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Somatic growth dynamics of West Atlantic hawksbill sea turtles: a spatio-temporal perspective

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Abstract. Somatic growth dynamics are an integrated response to environmental conditions. Hawksbill sea turtles (*Eretmochelys imbricata*) are long-lived, major consumers in coral reef habitats that move over broad geographic areas (hundreds to thousands of kilometers). We evaluated spatio-temporal effects on hawksbill growth dynamics over a 33-yr period and 24 study sites throughout the West Atlantic and explored relationships between growth dynamics and climate indices. We compiled the largest ever data set on somatic growth rates for hawksbills – 3541 growth increments from 1980 to 2013. Using generalized additive mixed model analyses, we evaluated 10 covariates, including spatial and temporal variation, that could affect growth rates. Growth rates throughout the region responded similarly over space and time. The lack of a spatial effect or spatio-temporal interaction and the very strong temporal effect reveal that growth rates in West Atlantic hawksbills are likely driven by region-wide forces. Between 1997 and 2013, mean growth rates declined significantly and steadily by 18%. Regional climate indices have significant relationships with annual growth rates with 0- or 1-yr lags: positive with the Multivariate El Niño Southern Oscillation Index (correlation = 0.99) and negative with Caribbean sea surface temperature (correlation = −0.85). Declines in growth rates between 1997 and 2013 throughout the West Atlantic most likely resulted from warming waters through indirect negative effects on foraging resources of hawksbills. These climatic influences are complex. With increasing temperatures, trajectories of decline of coral cover and availability in reef habitats of major prey species of hawksbills are not parallel. Knowledge of how choice of foraging habitats, prey selection, and prey abundance are affected by warming water temperatures is needed to understand how climate change will affect productivity of consumers that live in association with coral reefs.

Key words: climate effects; coral reefs; *Eretmochelys imbricata*; Greater Caribbean; marine turtles; multivariate ENSO index; sea surface temperature; somatic growth rates; West Atlantic.

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INTRODUCTION

Individual productivity – somatic growth and reproduction – is strongly influenced by environment, particularly in ectotherms. Rates of productivity are integrated responses to environmental conditions including temperature, habitat quality, salinity (in aquatic systems), and food quality and quantity. Thus, spatial and temporal variation in growth rates or reproductive output, either within or among individuals, carry a strong environmental signal that can be used to assess effects of long-term environmental conditions such as climate change (Ramos and González-Solís 2012).

Sea turtles are excellent models for tracking environmental change through variation in productivity. They are ectothermic and exhibit indeterminate growth, so their somatic growth rates are under strong environmental control. They are also long-lived, and members of individual populations forage over extensive areas. Both of these attributes tend to decrease effects of genetic variation on growth rates in long-term and geographically widespread studies that would occur if population turnover were rapid and genetically different populations lived in close proximity.

A challenge to studies of sea turtle growth dynamics is that, although sea turtles travel over large geographic ranges, individual studies tend to have small geographic ranges. A committee of the U.S. National Research Council (National Research Council 2010) recognized this challenge as a major impediment to assessing sea turtle populations and called for greater sharing of data among programs.

Here, we collaborate on a regional study to analyze somatic growth rates of hawksbill sea turtles (*Eretmochelys imbricata*) from 24 sites in the West Atlantic (Fig. 1) between 1980 and 2013. Individual hawksbills range widely throughout the West Atlantic. Lifestages and movement patterns have been documented by flipper tags, satellite telemetry, and genetic "tags" (reviews in Bolten 2003, Meylan et al. 2011, Campbell 2014). After spending the first years of life in oceanic habitats, hawksbills at a minimum size of about 20 cm carapace length (CL) recruit to neritic habitats. Immature hawksbills usually are resident in specific foraging areas for a few years before moving on to other foraging grounds, sometimes at considerable distances. As hawksbills approach sexual maturity, they often become site-fixed to a foraging ground that they will inhabit for many years, if not for life. These foraging aggregations are mixed stocks, drawn from rookeries throughout the West Atlantic.

Hawksbills are listed as Critically Endangered in the IUCN Red List of Threatened Species (IUCN 2015) largely due to hundreds of

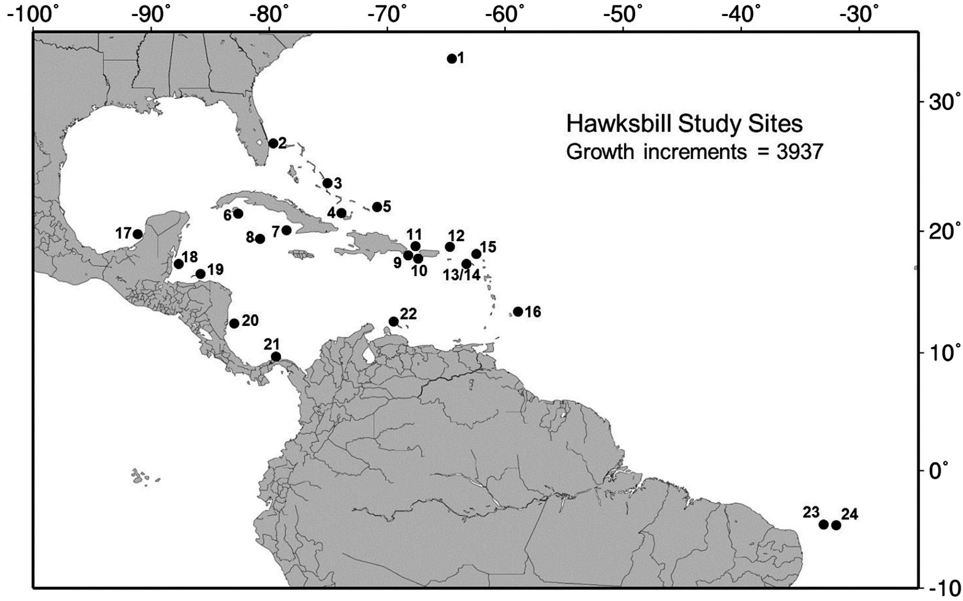

Fig. 1. Location of study sites and sample sizes based on data set with >59 d recapture durations. 1 = Bermuda (n = 6); 2 = Florida, USA (n = 36); 3 = Central Bahamas (n = 15); 4 = Great Inagua, Bahamas (n = 39); 5 = Turks and Caicos Islands (n = 65); 6 = Cuba (West) (n = 10); 7 = Cuba (East) (n = 41); 8 = Cayman Islands (n = 63); 9 = Monito Island, Puerto Rico (n = 342); 10 = Mona Island, Puerto Rico (n = 995); 11 = Desecheo Island, Puerto Rico (n = 68); 12 = Culebra Island, Puerto Rico (n = 56); 13 = St. Thomas, U.S. Virgin Islands (n = 16); 14 = Buck Island Reef National Monument, U.S. Virgin Islands (n = 19); 15 = British Virgin Islands (n = 87); 16 = Barbados (n = 886); 17 = Campeche, Mexico (n = 24); 18 = Belize (n = 29); 19 = Honduras (n = 41); 20 = Nicaragua (n = 35); 21 = Panama (n = 27); 22 = Bonaire (n = 181); 23 = Atol das Rocas, Brazil (n = 239); 24 = Fernando de Noronha, Brazil (n = 617). Created with Seaturtle.org Maptool (2002).

years of intense exploitation for tortoiseshell, meat, and eggs (Meylan and Donnelly 1999). Because of their large geographic range and reliance on coral reef habitats that are suffering degradation (Jackson et al. 2014), a regional approach is needed to understand hawksbill demography, management needs, and their roles in the structure and function of marine ecosystems.

Our study has two goals. First, we consolidate the largest ever data set for growth rates of West Atlantic hawksbills and determine spatiotemporal effects on their growth dynamics over a 33-yr period. Second, we explore the relationship between growth dynamics and climate indices in the region and the potential effect of climate change on hawksbill productivity.

METHODS

Data compilation

Data on hawksbill somatic growth rates were compiled from 24 projects from the West Atlantic (Fig. 1). Some of the growth data used in analyses in this study were used previously in accounts for individual sites (Boulon 1994, Diez and van Dam 2002, Blumenthal et al. 2009, Bjorndal and Bolten 2010, Krueger et al. 2011, Hart et al. 2013, Wood et al. 2013, Hawkes et al. 2014). All turtles were captured in neritic waters (not on nesting beaches) and tagged for individual identification. Data were collected on capture dates, CL, location, and habitat type (reef, hard bottom, cliff wall, seagrass, or mixed [includes "unknown"]). Sex was usually not determined, so was not included in analyses.

Carapace length is the most common measure of body size and is measured in a variety of ways (Bolten 1999). See Appendix S1 for treatment of various CL measurements. We used the average of CL at capture and recapture to estimate size for the growth increment (Chaloupka and Limpus 1997). Because measurement error can cause both over- and underestimation of size, negative growth rates, which result from either measurement error or damage to carapace margins, were included in analyses to avoid systematic bias.

The initial compilation of hawksbill growth data resulted in 4676 growth increments for 1822 individual hawksbills with durations from 1 to 5185 d. Minimum duration between capture and recapture is an important criterion in growth studies; including short intervals can substantially increase the sample size of growth increments (Hawkes et al. 2014). However, measurement error can be a large proportion of the change in size during a short duration, and, in seasonal habitats, short intervals may only encompass the peak or nadir of seasonal growth rates leading to large errors when extrapolated to annual growth rates. The standard duration in sea turtle studies for many years has been >11 months (Chaloupka and Limpus 1997) based on the rationale that this interval would avoid seasonal effects and measurement error would be an acceptably small proportion of the growth increment. However, in a recent study of hawksbill growth in the British Virgin Islands, 60 d was used as the minimum duration (Hawkes et al. 2014). To set the minimum duration for our study, we used the value above which duration did not have a significant effect on our growth models, which was 146 d (see Appendix S2).

Statistical methods

Factors and/or covariates affecting hawksbill somatic growth rates are explored using generalized additive nonparametric regression models with fixed and random or mixed effects, referred to as a generalized additive mixed model (GAMM). This modeling approach allows for flexible specification of both error and link functions, enables arbitrary specification of the functional form for each continuous covariate included in the model, and accounts for mixed effects from multiple measurements on the same sampling unit such as location (Fahrmeir and Lang 2001) and each individual turtle (Chaloupka and Balazs 2005). Descriptions of how GAMMs were fitted, and visualization of any GAMM-estimated spatial trend over time effect are given in Appendix S3.

The importance of explicitly accounting for the multilevel sampling heterogeneity (the random effects attributable to the sampling design constraints) using a GAMM was evaluated using the following approach presented in Gilman et al. (2012): (1) fit a generalized additive model (GAM) instead using the same data and fixed effect variables and extract the deviance residuals; (2) fit a linear mixed effects model to the residuals using a constant parameter-only model with the same random effects included in the GAMM; (3) fit a linear fixed effects model to the residuals using a constant parameter-only model; and (4) compare the fit of the two models using AIC or a log-likelihood ratio test (see Wood 2006) – where a smaller comparative AIC value indicates a relatively better fitting model. Hence, using both AIC as a guide and the log-likelihood ratio test as a formal test, we could determine whether inclusion of random effects was necessary. These linear mixed effects models (LME) were fit using the *lme*() function in the *nlme* R package (Pinheiro and Bates 2000) while linear fixed effects models (LM) were fit using the *lm*( ) R function (Pinheiro and Bates 2000).

There is no accepted way to formally estimate model fit for GAMMs (see Wood 2006), so we used an *ad hoc* approach (Gilman et al. 2012), by first fitting an equivalent GAM to derive the percent deviance explained (a measure of GAM goodness-of-fit: see Hastie and Tibshirani [1990]). If the inclusion of the random effects was found to be necessary then the GAMM should account for more of the deviance than the equivalent GAM.

We used a mixed longitudinal sampling design (sampling with partial replacement). In our primary data set with durations >145 d (see below), 47% of 1631 individual turtles were recaptured more than once. Our models had one response variable (somatic growth rate) and 10 potential covariates: seven fixed effects and three random effects (project, individual turtle, initial year of recapture interval). The seven fixed effects comprised five continuous covariates – mean CL, mean year, duration of growth increment, initial month of growth increment, and location (either spatio-temporal or just spatial depending on the model) and two factors: habitat and CL code (whether measured as straight CL [SCL] or curved CL [CCL]). Mean CL is the arithmetic mean of SCL notch to tip (see Appendix S1) at initial capture and recapture. Mean year is the calendar year of the midpoint of the recapture interval. This approach introduces little error in calendar year assignment because 77% of growth records had durations <2 yr. Recapture interval was included to evaluate any bias from variable durations. In our spatio-temporal model, we assigned growth increments to four epochs by mean year: 1980–1995, 1996–2001, 2002–2007, and 2008–2013 (number of growth increments = 206, 855, 1695, 785, respectively). Epochs were of equal length except the first, which was longer because of fewer data in those years. In GAMM analyses, each covariate is conditioned on all other covariates. For example, any differences in CL of turtles in different regions or different years would be accounted for in assessments of spatial or temporal effects. The GAMM code for the spatial model is: gamm4(grow.rate ~ habitat + cl.code + s(mean.cl) + s(mean.year) + s(log(duration)) + s(month, bs = ″cc″) + t2(lon, lat, bs = ″ds″, m = c(1,.5)), random = ~(1∣Year) + (1∣turtle) + (1∣project)).

RESULTS

Our data set – with durations >145 d – is composed of 3541 growth increments for 1631 individual hawksbills ranging in duration from 146 to 5185 d. SCLnt values from all turtle captures (n = 7082) range from 19.0 to 89.7 cm, and mean SCLnt values for all growth increments (n = 3541) range from 21.6 to 89.6 cm. Mean year of growth rate increments ranges from 1980 to 2013. Growth rates from all growth rate increments vary from −2.1 to 22.6 cm/yr with a mean ± SD of 3.1 ± 2.3 cm/yr. Mean CL of growth increments did not change over time (linear regression, $R^2 = 0.0007$, $P = 0.108$).

We conducted two GAMM analyses – a full spatio-temporal model and a spatial model collapsed over time – to explore fixed and random effects. The spatio-temporal interaction was not significant, so we only present the spatial model (Figs. 2 and 3). Lack of a significant spatio-temporal interaction indicates that changes in growth rates over time were consistent throughout the region.

The linear mixed model with random effects (LME) was a significantly better fitting model than a linear model (LM) that did not account for sampling year, project and turtle-specific heterogeneity (AIC for LME = 13,645.94 compared to LM AIC = 13,915.17, log-likelihood ratio test $\chi^2_{0.05} = 275.2$, df = 3, $P < 0.001$). Thus, inclusion of the random effects in the GAMM was warranted. In addition, the variance term for all random effects was >0, providing further support for inclusion of the three random effects. Because the generalized additive model (GAM) equivalent model accounted for 42% of the hawksbill

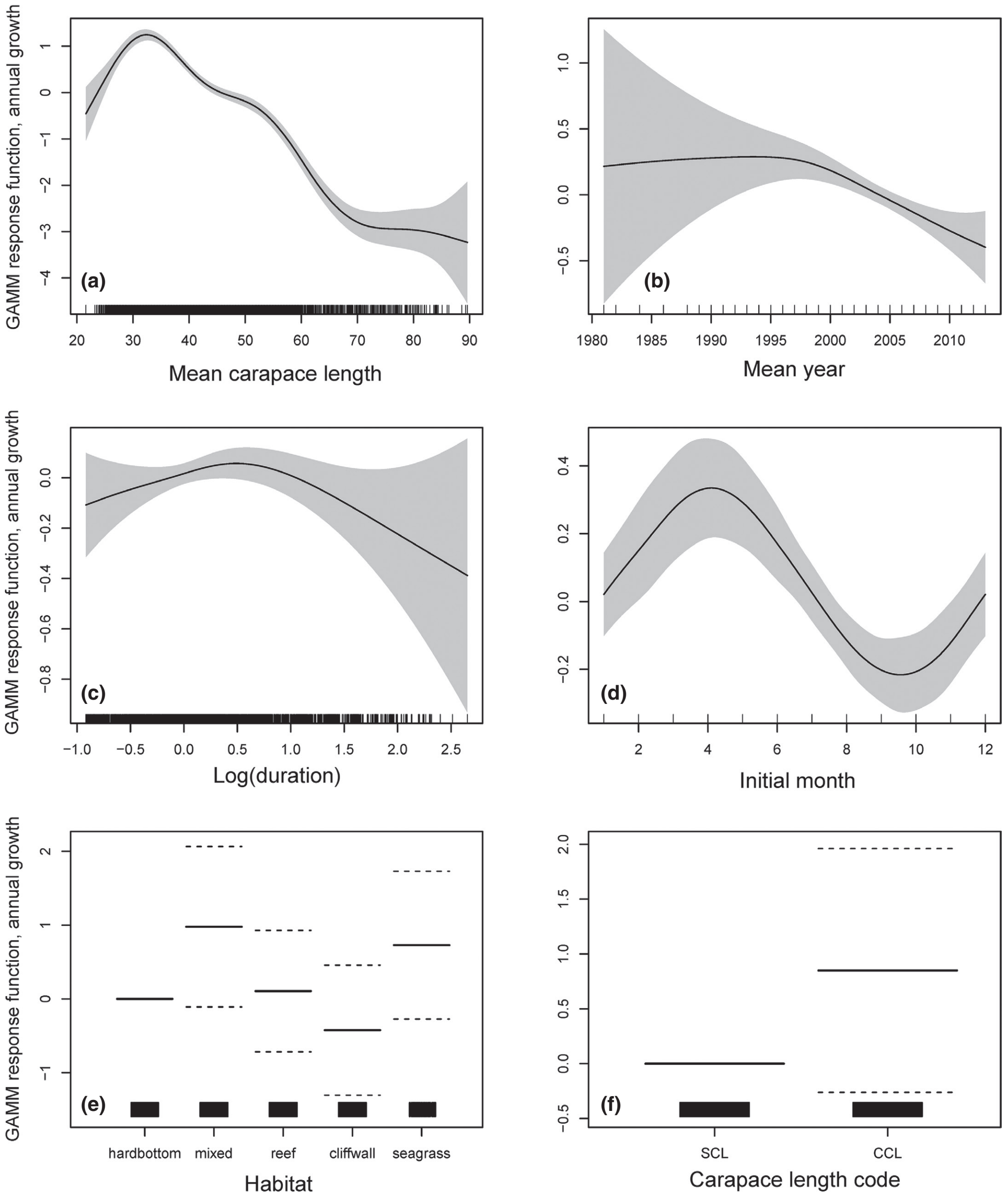

Fig. 2. Graphical summary of GAMM analysis. The response variable (mean annual growth rate) is shown on the *y*-axis as a centered smoothed function scale to ensure valid pointwise 95% confidence bands. The covariate is shown on the *x*-axis: (a) mean straight carapace length (cm) (df = 7.65), (b) mean year (df = 2.26), (c) duration (original data were in days) (df = 2.44), (d) initial month (df = 3.15), (e) habitat, (f) CL code for straight carapace length (SCL) or curved carapace length (CCL). Solid curves are the smoothing spline fits conditioned on all other covariates. Shaded areas are bounded by pointwise 95% confidence curves around the fits. All covariates are significant except duration, habitat and CL code. Rug plots indicate smaller sample sizes at large body size and long durations.

growth data variance, the GAMM model would explain >42% of the model deviance. Therefore, this GAMM was an adequate fit to the data with significant nonlinear effects and no aberrant residual behavior using *gam.check*() for model fit diagnostics (see Wood 2006).

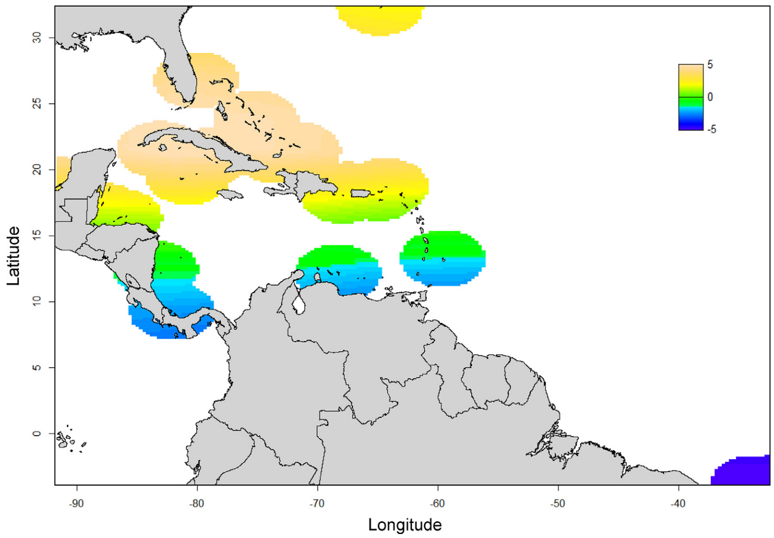

Fig. 3. Structured spatial effect from GAMM analysis. Trend for decreasing growth rates from north to south is not significant ($P = 0.480$). The color scale is the centered GAM scale as for all the GAM(M) plots (e.g., Fig. 2) to allow comparison among plots. Dark blue = lowest growth rates; beige = highest growth rates.

The nonsignificant fixed effects (Fig. 2) are duration ($P = 0.085$), CL code ($P = 0.127$), capture habitat (all habitats, $P > 0.05$), and capture location on the latitude/longitude surface ($P = 0.480$). We selected the range of recapture durations (>145 d) so that duration would not affect the model (Fig. 2c). Nonsignificance of CL code validates combining SCL and CCL growth data. Capture habitat was not characterized well at several of the 24 project sites, so the effect of this covariate should be further examined in future studies. Lack of a significant spatial effect indicates that growth rates in hawksbills throughout the region respond equivalently. There is, however, a nonsignificant trend for growth rates to decrease from north to south in our study region (Fig. 3). Significant spatial effects have been reported for hawksbills between two of our study sites, the Puerto Rican islands of Mona and Monito (Diez and van Dam 2002) that are separated by about 5.3 km. Such differences measured at sites at short distances from each other may well be swamped by the variation among the many sites at the regional scale of our study.

Significant fixed effects are mean CL ($P < 0.0001$, Fig. 2a), initial month of the growth increment ($P < 0.0001$, Fig. 2d), and mean year of the growth increment ($P = 0.0003$, Fig. 2b). Growth rates increase over the size range from 20 to 32 cm SCLnt and then decline to a size of about 70 cm SCLnt at which size hawksbills approach maturity and growth rates slow (Fig. 2a). Results of sea turtle growth studies are often presented for 10-cm CL size classes. To allow our results to be compared with future studies, we have provided the values in Appendix S4.

The significant effect of initial month is apparently a result of the greater probability of a growth increment including more time in months that best support growth when the interval begins in those months. When the model is run with durations limited to about 1 yr (330 to 400 d), this effect disappears (Appendix S5); the significance of all other covariates remained the same (Appendix S2: Table S1).

The significant effect of mean year begins in 1997, after which growth rates significantly decline (Figs. 2b and 4a) by 18% from an annual mean of 3.76 to 3.08 cm/yr. To evaluate possible environmental drivers for the significant region-wide effect of mean year on growth rates, we related mean annual growth rates generated from our GAMM analysis to Caribbean sea surface temperature (SST) and the Multivariate El Niño Southern Oscillation Index (MEI). We used the MEI due to the climatic teleconnections between the tropical Pacific and tropical Atlantic (Giannini et al. 2001). The MEI integrates six variables in the eastern tropical Pacific Ocean as a proxy for the El Niño Southern Oscillation: sea surface temperature, surface air temperature, sea-level pressure, two components of surface winds, and total cloudiness of the sky (Mazzarella et al. 2013). We sourced MEI bimonthly data from 1950 to present (http://www.esrl.noaa.gov/psd/enso/mei/table.html) and annualized the bimonthly index to an annualized index. We then ran a GAMM with autoregressive (AR1) error to reveal any underlying annual trend since 1950 (Fig. 4b) and lag plotted the GAMM trend MEI against mean annual growth rates (Fig. 5a, b) for 0- to 11-yr lags with *astsa* package for R (Stoffer 2014). We followed a similar approach with Caribbean SST data. The SST anomalies are based on NOAA erSST (version 3b; 2 × 2 degree; https://www.ncdc.noaa.gov/data-access/marineocean-data/extended-reconstructed-sea-surface-temperature-ersst-v3b) using climatology from 1980 to 2013 (Figs. 4c and 5c, d). The MEI has a positive relation with mean annual growth rates and a substantially better fit than SST, which has a negative relation with annual growth rate. The best fit for both MEI (correlation 0.99) and SST (correlation −0.85) is for a 0- or 1-yr lag, indicating that growth in a given year is a function of MEI or SST from the previous 12 months. There is a threshold between 26.4 °C and 26.5 °C for the relationship between SST and growth rates (Fig. 5c, d). At lower temperatures, SST has no effect on mean annual growth rates of hawksbills; above the threshold, SST is inversely related to growth rates.

Discussion

Effect of body size on growth rates

Body size almost always has a significant effect on sea turtle growth rates, although the shape of the response function varies (Chaloupka and Limpus 1997). In Atlantic hawksbills, growth functions are usually nonmonotonic with a peak at about 35 cm SCL, whereas in most Pacific hawksbill populations, growth rates peak at between 50 and 60 SCL (references in Bjorndal and Bolten 2010). These changes in slopes and variation in sizes at which peak growth occurs almost certainly represent important changes in lifestyle, such as gaining access to food resources at larger body sizes or differences in body size at recruitment to neritic habitats.

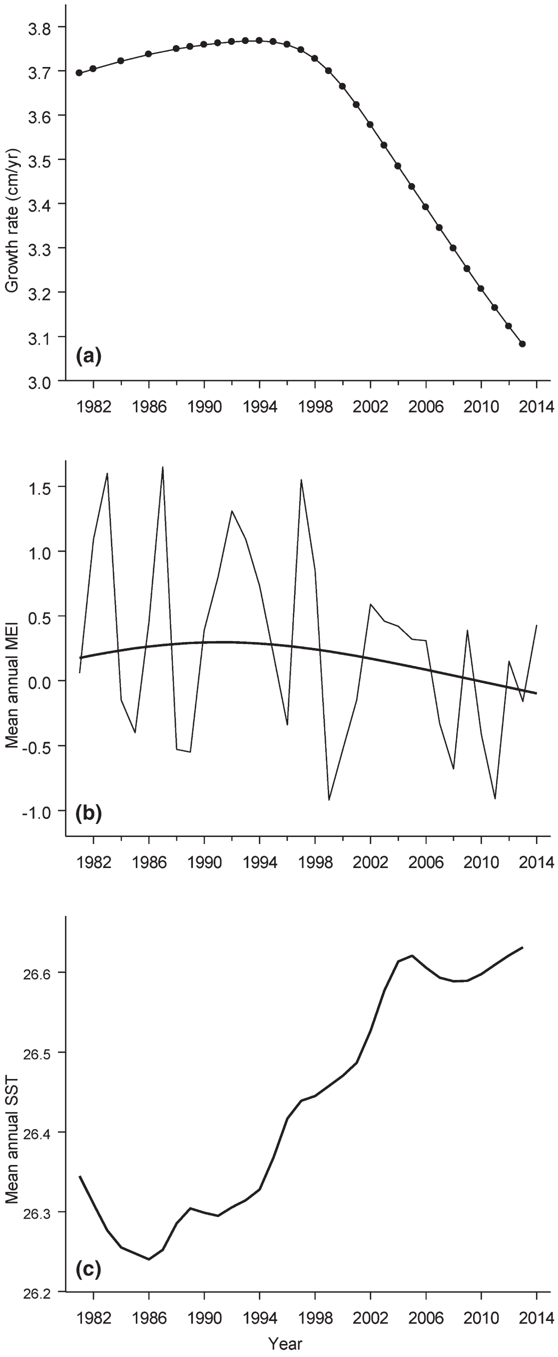

Fig. 4. Relationships between year and (a) mean annual growth rates (cm/yr) for hawksbills in the West Atlantic region, and annualized values for (b) Multivariate El Niño Southern Oscillation Index (MEI) and (c) Caribbean sea surface temperature °C (SST). Smooth line in (b) is from GAMM analysis showing underlying annual trend; MEI data from 1950 to 1980 are not shown so that *x*-axes are consistent among the graphs.

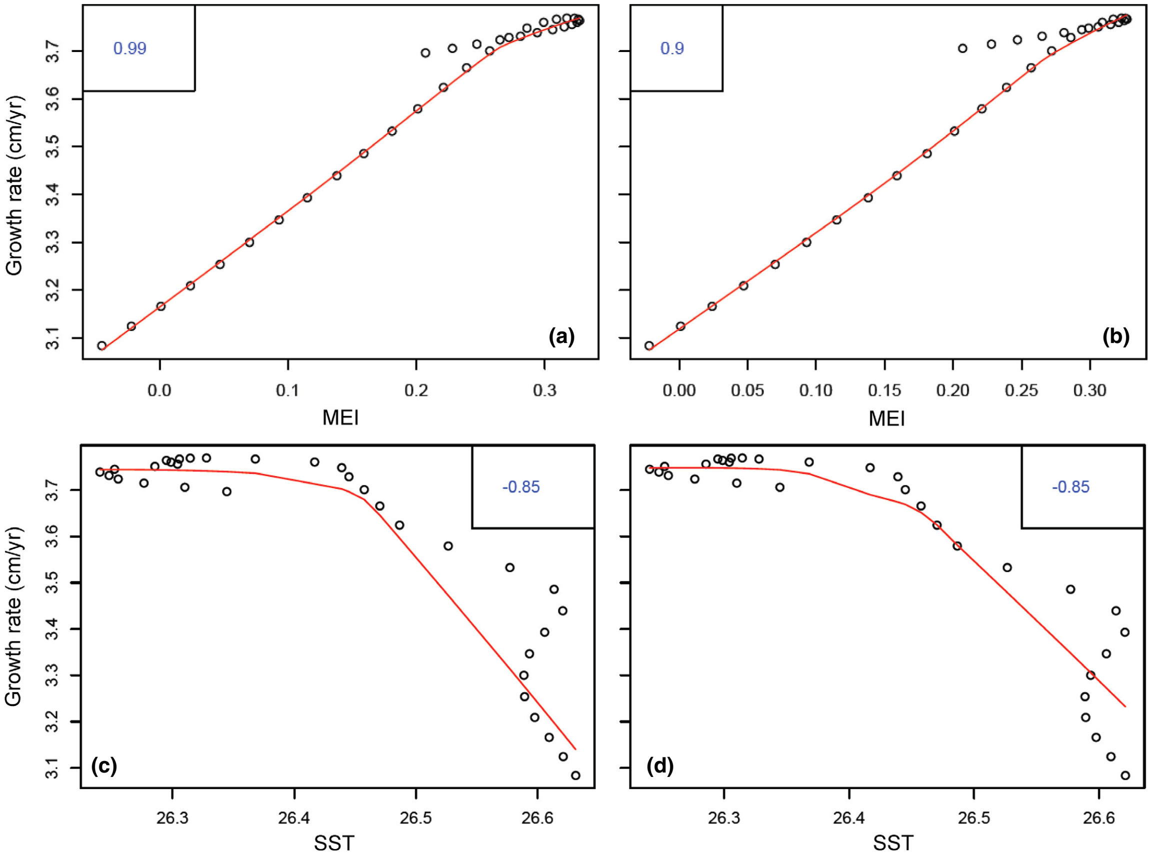

Fig. 5. GAMM trends (solid lines) of mean annual growth rates of hawksbills (open circles) lag-plotted against the annualized Multivariate El Niño Southern Oscillation Index (MEI) with (a) no lag and (b) 1-yr lag and against the annualized Caribbean sea surface temperature (SST, °C) with (c) no lag and (d) 1-yr lag. Correlation coefficients are in boxes within each graph. MEI has a substantially better fit to annual growth rates than does SST. Note the threshold between 26.4 °C and 26.5 °C for the relationship between SST and growth rates.

The slower growth rates in the smallest hawksbills in our study (Fig. 2a) probably result from nutritional challenges during the transition to neritic foraging grounds from oceanic habitats where they spend the first years of life feeding on gelatinous prey and other floating organisms (Bolten 2003). After recruiting to neritic habitats, they shift to diets dominated by sponges and other benthic invertebrates (Meylan 1988, Krueger et al. 2011). Sponges have both physical and chemical defenses that can make them difficult to digest by sea turtles (Bjorndal 1990). This period of limited nutrition during adjustment to a new habitat and diet could be followed by a period of compensatory growth during which turtles would exhibit more rapid growth. Compensatory growth and growth responses to periods of limited feeding followed by *ad libitum* feeding have been demonstrated in juvenile sea turtles (Bjorndal et al. 2003, Roark et al. 2009). Very rapid growth rates recorded for two small hawksbills in The Bahamas (14.3 and 15.6 cm/yr; Bjorndal and Bolten 2010) and one in the British Virgin Islands (10.9 cm/yr; Hawkes et al. 2014) may well represent compensatory growth.

After the peak at about 32 cm SCLnt, growth rates in our study decline until, upon reaching sexual maturity, growth greatly slows and approaches zero. Between about 45 and 52 cm SCLnt, the decline in growth rates slows (Fig. 2a). This period of slower decline is intriguing because of its similarity to the size at which many Pacific populations exhibit peak growth rates. Further interpretation of shapes of growth functions and comparisons among regions requires additional data on changes in habitat, prey selection, and food intake with increasing body size in hawksbills.

Environmental drivers of temporal changes in growth dynamics

The decline in West Atlantic hawksbill growth rates since 1997 is strongly correlated with warming sea surface temperatures (SST) and the Multivariate ENSO Index (MEI), with a better fit with the latter. The El Niño Southern Oscillation (ENSO) originates in the tropical Pacific and has strong global impacts on climate fluctuation over inter-annual time-scales (Mazzarella et al. 2013). The ENSO is represented by several indices, but the MEI is currently considered the most representative index (Mazzarella et al. 2013) because it combines six meteorological parameters as described above. The ENSO affects tropical Atlantic SST, rainfall, and associated regional-scale ocean-atmosphere anomalies in the region (Giannini et al. 2001). Strong correlations between the MEI, SST, and rainfall have been revealed throughout our study area (Spillman et al. 2011, Gouirand et al. 2014). The extent and possible drivers of the MEI teleconnection have been evaluated for the West Atlantic, including the Caribbean, northern and northeastern South America, Gulf of Mexico, and South Florida (Simonti and Eastman 2010, Gouirand et al. 2012, Gonzalez et al. 2013, Misra and DiNapoli 2013, Park and Dusec 2013, Munroe et al. 2014). The nonsignificant trend for hawksbill growth rates to decrease from north to south in our study region (Fig. 3) is consistent with our conclusion that growth rates are slower at higher temperatures in our study region.

Inverse relationships have also been shown between SST and sea turtle reproductive productivity. In Pacific loggerheads, *Caretta caretta*, regardless of whether the population was increasing or decreasing, nesting abundance was inversely correlated with mean annual SST in the major foraging region during the year before the summer nesting season (Chaloupka et al. 2008). The authors posited that cooler temperatures are associated with increased productivity and prey abundance in foraging habitats that result in increased loggerhead reproductive productivity. Correlations between SST or climate indices and numbers of nesting sea turtles with no or short lags have been reported for Pacific green turtles, *Chelonia mydas* (Limpus and Nicholls 2000, Chaloupka 2001), Pacific leatherbacks, *Dermochelys coriacea* (Saba et al. 2007), hawksbills in the Gulf of Mexico (del Monte-Luna et al. 2012), and Atlantic loggerheads (Arendt et al. 2013). However, Atlantic green turtles (Solow et al. 2002) exhibited a positive relationship between winter SST anomalies and annual breeding probability. Somatic growth rates in Atlantic loggerheads had a similar year effect to that reported in this study for hawksbills, with growth rates decreasing after 1997; water temperature was suggested as a primary cause (Bjorndal et al. 2013).

The inverse relationship between temperature and hawksbill growth rates – and, perhaps, reproductive productivity in other sea turtle species – most likely results from indirect effects such as benthic productivity, rather than from direct inhibition of hawksbill productivity through metabolic effects. The MEI, which is correlated with tropical Atlantic SST and other environmental variables that would affect ecosystem productivity, is a much better predictor of annual mean hawksbill growth rates than SST alone. In addition, the threshold between 26.4 °C and 26.5 °C mean annual Caribbean SST for the temperature effect on growth rates (Fig. 5c, d) may indicate that in years with mean temperatures above 26.5 °C, maximum temperatures are often high enough to trigger negative effects on hawksbill growth (e.g., 29 °C). The temperature threshold for mass bleaching events, which usually ranges from 29 °C to 32.8 °C, is "surprisingly low for tropical organisms to suffer high mortality" (Baird et al. 2009). In this same temperature range, hawksbills apparently function normally (Nodarse et al. 1998, NMFS and USFWS 2013, Pilcher et al. 2015). Usually during bleaching events, symbiotic organisms, such as corals, sea anemones, corallimorpharians, zoanthids, and sponges, suffer mortality (McClanahan et al. 2009). The last four groups are important prey for hawksbills in the West Atlantic.

Hawksbills live in close association with coral reefs throughout their Atlantic range (Campbell 2014). Therefore, it is tempting to suggest that the decline in hawksbill growth rates is directly related to the well-documented degradation of coral reefs in the Greater Caribbean and decrease in coral cover that have occurred over a similar time frame (Selig et al. 2012). Jackson et al. (2014) summarized data on past and present status of Caribbean coral reefs and concluded that the phase shift from coral to macro-algal dominance reached a peak in the mid-1990s and has continued in most areas to the present, resulting in a "modern era of massively degraded coral reefs."

Although hawksbill growth and coral reef declines are probably inter-related through a shared driver of climate, the relationship is not a simple one. Hawksbills throughout our study area feed primarily on sponges, zoanthids, corallimorpharians, and other benthic invertebrates associated with coral reefs rather than on corals themselves (references in Krueger et al. 2011). In some areas within our study region, abundances of sponges, corallimorpharians and zoanthids have declined as a result of diseases, thermal stress, or over-harvesting for the aquarium trade (Peterson et al. 2006, Wulff 2006, McClanahan et al. 2009, Torres-Pratts et al. 2011). In other areas, however, sponges – including species known to be preferred prey of hawksbills – and corallimorpharians are increasing on coral reefs, and models predict that their populations will increase with climate change and will not be negatively affected by ocean acidification (Hawkes et al. 2009, Norström et al. 2009, Colvard and Edmunds 2011, Bell et al. 2013, Loh et al. 2015).

These different trajectories in quality of coral reef habitats and potential abundance of hawksbill prey make it difficult to decipher effects of climate change on hawksbill growth dynamics. Data on effects of warming water temperatures on trophic dynamics in hawksbills (i.e., choice of foraging habitats, prey selection, and prey abundance) are needed to understand how climate change will affect hawksbill demographic parameters and productivity.

Density-dependent effects – although they cannot be dismissed – probably have not affected somatic growth rates on a region-wide basis given that modern populations of hawksbills in the West Atlantic are a fraction of historical population sizes as a result of historic over-exploitation (Meylan and Donnelly 1999, McClenachan et al. 2006). Increases in nest abundance reported for some areas in recent years have not been sufficient to recover these densities, even considering reductions in reef habitats (NMFS and USFWS 2013, Campbell 2014).

CONCLUSIONS

Our study underscores the value of combining studies for regional analyses of sea turtle biology with large spatial and temporal scales. The lack of a spatial effect or spatio-temporal interaction and the very strong temporal effect reveal that growth rates in West Atlantic hawksbills are driven by region-wide forces. The close association of annual growth rates with the MEI and Caribbean SST indicates that the decline in hawksbill growth rates since 1997 is probably an indirect response to increasing temperatures and climate.

A greater research emphasis is needed on environmental parameters during studies of sea turtle biology. Studies are needed on effects of habitat quality and prey density on sea turtle productivity; density-dependent effects; and changes in habitat, prey selection, and food intake with increasing body size in sea turtles. Knowledge of how choice of foraging habitats, prey selection, and prey abundance are affected by warming water temperatures is needed to understand how climate change will affect sea turtle demographic parameters and productivity. In addition, improved quantification of thermal limits on all sea turtle life stages is critical for evaluating effects of climate change on their ecology, behavior, physiology, and productivity.

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