all probably play a role in determining a green turtle's growth rate.

Habitat differences within a turtle population can result in very different growth rates. Balazs (1982) documented dramatic differences in the growth rates of green turtles in the Hawaiian archipelago from one feeding area to another. He suggested that the differences were due to

varying food quality among the feeding areas. On an even smaller scale, our data suggest that green turtles of the same size from two areas of Union Creek grow at significantly different rates. Studies are now underway to improve the description of the Union Creek habitat and to determine how much of the variation in growth rates can be attributed to the season in which the data were collected, the sex of the turtle, location within Union Creek, microhabitat and nutritional differences, annual variation, and individual, genetic variation.

We know diet quality is an important factor in determining growth rates in green turtles because captive green turtles fed diets high in animal protein grow much more rapidly than wild green turtles on herbivorous diets (Bjorndal, 1985). However, to measure diet quality, it is not sufficient to analyze available foods for nutrient composition. As discussed elsewhere (Bjorndal, unpubl.), diet quality should be measured by animal performance on the diet, e.g., by measuring intake and digestibility, as has been done with green turtles in Union Creek (Bjorndal, 1980).

Comparisons with other marine turtle species.—During our study on green turtles, we also collected data on growth in loggerheads (Bjorndal and Bolten, 1988) and hawksbills in Union Creek (Table 5). Hawksbills and loggerheads have trends similar to those of green turtles: rate of growth in CL decreases with increasing size, and rate of growth in mass is relatively constant with respect to size. However, the species grow at different rates. As one would predict from their diets (Mortimer, 1982), the herbivorous green turtle grows more slowly than the two carnivorous species. Loggerheads grow from 25–75 cm in 3–4 yr (Bjorndal and Bolten, 1988) whereas green turtles take approx. 17 yr to grow from 30–75 cm. Rate of mass gain is approx. 4 times greater in loggerheads than in green turtles.

Growth rate in mass is approx. 1.5 times greater in hawksbills than in green turtles. The growth rate of CL in the smallest hawksbill is much greater than that in green turtles of the same size (Table 5), but the growth rates of the larger hawksbills are within the range measured in green turtles of comparable size. However, because hawksbills mature at a smaller CL than green turtles, the hawksbills are closer to their asymptotic size and the comparison may not be valid. Growth rates calculated at equivalent por-

tions of the growth curve (in relation to inflection point, if any, and the asymptote) rather than at equivalent sizes would allow better species comparisons. When growth curves have been defined, the best comparisons will be between equivalent sizes expressed as a proportion of the estimated asymptote. More data are needed before such comparisons can be made between species.

In comparing growth rates of CL in sympatric populations of green turtles and loggerheads in Mosquito Lagoon, Florida, Mendonca (1981) found that loggerheads grew more rapidly, but the difference in the rates was not as great as we recorded in Union Creek. In contrast, Limpus (1985) reported that sympatric populations of green turtles and loggerheads on the southern Great Barrier Reef, Australia, grow at approximately the same rate. However, the Australian turtles are large and growing slowly.

Conclusions.—Growth rates can be used to assess the effect of environmental variables on green turtle productivity. More data on growth rates for CL and body mass are needed for green turtles living in quantified habitats (e.g., temperature, food quantity and quality, water depth, substrate type and turtle population density), so that the degree to which the different sources of variation influence growth rates can be defined. These data would also allow the use of growth rates to assess relative habitat quality for green turtles, and to determine the characteristics of good quality feeding habitats so that critical feeding areas can be conserved to protect this endangered species.

To facilitate comparisons of growth rates among populations and species, methods of measurement should be standardized. Barring that, methods of measurement should be described in detail, and the relationship between growth rates based on curved and on straight-line measurements should be established to permit conversions. Zero and negative growth increments should be included in calculations of growth rates, and a measure of the precision or repeatability of measurements should be presented with all growth data.

Note added in press.—After this paper was submitted, further field work has increased our sample size of growth increments for the same size range of turtles as reported here to 270 for CL, 229 for CLm, 263 for CW, 268 for PL, and 270 for mass. Results of analyses of this larger

data set confirm all of the conclusions presented in this paper.

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