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Ecological regime shift drives declining growth rates of sea turtles throughout the West Atlantic

Running head: Regime shift drives declining growth rates

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Abstract

Somatic growth is an integrated, individual-based response to environmental conditions, especially in ectotherms. Growth dynamics of large, mobile animals are particularly useful as bio-indicators of environmental change at regional scales. We assembled growth rate data from throughout the West Atlantic for green turtles, *Chelonia mydas*, which are long-lived, highly migratory, primarily herbivorous mega-consumers that may migrate over hundreds to thousands of kilometers. Our dataset, the largest ever compiled for sea turtles, has 9690 growth increments from 30 sites from Bermuda to Uruguay from 1973 to 2015. Using generalized additive mixed models, we evaluated covariates that could affect growth rates; body size, diet, and year have significant effects on growth. Growth increases in early years until 1999, then declines by 26% to 2015. The temporal (year) effect is of particular interest because two carnivorous species of sea turtles – hawksbills, *Eretmochelys imbricata,* and loggerheads, *Caretta caretta* – exhibited similar significant declines in growth rates starting in 1997 in the West Atlantic, based on previous studies. These synchronous declines in productivity among three sea turtle species across a trophic spectrum provide strong evidence that an ecological regime shift (ERS) in the Atlantic is driving growth dynamics. The ERS resulted from a synergy of the 1997/1998 El Niño Southern Oscillation (ENSO) – the strongest on record – combined with an unprecedented warming rate over the last two to three decades. Further support is provided by the strong correlations between annualized mean growth rates of green turtles and both sea surface temperatures (SST) in the West Atlantic for years of declining growth rates (r = -0.94) and the Multivariate ENSO Index (MEI) for all years (r = 0.74). Granger-causality analysis also supports the latter finding. We discuss multiple stressors that could reinforce and prolong the effect of the ERS. This study demonstrates the importance of region-wide collaborations.

Introduction

Marine systems have undergone great changes in ecosystem function and species distribution and abundance in the Anthropocene (Jackson *et al.*, 2001; Lotze *et al.*, 2006; Alheit 2009; Halpern *et al.*, 2015; McCauley *et al.*, 2015). Some of these changes have resulted in or resulted from ecological regime shifts (ERS), defined by Conversi *et al.* (2015) as "dramatic, abrupt changes in the community structure that are persistent in time, encompass multiple variables, and include key structural species – independently of the mechanisms causing them." Many studies have evaluated the changes that result from ERS in structure and function of ecosystems; biogeography, phenology, and abundance of species; and foodwebs or trophodynamics (references in Alheit & Bakun, 2010; Rocha *et al.*, 2015; Young *et al.*, 2015). However, fewer studies have addressed longterm physiological changes at the individual level across regional landscapes in this era of changing seas. Here we evaluate somatic growth dynamics of the green turtle (*Chelonia mydas*) throughout the West Atlantic across more than four decades (1973-2015).

Somatic growth rates of ectotherms are valuable bio-indicators of environmental change because their growth dynamics are strongly influenced by environmental conditions and are an integrated response to changes in these conditions. Sea turtles are long-lived, highly migratory mega-consumers and are therefore excellent models for such environmental monitoring. Green turtles, hawksbills (*Eretmochelys imbricata*), and loggerheads (*Caretta caretta*) spend decades in neritic habitats growing to sexual maturity. During this immature period, individuals may move hundreds to thousands of kilometers among foraging grounds (Musick & Limpus, 1997).

Many of the authors of the present study collaborated on earlier studies of somatic growth dynamics in West Atlantic hawksbills (Bjorndal *et al.*, 2016) and Northwest Atlantic loggerheads (Bjorndal *et al.*, 2013) based on capture-mark-recapture data and using a similar modeling approach. These studies revealed that growth rates for hawksbills and loggerheads exhibited similar, continuing declines beginning in 1997. The same pattern of decline was reported for North Atlantic loggerheads based on a different technique (skeletochronology) and a different sample of loggerheads (Avens *et al.*, 2015). Hawksbills and loggerheads are primarily carnivorous, although they feed on different types of prey. Hawksbills feed mostly on sponges, corallimorpharians, zoanthids, and sea anemones associated with coral reefs (references in Krueger *et al.*, 2011). Loggerheads prey most commonly on slow-moving or sessile, hardshelled benthic invertebrates (Hopkins-Murphy *et al.,* 2003).

In 1997/1998, an ERS occurred in the Atlantic as a result of a synergy between the abrupt warming from the strongest El Niño Southern Oscillation (ENSO) event ever recorded and the unprecedented warming rate over the last two to three decades (Martinson *et al.,* 2008; Reid & Beaugrand, 2012; IPCC, 2014; Beaugrand *et al.,* 2015; Wijffels *et al.*, 2016). The decline in hawksbill and loggerhead growth rates may have been a response to this ERS. A study of somatic growth dynamics of the primarily herbivorous green turtle would reveal the extent to which patterns of regional changes in productivity hold across trophic levels. If growth in green turtles follows the same pattern, the probability that the growth dynamics of all three species are responses to widespread climatic drivers and an ERS would be greatly increased. Therefore, we assembled growth rate data for West Atlantic green turtles resulting in the largest (n = 9690 growth increments, longest (from 1973 through 2015), and most widespread (from Bermuda to Uruguay) dataset ever compiled for sea turtles.

In this paper, we have three objectives: (1) evaluate West Atlantic green turtle growth dynamics with generalized additive mixed models, (2) compare the temporal dynamics of green turtles with those of West Atlantic hawksbills and North Atlantic loggerheads, and (3) explore relationships of temporal growth trajectories with Multivariate El Niño Southern Oscillation Index (MEI) and sea surface temperature (SST). These drivers were selected because they are the most likely drivers of the ERS in the late 1990s (Martinson *et al.*, 2008; Reid & Beaugrand, 2012; Beaugrand *et al.*, 2015).

Materials and Methods

Data assembly

Green turtle growth rate data were combined from 30 projects in the West Atlantic (Fig. 1). Some of these data have been published in studies for individual sites, but never in regional assessments. Turtles were captured by a variety of methods in foraging areas in neritic habitats and not on nesting beaches. Turtles were tagged, usually with flipper tags, for individual identification. Data used in this study are capture date and location (latitude/longitude), carapace length (CL, the most common measure of body size in sea turtles), and primary diet at each site. Sex is known for a small fraction of individuals so is not used in our analyses. Body size for each growth increment is the average of CL at capture and recapture (Chaloupka & Limpus, 1997). Negative growth rates, which result from either measurement error or damage to carapace margins, are included in analyses to avoid systematic bias.

When the growth data were first assembled, durations (time-at-large) of the growth increments varied from 1 to 7636 d. Including growth increments with short or long durations can introduce substantial error. Short durations may only capture the fastest or slowest of seasonal growth rates, resulting in large errors when extrapolated to estimates of annual growth, or the change in size may be so small that measurement error is a large proportion of actual growth. During long durations, average CL may not represent a good estimate of body size for the interval. To set the minimum and maximum durations for our analyses, we followed Bjorndal *et al.* (2016) to determine the limits within which duration did not significantly affect our growth model. We created a dataset in which 60 days was the minimum duration (n = 9690) and, based on the generalized additive mixed model (below), determined that 330 and 1644 d were the minimum and maximum values. Our minimum value is the same as the standard that has been used for many years in sea turtle studies (Chaloupka & Limpus, 1997), giving further support to the standard minimum. To increase sample size, successive growth increments for individual turtles below the 330 d limit were combined to exceed the minimum duration when possible.

Statistical methods

Generalized additive nonparametric regression models with fixed and random effects – often referred to as generalized additive mixed models (GAMM) – were used to explore somatic growth rates. 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 & Lang, 2001). Our model used scaled Student-t (scat) likelihood based on findings from a gamboostLSS model as in Gilman *et al.* (2016) that showed Student-t likelihood is better than Gaussian for our model.

The GAMMs were fitted using the following: (1) thin plate regression splines to model nonlinear covariate effects; (2) a two-dimensional Duchon-spline surface smoother to account for structured spatial effects attributable to the geospatial location (latitude, longitude) of each project site; (3) a tensor product of a 2D Duchon-spline surface and a time effect with cubic regression spline basis to account for any spatial trend in time (Marra *et al.*, 2012), where time is blocks of years (= epochs); and (4) project-specific heterogeneity incorporated as a random effect term to account for the multilevel sampling structure of the dataset. This spatially explicit GAMM is generally referred to as a geoadditive GAMM (Kammann & Wand, 2003). All GAMM models were fitted using the *mgcv* package for R (Wood & Scheipl, 2014) with the smoothness parameters estimated using REML (Wood, 2006).

We use a mixed longitudinal sampling design (sampling with partial replacement); 1318 (33%) of 3958 individual turtles were recaptured more than once. In our GAMM analyses, we assess six fixed effects and one random effect (project collecting the data, n = 30) on one response variable (somatic growth rate). Of the six fixed effects, two (diet and CL type) are each four-level factors. Diet is the primary diet for the site: seagrass, algae, seagrass/algae mix, and omnivorous. CL type is the specific CL metric used (see Appendix S1 in Supporting Information). The other four fixed effects are continuous covariates (mean CL of growth increment, mean year of growth increment, duration of growth increment, and location on a latitude/longitude surface or a location/temporal interaction term). Mean CL is the arithmetic mean of straight CL notch to tip (SCLnt, see Fig. S1-1 in Appendix S1 Supporting Information) 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 72% of growth records had durations <2 yr. Recapture interval was included to evaluate any bias from variable durations. For the spatio-temporal interaction, we use an interaction term of location by epoch. The four epochs have nearly equal sample sizes based on mean year (1974-1999, 2000-2006, 2007-2010, 2011-2015). Number of growth increments in each epoch is 1470, 1421, 1486, and 1824, respectively. We conducted two GAMM analyses – a spatial model and a spatio-temporal model – to explore the importance of spatio-temporal interaction. 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 R code for the spatio-temporal model is: `mgcv(data.gam <- gam(grow.rate ~ diet + cl.type + s(mean.size) + s(mean.year, k=4) + s(duration) + te(lon, lat, by=decade, bs="ds", m=c(1,.5)) + s(project, bs="re"), family=scat(link="identity"), method="REML")`.

Annualized mean growth rates are expressed as standardized values ([Annual value - mean of annual values]/SD of annual values) to allow direct comparison among the three sea turtle species. To evaluate whether the significant region-wide effect of mean year on growth rates was related to the two drivers proposed for the Atlantic ERS beginning in the mid-1990s (ENSO and ocean heating), we related annualized mean growth rates generated from our GAMM analysis to the MEI and SST. We selected the MEI to represent ENSO because it is currently considered the most representative index (Mazzarella *et al.*, 2013) and reflects ecological changes well because it integrates six variables in the eastern tropical Pacific Ocean as a proxy for the ENSO: SST, surface air temperature, sea-level pressure, two components of surface winds, and total cloudiness of the sky (Mazzarella *et al.*, 2013). Climate teleconnection between the Pacific and Atlantic is strong with the ENSO affecting Atlantic SST, rainfall, and associated regional-scale ocean-atmosphere anomalies in our study region (Giannini *et al.*, 2001; Spillman *et al.*, 2011; Gouirand *et al.*, 2014) and Atlantic warming possibly triggering ENSO events in the Pacific (Ham *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 and lag plotted the GAMM trend MEI against annualized mean growth rates for 0- to 11-yr lags with *astsa* package for R (Stoffer, 2014). We followed a similar approach with SST data. Because of the variation in temporal and spatial coverage of our growth data, rather than use the SST values for the entire region, we used mean SST values from 625 km^2 around three sites (Bermuda; Inagua, The Bahamas; and Fernando de Noronha, Brazil) (Fig. 1). These three sites represent 53% of the growth increments in our study, 100% of the temporal range, and the latitudinal range of 93% of our study sites. SST data were sourced from NOAA OISST (Optimum Interpolation Sea Surface Temperature) AVHRR (Advanced Very High Resolution Radiometer) satellite data (25-km x 25-km (1/4 degree) https://www.ncdc.noaa.gov/oisst). SST data begin in 1982 when the satellite started recording data.

We also explored the relationship between somatic growth rates and MEI using a statistical forecasting approach. For instance, does an environmental driver such as MEI improve the forecasting performance of expected somatic growth rates for West Atlantic green turtles? A common test of this forecasting performance is Granger-causality analysis (Enders, 1995; Triacca, 2005). This analysis in no way assesses true causality and refers only to forecast ability while also assuming a linear dependence between the response variable and the predictor (Mariusz, 2015). See Appendix S1 (Supporting Information) for details of the Granger-causality analysis.

Results

Dataset and GAMM results

Green turtles were sampled in mixed stock foraging aggregations that include turtles from all five Atlantic regional management units (Bjorndal & Bolten, 2008; Wallace *et al.*, 2010). Our initial dataset (n = 9690) with a 60 d minimum duration for growth increments was revised to a dataset with durations from 330 to 1640 d. Our final dataset has 6201 growth increments for 3958 individual green turtles. Number of growth increments for individual turtles varies from 1 to 10 with a mean ± SD of 1.6 ± 1.1. Growth rates from all growth increments vary from −0.9 to 11.9 cm/yr with a mean ± SD of 3.4 ± 2.0 cm/yr. Green turtles were captured from 1973 through 2015, and mean year of growth increments is from 1974 through 2015. SCLnt values from all turtle captures (n = 12,402) vary from 23.2 to 117.0 cm, and mean SCLnt values for all growth increments (n = 6201) range from 24.6 to 117.0 cm. Mean CL of growth increments did not change over time (linear regression, n = 6201, P = 0.289).

In a comparison of the spatial-only and the spatio-temporal GAMM analyses, the spatio-temporal interaction is significant for each of the four epochs ($P < 0.007$), so we only present results from the spatio-temporal model (Fig. 2, Fig. S2-1 in Appendix S2 Supporting Information). The spatio-temporal model explains 34.3% of the model deviance and is an adequate fit to the data with significant nonlinear effects. Including the spatio-temporal interaction in the model only increases the deviance explained by 1.3%. Of the seven covariates in the model, four of the six fixed effects and the one random effect (projects) are significant.

Mean CL is a significant fixed effect ($P < 0.0001$; Fig. 2a). Growth rates initially increase from 25 to ~40 cm SCLnt, probably as a result of increased nutrient gain as new recruits improve foraging behavior, diet selection, and digestive processing. Growth rates then decline to a size of about 90 cm SCLnt at which size green turtles approach maturity and growth rates slow as resource allocation is shifted from growth to reproduction. The slope of the decline becomes substantially steeper around 70 cm SCLnt, perhaps because of changes in habitat, diet selection, and food intake with increasing body size. A graph of predicted growth rates (cm/yr) plotted against mean CL is presented in Fig. S2-2 (in Appendix S2 Supporting Information). For discussion of size-specific growth dynamics see Appendix S3 Supporting Information.

Mean year of the growth increment also has a significant effect ($P < 0.0001$; Fig. 2b). Growth rates increase from 1974 to 1999, although the 95% confidence interval is broad until ~1985. After 1999, growth rates exhibit a steady decline. This decline is not a result of changes in CL because, as noted above, covariates in the GAMM are conditioned on each other and mean CL values do not change over years. See Fig. S2-3 (in Appendix S2 Supporting Information) for a graph of predicted growth rates (cm/yr) plotted against mean year.

Growth rates differ significantly among diet categories (Fig. 2c). Green turtles on seagrass diets grow more rapidly than green turtles on mixed seagrass/algae, algae, and omnivorous diets ($P < 0.0001$, $P = 0.009$, and $P = 0.033$, respectively). There are no significant differences among growth rates on seagrass/algae, algae and omnivorous diets, although the difference between seagrass/algae and algae approaches significance (Fig. 2c). For discussion of role of diet in growth dynamics see Appendix S3 (Supporting Information).

The spatio-temporal interaction was significant for all epochs ($P < 0.007$; Fig. S2-1 in Appendix 2 Supporting Information) and is confounded with all remaining heterogeneity in growth rates not accounted for by the six other covariates in our model (body size, mean year, duration, diet type, CL type, and project). Differences in growth rates indicated in Fig. S2-1 (in Appendix 2 Supporting Information) by differences in color within an epoch and among epochs represent site-specific responses to other covariates not included in our model (e.g., food quality or quantity). If we could include other meaningful covariates in our model, the spatio-temporal plots presented here would probably present different patterns.

The nonsignificant fixed effects are duration ($P = 0.076$) and CL type ($P > 0.235$ for all comparisons). We set the range of recapture durations from 330 to 1644 d so that duration would not affect the model (Fig. 2d). Lack of significant difference among the four CL metrics (Fig. 2e) justifies combining the growth data for the four measurement types.

Results of sea turtle growth studies are often presented for 10-cm carapace length size classes. To allow our results to be compared with other studies, we have provided these values in Table S2-1 (in Appendix S2 Supporting Information).

Drivers of mean year effect

Annualized mean growth rates increase to a high value in 1999 and then decline by 26% to 2015

(Fig. 3a). The correlation of this pattern with SST values from 1982 to 2015 is moderate (r = -0.43 to -0.54 with 0 to 11 yr lags; Fig. S2-4 in Appendix S2 Supporting Information). Correlation improves greatly when data are restricted to years with stable and declining growth starting in 1997 (r = -0.94 for 0-yr lag; Fig. 4). There is an apparent threshold temperature between 25.9 °C and 26.0 °C below which growth rates tend to increase with increasing SST and above which growth rates decline as SST increases.

Annualized mean growth rates for all years (1974 to 2015) correlate strongly (r = 0.74) with annualized MEI with 2- to 4-yr distributed lags (Fig. 5). An inverse-precision weighted GAMM (Fig. S2-5 in Appendix S2 Supporting Information) with 3-yr lagged MEI accounts for ~52% of the variance in the annualized mean growth rates. We found a statistically significant 2-year lag between annualized MEI and annualized somatic growth rates using the Granger-causality test [VAR(p = 2) model was best fit for p ranging from 1:10, F-test = 93.1, df = c(1,66), $P < 0.0001$]. Forecasting performance declined rapidly with increasing lags 3-10. Thus, including MEI from 2 years prior significantly improves the forecast performance of predicting current somatic growth above and beyond just simply using the growth rates themselves. This finding is consistent with the simpler lagged plot approach (Fig. 5). Our results indicate that green turtle growth rates decrease with increasing SST above a threshold between 25.9 and 26.0 °C (Figs. 3a,b, 4) and increase with increasing MEI (Figs. 3a,c, 5 and Fig. S2-5 in Appendix S2 Supporting Information).

Discussion

Region-wide drivers of sea turtle growth declines

The significant regional decrease in green turtle growth rates after 1999 confirms that the pattern of decreasing growth rates in sea turtles beginning in the late 1990s and continuing to the present is consistent across trophic levels. Similar declines occur in annualized mean growth rates in two carnivorous species – West Atlantic hawksbills (Fig. 3d) and North Atlantic loggerheads (Fig. 3e,f) – following the highest growth rates in 1997. The growth functions for hawksbills (Fig. 3d) and loggerheads (Fig. 3e) were based on studies using capture-mark-recapture data and analyses similar to those in the present study (Bjorndal *et al.*, 2013, 2016). The second loggerhead function (Fig. 3f) was generated based on a very different approach using skeletochronology, different analyses, and a different loggerhead dataset (Avens *et al.*, 2015) that reinforces the observed decline presented here. The different initial years of the declines among the three sea turtle species may represent different lag times in responding to environmental forces among the three species, but 1997 also falls within the 95% confidence interval for the highest growth rates in green turtles in 1999 (Fig. 3a). One difference in these growth functions is the upturn in one of the loggerhead studies (Fig. 3e) after 2007, but the confidence interval at that point would allow for a continued decline in growth rates.

Based on the similar growth dynamics among three sea turtle species across a trophic spectrum and on strong correlations with MEI and SST, we conclude that the declining growth trajectories are most likely a result of the ERS that occurred in the late 1990s. The ERS is believed to be a result of the synergistic effect of two strong thermal processes: abrupt warming during the strong ENSO event of 1997/1998 and the intensification of warming rate over the last two to three decades (Martinson *et al.*, 2008; Reid & Beaugrand, 2012; IPCC, 2014; Beaugrand *et al.*, 2015; Wijffels *et al.*, 2016). During this ERS, abrupt ecological changes occurred in the Atlantic from the North Sea to the Antarctic shelf, including substantial loss of Antarctic sea ice, extreme global bleaching event of corals, and shifts in distribution and phenology in populations of phytoplankton, zooplankton, molluscs, echinoderms, fish, and seabirds (Hoegh-Guldberg, 2007; Martinson *et al.*, 2008; Luczak *et al.*, 2011; Beaugrand *et al.*, 2013, 2015; Ortega *et al.*, 2013).

The correlation between MEI and the green turtle growth function is strong (r = 0.74) throughout the study period whereas SST is moderately correlated (r = -0.54) with the entire growth function but strongly negatively correlated (r = -0.94) with the declining growth function in years following the El Niño year and above the threshold between 25.9 and 26.0 °C. The cause of this threshold is not known. It does not appear to be a threshold for green turtle functioning (see discussion of thermal effects below) unless maximum SST values surpass the optimal thermal zone of green turtles in their habitats in years with an annualized value of 26 °C.

The decline in hawksbill growth rates was also strongly correlated with warming SST in the Caribbean and declining MEI values, with a better fit with the latter (Bjorndal *et al.*, 2016). The MEI and SST effects were attributed to indirect negative effects of rising temperatures on foraging habitats (primarily coral reefs) and prey organisms. Similar explorations of climatic indices were not conducted in the loggerhead growth study although water temperature was suggested as a primary driver for the decline in growth rates (Bjorndal *et al.*, 2013).

Multiple Stressors

Effects of ERS can be reinforced and prolonged by synergistic interactions of multiple stressors (Conversi *et al.*, 2015). The decline in sea turtle growth rates may be a result of multiple stressors that are directly related to MEI or coincidental. Temperature can affect growth rates either directly, through physiological processes of sea turtles, or indirectly through effects on quality and quantity of food resources. Direct effects seem unlikely because the maximum SST values are well within the thermal activity range for sea turtles (Spotila *et al.*, 1997). Therefore, any temperature influence would probably be indirect through effects on habitats and food resources, as reported for hawksbill growth rates (Bjorndal *et al.*, 2016). Different aggregations of green turtles will not all exhibit the same temporal pattern in growth dynamics as the region-wide response in this study because of local differences in strength of stressors and the proximity of the green turtles to the edge of their thermal niche (Beaugrand *et al.*, 2015).

In our study, 63% and 22% of growth increments are for turtles with primary diets of seagrasses (most commonly *Thalassia testudinum*) and seagrass/algae, respectively. Many reports exist of seagrasses living near their thermal maxima for both temperate and tropical species (Collier & Waycott, 2014; Thomson *et al.*, 2015; Pedersen *et al.*, 2016). Increasing temperatures can have direct effects on physiological functions such as photosynthesis and reproduction (Bulthuis, 1987; Short & Neckles, 1999). Optimal temperatures for maximum productivity of *T. testudinum* range from 28 to 31 °C (Lee *et al.*, 2007), and the threshold for *T. testudinum* under sustained exposure is ~33 °C (Koch *et al.*, 2007). Direct thermal effects on *T. testudinum* may seem unlikely with high values of monthly SST at 30 °C in our study region. However, *T. testudinum* meadows often grow in shallow, protected waters that may experience water temperatures well above regional monthly SST and above the optimal thermal zone of the seagrass, especially at low tides (Collier & Waycott, 2014). Many indirect effects of increased temperatures on productivity, mortality, abundance, and distribution of seagrasses have been identified, including decrease in light penetration resulting from thermal-induced eutrophication, changes in salinity, and increased epiphytic algae, water depths, phytotoxins, and incidence of diseases (Short & Neckles, 1999; Koch *et al.*, 2007).

Sea turtle foraging habitats are negatively impacted by many anthropogenic effects in addition to rising temperatures (Rees *et al.* 2016). The great increase in human populations in coastal areas (Norström *et al.*, 2016) brings a plethora of threats to sea turtles and their habitats on continental shelves. Net human migration to coastal areas both globally and in areas of coral reefs remained constant in the 1970s and 1980s and increased greatly in the 1990s by factors of 2.7 and 5, respectively (Norström *et al.*, 2016). The timing of this migration fits with the initiation of declines in sea turtle growth rates in the late 1990s and the dramatic decline in seagrass pastures. Annual rates of loss of seagrass pastures have increased over the past decades, resulting in the loss of substantial seagrass area since the 1990s (Waycott *et al.*, 2009; Mcleod *et al.*, 2011). These are global seagrass losses, but within our study region seagrass loss has been substantial (Short & Wyllie-Echeverria, 1996). A network of 52 seagrass (primarily *T. testudinum*) sampling sites across the Greater Caribbean was monitored by CARICOMP from 1993 to the present (van Tussenbroek *et al.*, 2014). Of the 35 sites that allowed longterm monitoring, 15 (43%) had clear trends indicating environmental deterioration and 25 (71%) exhibited at least one of the six indicators of environmental deterioration (van Tussenbroek *et al.*, 2014).

Although some seagrass loss is from natural causes such as hurricanes, earthquakes, and foraging activities by a variety of species, the vast majority of loss is from anthropogenic activities. Industrial and agricultural run-off resulting in eutrophication, coastal infrastructure development, dredging, aquaculture development, algal blooms, trawling, and boat damage are some of the more important human activities that destroy seagrass pastures (Orth *et al.*, 2006; Grech *et al.*, 2012; Wells *et al.*, 2015). The CARICOMP program identified increased terrestrial run-off of fertilizers, sewage, and sediments as the primary negative anthropogenic effects in the region (Linton & Fisher, 2004). The introduction of the invasive seagrass *Halophila stipulacea* in the eastern Caribbean is another potential stressor, and the combined environmental degradation may induce fibropapillomatosis, a green turtle disease that can reach high incidence (for discussion of both, see Appendix S3 in Supporting Information). As seagrass ecosystems decline, green turtles will shift to other diets of algae and invertebrates, if available. Based on our study, these diets support slower green turtle growth rates, thus the decline in growth rates will be exacerbated.

Anthropogenic degradation of foraging grounds of hawksbills and loggerheads are also well documented. Hawksbills are closely associated with coral reefs, and extent and health of reef habitats in the West Atlantic have suffered serious declines (references in Jackson *et al.*, 2014). Coral bleaching, acidification, and diseases interact synergistically with local stressors such as sedimentation, eutrophication, and overfishing to extend the effects of the ERS (Ateweberhan *et al.*, 2013). Loggerheads are the most generalist of sea turtle species (Bolten, 2003) and occupy many habitats including seagrass pastures, hard bottom and soft bottom habitats. Although diverse habitat use makes loggerheads less vulnerable to habitat destruction, they are not immune. Trawl fisheries and loggerhead foraging areas often overlap; trawl fishing drastically degrades bottom habitats and removes loggerhead prey (Bjorndal, 1997; National Research Council, 2002). All sea turtle habitats are also seriously degraded by accumulation of anthropogenic debris. Ingestion of marine debris by sea turtles has increased in the last few decades (Nelms *et al.*, 2015) and can decrease nutrient gain in sea turtles through nutrient dilution which decreases growth rates (McCauley & Bjorndal, 1999).

Density dependence may be a factor in the decline of growth rates after the late 1990s because West Atlantic green turtle populations appear to be increasing in abundance (Chaloupka *et al.*, 2008; Weber *et al.*, 2014; Garcia-Cruz *et al.*, 2015). Also, as stated above, quality and quantity of foraging areas for sea turtles are declining, thus lowering the population levels of green turtles at which density-dependent effects would be invoked. Evidence for density-dependent regulation of growth rates was reported for three green turtle study sites (The Bahamas, Florida, USA, and México; Bjorndal *et al.*, 2000; Kubis *et al.*, 2009; Labrada-Martagón *et al.* 2017), but no evidence of a density-dependent effect was found in a green turtle aggregation in Puerto Rico (Patrício *et al.*, 2014). Density dependence cannot be the major driver because the three species of sea turtles would not simultaneously reach the population levels at which density dependence would begin to regulate somatic growth on a region-wide basis. Modern populations of hawksbills in the West Atlantic are a fraction of historical population sizes as a result of historic over-exploitation (Meylan & Donnelly, 1999; McClenachan *et al.*, 2006). Increases in nest abundance for hawksbills reported for some areas in recent years have not been sufficient to recover these densities, even considering reductions in reef habitats (NMFS & USFWS, 2013; Campbell, 2014).

We conclude that the declining growth rates in sea turtles are most likely a result of an ERS that occurred in the late 1990s and exacerbated by the cumulative impacts of ongoing anthropogenic degradation of foraging habitats in the region. Determining the relative importance of individual stressors on growth rates is not possible at this time and deserves further research. Regardless of the mechanisms, the summary conclusion that productivity of sea turtles is lower at warmer temperatures is not good news in an age of warming seas.

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Figure Legends

Fig. 1: Location of study sites based on dataset with recapture durations > 330 d and < 1644 d (*n* = 6201). 1 = Bermuda (*n* = 845); 2 – 5 = Florida East Coast, USA (*n* = 878); 6 = Dry Tortugas,

Florida, USA (*n* = 53); 7 = St. Joseph Bay, Florida, USA (*n* = 64); 8 = Mansfield Channel, Texas, USA (*n* = 14); 9 = Laguna Madre, Texas, USA (*n* = 15); 10 = Campeche, México (*n* = 17); 11 = Akumal, México (*n* = 80); 12 = Cayman Islands (*n* = 9); 13 – 16 = Bahamas North & Central (*n* = 1111); 17 = Great Inagua, Bahamas (*n* = 1119); 18 = Turks and Caicos Islands (*n* = 15); 19 – 20 = Puerto Rico (*n* = 284); 21 = British Virgin Islands (*n* = 7); 22 – 23 = US Virgin Islands (*n* = 95); 24 = Pearl Cays, Nicaragua (*n* = 7); 25 = Panama (*n* = 36); 26 = Bonaire (*n* = 191); 27 = Fernando de Noronha, Brazil (*n* = 1206); 28 = Atol das Rocas, Brazil (*n* = 89); 29 = Praia do Forte, Brazil (*n* = 39); 30 = Uruguay (*n* = 27).

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 and allow direct comparisons of effect strength among covariates. The covariate is shown on the *x*-axis: mean SCL (straight carapace length, cm) (a); mean year (b); diet (S is seagrass, S/A is seagrass and algae, A is algae, O is omnivorous) (c); duration (yr) (d); CL (carapace length) measurement type (SNT is straight CL notch to tip, CNT is curved CL notch to tip, SNN is minimum straight CL, CNN is minimum curved CL, see Appendix S1 in Supporting Information) (e). Solid curves are the smoothing spline fits conditioned on all other covariates. Dashed lines are pointwise 95% confidence curves around the fits. All covariates are significant except duration and CL type. Rug plot indicates smaller sample sizes at large body size.

Fig. 3. Annualized mean growth rates (standardized) for green turtles (a); annualized sea surface temperature (SST, °C) (b); annualized Multivariate El Niño Southern Oscillation Index (MEI) (c); annualized mean growth rates for hawksbills (standardized), modified from Bjorndal *et al.* (2016) (d); annualized mean growth rates (standardized) for loggerheads, modified from Bjorndal *et al.* (2013) (e); and loggerhead growth rates with centered smoothed GAMM function scale on the *y*-axis, modified from Avens *et al.* (2015) (f). For growth rates (a,d,e,f) solid lines are smoothing spline fits conditioned on all other covariates and dashed lines are pointwise 95% confidence curves around the fits. For SST and MEI (b,c) solid lines are annualized values and dashed lines are from GAMM analyses showing underlying annual trend; MEI data from 1950 to 1974 are not shown so that *x*-axes are consistent among graphs.

Fig. 4. Annualized mean growth rates (standardized) of green turtles from 1997 to 2015 (open circles) against the annualized sea surface temperature (SST, °C) with no lag, solid line is the GAMM trend (see text). Correlation coefficient is in a box within the graph. Note the threshold between 25.9 and 26.0 °C above which growth rates decline with increasing SST.

Fig. 5. Annualized mean growth rates (standardized) of green turtles for 1974 to 2015 (open circles) lag-plotted against the annualized Multivariate El Niño Southern Oscillation Index (MEI) with 2-yr lag (a), 3-yr lag (b), and 4-yr lag (c). Solid lines are the GAMM trends (see text). Correlation coefficients are in boxes within each graph.

Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supplemental Methods

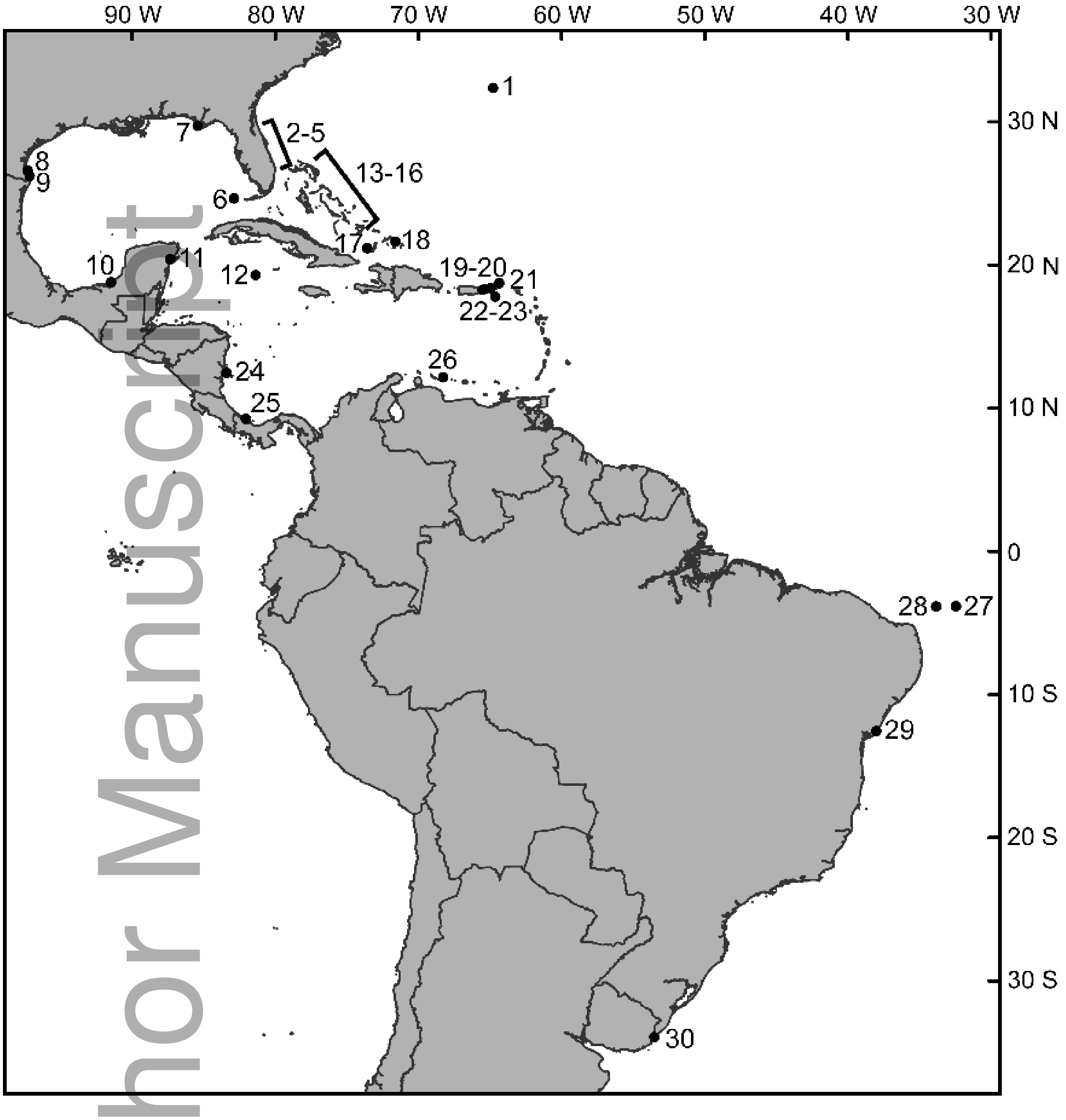
- Treatment of various carapace length measurements
- Figure S1-1. Anterior and posterior pairs of anatomical points for carapace length measurements
- Granger-causality analysis

Appendix S2. Supplemental Results

- Figure S2-1. Spatio-temporal interaction plots for the four epochs
- Figure S2-2. Straight carapace length (SCL) growth rate (cm/yr) predicted by the GAMM analysis plotted against the mean SCL (cm) of each growth increment
- Figure S2-3. Straight carapace length growth rate (cm/yr) predicted by the GAMM analysis plotted against the mean year of each growth increment
- Figure S2-4. GAMM trends of annualized mean growth rates and annualized sea surface temperatures
- Figure S2-5. Predicted year-specific standardized straight carapace length growth rates as a function of 3-yr lagged annualized Multivariate El Niño Southern Oscillation Index
- Table S2-1. Growth rates (cm/yr) for 10-cm size classes

Appendix S3. Supplemental Discussion

Appendix S4. Acknowledgements for individual projects



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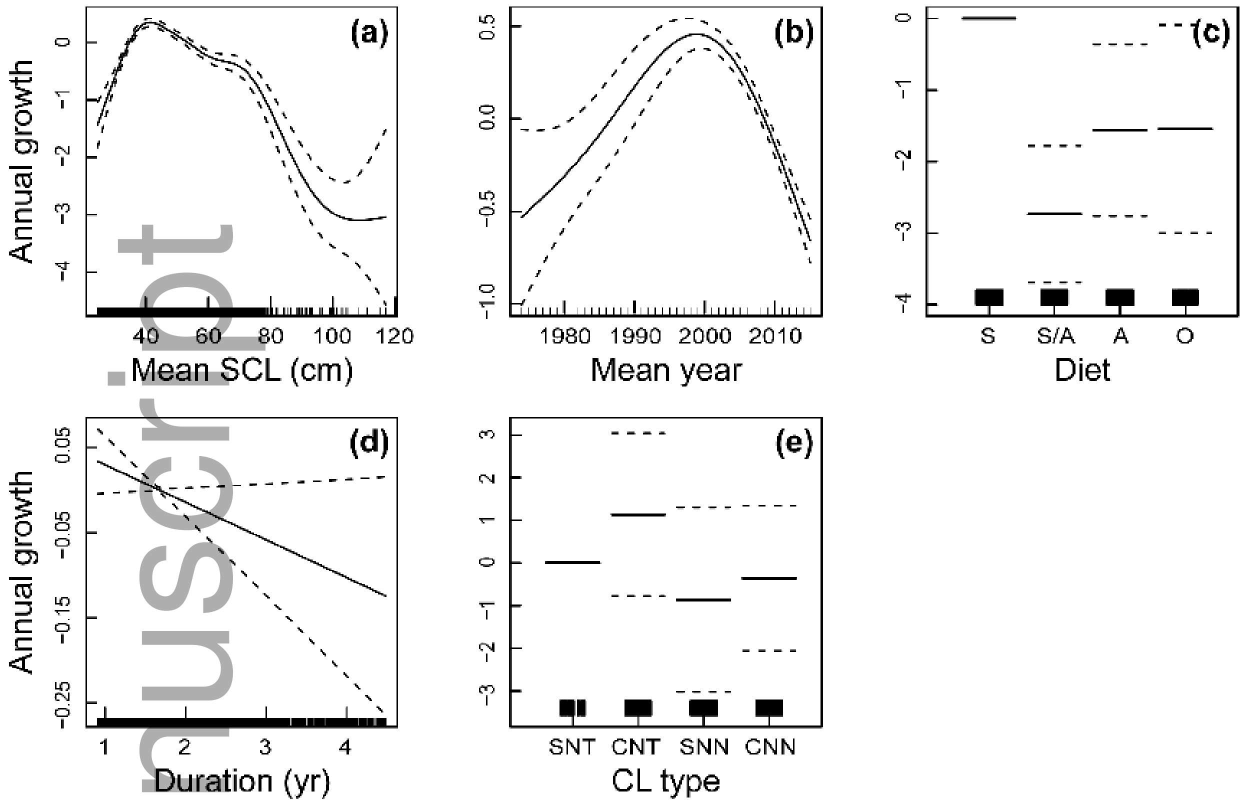

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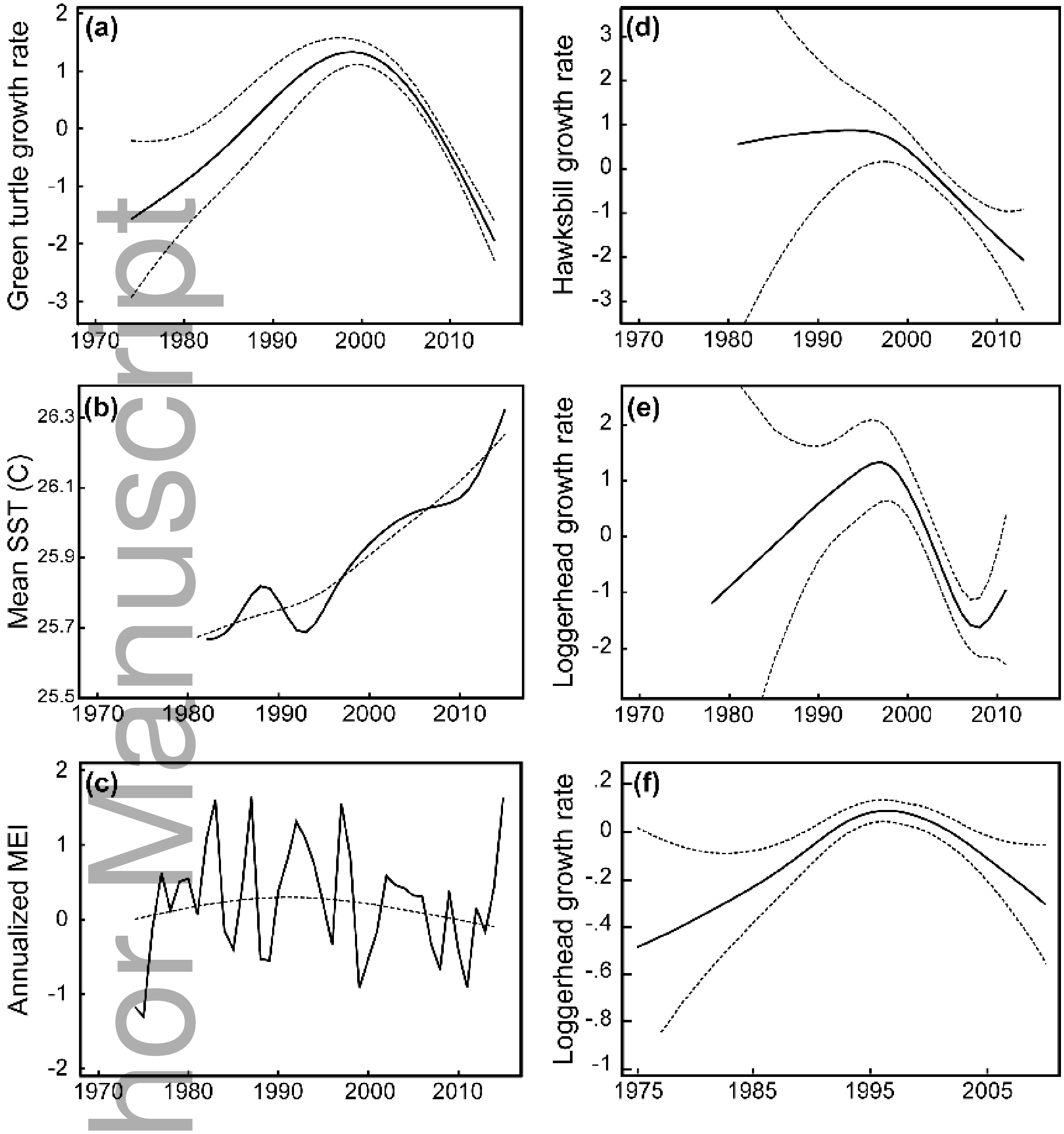

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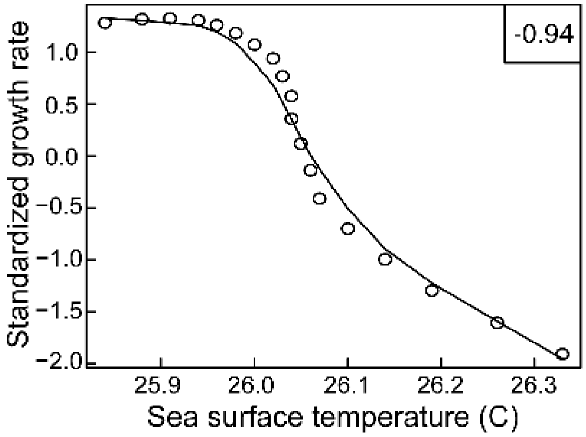

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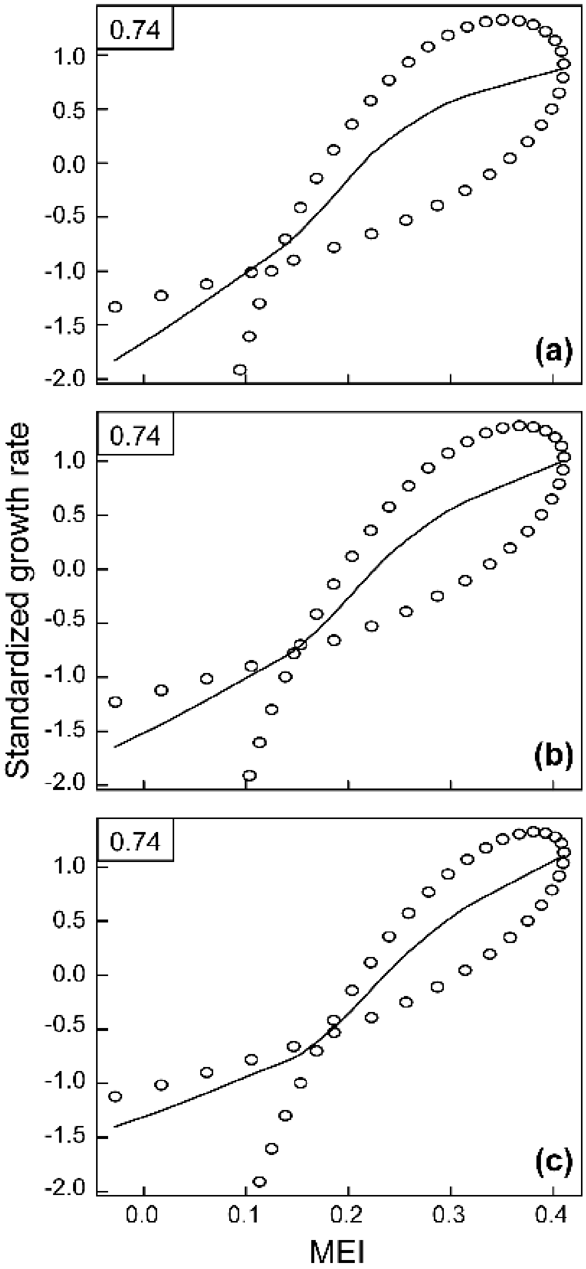

gcb_13712_f5.tif