

GREEN TURTLE SOMATIC GROWTH MODEL: EVIDENCE FOR DENSITY DEPENDENCE

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Abstract. The green turtle, *Chelonia mydas*, is a circumglobal species and a primary herbivore in marine ecosystems. Overexploitation as a food resource for human populations has resulted in drastic declines or extinction of green turtle populations in the Greater Caribbean. Attempts to manage the remaining populations on a sustainable basis are hampered by insufficient knowledge of demographic parameters. In particular, compensatory responses resulting from density-dependent effects have not been evaluated for any sea turtle population and thus have not been explicitly included in any population models.

Growth rates of immature green turtles were measured during an 18-yr study in Union Creek, a wildlife reserve in the southern Bahamas. We have evaluated the growth data for both straight carapace length (SCL) and body mass with nonparametric regression models that had one response variable (absolute growth rate) and five potential covariates: sex, site, year, mean size, and recapture interval. The SCL model of size-specific growth rates was a good fit to the data and accounted for 59% of the variance. The body-mass model was not a good fit to the data, accounting for only 26% of the variance. In the SCL model, sex, site, year, and mean size all had significant effects, whereas recapture interval did not.

We used results of the SCL model to evaluate a density-dependent effect on somatic growth rates. Over the 18 yr of our study, relative population density underwent a sixfold increase followed by a threefold decrease in Union Creek as a result of natural immigration and emigration. Three lines of evidence support a density-dependent effect. First, there is a significant inverse correlation between population density and mean annual growth rate. Second, the condition index ($\text{mass}/(\text{SCL})^3$) of green turtles in Union Creek is positively correlated with mean annual growth rates and was negatively correlated with population density, indicating that the green turtles were nutrient limited during periods of low growth and high population densities. Third, the population in Union Creek fluctuated around carrying capacity during our study and thus was at levels likely to experience density-dependent effects that could be measured.

We estimate the carrying capacity of pastures of the seagrass *Thalassia testudinum*, the major diet plant of the green turtle, as a range from 122 to 4439 kg green turtles/ha or 16–586 million 50-kg green turtles in the Caribbean. Because green turtle populations are probably regulated by food limitation under natural conditions, carrying capacity can serve as a baseline to estimate changes in green turtle populations in the Caribbean since pre-Columbian times and to set a goal for recovery for these depleted populations.

Finally, we compare the growth functions for green turtle populations in the Atlantic and Pacific oceans. Not only does the form of the size-specific growth functions differ between the two regions (monotonic declining in the Atlantic and nonmonotonic in the Pacific), but also small juvenile green turtles in the Atlantic have substantially higher growth rates than those in the Pacific. Research is needed to evaluate the causes of these differences, but our results indicate that demographic parameters between ocean basins should only be extrapolated with great caution.

Key words: Australia; Bahamas; carrying capacity; *Chelonia mydas*; demography; density-dependent effect; green turtles; growth models; growth rate; marine turtles; nonparametric regression; sustainable use.

INTRODUCTION

The conservation of marine biodiversity is recognized as a critical need (Norse 1993, National Research

Council 1995). Sustainable management of marine resources has proven to be difficult and fraught with population collapses of target and nontarget species as well as extensive habitat degradation (Dayton et al. 1995, Mooney 1998, Pauly et al. 1998). Populations of many marine species of invertebrates, fish, turtles, and mammals have plummeted as a result of unsustainable ex-

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ploitation. The drastic decline in one such species—the green turtle, *Chelonia mydas*, the “world’s most valuable reptile” (Parsons 1962:1)—has recently been highlighted (Jackson 1997). The decline in the number of green turtles in the Caribbean since the arrival of Columbus has been estimated to be as high as 99% (Bowen and Avise 1995, Jackson 1997). How many green turtles inhabited the Greater Caribbean when Columbus arrived? Much of the decline occurred before green turtle population levels were recorded, making it difficult to assess early population levels and thus to identify appropriate goals for recovery of green turtle populations in the Caribbean.

To design effective management plans to reverse the population decline of green turtles, demographic processes must be quantified, and the potential for density-dependent effects on these processes needs to be evaluated. The density dependence of demographic parameters is critical for modeling population growth, for understanding recovery of depleted populations, and for estimating the extent to which natural populations can be harvested on a sustainable basis (Dempster 1975, Robinson 1993, Getz 1996, Hixon and Carr 1997). One of the avenues of research highlighted in the Sustainable Biosphere Initiative (Lubchenco et al. 1991) was the degree to which processes that control population growth are density dependent. Over the 18 yr of our study, the population of green turtles in Union Creek, Great Inagua, Bahamas, underwent an approximate six-fold increase in relative population density, followed by an approximate three-fold decrease as a result of immigration and emigration. These substantial changes in relative density allowed us to evaluate density-dependent effects on somatic growth rates.

A major challenge to the study of demography and life history patterns of green turtles is the juvenile stage, which lasts several decades (Bjorndal and Zug 1995, Limpus and Chaloupka 1997) and is characterized by obscure and wide-ranging movements (Carr 1980). Upon leaving their nesting beach, green turtle hatchlings disappear into what has been termed the “lost year,” a lifestage of unknown duration, which we believe is passed in pelagic habitats, but the location or any aspect of the biology of this stage in green turtles has never been discovered (Bolten and Balazs 1995). When green turtles attain a size of 25 to 35 cm carapace length, they appear on benthic foraging grounds in relatively shallow waters and adopt an herbivorous diet (Bjorndal 1985). During this stage, green turtles are more amenable to study. However, long-term studies of natural populations are difficult, due to the extensive developmental migrations undertaken by green turtles—movements among foraging areas that are triggered by unknown cues and may involve travel over thousands of kilometers—and high human-induced mortality that can extirpate a study population in a short time.

Because of the difficulty in obtaining quantitative

demographic data, it is tempting to extrapolate values measured for a green turtle population in one region to populations in other regions. For example, Crowder et al. (1994) used survivorship estimates for a relatively unexploited loggerhead population in Australia to predict the impact of turtle excluder devices on loggerhead populations in the southeastern USA. They explicitly stated the risk of such extrapolation, but no data were available for Atlantic populations. Comparisons of parameters among regions to evaluate the validity of such extrapolations are lacking.

In this paper, we use nonparametric regression modeling to analyze growth rates of immature green turtles in a wildlife reserve in the southern Bahamas. We evaluate not only the form of the growth rate function, but also the effects of both continuous and discrete or nominal covariates (body size, sex, site of capture, year, and duration of growth interval) on growth rates. Assessment of these covariates leads to new insights into density-dependent regulation of growth rates in immature green turtles. We compare the mean size-specific growth function of the turtles in our study to the very different mean size-specific growth function of Australian green turtles (Limpus and Chaloupka 1997). Finally, we calculate a range of estimates for the carrying capacity of seagrass pastures in the Caribbean for green turtles to provide population estimates for pre-Columbian populations and thus goals for population recovery.

METHODS

Growth data

This analysis is part of an ongoing study conducted on green turtle foraging grounds in Union Creek on the north coast of Great Inagua, the southernmost island in The Bahamas (21.17° N, 73.57° W). Union Creek Reserve is a Protected Area within The Bahamas National Park system, and green turtles within its boundaries are protected from exploitation. In The Bahamas, a creek is a saltwater bay or passage, not associated with freshwater, as the name would suggest in other countries. Union Creek is ~20 km² in area, is surrounded by and interspersed with mangroves, and has pastures of the seagrass *Thalassia testudinum*, which is the primary diet plant of green turtles in the Greater Caribbean (Bjorndal 1997). Union Creek can be divided into two areas: the Upper Sound and the Lower Sound. The Lower Sound is characterized by shallower water and *Thalassia* pastures that sometimes show signs of stress (brown leaf tips and narrower leaf blades) compared to the deeper waters and healthy stands of *Thalassia* in the Upper Sound.

The study population comprises only immature green turtles that enter Union Creek and then emigrate to other habitats elsewhere in the Caribbean prior to the onset of sexual maturity. Our studies of the ecology of this population began in 1975; growth data presented

here were collected from 1979 through 1996. Each year, except 1981 and 1995, green turtles were captured during a one- to two-week interval by jumping on them from the bow of a motorboat following a brief chase. Turtles were tagged with flipper tags bearing an identification number, return address, and offer of a reward for the return of the tag. Site of capture (Upper or Lower Sound) was recorded. Turtles were measured with anthropometer calipers (GPM model 101, Switzerland) to the nearest 0.1 cm. The linear metric used in this study is straight carapace length measured from the anterior midpoint of the nuchal scute to the posterior tip of the longer of the pair of posterior marginal scutes. The precision of this measurement, determined as mean discrepancy between repeated measurements, is 0.046 cm (Bjorndal and Bolten 1988). Turtles were weighed on either a 20-kg capacity spring scale to the nearest 0.1 kg or, if the mass of the turtle was >20 kg, on a 225-kg capacity spring scale to the nearest 0.5 kg. In some years, blood samples were collected for sex identification, using circulating levels of testosterone and/or for mtDNA sequencing for haplotype determination (Bolten et al. 1992, Lahanas et al. 1998). A strip of pink flagging was attached to the turtle before release to avoid capturing the same individual again and to allow for population estimates based on numbers of turtles seen with and without flagging at the end of the sampling period.

A condition index ($CI = \text{body mass}/SCL^3$) was calculated for all green turtles with $SCL < 70$ cm ($n = 701$) captured in Union Creek from 1979 through 1987 and in 1998, the years in which mass was recorded for all turtles. By evaluating only turtles with $SCL < 70$ cm, CI was not significantly correlated with SCL (Spearman's $\rho = 0.073$, $P > 0.05$), and size ranges were the same among years. Therefore, CI values could be compared among years (Bolger and Connolly 1989).

Sampling design and statistical modeling approach

The implicit sampling design in this study was mixed longitudinal sampling (sampling with partial replacement) with 41% of the 333 individual green turtles recaptured two or more times. Age was unknown (Bjorndal et al. 1998), as in most sea turtle studies, so that the implicit sampling design here confounds the year and cohort effects. A discussion of time-dependent demographic sampling designs in relation to sea turtle studies is found in Chaloupka and Musick (1997).

Capture-recapture profiles for each of the 333 turtles in the Union Creek study included the following: (1) straight carapace length (cm SCL) at first capture and at each recapture, (2) sex determined from blood sampling where possible or coded as unknown, (3) date of first capture, and (4) time at large since first capture or previous recapture. Body mass (kg) was also recorded at first capture and at each recapture for 179 of the 333 turtles in the study.

Only green turtles with recapture intervals >11 mo

were included to minimize errors in growth rate estimation for turtles yet to undergo a full year of growth (Chaloupka and Musick 1997). Absolute growth rates were derived from these capture-recapture profiles, with both negative and zero growth rates included in the analysis since there is no valid reason to do otherwise (Bjorndal and Bolten 1988, Chaloupka and Limpus 1997).

The usual approach used for analysis of sea turtle growth with unknown age has been size-based analogues of age-based parametric growth curves, which has several shortcomings (Chaloupka and Musick 1997). The two-stage modeling approach of Chaloupka and Limpus (1997) and Limpus and Chaloupka (1997) was adopted in the current study to overcome these problems associated with modeling growth for animals of unknown age. The approach comprised: (1) a robust nonparametric statistical model of growth rates for sea turtles of unknown age to derive the expected size-specific growth rate function conditioned on the covariates followed by (2) numerical integration of that size-specific growth rate function to derive the expected size-at-age growth function. Numerical differentiation can then be used to derive the age-specific growth rate function from the expected size-at-age growth function (see Limpus and Chaloupka 1997). The expected size-at-age and age-specific growth functions were therefore derived without recourse to size-based growth analogues.

The relationship between absolute growth rates recorded for each turtle and specific growth rate covariates was modeled statistically in the first stage of the current study using a generalized additive modeling approach (GAM, Hastie and Tibshirani 1990) applied to sea turtle growth studies by Chaloupka and Limpus (1997) and Limpus and Chaloupka (1997). GAM enables robust analysis of regression models with nonlinear covariate functional form and a range of non-normal error terms (Hastie and Tibshirani 1990).

The specific GAM regression model used here comprised: (1) an identity link, (2) a robust quasi-likelihood error function, and (3) flexible cubic smoothing splines to model the nonlinear functional relationship between the response variable (growth rate) and the continuous covariates (year, mean carapace size, recapture interval). A quasi-likelihood error function is general, depending only on an empirical mean-variance relationship derived from the data (Hastie and Tibshirani 1990). Unlike a parametric error function, a quasi-likelihood error function requires no prior knowledge of the error distribution and is also useful for accounting for potential correlated error inherent in mixed longitudinal data sets. The GAM fit summary (Table 1) comprises: (1) an estimate of the contribution of each covariate to the overall model fit using t ratio statistical inference, and (2) an estimate of the nonlinearity for each continuous covariate (nonparametric term) using a nonparametric F ratio test. A more detailed expla-

TABLE 1. Summary of GAM models (identity link, quasi-likelihood error, cubic smoothing splines) fitted to Union Creek immature green turtle growth rates.

Parameter	Asymptotic				Nonlinear effects (nonparametric)		
	Estimate	Standard error	<i>t</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Absolute growth rate metric = cm SCL/yr (see Fig. 1a–e)†							
Constant	10.4001	1.5392	6.757				
Sex (M vs. F)	−0.8006	0.2085	−3.839	< 0.001			
Sex (M vs. Unknown)	−0.1219	0.1783	−0.684	NS			
Site (1 vs. 2)	−0.1628	0.2223	−0.732	NS			
Site (1 vs. 3)	−0.4845	0.2013	−2.406	< 0.02			
Year	0.0471	0.0159	2.968	< 0.01	3.0	8.278	< 0.0001
Mean size (SCL)	−0.2002	0.0077	−26.145	< 0.001	4.9	2.664	< 0.02
Recapture interval	0.0907	0.0794	1.141	NS	3.0	1.081	NS
Absolute growth rate metric = kg body mass/yr (see Fig. 1f–j)‡							
Constant	18.0159	6.8910	2.614				
Sex (M vs. F)	−0.5925	0.4404	−1.345	NS			
Sex (M vs. Unknown)	−0.4503	0.3738	−1.205	NS			
Site (1 vs. 2)	−0.1567	0.2608	−0.601	NS			
Site (1 vs. 3)	−0.6588	0.3026	−2.177	< 0.05			
Year	−0.1576	0.0787	−2.004	< 0.05	2.9	0.428	NS
Mean size (mass)	−0.0489	0.0101	−4.838	< 0.001	4.9	3.509	< 0.005
Recapture interval	0.2617	0.1427	1.834	NS	3.0	0.276	NS

Notes: Probabilities (*P*) reported for *F* values are based on nonparametric df and residual deviance df. A significant nonparametric *F* means that the covariate was nonlinear. If the *t* test for a covariate is not significant (NS) then the nonparametric *F* test for nonlinearity is irrelevant. Site codes are defined in Fig. 1.

† Null deviance = 2499.1, null df = 538, residual deviance = 1013.6, residual df = 520.1, quasi-likelihood dispersion parameter = 1.69, $R^2 = (2499.1 - 1013.6)/2499.1 = 0.59$.

‡ Null deviance = 677.9, null df = 238, residual deviance = 505.03, residual df = 220.2, quasi-likelihood dispersion parameter = 1.89, $R^2 = (677.9 - 505.03)/677.9 = 0.26$.

nation of the GAM approach, its relationship to standard general linear regression modeling approaches, and the GAM summary format used here is presented in Chaloupka and Limpus (1997).

The GAM models for growth in carapace length and growth in body mass each had one response variable (absolute growth rates) and five potential growth covariates (sex, site, year, mean size, and recapture interval). Sex was coded as males, females, or unknown sex. The site covariate was included in the models to evaluate the effect of location within Union Creek. Three site codes were assigned: intervals with the same location at capture and recapture ("stayers" in the Upper Sound and "stayers" in the Lower Sound) and intervals during which the turtle had moved from the Lower Sound at first capture to the Upper Sound at recapture ("movers"). No turtles moved from the Upper Sound to the Lower Sound.

Year is the calendar year of the growth record and was included to account for the implicit time-dependent sampling design. The year of recapture was assigned to each growth interval. This approach introduces little error in calendar year assignment because most (77%) of the growth records were for recapture intervals of < 2 yr. The year covariate accounts for variation in growth resulting from variation in environmental factors and/or cohort (age class) effects. Because the ages of the turtles were not known, the effect of annual variation in environmental factors cannot be distinguished from cohort effects. Despite this confounding

of environmental and cohort effects, the year covariate must be included in the models because it is a constraint of time series sampling design inherent in all mark-recapture studies.

Mean size (either mean SCL or mean mass) is the arithmetic mean of size at first capture and size at recapture. Mean size is the best approximation of size for a growth interval, particularly if the intervals are sufficiently short so that growth during the interval is linear. The recapture-interval covariate was included in the models to account for any bias introduced by variable lengths of recapture intervals.

RESULTS

Growth data

From 1979 through 1996, 539 growth increments for straight carapace length (SCL) were measured over intervals of at least 330 d for 333 individual green turtles. Of these increments, 69 were recorded for males, 104 for females, and 366 for turtles of unknown sex (sex cannot be identified from external characteristics in immature sea turtles). The data included growth records for turtles spanning the postrecruitment developmental phase from 25.3 to 82.3 cm SCL. Growth rates varied from 0.1 to 10.8 cm/yr, with a mean of 4.2 cm/yr and a median of 4.3 cm/yr. Recapture intervals ranged from 330 d to 6 yr, with a median interval of 1.3 yr; 77% were between 330 and 730 d in duration.

From 1979 through 1989, 239 growth increments for

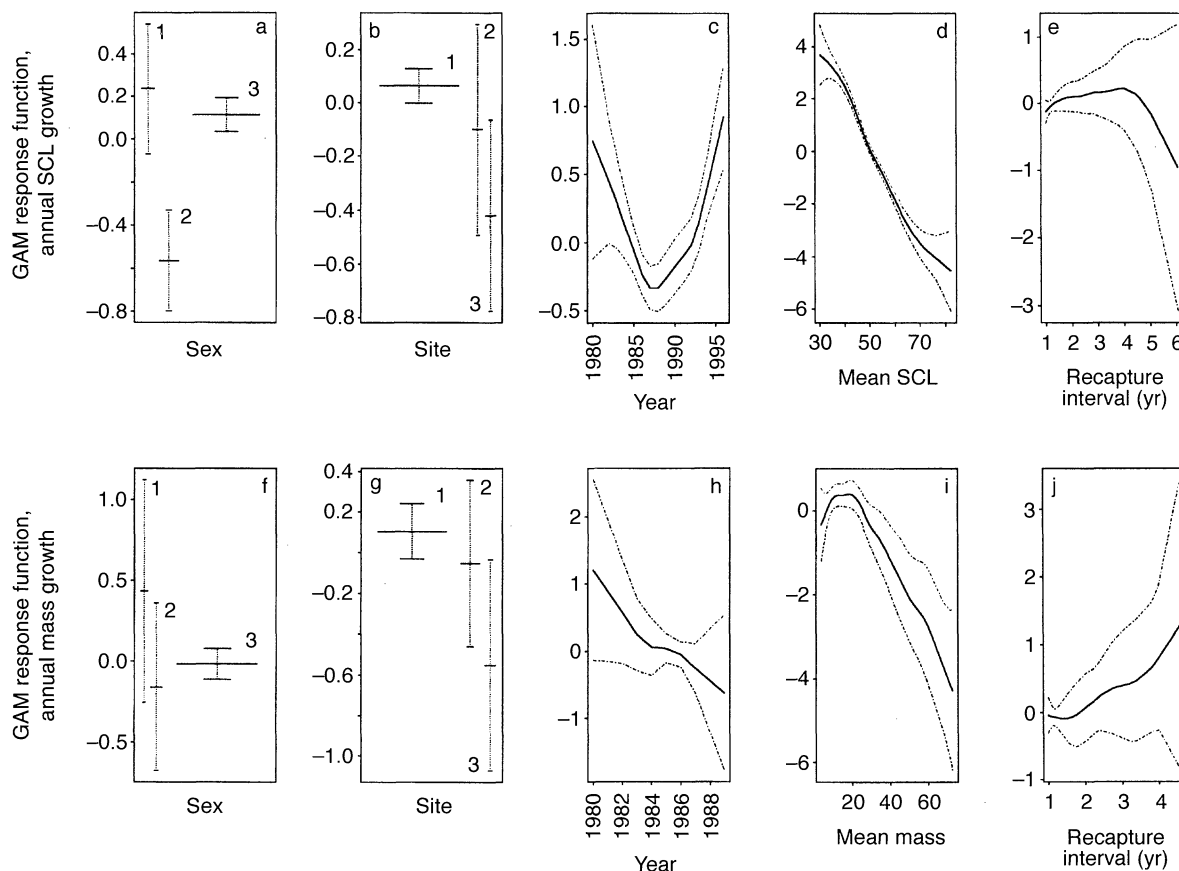


FIG. 1. Graphical summary of GAM analysis of growth covariates summarized in Table 1: annual SCL growth in panels (a)–(e); annual mass growth in panels (f)–(j). The response variable (mean annual growth rate) is shown on the y-axis as a centered smoothed function scale to ensure valid pointwise 95% confidence bands. The covariate is shown on the x-axis: (a, f) sex (1 = male, 2 = female, 3 = unknown); (b, g) site (1 = stayer in Upper Sound, 2 = stayer in Lower Sound, 3 = mover from Lower Sound to Upper Sound); (c, h) year; (d, i) mean size between first capture and next capture; (e, j) recapture interval in years. For (a), (b), (f), and (g), width of the mean covariate response is proportional to sample size with the 95% confidence interval shown by cross bars. Solid curves in (c)–(e) and (h)–(j) are the cubic smoothing spline fits for each continuous covariate conditioned on all other covariates in the GAM model (see Table 1). Dotted curves are pointwise 95% confidence curves around the fits.

body mass were measured over intervals of at least 330 d for 179 individual green turtles. Of these increments, 17 were for males, 28 for females, and 194 for turtles of unknown sex. Most of these growth increments were recorded before 1987, because few turtles were weighed after that year. Mass of the turtles ranged from 2.0 to 73.5 kg. Growth rates varied from -1.7 to 9.1 kg/yr, with a mean of 3.5 kg/yr and a median of 3.6 kg/yr. Of the growth intervals, 84% were between 330 and 730 d in duration.

Growth model

For growth in carapace length, the GAM regression analysis indicated that sex, site, year, and mean size all had significant effects, whereas recapture interval did not have a significant effect (Table 1, Fig. 1a–e). For the sex covariate, females had significantly slower growth rates than did males and turtles of unknown sex; the latter two groups were not significantly dif-

ferent from each other (Table 1, Fig. 1a). For the site covariate, turtles that remained in the Upper Sound had size-specific growth rates significantly faster for a given size than turtles that moved from the Lower Sound to the Upper Sound. There was no significant difference in growth rates between turtles that remained in the Upper Sound and those that remained in the Lower Sound or between turtles that remained in the Lower Sound and those that moved from Lower to Upper Sound (Table 1, Fig. 1b). The two continuous covariates (year and mean SCL) were significant nonlinear effects (Table 1, Fig. 1c, d).

For growth in mass, the GAM regression analysis identified site, year, and mean mass as significant covariates (Fig. 1g–i); sex and recapture intervals were not significant (Table 1). The effect of site was the same as for SCL growth—that is, the only significant difference was between turtles that remained in the Upper Sound and turtles that moved from the Lower Sound

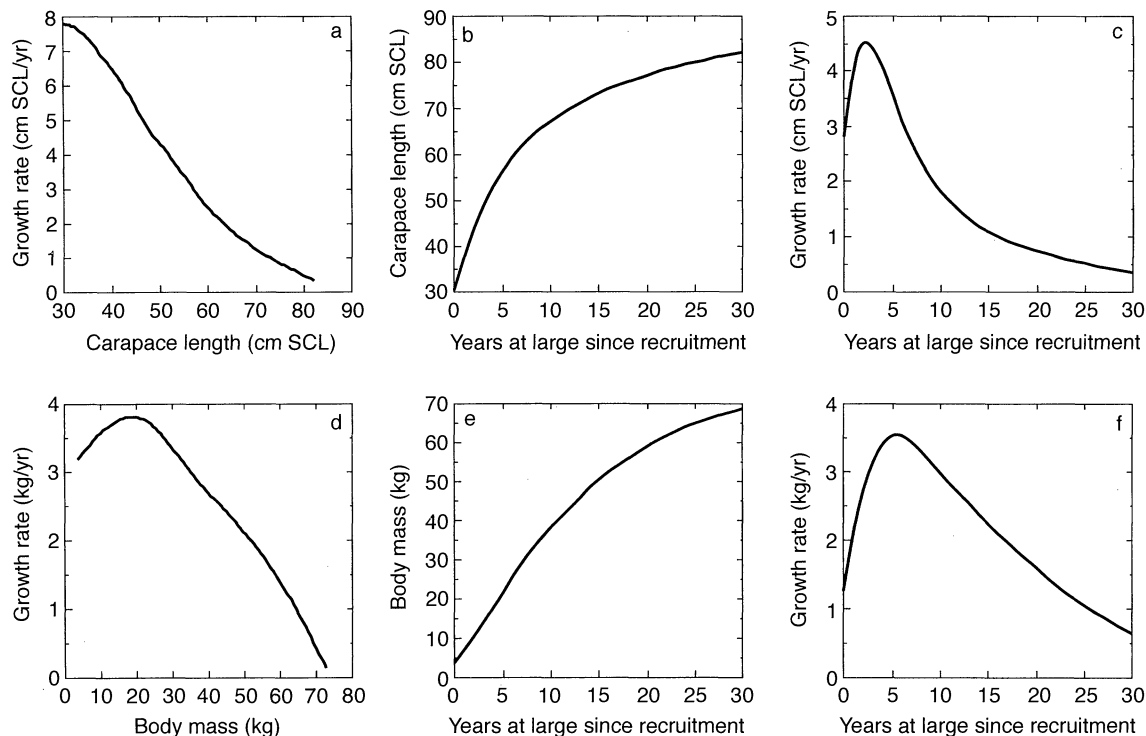


FIG. 2. Estimated size- and age-specific growth rate functions derived from the GAM model fit that was conditioned on all the covariates (Table 1): SCL growth in panels (a)–(c); mass growth in panels (d)–(f). (a, d) Expected or mean size-specific growth rate function extracted from the GAM results with growth rates on original scale rather than on the GAM scale. Extraction was by cubic B-spline smooths to fitted GAM values. (b, e) Numerical integration of the expected size-specific growth functions in Fig. 2a and 2d, to derive the expected size-at-age functions, where age is years at large since recruitment. (c, f) Numerical differentiation of the expected size-at-age functions (Fig. 2b and 2e) to derive the expected age-specific growth rate functions.

to the Upper Sound (Table 1, Fig. 1g). Year has a significant linear effect, as opposed to a significant nonlinear effect in the SCL model (compare Fig. 1c, h). Mass data, however, were available only for the earlier years of the study, so the downward trend for the year effect in the mass model (Fig. 1h) is similar to the trend over the same years for the year effect in the SCL model (Fig. 1c). Mean mass has a significant nonlinear effect (Table 1, Fig. 1i).

Covariate function plots for a GAM model fit (Fig. 1) are centered on the response scale by subtracting a weighted mean to ensure valid pointwise 95% confidence bands (Hastie and Tibshirani 1990). Although essential for analyses, these plots are more difficult to decode on the original response (i.e., growth rate) scale. To assist evaluation of the SCL-specific growth functions, a cubic B-spline smooth was extracted from the GAM results for Fig. 1d and plotted on the uncentered growth rate scale to highlight the underlying nonlinear function on the original growth rate scale (Fig. 2a). The curve is a monotonic declining function.

The expected SCL-at-age function (Fig. 2b) was derived by numerical integration of the expected SCL-specific growth function (Fig. 2a). It is important to note that “age” is expressed as years since recruitment,

because the age at recruitment and the form of the growth curve prior to recruitment are unknown. Although green turtles as small as 25 cm SCL have been captured in Union Creek, the smallest mean size of a green turtle measured at the beginning and end of a growth interval was 30 cm. It is apparent from Fig. 2b that growth from mean size at recruitment (30 cm) to maximum size (82 cm) observed in Union Creek requires ~30 yr. However, because growth at the largest sizes is very slow in Union Creek, nearly half of that time interval represents the time required to grow the last few centimeters. Most green turtles (98%) have left Union Creek before they reach 75 cm SCL; growth from recruitment (30 cm) to 75 cm, by which size most turtles have left Union Creek, would require only ~17 yr (Fig. 2b).

The expected SCL-at-age function (Fig. 2b) appears in this form to be a von Bertalanffy curve, but there is actually a very early rapid growth spurt that can be seen in the expected age-specific growth rate function (Fig. 2c), which was derived by numerical differentiation of the expected SCL-at-age function (Fig. 2b). This difference in interpretation illustrates why evaluations based on size- or age-specific growth rates are preferable to evaluations of just size-at-age, which can

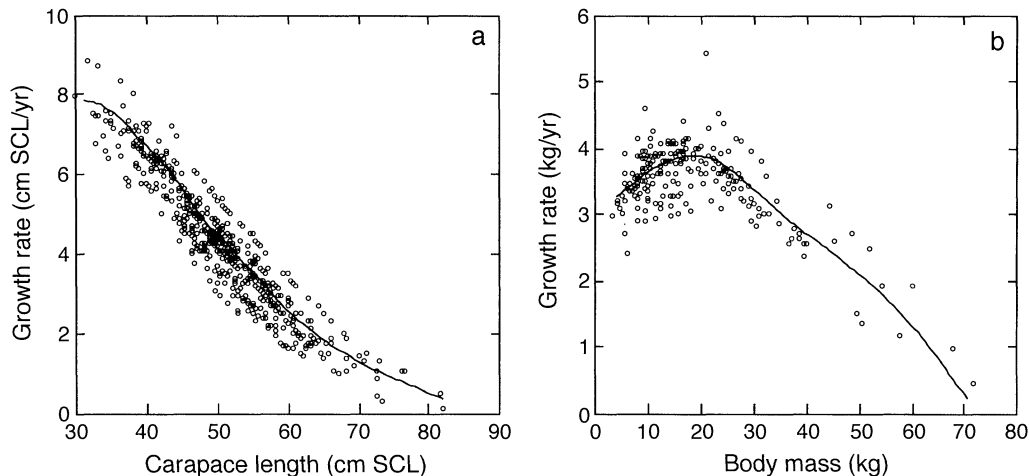


FIG. 3. Estimated size-specific growth rate function for (a) SCL growth and (b) mass growth for green turtles in Union Creek derived from the GAM model fit summarized in Table 1. Fitted values are from the GAM model; some plotted circles appear as filled because of many overlapping values. The solid curve in each panel is a cubic B-spline smooth fitted to those predicted GAM model values to highlight the underlying size-specific growth rate function conditioned on all the covariates (see Fig. 2a and 2d).

be misleading. Maximum age-specific growth rates in SCL were attained ~ 2 yr post recruitment.

A similar set of plots was generated for the body mass model (Fig. 2d–f). The expected mass-specific growth rate function (Fig. 2d) is a nonmonotonic curve. Maximum mass-specific growth rates are reached at a body mass of ~ 20 kg. The maximum body mass of turtles in Union Creek (69 kg) was reached at 30 yr postrecruitment (Fig. 2e), and the maximum age-specific growth rates in mass were reached around 5 yr postrecruitment (Fig. 2f).

The SCL model (size-specific growth rates) was a good fit to the data. While there is substantial variability, the model accounts for at least 59% of the variance (Table 1, Fig. 3a). Unlike the SCL model, the body mass model was not a good fit to the data. There is substantial variability, and the GAM model accounts

for only 26% of the variance (Table 1, Fig. 3b). The discussion, therefore, will focus on the SCL model.

Year effect and density-dependent effects

There is a significant inverse correlation (Spearman's $\rho = -0.589$, $n = 14$, $P = 0.027$) between the annual estimated population density of green turtles in Union Creek and the mean annual growth rate estimates (Fig. 4). Although the number of turtles captured during each sampling period is not a quantitative measure of density, we are confident that it is a reliable relative population index because of consistency in capture methods and duration of sampling period. Estimates are not available for 1981 and 1995 because no field work was conducted during those years, and for 1987 because severe storms and boat failure changed our sampling procedure. Although, as explained above, the year effect is confounded with cohort effects (see review in Chaloupka and Musick 1997) and somewhat obscured by the fact that some recapture intervals are longer than 1 yr, the pattern in Fig. 4 suggests that the year effect is real and that a density-dependent effect is apparent.

The condition index ($CI = \text{body mass}/\text{SCL}^3$) was negatively correlated with year from 1979 to 1987, the period of decreasing growth rates (Spearman's $\rho = -0.131$, $n = 640$, $P < 0.001$). CI also decreased significantly with decrease in the mean annual growth rate estimates (Spearman's $\rho = 0.113$, $n = 628$, $P = 0.005$) for 1980–1987 (years for which mass data and annual growth rate estimates are available), and decreased significantly with increasing population density (Fig. 5, Spearman's $\rho = -0.158$, $n = 639$, $P < 0.001$) for 1979–1987 and 1998 (years for which mass data and population density values are available).

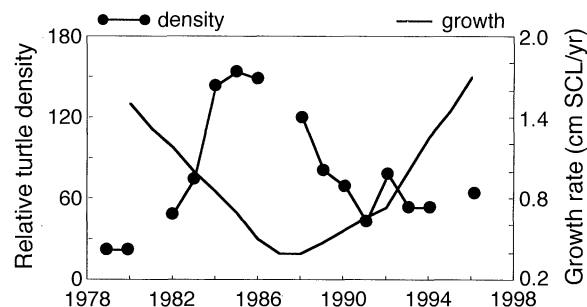


FIG. 4. Relative density of green turtles in Union Creek (number of turtles captured/sampling period) for each year superimposed on response variable (growth rate) curve for the year effect function shown in Fig. 1c. Note the 1- to 2-yr lag between density and growth rate changes. No density estimates are available for 1981, 1987, and 1995.

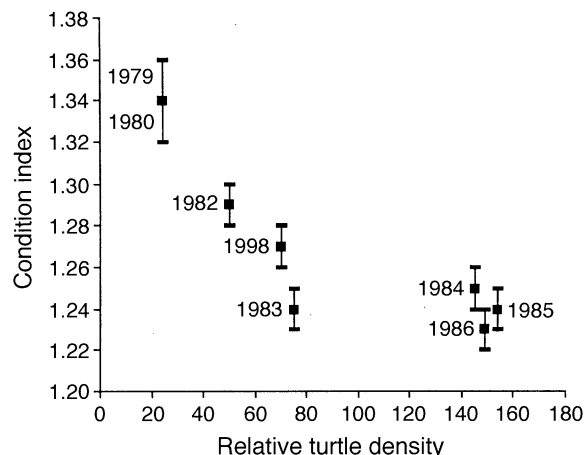


FIG. 5. Relation between condition index [$CI = \text{mass}/(\text{SCL})^3$] and relative turtle density in Union Creek for years in which both mass data and turtle density values are available (Spearman's $\rho = -0.158$, $n = 639$, $P < 0.001$). Values are mean ± 1 SE and are identified by year.

DISCUSSION

Sex and site effects

Although sex was identified as a statistically significant covariate, the biological reality of the difference is not certain. The number of growth intervals that can be attributed to turtles of known sex is relatively small (32%), and the growth intervals of males and females are differentially distributed over years, mean SCL, and site. Females have greater representation in earlier years (1986 to 1989), in larger size classes, and in the Lower Sound, all of which would tend to decrease growth rates relative to males. These confounding factors and small sample size preclude drawing firm conclusions about apparent sex-specific growth rate differences.

Further evidence that the slower growth rates of females may be an artifact of sampling comes from two sources. First, in Fig. 1a, the large group of turtles of unknown sex falls out with the males rather than between the males and females as would be expected, based on the assumption that the unknown sex group was composed of at least an equal number of females and males. The female-to-male ratio of a sample of 111 green turtles in the Union Creek population collected in 1988 was 1.4:1.0 (Bolten et al. 1992). Second, an earlier analysis of sex-specific growth rates for the Union Creek green turtle population, using a linear regression model, found no significant sex effect (Bolten et al. 1992).

Significant sex-specific growth rates have been reported for green turtles in the southern Great Barrier Reef (Limpus and Chaloupka 1997), the only other green turtle population that has been evaluated for sex-specific growth. At sizes >60 cm curved carapace length (CCL), southern Great Barrier Reef females grow significantly faster than do males—the opposite

of the effect reported here. The difference in sex-specific growth rates has been attributed to sexual dimorphism in body size (Limpus and Chaloupka 1997). In the green turtle population in the southern Great Barrier Reef, mean CCL of breeding males is significantly smaller than that of breeding females, with an estimated difference of 7 cm (Limpus and Chaloupka 1997). Unfortunately, we know of no data on relative sizes of mature male and female green turtles in the Greater Caribbean.

The difference in the results of our study and that from Australia might be due in part to a difference in the size distribution of the study populations. The Australian study included the entire postrecruitment phase from 39 to 116 cm CCL, including a substantial proportion of sexually mature females and males. The difference in growth rates between the sexes occurred between 60 cm CCL and attainment of sexual maturity around 95 cm CCL; much of that size range (>80 cm SCL) is absent from the Union Creek population.

The significant site effect in our model indicates that even in relatively small (20 km²), foraging habitats, habitat selection by individual turtles may have significant effects on size-specific growth rates. Habitat selection may be responsible for some of the unexplained variation in this and other growth rate studies. The significantly lower growth rates of turtles that moved from a lower quality habitat to a higher quality habitat (movers) compared with those of green turtles that remained within either habitat (stayers) suggest that developmental migrations may be a response to nutrient limitation and/or decreased growth rates.

Regional growth patterns: Atlantic region

The SCL-specific growth rate function for green turtles in Union Creek is a monotonic nonlinear declining function (Fig. 2a). Earlier studies in Union Creek (Bjorndal and Bolten 1988, Bjorndal et al. 1995) and studies of other populations of green turtles in the Caribbean (Schmidt 1916, Boulon and Frazer 1990) and U.S. Atlantic waters (Mendonça 1981, Frazer and Ehrhart 1985, Shaver 1994) have reported similar patterns of continual decline in growth rates with increasing carapace length. Only one study has reported a non-monotonic pattern of carapace length growth for green turtles in the Atlantic (Culebra, Puerto Rico; Collazo et al. 1992), but the study was based on a small sample size with recapture intervals as short as 3 mo. More data are needed for the Culebra population, because extrapolation to annual growth rates from short recapture intervals is extremely problematic (Chaloupka and Musick 1997).

The similarity of this continual declining growth function with increasing body size to the von Bertalanffy curve (Ratkowsky 1986) encouraged researchers to use the von Bertalanffy model to describe growth within the size range studied (Bjorndal and Bolten 1988, 1995, Bjorndal et al. 1995) and to extrapolate

outside the size range to estimate ages at sexual maturity (Frazer and Ehrhart 1985, Frazer and Ladner 1986, Boulon and Frazer 1990). Chaloupka and Musick (1997) observed that the application of the von Bertalanffy to sea turtle populations had often involved statistically incorrect techniques and inappropriate extrapolations outside the size range of the studies. Results from our study indicate that the monotonic declining SCL-specific growth function (Fig. 2a) is not a von Bertalanffy curve.

However, because of the similarity between our model based on GAM regression analysis and that of a von Bertalanffy model, descriptions of growth within the studied size range (30–80 cm SCL) may not be greatly different. In an earlier study of growth rates in the Union Creek green turtle population (Bjorndal et al. 1995), results from two applications of a von Bertalanffy model using nonlinear regression analysis and length-frequency analysis (MULTIFAN software) were compared with a growth curve calculated for 5-cm increments. The last procedure involved calculating the mean time intervals required for turtles to grow between 5-cm SCL increments, based on the mean growth rates for each 5-cm size class. The time required for green turtles in Union Creek to grow from 30 to 70 cm was estimated as 12 yr by the von Bertalanffy length-frequency technique, as 13 yr by the von Bertalanffy nonlinear regression technique, and as 13 yr by the 5-cm increment calculations. Our GAM regression analysis estimates 12 yr as the interval between 30 and 70 cm (Fig. 2b). Although the four techniques generated similar estimates for this parameter, the GAM regression analysis is superior because the data determine the underlying growth function and because covariates—both continuous and discrete—can be evaluated for their independent effect on the growth function (Chaloupka and Musick 1997, Limpus and Chaloupka 1997).

The real concern is the use of the von Bertalanffy model to extrapolate outside the size range of the study (Bjorndal and Bolten 1988, Day and Taylor 1997), which is a common practice to estimate age at sexual maturity (Chaloupka and Musick 1997). There is no reason to expect that green turtles in the early pelagic stage between hatching (5 cm SCL) and recruitment to benthic foraging habitats (25 to 35 cm SCL) follow the same growth function as larger immature green turtles on benthic foraging grounds. In fact, because pelagic green turtles probably consume a very different diet and occupy very different habitats, there are good reasons to predict that their growth function would be different. It is also inappropriate to extrapolate to the larger “missing” size class of turtles between 80 cm and sexual maturity. No growth data are available for Atlantic green turtles in this size range. To date, growth studies in the Atlantic have been limited to relatively shallow water areas largely because of depth-limited capture techniques, turtle population densities, and convenience. As green turtles approach 70 to 80 cm

SCL, they leave these shallow water habitats and may experience a growth spurt if they take up residence in habitats that can support more rapid growth.

One source of variation in somatic growth functions of green turtles, both within and among Atlantic feeding grounds, might be differences in adult body size of distinct green turtle nesting populations in the Greater Caribbean, because adult size may affect rates of growth of immatures. We know that the population of immature green turtles in Union Creek is a mixed stock, with individuals derived from several nesting populations, based on mitochondrial DNA sequences (Lahanas et al. 1998). The mean size of mature female green turtles varies substantially among these contributing populations, from a mean carapace length of 100.2 cm for the population nesting at Tortuguero, Costa Rica, to 111.8 cm for green turtles nesting in Surinam (Pritchard 1969, Bjorndal and Carr 1989). As discussed above, a significant difference in growth rates between male and female green turtles from the southern Great Barrier Reef has been attributed to a difference of 7 cm in mean carapace length of mature males and females in that population (Limpus and Chaloupka 1997). The 11-cm range in mean carapace lengths of nesting females in the source populations that contribute to the Union Creek population suggests that the growth functions of these source populations could be significantly different. Therefore, in a mixed stock, immature green turtles of the same size and/or age from different breeding populations could grow at different rates, even when sharing foraging grounds. When genetic surveys are completed, we will incorporate source rookery as a potential growth covariate in our model to evaluate this source of variation.

Regional growth patterns: comparison with populations in the Pacific Ocean

In contrast to the Atlantic populations, size-specific growth functions of green turtles in the Pacific are non-monotonic. In green turtles from the southern Great Barrier Reef (Limpus and Chaloupka 1997), growth rates increase with increasing carapace length from 39 cm CCL to maximum values between 60 and 63 cm, and then decline until growth becomes negligible approaching the onset of sexual maturity (Fig. 6). Growth rates measured in green turtles in Hawaii (Balazs 1982, Balazs et al. 1994) and the Galápagos Islands (Green 1993), based on much smaller sample sizes than the Australian sample, have a similar pattern of increasing juvenile growth rates followed by declining subadult rates. Despite the differences in growth rates between the Atlantic and Pacific, the mean sizes of nesting females are quite similar: 106 cm CCL for green turtles nesting in the southern Great Barrier Reef (Limpus and Chaloupka 1997) and 104 cm CCL (converted from mean of 100 cm SCL; Bjorndal and Carr 1989) for green turtles nesting at Tortuguero, Costa Rica, the rookery from which the majority of Union Creek turtles

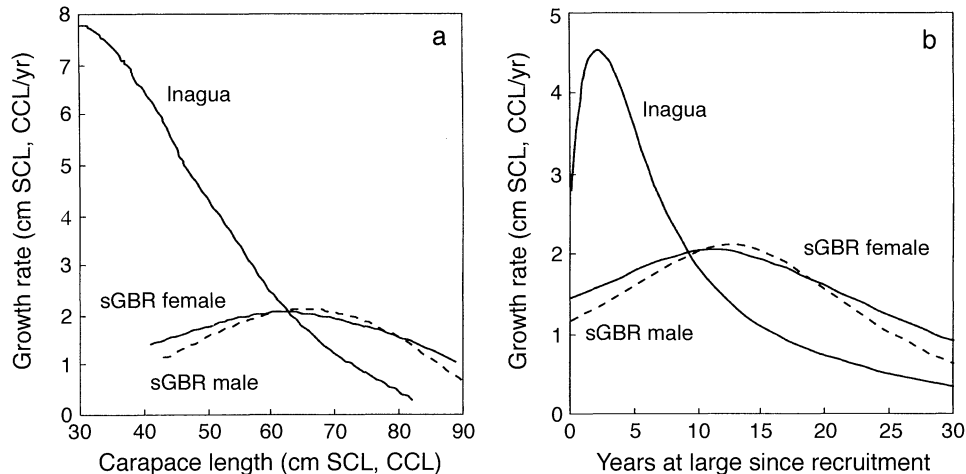


FIG. 6. Comparative (a) size-specific and (b) age-specific growth rate functions for the southern Great Barrier Reef (sGBR) population of immature green turtles (Limpus and Chaloupka 1997) and the Union Creek (Inagua) population of immature green turtles. The Australian study was based on curved carapace length (CCL) measurements, whereas the Union Creek study was based on SCL measurements. The difference between SCL and CCL is minor (Bjorndal and Bolten 1989) and does not affect the qualitative comparisons for immatures presented here.

are derived (Lahanas et al. 1998). A similar dichotomy exists in growth functions of hawksbill sea turtles (*Eretmochelys imbricata*) between the southern Great Barrier Reef and the Caribbean (Bjorndal and Bolten 1988, Boulon 1994, Chaloupka and Limpus 1997).

Why do small juvenile sea turtles, both green turtles and hawksbills, grow so much more slowly at an equivalent size in Australian waters than in the Greater Caribbean? No data on population densities are available for the two regions, but Australian green turtle and hawksbill populations have been exploited to a lesser extent than have Caribbean populations (Limpus 1995). Density-dependent effects similar to those proposed in this study may be an important regulating mechanism for somatic growth rates in Australian immature green turtles. If the difference in growth function is a result of higher population density in Australia, Caribbean green turtle growth functions may change to the Australian pattern if their populations are allowed to rebuild towards pre-exploitation levels. Comparative studies of population densities, nutrition, and growth between the two regions are needed to assess the relative influences of genetics and environment on the growth functions.

Density-dependent effect on somatic growth

For large herbivores that outgrow most predators, such as the larger ungulates in the Serengeti, population size is regulated by nutrient limitation at or near carrying capacity (K) of forages (Sinclair 1995). Green turtles are the marine equivalents of these large ungulates, and, in the absence of exploitation by humans, their populations are probably regulated by food availability (Bjorndal 1982, Jackson 1997). Density-dependent effects result from competition for limiting resources and increase as population levels approach or

exceed K . Density-dependent effects on somatic growth have been reported for a wide range of organisms, including fish (Booth 1995), salamanders (van Buskirk and Smith 1991), tortoises (Stubbs et al. 1985), and meadow voles (Ostfeld and Canham 1995).

Three lines of evidence support our conclusion that the significant year effect in our growth model is a density-dependent effect. First, there is a significant inverse correlation between population density and mean annual growth rate (Fig. 4). Second, changes in the condition index (mass/SCL^3) reflect changes in mean annual growth rates and population density (Fig. 5). Third, the population in Union Creek fluctuated around K during our study and thus was at levels likely to experience density-dependent effects that could be measured.

The inverse correlation between population density and mean annual growth rate (Fig. 4) indicates that as density increased, growth rates decreased. The 1- to 2-yr lag between changes in the relative density estimate and changes in mean growth rate results from two causes. First, the recapture year—or the end of the growth interval—is the year assigned for the year effect, whereas the density estimate for each year is an instantaneous measure. Second, the lag represents the time between depletion of food resources, the resulting feedback mechanism cueing the turtles that their rates of nutrient gain and/or growth have decreased, and the departure of the turtles for other foraging habitats.

The condition index (CI) was positively correlated with mean annual growth rate and negatively correlated with population density (Fig. 5). That is, green turtles of a given carapace length had relatively lighter body mass when growth rates were low and when population densities were high, indicating that the animals were

TABLE 2. Carrying capacities for green turtles on *Thalassia testudinum* pastures in the Caribbean. Calculations are based on three levels of intake estimated by three different methods and on two levels of *T. testudinum* productivity.

Thalassia productivity (kg DM·ha ⁻¹ ·yr ⁻¹)	Intake level (kg DM <i>Thalassia</i> ·(kg green turtle) ⁻¹ ·yr ⁻¹)					
	0.74†		1.17‡		1.77§	
	Turtle mass per area (kg/ha)	Number of turtles in Caribbean¶	Turtle mass per area (kg/ha)	Number of turtles in Caribbean	Turtle mass per area (kg/ha)	Number of turtles in Caribbean
216 (heavy grazing)¶	292	38 544 000	185	24 420 000	122	16 104 000
3285 (moderate grazing)#	4439	585 948 000	2808	370 656 000	1856	244 992 000

Note: DM indicates dry mass.

† Bjorndal (1982); based on calculation of energy budget for adult female.

‡ Bjorndal (1980); based on indigestible lignin ratio and daily feces production.

§ Williams (1988); based on estimates of daily bite counts and bite size.

¶ Based on 6 600 000 ha *Thalassia* in the Caribbean (Jackson 1997) and turtle size = 50 kg.

¶ Recalculated from Williams (1988: Table 4).

Zieman et al. (1984).

nutrient-limited. CI values for green turtles weighed in 1998 are consistent with the relation between CI and population density established in the early years of the study (Fig. 5).

The population densities in Fig. 4 represent a change from population levels below K in the first years of the study to higher levels (~6 times greater than initial population densities) through immigration in the middle years of the study. This high population density resulted in a decrease in the standing crop of *Thalassia testudinum*, as recorded in qualitative observations (K. A. Bjorndal and A. B. Bolten, *personal observation*), followed by net emigration of green turtles (documented by recaptures of tagged green turtles throughout the Greater Caribbean). In the final years of the study, the green turtle population stabilized near the estimated K (40% of the population density during the high years) of *T. testudinum* pastures in Union Creek. An estimate of K for green turtles foraging on the 10 ha of *T. testudinum* in the Upper Sound of Union Creek can be calculated from the values presented in Table 2 for the intake values measured in Union Creek (Bjorndal 1980) and the production of *T. testudinum* in a heavily grazed area (Williams 1988). The estimate is 1850 kg of green turtles, or 105 individual green turtles, because the mean mass of green turtles in Union Creek is 17.6 kg. From 1989 to 1998, our mean annual population estimate for green turtles in the Upper Sound of Union Creek was 98, a value very similar to the K estimate of 105.

This density-dependent effect on growth rates is the first described for any sea turtle population. Description of density-dependent effects in sea turtle populations has been limited to a simulation model of increased nest destruction with increased density of nesting turtles (Bustard and Tognetti 1969), which is assumed to occur, but has never been quantified, at beaches with high densities of nesting activity. An understanding of the extent to which density-dependent effects and compensatory gain influence demography is critical for the development of demographic models and strategies for

sustainable harvest. None of the sea turtle population models has accounted explicitly for density-dependent demographic effects (see review in Chaloupka and Musick 1997). The density-dependent effect on growth in Union Creek was a local phenomenon, but probably represents the effect that would occur on a wider scale if green turtle populations were allowed to rebuild. Thus, our results can be used as a starting point to incorporate density-dependent effects into population models.

The foraging behavior of green turtles may promote density-dependent effects. Green turtles maintain grazing plots in *Thalassia* pastures by continually recropping grazed areas (Bjorndal 1980, Ogden et al. 1983). This pattern of grazing provides a higher quality diet for green turtles (Bjorndal 1980), initially stimulates more rapid growth of the *Thalassia* blades (Greenway 1974, Thayer et al. 1984), and increases the rate of nutrient recycling within the seagrass pasture (Thayer et al. 1982). These grazing plots may be maintained for over a year and are used by many green turtles (Bjorndal 1980, Thayer et al. 1984). In areas of high turtle density and/or low *Thalassia* density, grazing plots may merge so that the entire pasture is cropped (Williams 1988). However, after a period of repeated clipping (measured to be ~1 yr in Jamaica), production of *Thalassia* blades declines, presumably as nutrient stores are depleted (Greenway 1974). Thus, by their grazing, green turtles create a cycle of food resource stimulation in both quantity and quality followed by decline of the resource—a pattern not unlike slash-and-burn agriculture. This cycle would promote the accumulation of dense localized green turtle populations with high somatic growth rates followed by decline in growth rates as the food resources are depleted, possible dispersal of the aggregation, and creation of new grazing plots.

Setting a benchmark for green turtles in the Caribbean

Throughout the Caribbean, green turtle populations are far below historical levels as a result of overex-

exploitation by humans (Parsons 1962, Jackson 1997). Sailors in the Gulf of Batabanó, Cuba, no longer encounter groups of green turtles so large that it seems "as if the ships would run aground on them and their shells actually clattered" along the hulls as they did in the time of Columbus (Morison 1942:150). In 1774, Long wrote, "Vessels, which have lost their latitude in hazy weather, have steered entirely by the noise that these creatures [green turtles] make in swimming to attain the Caymanas isles" (cited in Lewis 1940:57). It is fortunate that modern navigators can rely on GPS systems; green turtles no longer swim to the Cayman Islands to breed.

Before the arrival of Europeans, green turtle populations in the Greater Caribbean may well have been controlled by food limitation (Bjorndal 1982, Jackson 1997), and density-dependent effects would have regulated productivity of green turtles. Seagrass ecosystems in the Caribbean would undoubtedly have had very different structures and functions under such heavy grazing regimes from those they have today. Recent studies (Pauly 1995, Jackson 1997, Dayton et al. 1998) have emphasized the need for accurate baselines to measure population changes and ecosystem degradation as well as to set goals for recovery of populations and restoration of ecosystems.

What is the best benchmark to use for Caribbean green turtles? If green turtle populations were regulated by food limitations, the K of Caribbean seagrass beds for the green turtle would be a maximum estimate. Jackson (1997) calculated a population estimate for pre-Columbian green turtles based on an estimate of K presented by Bjorndal (1982). However, the value from Greenway (1974) for productivity of *T. testudinum* used by Bjorndal (1982) was too high. More recent estimates of *T. testudinum* productivity allow us to improve estimates of K (Table 2). The three values for intake of *T. testudinum* by green turtles (Table 2) are strikingly similar given that they are based on three very different methods: an energy budget for adult female green turtles (Bjorndal 1982), indigestible lignin ratio and daily feces production (Bjorndal 1980), and daily bite counts and bite size (Williams 1988).

Our estimates of K vary by an order of magnitude based on the two productivity levels of *T. testudinum* measured in areas heavily grazed and more moderately grazed by green turtles (Table 2). This variation is not surprising. The biomass, rate of production, and quality of seagrasses are all affected by grazing (Thayer et al. 1984). In grazing systems, highest plant productivity is often associated with light to moderate grazing (McNaughton 1985). More estimates of *T. testudinum* under various grazing pressures are needed to improve our estimates of K .

In addition to the population estimate based on K , Jackson (1997) also took a very different approach to estimate the number of green turtles in the Caribbean before the arrival of Columbus. Based on hunting rec-

ords from the Cayman Islands in the 17th century, he estimated that there were 33–39 million adult green turtles in the pre-Columbian Caribbean and an unknown, but large, number of immature green turtles. These values fall within the range of population estimates in Table 2.

The similarity of these population estimates that are based on very different types of data provides encouragement that this approach to establishing a benchmark is appropriate. With further refinement of estimates of *T. testudinum* productivity, mean size of green turtles in stable populations, and area of *T. testudinum* in the Caribbean, we will be able to improve our estimates of the size of the green turtle population in the Caribbean before the arrival of Europeans and improve our goals for population recovery.

Conservation and management implications

When evaluating the implications of the density-dependent effect for the harvest of green turtles in the Greater Caribbean, it is important to note that most green turtle populations are probably well below the level at which further depletion would stimulate a compensatory density-dependent effect in growth rates or reproductive output. Union Creek is a relatively small area with unusually good protection from human-caused mortality, both direct and incidental. Green turtle populations can reach high densities in such protected areas, but green turtle foraging areas that are free of directed harvests and human-induced incidental mortality are rare in the Greater Caribbean. At its highest density, the population in Union Creek was the most dense that we have found in our studies of Caribbean green turtles (K. A. Bjorndal and A. B. Bolten, *personal observation*).

The regional differences in growth rates reported here for the Atlantic and Pacific may be reflected in other demographic parameters as well. Extreme caution should be used if demographic parameters are extrapolated between regions. The fundamental differences in growth functions indicate that management plans and strategies for sustainable use may have to vary substantially among regions. Comparative studies of the mechanisms that regulate growth in green turtles in the Atlantic and Pacific—and on the extent to which these mechanisms are density-dependent—are essential to addressing these issues.

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LITERATURE CITED

- Balazs, G. H. 1982. Growth rates of immature green turtles in the Hawaiian Archipelago. Pages 117–125 in K. A. Bjorndal, editor. *Biology and conservation of sea turtles*. Smithsonian Institution Press, Washington, D.C., USA.
- Balazs, G. H., W. C. Dudley, L. E. Hallacher, J. P. Coney, and S. K. Koga. 1994. Ecology and cultural significance of sea turtles at Punalu'u, Hawaii. Pages 10–13 in K. A. Bjorndal, A. B. Bolten, D. A. Johnson, and P. J. Eliazar, compilers. *Proceedings of the Fourteenth Annual Symposium on Sea Turtle Biology and Conservation*. NOAA Technical Memorandum NMFS-SEFSC-351, Miami, Florida, USA.
- Bjorndal, K. A. 1980. Nutrition and grazing behavior of the green turtle, *Chelonia mydas*. *Marine Biology* **56**:147–154.
- Bjorndal, K. A. 1982. The consequences of herbivory for the life history pattern of the Caribbean green turtle. Pages 111–116 in K. A. Bjorndal, editor. *Biology and conservation of sea turtles*. Smithsonian Institution Press, Washington, D.C., USA.
- Bjorndal, K. A. 1985. Nutritional ecology of sea turtles. *Copeia* **1985**:736–751.
- Bjorndal, K. A. 1997. Foraging ecology and nutrition of sea turtles. Pages 199–231 in P. L. Lutz and J. A. Musick, editors. *The biology of sea turtles*. CRC Press, Boca Raton, Florida, USA.
- Bjorndal, K. A., and A. B. Bolten. 1988. Growth rates of immature green turtles, *Chelonia mydas*, on feeding grounds in the southern Bahamas. *Copeia* **1988**:555–564.
- Bjorndal, K. A., and A. B. Bolten. 1989. Comparison of straight-line and over-the-curve measurements for growth rates of green turtles, *Chelonia mydas*. *Bulletin of Marine Science* **45**:189–192.
- Bjorndal, K. A., and A. B. Bolten. 1995. Comparison of length–frequency analyses for estimation of growth parameters for a population of green turtles. *Herpetologica* **51**:160–167.
- Bjorndal, K. A., A. B. Bolten, R. A. Bennett, E. R. Jacobson, T. J. Wronski, J. J. Valeski, and P. J. Eliazar. 1998. Age and growth in sea turtles: limitations of skeletochronology for demographic studies. *Copeia* **1998**:23–30.
- Bjorndal, K. A., A. B. Bolten, A. L. Coan, Jr., and P. Kleiber. 1995. Estimation of green turtle (*Chelonia mydas*) growth rates from length–frequency analysis. *Copeia* **1995**:71–77.
- Bjorndal, K. A., and A. Carr. 1989. Variation in clutch size and egg size in the green turtle nesting population at Tortuguero, Costa Rica. *Herpetologica* **45**:181–189.
- Bjorndal, K. A., and G. R. Zug. 1995. Growth and age of sea turtles. Pages 599–600 in K. A. Bjorndal, editor. *Biology and conservation of sea turtles*, revised edition. Smithsonian Institution Press, Washington, D.C., USA.
- Bolger, T., and P. L. Connolly. 1989. The selection of suitable indices for the measurement and analysis of fish condition. *Journal of Fish Biology* **34**:171–182.
- Bolten, A. B., and G. H. Balazs. 1995. Biology of the early pelagic stage—the “lost year.” Pages 575–581 in K. A. Bjorndal, editor. *Biology and conservation of sea turtles*, revised edition. Smithsonian Institution Press, Washington, D.C., USA.
- Bolten, A. B., K. A. Bjorndal, J. S. Grumbles, and D. W. Owens. 1992. Sex ratio and sex-specific growth rates of immature green turtles, *Chelonia mydas*, in the southern Bahamas. *Copeia* **1992**:1098–1103.
- Booth, D. J. 1995. Individual fitness and demography in juvenile groups of Hawaiian coral-reef damselfish. *Ecology* **76**:91–106.
- Boulon, R. H., Jr. 1994. Growth rates of wild juvenile hawksbill turtles, *Eretmochelys imbricata*, in St. Thomas, United States Virgin Islands. *Copeia* **1994**:811–814.
- Boulon, R. H., Jr., and N. B. Frazer. 1990. Growth of wild juvenile Caribbean green turtles, *Chelonia mydas*. *Journal of Herpetology* **24**:441–445.
- Bowen, B. W., and J. C. Avice. 1995. Conservation genetics of marine turtles. Pages 190–237 in J. C. Avice and J. L. Hamrick, editors. *Conservation genetics: case histories from nature*. Chapman and Hall, New York, New York, USA.
- Bustard, H. R., and K. P. Tognetti. 1969. Green sea turtles: a discrete simulation of density-dependent population regulation. *Science* **163**:939–941.
- Carr, A. 1980. Some problems of sea turtle ecology. *American Zoologist* **20**:489–498.
- Chaloupka, M. Y., and C. J. Limpus. 1997. Robust statistical modeling of hawksbill sea turtle growth rates (southern Great Barrier Reef). *Marine Ecology Progress Series* **146**:1–8.
- Chaloupka, M. Y., and J. A. Musick. 1997. Age, growth, and populations dynamics. Pages 233–276 in P. L. Lutz and J. A. Musick, editors. *The biology of sea turtles*. CRC Press, Boca Raton, Florida, USA.
- Collazo, J. A., R. Boulon, Jr., and T. L. Tallevast. 1992. Abundance and growth patterns of *Chelonia mydas* in Culebra, Puerto Rico. *Journal of Herpetology* **26**:293–300.
- Crowder, L. B., D. T. Crouse, S. S. Heppell, and T. H. Martin. 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. *Ecological Applications* **4**:437–445.
- Day, T., and P. D. Taylor. 1997. Von Bertalanffy's growth equation should not be used to model age and size at maturity. *American Naturalist* **149**:381–393.
- Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser. 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Ecological Applications* **8**:309–322.
- Dayton, P. K., S. F. Thrush, M. T. Agardy, and R. J. Hofman. 1995. Environmental effects of marine fishing. *Aquatic Conservation: Marine and Freshwater Ecosystems* **5**:205–232.
- Dempster, J. P. 1975. *Animal population ecology*. Academic Press, London, UK.
- Frazer, N. B., and L. M. Ehrhart. 1985. Preliminary growth models for green, *Chelonia mydas*, and loggerhead, *Caretta caretta*, turtles in the wild. *Copeia* **1985**:73–79.
- Frazer, N. B., and R. C. Ladner. 1986. A growth curve for green sea turtles, *Chelonia mydas*, in the U.S. Virgin Islands, 1913–14. *Copeia* **1986**:798–802.
- Getz, W. M. 1996. A hypothesis regarding the abruptness of density dependence and the growth rate of populations. *Ecology* **77**:2014–2026.
- Green, D. 1993. Growth rates of wild immature green turtles in the Galápagos Islands, Ecuador. *Journal of Herpetology* **27**:338–341.
- Greenway, M. 1974. The effects of cropping on the growth of *Thalassia testudinum* (König) in Jamaica. *Aquaculture* **4**:199–206.
- Hastie, T. J., and R. J. Tibshirani. 1990. Generalized additive models. *Monographs on statistic and applied probability*, volume 43. Chapman and Hall, London, UK.
- Hixon, M. A., and M. H. Carr. 1997. Synergistic predation, density dependence, and population regulation in marine fish. *Science* **277**:946–949.
- Jackson, J. B. C. 1997. Reefs since Columbus. *Coral Reefs* **16**, Supplement:S23–S33.
- Lahanas, P. N., K. A. Bjorndal, A. B. Bolten, S. Encalada, M. M. Miyamoto, R. A. Valverde, and B. W. Bowen. 1998. Genetic composition of a green turtle (*Chelonia mydas*)

- feeding ground population: evidence for multiple origins. *Marine Biology* **130**:345–352.
- Lewis, C. B. 1940. The Cayman Islands and marine turtle. *Bulletin of the Institute of Jamaica Science Series* **2**:56–65.
- Limpus, C. J. 1995. Global overview of the status of marine turtles: a 1995 viewpoint. Pages 605–609 in K. A. Bjorndal, editor. *Biology and conservation of sea turtles*, revised edition. Smithsonian Institution Press, Washington, D.C., USA.
- Limpus, C., and M. Chaloupka. 1997. Nonparametric regression modelling of green sea turtle growth rates (southern Great Barrier Reef). *Marine Ecology Progress Series* **149**:23–34.
- Lubchenco, J., A. M. Olson, L. B. Brubaker, S. R. Carpenter, M. M. Holland, S. P. Hubbell, S. A. Levin, J. A. MacMahon, P. A. Matson, J. M. Melillo, H. A. Mooney, C. H. Peterson, H. R. Pulliam, L. A. Real, P. J. Regal, and P. G. Risser. 1991. The Sustainable Biosphere Initiative: an ecological research agenda. *Ecology* **72**:371–412.
- McNaughton, S. J. 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs* **55**:259–294.
- Mendonça, M. T. 1981. Comparative growth rates of wild immature *Chelonia mydas* and *Caretta caretta* in Florida. *Journal of Herpetology* **15**:447–451.
- Mooney, H. A., editor. 1998. Ecosystem management for sustainable marine fisheries. *Ecological Applications* **8**, Supplement:S1–S174.
- Morison, S. E. 1942. *Admiral of the ocean sea, a life of Christopher Columbus*. Little, Brown and Co., Boston, Massachusetts, USA.
- National Research Council. 1995. *Understanding marine biodiversity*. National Academy Press, Washington, D.C., USA.
- Norse, E. A., editor. 1993. *Global marine biological diversity*. Island Press, Washington, D.C., USA.
- Ogden, J. C., L. Robinson, K. Whitlock, H. Daganhardt, and R. Cebula. 1983. Diel foraging patterns in juvenile green turtles (*Chelonia mydas* L.) in St. Croix, United States Virgin Island. *Journal of Experimental Marine Biology and Ecology* **66**:199–205.
- Ostfeld, R. S., and C. D. Canham. 1995. Density-dependent processes in meadow voles: an experimental approach. *Ecology* **76**:521–532.
- Parsons, J. J. 1962. *The green turtle and man*. University of Florida Press, Gainesville, Florida, USA.
- Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology and Evolution* **10**:430.
- Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres, Jr. 1998. Fishing down marine food webs. *Science* **279**:860–863.
- Pritchard, P. C. H. 1969. Sea turtles of the Guianas. *Bulletin of the Florida State Museum, Biological Sciences* **13**:85–140.
- Ratkowsky, D. A. 1986. Statistical properties of alternative parameterizations of the von Bertalanffy growth curve. *Canadian Journal of Fisheries and Aquatic Sciences* **43**:742–747.
- Robinson, J. G. 1993. The limits to caring: sustainable living and the loss of biodiversity. *Conservation Biology* **7**:20–28.
- Schmidt, J. 1916. Marking experiments with turtles in the Danish West Indies. *Meddelelser fra Kommissionen for Havundersøgelser, Serie Fiskeri* **5**:1–26.
- Shaver, D. J. 1994. Relative abundance, temporal patterns, and growth of sea turtles at the Mansfield Channel, Texas. *Journal of Herpetology* **28**:491–497.
- Sinclair, A. R. E. 1995. Serengeti past and present. Pages 3–30 in A. R. E. Sinclair and P. Arcese, editors. *Serengeti II: dynamics, management, and conservation of an ecosystem*. University of Chicago Press, Chicago, Illinois, USA.
- Stubbs, D., I. R. Swingland, A. Hailey, and E. Pulford. 1985. The ecology of the Mediterranean tortoise *Testudo hermanni* in northern Greece (the effects of a catastrophe on population structure and density). *Biological Conservation* **31**:125–152.
- Thayer, G. W., K. A. Bjorndal, J. C. Ogden, S. L. Williams, and J. C. Ziemann. 1984. Role of larger herbivores in seagrass communities. *Estuaries* **7**:351–376.
- Thayer, G. W., D. W. Engel, and K. A. Bjorndal. 1982. Evidence of short-circuiting of the detritus cycle of seagrass beds by the green turtle, *Chelonia mydas* L. *Journal of Experimental Marine Biology and Ecology* **62**:173–183.
- Van Buskirk, J., and D. C. Smith. 1991. Density-dependent population regulation in a salamander. *Ecology* **72**:1747–1756.
- Williams, S. L. 1988. *Thalassia testudinum* productivity and grazing by green turtles in a highly disturbed seagrass bed. *Marine Biology* **98**:447–455.
- Ziemann, J. C., R. L. Iverson, and J. C. Ogden. 1984. Herbivory effects on *Thalassia testudinum* leaf growth and nitrogen content. *Marine Ecology Progress Series* **15**:151–158.