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Temporal, spatial, and body size effects on growth rates of loggerhead sea turtles (*Caretta caretta*) in the Northwest Atlantic

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Abstract In response to a call from the US National Research Council for research programs to combine their data to improve sea turtle population assessments, we analyzed somatic growth data for Northwest Atlantic (NWA) loggerhead sea turtles (*Caretta caretta*) from 10 research programs. We assessed growth dynamics over wide ranges of geography (9–33°N latitude), time (1978–2012), and body size (35.4–103.3 cm carapace length). Generalized additive models revealed significant spatial and temporal variation in growth rates and a significant decline in growth rates with increasing body size. Growth was more rapid in waters south of the USA (<24°N) than in USA waters. Growth dynamics in southern waters in the NWA need more study because sample size was small. Within USA waters, the significant spatial effect in growth rates of immature loggerheads did not exhibit a consistent latitudinal trend. Growth rates declined significantly from 1997 through 2007 and then leveled off or increased. During this same interval, annual nest counts in Florida declined by 43 % (Witherington et al. in Ecol Appl 19:30–54, 2009) before rebounding. Whether these simultaneous declines reflect responses in productivity to a common environmental change should be explored to determine whether somatic growth rates can help interpret population trends based on annual counts of nests or nesting females. Because of the significant spatial and temporal variation in growth rates, population models of NWA loggerheads should avoid employing growth data from restricted spatial or temporal coverage to calculate demographic metrics such as age at sexual maturity.

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Introduction

A long-term regional approach is essential to understand the somatic growth dynamics of the Northwest Atlantic (NWA)

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loggerhead sea turtle (*Caretta caretta*) stock that nests along the southeast coast of the USA. Female loggerheads that nest in the southeast USA have been reported foraging as far north as Atlantic City, NJ, USA (39.35°N), and as far south as Belize (~17°N) (Meylan 1982). Based on mixed stock analyses, flipper tag returns, and satellite telemetry, immature loggerheads of this population move long distances and occur at least as far south as Panama (9°N) and as far north as Massachusetts, USA (42°N) (Engstrom et al. 2002; Hopkins-Murphy et al. 2003; Bowen et al. 2004; Hawkes et al. 2007; Mansfield et al. 2009; Arendt et al. 2012). Differences in environmental conditions such as temperature and food resources throughout the region would be expected to result in differences in growth rates. The importance of assessing somatic growth using a long-term regional approach is underscored by 3 studies that found significant spatial and temporal variation in growth rates of green turtles (*Chelonia mydas*) in Hawaii, USA (Balazs and Chaloupka 2004), Australia (Chaloupka et al. 2004), and central Florida, USA (Kubis et al. 2009).

Spatial and temporal variation in growth rates could have substantial effects on our understanding of loggerhead population dynamics. For this endangered species (IUCN 2012) in the NWA, current population models rely on estimating key parameters such as lifestage duration and age at sexual maturity based on the time required to grow to given sizes (Heppell et al. 2003; National Research Council 2010). These models are critical for the development and evaluation of management plans and management options for loggerheads. Population models could be improved if growth rate estimates used in the models incorporate appropriate levels of variance. Age at sexual maturity in wild sea turtles is almost certainly highly variable (Scott et al. 2012; Bjorndal et al. 2013). Understanding the source of the variation would allow investigators to apportion the variation correctly. In addition, information on variable growth rates among geographic regions may provide insights into why turtles undertake extensive movements among foraging grounds (Meylan et al. 2011) and on the possible effects of such movements on growth, age at sexual maturity, and reproductive output of individuals.

Data on loggerhead growth rates in the NWA have been collected by many individual research projects, but there has been no coordinating effort to evaluate these data on a regional basis. The National Research Council (2010), in their evaluation of how to improve sea turtle population assessments in the USA, recognized "The fractured status and lack of coordination of sea turtle databases are major impediments to the management and conservation of sea turtles [p. 110]." The National Research Council (2010) called for programs to collaborate and combine their data for analysis. We have responded to that call in our study by integrating loggerhead mark-recapture data from 10 research programs (Fig. 1). Data were collected in neritic waters over a broad spatial scale (8.98–32.82°N latitude) from 1978 to 2012 for loggerheads ranging from 35.4 to 103.3 cm straight carapace length. Our sample included adult turtles—based on body size—captured at sea. Female loggerheads nesting on Florida beaches range from 74.9 to 109.2 cm straight carapace length ($N = 661$, Bjorndal et al. 1983). We combined the mark-recapture data to evaluate spatial and temporal variation in growth rates of neritic loggerheads and assess the effect of body size on growth rates.

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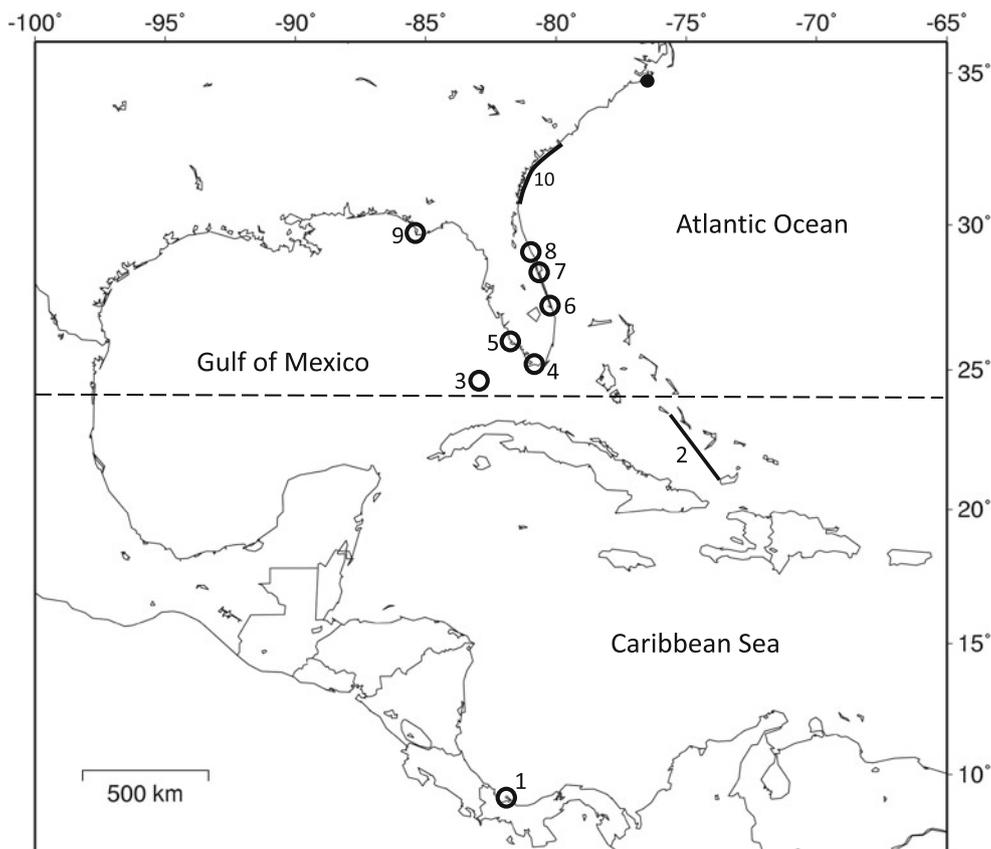
Methods

Order of authorship, except first and last authors, was determined by number of growth increments contributed to this study.

Turtle capture and data collection

Loggerheads were captured at 10 sites as numbered on the map (Fig. 1): (1) Secretary, Panamá, (2) central and southern Bahamas, (3) Dry Tortugas, Florida (FL), USA, (4) Florida Bay, FL, (5) Gullivan Bay, FL, (6) St Lucie Power Plant, FL, (7) Cape Canaveral, FL, (8) Mosquito Lagoon, FL, (9) St Joseph Bay, FL, and (10) coast of Georgia and South Carolina from 30.5 to 32.8°N. All loggerheads in this study were captured in neritic waters (not on nesting beaches) using several methods: hand capture while swimming, hand capture after diving from a boat, trawling, and entanglement nets. All turtles were

Fig. 1 Map showing the 10 study areas (*open circles* and *solid lines*), numbered south to north: *1* Secretary, Panamá, *2* central and southern Bahamas, *3* Dry Tortugas, Florida (FL), USA, *4* Florida Bay, FL, *5* Gullivan Bay, FL, *6* St Lucie Power Plant, FL, *7* Cape Canaveral, FL, *8* Mosquito Lagoon, FL, *9* St Joseph Bay, FL, and *10* coast of Georgia and South Carolina from 30.5 to 32.8°N. *Solid circle* is Core Sound, North Carolina, USA. *Dashed line* is 24°N latitude

tagged with flipper tags and some with internal PIT (passive integrated transponder) tags for individual identification. Carapace length was measured to the nearest 0.1 cm in 3 different ways (Bolten 1999): minimum straight carapace length (SCLmin), SCL notch-to-tip (SCLnt), and curved carapace length notch-to-tip (CCLnt). Calipers were used for SCL and flexible fiberglass tape measures for CCL. Minimum length was measured from the anterior midpoint of the nuchal scute to the posterior notch at midline between the posterior marginal scutes. Notch-to-tip lengths were measured from the anterior midpoint of the nuchal scute to the posterior tip of the posterior marginal scutes. Many turtles had more than 1 carapace length measurement recorded at each capture. Whenever possible, we used SCLmin, which is the preferred measure for growth because it is not affected by breakage or wear of the postmarginal scute tips (Bolten 1999). All measurements were taken by individuals trained in standard measurement techniques for sea turtles. Almost all turtles were recaptured within relatively close proximity of the first capture, but we cannot assume that turtles remained in the area during the recapture interval. Four of the growth

increments were recaptures of turtles that had been held in captivity for about 1-year post-hatching before release (=captive-released turtles).

Data analysis

We minimized the number of conversions between different carapace length measurements to reduce error introduced from such conversions. Our growth rates are measured either as changes in SCLmin ($N = 506$) or SCLnt ($N = 46$, including the 4 captive-released turtles and 1 of the turtles <50 cm—see below), and these values are treated as equivalent. Only 14 growth increments had different CL measurements taken for 1st and 2nd captures, so 14 values had to be converted (see Online Resource 1 for conversion equations). Recapture intervals <330 days were not included in the analyses to minimize errors in growth rate estimation (Chaloupka and Musick 1997). Negative growth rates, which almost certainly result from measurement error or carapace damage, were included in the analyses.

We used a mixed longitudinal sampling design (sampling with partial replacement) with 22 % of the 401

individual turtles recaptured more than once. Age of the loggerheads was not known, as in most sea turtle studies, so year and cohort effects are confounded. Despite this confounding of environmental and cohort effects, year was included as a covariate.

We modeled somatic growth statistically using generalized additive models (GAMs). Our models had 1 response variable (somatic growth rate) and 4 potential growth covariates, which were all continuous: mean SCLmin, latitude of initial capture, year, and recapture interval. Mean SCL is the arithmetic mean of SCL at initial capture and recapture. All mean SCLs are expressed as mean of SCLmin; mean SCL values for the 46 SCLnt growth increments were converted to SCLmin using the equation based on measurements from 306 loggerheads in Online Resource 1. Year was assigned as the calendar year of the midpoint of the recapture interval. Recapture interval was included in the model to assess any bias from variable durations of these intervals.

The GAM had an identity link, a quasilikelihood error function, and cubic smoothing splines. In GAM analyses, each covariate is conditioned on all other covariates. The significance of the contribution of each covariate to the overall model fit was evaluated with t ratio statistical inference. Significant covariates were evaluated for nonlinearity using a nonparametric F ratio test. The value of R^2 was calculated as (null deviance—residual deviance)/null deviance.

Four datasets were analyzed to address different questions.

Dataset #1 ($N = 552$ increments): All growth increments including recaptures of 4 small captive-released turtles and 2 small turtles (35.4 and 38.8 cm mean SCLmin) that fell well below the minimum size (50.4 cm SCLmin) of the rest of the growth increments. This dataset was only analyzed to show graphically the rapid growth rate in these 6 small turtles.

Dataset #2 ($N = 546$ increments): The 4 captive-release and 2 small turtles were removed to provide continuous size distribution (>50 cm mean SCLmin) and to avoid potential long-term effects of captive rearing.

Dataset #3 ($N = 534$ increments): Turtle captures south of continental USA (latitude < 24° N) were removed from Dataset #2 to provide continuous latitudinal distribution.

Dataset #4 ($N = 370$ increments): Turtles with mean SCLmin > 80 cm were deleted from Dataset #3 to remove the turtles with very slow growth rates approaching or at sexual maturity. A small proportion of loggerheads attain sexual maturity between the minimum size (74.9 cm SCLmin) and 80-cm SCLmin (Bjorndal et al. 1983).

We used S-Plus software (TIBCO Spotfire S + Version 8.2.0) for all statistical analyses. We used alpha = 0.05 for all analyses.

Results

Our combined studies yielded 552 growth increments for 401 loggerheads (Dataset #1; Table 1; Figure S-1 in Online Resource 1). Because of the large gap in mean SCLmin between 38.8 and 50.4 cm and concerns over lingering effects of captive rearing, we ran our first GAM analysis without the 4 captive-released turtles and 2 turtles <50 cm mean SCLmin (Dataset #2; Table 1). Of the continuous covariates—mean SCLmin, latitude of first capture, year, and recapture interval—only recapture interval was not significant ($t = 1.133$, $0.2 < P < 0.5$). The GAM was re-run without recapture interval, and analysis of deviance revealed no significant difference between the 2 models. The results of the second model (Table 2a and Fig. 2) revealed that the response functions of the 3 remaining covariates were significantly nonlinear, and the model had a good fit, accounting for 64.1 % of the variation in growth rates. Growth rates decreased with increasing body size (Fig. 2a). Most of the spatial (latitude) effect was between growth rates measured south and north of 24° N (Fig. 2b). Year had no significant effect until 1997, after which growth rates significantly declined until 2007 (Fig. 2c, d).

The significant spatial effect for growth rate (Fig. 3) was confirmed with a Wilcoxon rank-sum test ($Z = -5.0364$, $P < 0.0001$) for the size range shared by turtles north and south of 24° N (54–76 cm mean SCLmin). Loggerheads south of USA waters (<24° N) grew more rapidly (mean ± SD = 5.2 ± 2.8; $N = 12$) than USA turtles (1.4 ± 1.4, $N = 332$).

Mean SCLmin and years were both significant covariates, but they were not evenly distributed north and south of 24° N (Table 2b). Therefore, we next deleted all growth increments from latitude <24° N (Dataset #3, Table 1) to evaluate the spatial effect across a latitude distribution with even distributions of mean SCLmin and years. For this model, mean SCLmin and year, both had significant and nonlinear effects on growth rates (Table 2b), whereas recapture interval ($t = 1.245$, $0.2 < P < 0.5$) and latitude ($t = -1.449$, $0.1 < P < 0.2$) were not significant. This model accounted for 51.7 % of the variation in growth rates. Except for latitude, the GAM graphical presentation from Dataset #2 (Fig. 2) was almost identical to that of Dataset #3.

To assess whether the large proportion of slow growing mature turtles or turtles approaching maturity was masking a spatial effect in USA waters (>24°), we repeated the GAM analysis with Dataset #4 from which we deleted all growth increments with mean SCLmin >80 cm (Table 1). For this model (Table 2c), mean SCLmin had a significant effect, but now, the decline in growth rate with increasing size was nonlinear (Fig. 4c). Latitude was again a significant and nonlinear covariate, but there was no consistent trend for growth rate to increase or decrease with latitude.

Table 1 Characteristics of the 4 datasets used in this study

	Dataset #1[a]	Dataset #2[b]	Dataset #3[c]	Dataset #4[d]
Sample size	552	546	534	370
SCL GR (cm/year)	1.2 ± 1.9	1.1 ± 1.5	1.0 ± 1.3	1.3 ± 1.4
	−1.4 to 17.0	−1.4 to 12.6	−1.4 to 8.8	−1.4 to 8.8
Mean SCLmin (cm)	72.8 ± 11.3	73.1 ± 10.9	73.3 ± 11.0	67.1 ± 6.4
	35.4 to 103.3	50.4 to 103.3	50.4 to 103.3	50.4 to 80.0
Latitude	8.98 to 32.82°N	8.98 to 32.82°N	24.09 to 32.82°N	24.09 to 32.82°N
Capture dates	24 July 1975 to 1 July 2012	19 June 1978 to 1 July 2012	9 March 1983 to 1 July 2012	9 March 1983 to 1 July 2012
Year	1977 to 2011	1978 to 2011[e]	1985 to 2011	1985 to 2011
Recapture interval (days)	732 (median)	732 (median)	732 (median)	725 (median)
	330 to 4807	330 to 4807	330 to 4807	330 to 4291

Values are mean ± standard deviation and range, unless otherwise stated. SCL GR is growth rate of straight carapace length, mean SCLmin is the mean SCLmin of the first and second capture, and latitude is for first capture. Mean SCL GR must be interpreted with caution because significant body size, spatial, and temporal effects are confounded in these means

[a] All growth increments

[b] Dataset #1 without 4 captive-reared and 2 turtles < 50.0 cm mean SCLmin

[c] Dataset #2 without latitudes <24°N

[d] Dataset #3 without mean SCLmin >80 cm

[e] Only 14 increments had a year value <1990

Table 2 Summaries of general additive regression models with all significant parameters (identity link, robust quasi-likelihood error function and cubic smoothing splines)

Parameter	Estimate	ASE	t ratio	Prob(t)	Nonlinear effects (nonparametric)		
					df	F	P
a. Model with all turtles >50 cm mean SCL[a]							
Constant	63.629	12.278	5.182				
Mean SCLmin	−0.0532	0.0032	−16.455	<0.001	2.9	4.605	0.0038
Latitude	−0.1389	0.0130	−10.669	<0.001	10.6	16.580	<0.001
Year	−0.0276	0.0061	−4.494	<0.001	2.9	8.559	<0.001
b. Model with turtles >50 cm mean SCL and north of 24° north latitude[b]							
Constant	68.201	13.151	5.186				
Mean SCLmin	−0.0435	0.0033	−13.322	<0.001	2.9	3.256	0.0226
Year	−0.0321	0.0066	−4.875	<0.001	2.9	5.377	0.0014
c. Model with turtles >50 cm and <80 cm mean SCL and north of 24° north latitude[c]							
Constant	80.489	18.596	4.328				
Mean SCLmin	−0.0507	0.0084	−6.026	<0.001	2.9	1.839	0.141
Latitude	−0.0599	0.0265	−2.259	<0.05	8.1	8.282	<0.001
Year	−0.0372	0.0092	−4.017	<0.001	2.9	12.647	<0.001

ASE is asymptotic standard error, mean size is the mean of the straight carapace lengths (SCL) at the beginning and end of the growth increment, latitude is location of first capture, and year is the midpoint of the growth increment

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. R^2 = (null deviance − residual deviance)/null deviance

[a] Dataset #2: Null deviance = 1202.68, null df = 545, residual deviance = 432.03, residual df = 525.6, robust quasi-likelihood dispersion parameter = 0.605, R^2 = 0.641

[b] Dataset #3: Null deviance = 907.30, null df = 533, residual deviance = 438.59, residual df = 525.2, robust quasi-likelihood dispersion parameter = 0.594, R^2 = 0.517

[c] Dataset #4: Null deviance = 728.33, null df = 369, residual deviance = 385.47, residual df = 348.1, robust quasi-likelihood dispersion parameter = 0.848, R^2 = 0.471
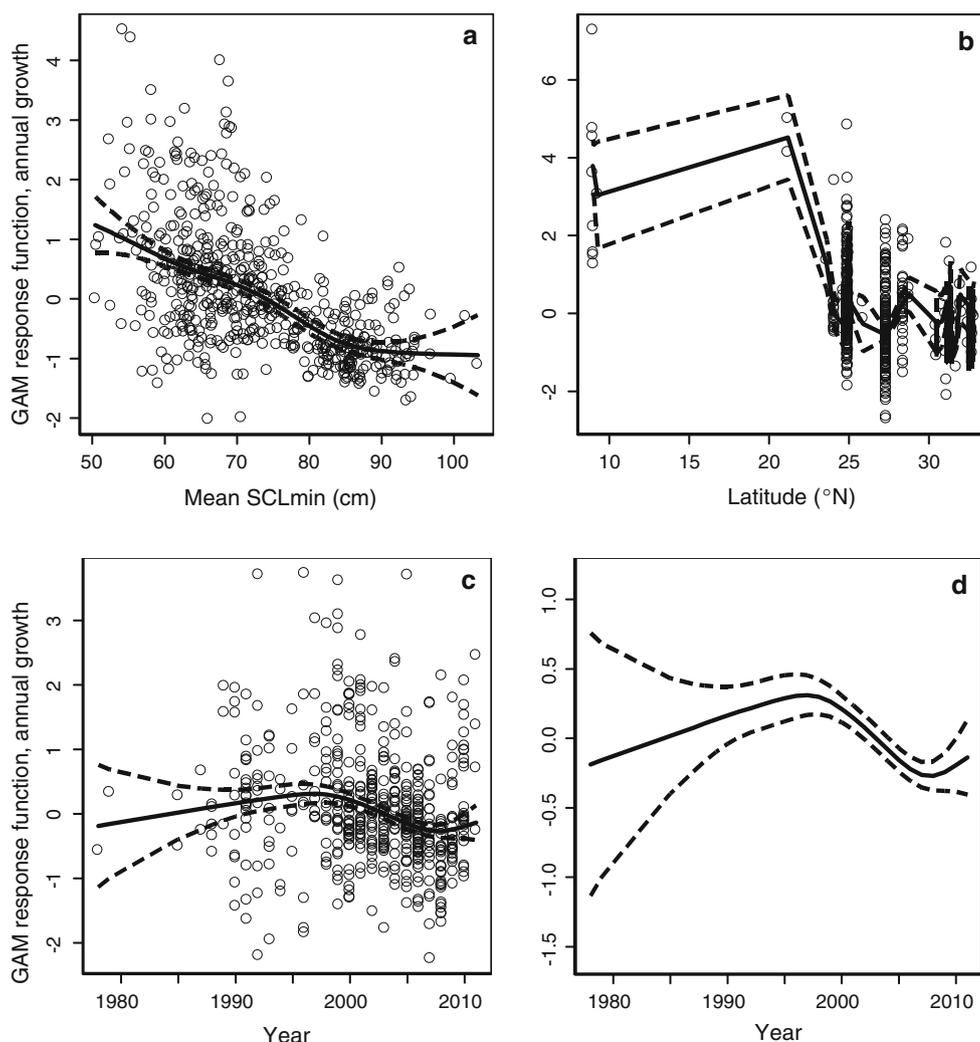
Fig. 2 Graphical summaries of general additive regression analyses of growth covariates of **a** mean size, **b** latitude, and **c**, **d** year for Dataset #2. The response variable (annual carapace growth rate) is shown on the y-axis as a centered smoothed function scale to ensure valid pointwise 95 % confidence bands. The *solid lines* are the cubic smoothing spline fits for each covariate conditioned on all other covariates in the analyses (Table 2). *Dashed lines* are pointwise 95 % confidence lines around the fits. *Open circles* are residuals. Year covariate is also shown (**d**) without residuals on an expanded y-axis to reveal the smoothing spline

Year had a significant and nonlinear effect. This model accounted for 47.1 % of the variation in growth rates.

Discussion

Size-specific variation in growth rates

We found that body size had a significant effect on growth rates for all of the datasets we evaluated; in all cases, growth rates declined with increasing body size. The response function for the entire continuous size range (50.4–103.3 cm mean SCLmin) was nonlinear due to the nearly horizontal segment of the function for turtles greater than ~87 cm mean SCLmin. When these large turtles were excluded, the response function was linear (Fig. 4).

Almost every study of somatic growth rates in sea turtles has reported a significant effect of body size, although the shape of the response function varies (e.g., Balazs and Chaloupka 2004; Kubis et al. 2009; Bjorndal and Bolten 2010). One of the few exceptions is a study conducted with loggerheads in Core Sound, North Carolina, USA (34.8°N; Fig. 1) that lies to the north of our study range (Braun-McNeill et al. 2008). This mark-recapture study with large sample size ($N = 209$) found no effect of body size for loggerheads between 50 and 80 cm SCL. Braun-McNeill et al. (2008) suggested that the lack of body size effect may have resulted from the restricted size range in their study. We evaluated the 50–80 cm mean SCLmin size range in our data and found a significant, declining function (Fig. 4c). Loggerheads leave Core Sound in winter months and migrate to 3 primary areas (Florida, offshore North
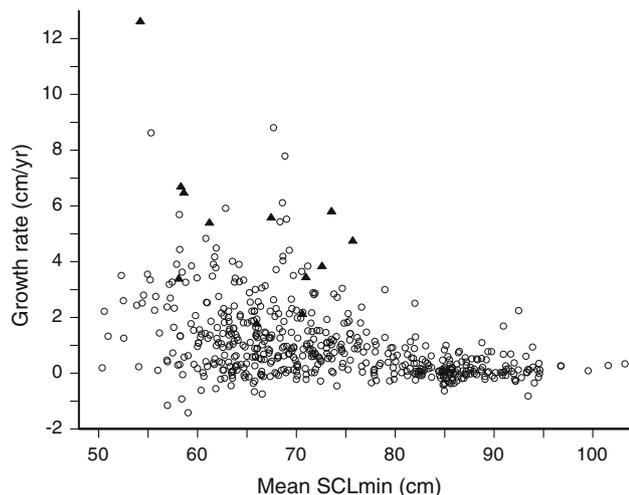
Fig. 3 Relation of growth rate (cm/year) to mean minimum straight carapace length (SCLmin, cm) for loggerheads >50 cm SCLmin that were not captive releases. *Solid triangles* are loggerheads from <24° N (central and southern Bahamas and Panama; $N = 12$); *open circles* are loggerheads from >24° N (USA waters; $N = 534$)

Carolina, and offshore waters north of North Carolina). Braun-McNeill et al. (2008) suggested that differential costs and benefits of these over-wintering sites might contribute to the variation in growth rates that they measured. If selection of an over-wintering site is size-dependent, the differential cost/benefit ratio of the 3 sites could contribute to the lack of body size effect on growth rates. That is, if small turtles over-winter in poor quality sites while large turtles over-winter in high-quality sites, the resulting decrease and increase in relative growth rates of small and large turtles, respectively, could result in the lack of size effect found in Core Sound loggerheads.

Our dataset included only 6 growth increments with a mean SCLmin <50 cm. When these data were included in a GAM analysis, the declining function of growth rate with body size was extended to these small sizes (Fig. 4a). However, these data must be interpreted with caution. Four of the growth increments were for recaptures of captive-released turtles that had been held in captivity for about 1 year. Data from captive-released turtles may be biased because early periods of high-quality nutrition and rapid growth can entrain later growth trajectories in reptiles despite changes in nutrient resources—termed the "silver spoon" effect (Madsen and Shine 2000). That leaves only 2 growth increments for turtles with initial sizes of 32.5 and 31.7 cm SCLmin, mean SCLmin of 35.4 and 38.9 cm and latitudes of 24.9 and 29.8°N, respectively. Loggerheads in this size range have usually not recruited to neritic habitats from the oceanic habitats of their early life stage (Bolten 2003). These 2 growth increments indicate that small loggerheads can grow rapidly in neritic habitats. More research is needed on growth rates of small loggerheads, both in oceanic and neritic habitats.

Spatial variation in growth rates

We used latitude as a measure of relative geographic position. Although almost all turtles were recaptured within the same foraging area, we cannot assume all loggerheads remained in the area throughout the release–recapture interval. These movements introduce some uncertainty into our spatial analysis. When growth rates were assessed over the full latitude range (9–33°N), there was a significant effect, with turtles south of USA waters (<24°N) growing significantly more rapidly than turtles in USA waters. We have few data for southern loggerheads ($N = 12$), and 2 of these growth measurements were taken in years prior to those measured in USA waters. Given the significant year effect in our study, these data must be interpreted with caution. However, the indication that loggerheads grow more rapidly in waters south of the USA needs to be further explored.

Studies of distribution, abundance, and growth of loggerheads in the NWA have focused on USA waters. Part of the large loggerhead population that nests in the southeastern USA forages in waters to the south of the USA, but the proportion that inhabits these southern waters—particularly immature turtles—is not known. The proportion could be sufficient to affect estimates of growth rates, durations of lifestages, and age at sexual maturity for the USA stock. Of the 13 flipper tag returns that two of us (ABB and KAB, unpubl. data) have received from loggerheads tagged in oceanic habitats in the North Atlantic and recaptured in neritic habits in the NWA, 6 have been returned from USA waters and 7 have come from turtles captured south of the USA. This distribution is probably biased in favor of USA waters because of greater effort expended to capture immature loggerheads in USA waters than in more southern waters. A study of loggerheads in Chiriqui Lagoon, Panama, suggested that the South Florida nesting population may contribute up to 70 % of this tropical, juvenile-dominated, foraging aggregation based on a mixed stock analysis using mtDNA sequences (Engstrom et al. 2002).

Latitude was not a significant covariate in the GAM for all loggerheads in USA waters. However, when we removed the large turtles (>80 cm) that were approaching or at sexual maturity and thus growing very slowly, latitude was significant for loggerheads with mean SCLmin between 50 and 80 cm. Growth rates varied significantly among foraging grounds, but there was no overall trend for growth rates to increase or decrease with increasing latitude. Because loggerheads on these foraging grounds are mixed stocks (Bowen et al. 2004), it is unlikely that this variation is a result of genetic differences. Environmental variables, such as abundance and quality of prey species, together with migration strategies, probably have a greater influence; more research is needed on these relationships.

Fig. 4 Effect of body size on growth functions for datasets with different ranges of mean SCLmin. **a** Dataset #1: 35.4–103.3 cm; significant and nonlinear **b** Dataset #2: 50.4–103.3 cm; significant and nonlinear **c** Dataset #4: 50.4–80.0 cm; significant and linear. The response variable (annual carapace growth rate) is shown on the y-axis as a centered smoothed function scale to ensure valid pointwise 95 % confidence bands. *Solid lines* are the cubic smoothing spline fits for each covariate conditioned on all other covariates in the analyses (Table 2); *dashed lines* are pointwise 95 % confidence lines around the fits; *open circles* are residuals. All are plotted on the same x- and y-axes to allow comparisons
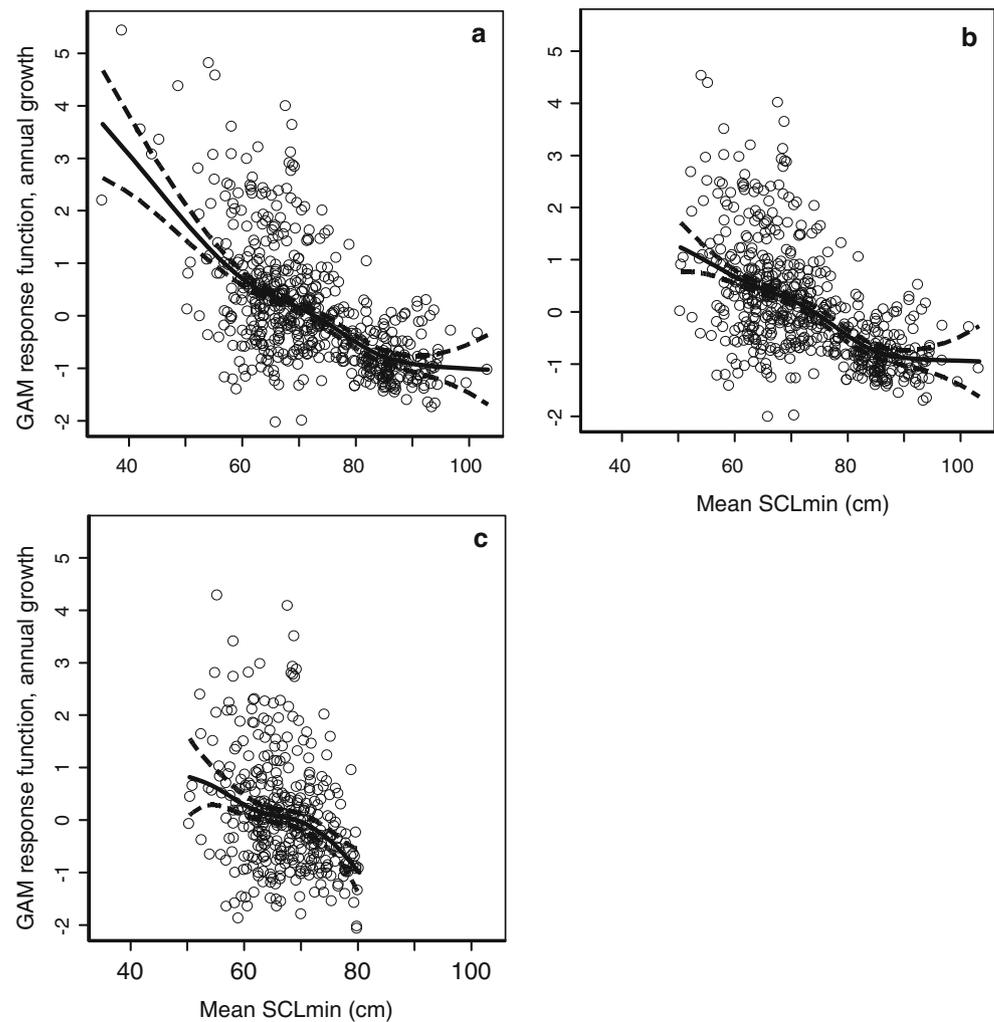
The only other available mark-recapture study of growth in NWA loggerheads with substantial sample sizes is from Core Sound, North Carolina, USA (Braun-McNeill et al. 2008). To compare our data with that study (Table 3), we limited our data to loggerheads captured and recaptured from 1994 to 2005 and compared growth rates for 10-cm size classes presented by Braun-McNeill et al. (2008). No statistical comparisons are possible, but based on mean values, the NC 50–59-cm size class appears to grow more slowly, and the 60–69-cm size classes appear to have similar growth rates. The NC 70–79-cm size class appears to grow more rapidly, but most of the NC loggerheads were in the smaller portion of this size class, which grow more rapidly than the larger turtles in that size class in our study (Fig. 3).

Kubis et al. (2009) also found a significant geographic effect among green turtle foraging grounds along a much smaller scale in central Florida. Green turtles from 4 foraging grounds from 27.34 to 28.42°N with different forage availability grew at significantly different rates. Similar

results have been found in studies that examined green turtle growth rates from a series of geographically distinct foraging grounds in Australia over a range of 14° latitude (Chaloupka et al. 2004) and Hawaii over a range of 3° (Balazs and Chaloupka 2004). Both studies reported site-specific growth rates that were significantly different. In all 3 studies, growth rates did not increase or decrease with latitude, and all authors concluded that the variation was probably a result of local differences in food quality and quantity.

The spatial variation in growth rates leads to 3 important conclusions. First, these spatial differences and movements of turtles among spatially distinct foraging grounds create a complex pattern with substantial variation in growth rates for the NWA loggerhead population. Second, growth data from multiple foraging grounds should be integrated to generate growth or population models for a regional population. Third, differences in growth rates are a relative measure of habitat quality for loggerheads. As such, growth rates may help interpret the causes of movements among

Table 3 Mean ± SD (range) growth rates for straight carapace length (SCL) divided into 10-cm size classes by mean SCLmin

Mean SCLmin size classes (cm)	Growth rates (cm/year)		
	This study	This study restricted to 1994–2005 & 50–79 cm SCLmin	Core Sound, North Carolina, 1994–2005[a]
30–39	5.9 (2.9 & 8.9) $N = 2$		
40–49	–		
50–59	2.4 ± 2.5 (−1.4 to 12.6) $N = 47$	2.0 ± 2.2 (−1.4 to 8.6) $N = 26$	1.58 (1.17 to 2.04) $N = 44$
60–69	1.5 ± 1.5 (−0.8 to 8.8) $N = 196$	1.8 ± 1.8 (−0.7 to 8.8) $N = 89$	1.82 (1.59 to 2.05) $N = 122$
70–79	1.1 ± 1.1 (−0.5 to 5.8) $N = 130$	1.1 ± 1.0 (−0.4 to 3.8) $N = 48$	1.63 (1.25 to 2.05) $N = 43$
80–89	0.2 ± 0.4 (−0.7 to 2.5) $N = 129$		
90–99	0.2 ± 0.5 (−0.8 to 2.2) $N = 41$		
100–109	0.2 ± 0.1 (0.1 to 0.3) $N = 3$		

Values for all loggerheads except captive-released turtles are shown. Restricted data from our study are presented for comparison with data from Core Sound, North Carolina, USA. Values from our study must be used with caution because data from all years and latitudes—both of which have a significant effect on growth—are combined. N is number of growth increments

[a] Data from Braun-McNeill et al. (2008)

foraging grounds and the effects of these movements on age at maturity and reproductive output of individuals.

Temporal variation in growth rates

As in our study, analyses of temporal effects on growth rates in wild sea turtles usually confound cohort effects (largely genetic or density-dependent) with year effects (largely environmental) because the ages of the turtles are not known (Chaloupka and Musick 1997). In a study of growth in oceanic-stage loggerheads, Bjorndal et al. (2003) distinguished between year and cohort effects in known-age loggerheads based on skeletochronology. Year, but not cohort, was significant. They concluded that the lack of a significant cohort effect probably resulted from the variation in ambient temperatures and quantity of food resources experienced by individuals within each cohort during each year that would overwhelm any cohort effect. This conclusion may hold for the loggerheads in our study. Significant year effects on growth rates in green turtles have been attributed to density-dependent effects (Bjorndal et al. 2000; Balazs and Chaloupka 2004; Kubis et al. 2009), and this possibility should be explored with loggerheads.

In all of the datasets we examined, there was an insignificant trend for increasing growth rates up to 1997, when a significant decline in growth rates occurred through 2007. After 2007, growth rates leveled off or possibly began to increase (Fig. 2c,d). This function for year is conditioned on all other covariates. The North Carolina data collected from 1994 through 2005 were not analyzed for a year effect (Braun-McNeill et al. 2008); it would be interesting to determine whether there was a similar decline in growth rates in that area for the same period.

This decline in growth rates matches the period of time (1998–2007) during which there was a significant decline (43 %) in the numbers of loggerhead nests deposited in the "index survey" beaches in Florida (Witherington et al. 2009). The numbers of nests have since rebounded to 1998 levels (Florida Fish and Wildlife Conservation Commission 2012). The simultaneous declines in growth rates and nest abundance may be coincidence, but they may represent similar declines in productivity (growth and egg production) resulting from changes in the same environmental parameter(s). If changes in growth rates can be used to assess whether changes in nesting abundance are a result of environmental changes or actual changes in female

population size, then the study of growth rates would be a valuable tool in population assessment.

Trends in sea turtle abundance are primarily monitored by annual counts of nests or nesting females on nesting beaches (TEWG 2009; National Research Council 2010). Assessing population trends is critical for managing these threatened and endangered species, but difficult to accomplish. Interpreting changes in abundance without other demographic information to diagnose the cause(s) of the changes can lead to serious misinterpretations (TEWG 2009; National Research Council 2010; Bjorndal et al. 2011).

Anthropogenic threats (Jackson et al. 2001; Witherington et al. 2009) and changing environmental conditions (Chaloupka et al. 2008; Van Houtan and Halley 2011; Saba et al. 2012) have been proposed as the main drivers of fluctuations in annual numbers of nests or nesting females. Wherever immature sea turtles inhabit foraging grounds that share environmental conditions with foraging grounds of adult females, simultaneously monitoring growth rates of immature turtles and annual counts of nests or nesting females could indicate which of these drivers may be causing a given population trend. If changes in annual nest or female counts are a result of environmental factors affecting productivity, then growth rates of immature turtles should be positively correlated with counts. If an actual change in abundance is causing the change in annual counts of nests or females, then growth rates should either not change or be negatively correlated with population size because of density-dependent effects.

Kubis et al. (2009) found significant declines in green turtle growth rates from 1998 through 2005, when the study ended, at 3 coastal sites along the central Florida coast, but an inshore site, the Indian River Lagoon, had no significant change. The declines at the 3 coastal sites could suggest that growth rates in loggerheads in our study and green turtles were responding to a shared environmental parameter. Because green turtles in this area are primarily herbivorous (Kubis et al. 2009), whereas loggerheads are primarily carnivorous (Hopkins-Murphy et al. 2003), the effect is not diet specific. Factors that affect productivity across trophic levels, such as temperature, may be important.

Conclusions

Our study demonstrates the value of combining datasets from a number of research programs, as called for by the National Research Council (2010). By combining the data, we were able to evaluate spatial effects over a wide latitudinal range and to assess temporal and size-specific effects with robust sample sizes.

The significant spatial and temporal variation in growth rates of loggerheads among foraging grounds has important implications for population models. A better knowledge of the factors causing these differences in growth rates—such as environmental parameters, residence times, and movements among foraging grounds—is critical for understanding how growth rates vary among and within individuals of this long-lived species.

Several topics were identified as needing more research including growth rates of small loggerheads (<50 cm SCL) in both neritic and oceanic habitats and growth rates of loggerheads in waters south of the USA. More information on the proportion of loggerheads in the USA nesting stock that inhabit subtropical and tropical waters south of the USA is also needed. If these southern turtles do grow more rapidly, as indicated in our study, the higher productivity could have a substantial effect on population models for the USA nesting stock.

Loggerheads in our study exhibited declining growth rates with increasing size. This is a common pattern in sea turtles, but in contrast to the pattern of constant growth between 50 and 80 cm SCL found in Core Sound, North Carolina. The lack of size effect in Core Sound should be further explored; valuable insights into the regulation of growth rates could be revealed.

The potential link between growth rates of immature sea turtles and annual counts of nests or nesting females should be evaluated wherever immature sea turtles inhabit foraging grounds that share environmental conditions with foraging grounds of adult females. If changes in growth rates can be used to interpret trends in counts of nests or nesting females by distinguishing between changes in environmental factors or population abundance, this would provide an important new tool. Demographic parameters should be integrated with abundance estimates to evaluate trends in nest and female counts on nesting beaches (TEWG 2009; National Research Council 2010; Bjorndal et al. 2011).

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