

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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1 **Abstract**

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

25 **Introduction**

26 Marine systems have undergone great changes in ecosystem function and species
27 distribution and abundance in the Anthropocene (Jackson *et al.*, 2001; Lotze *et al.*, 2006; Alheit
28 2009; Halpern *et al.*, 2015; McCauley *et al.*, 2015). Some of these changes have resulted in or
29 resulted from ecological regime shifts (ERS), defined by Conversi *et al.* (2015) as “dramatic,
30 abrupt changes in the community structure that are persistent in time, encompass multiple
31 variables, and include key structural species – independently of the mechanisms causing them.”
32 Many studies have evaluated the changes that result from ERS in structure and function of
33 ecosystems; biogeography, phenology, and abundance of species; and foodwebs or
34 trophodynamics (references in Alheit & Bakun, 2010; Rocha *et al.*, 2015; Young *et al.*, 2015).
35 However, fewer studies have addressed longterm physiological changes at the individual level
36 across regional landscapes in this era of changing seas. Here we evaluate somatic growth
37 dynamics of the green turtle (*Chelonia mydas*) throughout the West Atlantic across more than
38 four decades (1973-2015).

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

46 Many of the authors of the present study collaborated on earlier studies of somatic growth
47 dynamics in West Atlantic hawksbills (Bjorndal *et al.*, 2016) and Northwest Atlantic loggerheads

48 (Bjorndal *et al.*, 2013) based on capture-mark-recapture data and using a similar modeling
49 approach. These studies revealed that growth rates for hawksbills and loggerheads exhibited
50 similar, continuing declines beginning in 1997. The same pattern of decline was reported for
51 North Atlantic loggerheads based on a different technique (skeletochronology) and a different
52 sample of loggerheads (Avens *et al.*, 2015). Hawksbills and loggerheads are primarily
53 carnivorous, although they feed on different types of prey. Hawksbills feed mostly on sponges,
54 corallimorpharians, zoanthids, and sea anemones associated with coral reefs (references in
55 Krueger *et al.*, 2011). Loggerheads prey most commonly on slow-moving or sessile, hard-
56 shelled benthic invertebrates (Hopkins-Murphy *et al.*, 2003).

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

69 In this paper, we have three objectives: (1) evaluate West Atlantic green turtle growth
70 dynamics with generalized additive mixed models, (2) compare the temporal dynamics of green

71 turtles with those of West Atlantic hawksbills and North Atlantic loggerheads, and (3) explore
72 relationships of temporal growth trajectories with Multivariate El Niño Southern Oscillation
73 Index (MEI) and sea surface temperature (SST). These drivers were selected because they are
74 the most likely drivers of the ERS in the late 1990s (Martinson *et al.*, 2008; Reid & Beaugrand,
75 2012; Beaugrand *et al.*, 2015).

76

77 **Methods**

78 *Data assembly*

79 Green turtle growth rate data were combined from 30 projects in the West Atlantic (Fig. 1).
80 Some of these data have been published in studies for individual sites, but never in regional
81 assessments. Turtles were captured by a variety of methods in foraging areas in neritic habitats
82 and not on nesting beaches. Turtles were tagged, usually with flipper tags, for individual
83 identification. Data used in this study are capture date and location (latitude/longitude), carapace
84 length (CL, the most common measure of body size in sea turtles), and primary diet at each site.
85 Sex is known for a small fraction of individuals so is not used in our analyses. Body size for
86 each growth increment is the average of CL at capture and recapture (Chaloupka & Limpus,
87 1997). Negative growth rates, which result from either measurement error or damage to
88 carapace margins, are included in analyses to avoid systematic bias.

89 When the growth data were first assembled, durations (time-at-large) of the growth
90 increments varied from 1 to 7636 d. Including growth increments with short or long durations
91 can introduce substantial error. Short durations may only capture the fastest or slowest of
92 seasonal growth rates, resulting in large errors when extrapolated to estimates of annual growth,
93 or the change in size may be so small that measurement error is a large proportion of actual

94 growth. During long durations, average CL may not represent a good estimate of body size for
95 the interval. To set the minimum and maximum durations for our analyses, we followed
96 Bjorndal *et al.* (2016) to determine the limits within which duration did not significantly affect
97 our growth model. We created a dataset in which 60 days was the minimum duration ($n = 9690$)
98 and, based on the generalized additive mixed model (below), determined that 330 and 1644 d
99 were the minimum and maximum values. Our minimum value is the same as the standard that
100 has been used for many years in sea turtle studies (Chaloupka & Limpus, 1997), giving further
101 support to the standard minimum. To increase sample size, successive growth increments for
102 individual turtles below the 330 d limit were combined to exceed the minimum duration when
103 possible.

104 *Statistical methods*

105 Generalized additive nonparametric regression models with fixed and random effects –
106 often referred to as generalized additive mixed models (GAMM) – were used to explore somatic
107 growth rates. This modeling approach allows for flexible specification of both error and link
108 functions, enables arbitrary specification of the functional form for each continuous covariate
109 included in the model, and accounts for mixed effects from multiple measurements on the same
110 sampling unit such as location (Fahrmeir & Lang, 2001). Our model used scaled Student-t (scat)
111 likelihood based on findings from a gamboostLSS model as in Gilman *et al.* (2016) that showed
112 Student-t likelihood is better than Gaussian for our model.

113 The GAMMs were fitted using the following: (1) thin plate regression splines to model
114 nonlinear covariate effects; (2) a two-dimensional Duchon-spline surface smoother to account
115 for structured spatial effects attributable to the geospatial location (latitude, longitude) of each
116 project site; (3) a tensor product of a 2D Duchon-spline surface and a time effect with cubic

117 regression spline basis to account for any spatial trend in time (Marra *et al.*, 2012), where time is
118 blocks of years (= epochs); and (4) project-specific heterogeneity incorporated as a random
119 effect term to account for the multilevel sampling structure of the dataset. This spatially explicit
120 GAMM is generally referred to as a geoadditive GAMM (Kammann & Wand, 2003). All
121 GAMM models were fitted using the *mgcv* package for R (Wood & Scheipl, 2014) with the
122 smoothness parameters estimated using REML (Wood, 2006).

123 We use a mixed longitudinal sampling design (sampling with partial replacement); 1318
124 (33%) of 3958 individual turtles were recaptured more than once. In our GAMM analyses, we
125 assess six fixed effects and one random effect (project collecting the data, $n = 30$) on one
126 response variable (somatic growth rate). Of the six fixed effects, two (diet and CL type) are each
127 four-level factors. Diet is the primary diet for the site: seagrass, algae, seagrass/algae mix, and
128 omnivorous. CL type is the specific CL metric used (see Appendix S1 in Supporting
129 Information). The other four fixed effects are continuous covariates (mean CL of growth
130 increment, mean year of growth increment, duration of growth increment, and location on a
131 latitude/longitude surface or a location/temporal interaction term). Mean CL is the arithmetic
132 mean of straight CL notch to tip (SCLnt, see Fig. S1-1 in Appendix S1 Supporting Information)
133 at initial capture and recapture. Mean year is the calendar year of the midpoint of the recapture
134 interval. This approach introduces little error in calendar year assignment because 72% of
135 growth records had durations <2 yr. Recapture interval was included to evaluate any bias from
136 variable durations. For the spatio-temporal interaction, we use an interaction term of location by
137 epoch. The four epochs have nearly equal sample sizes based on mean year (1974-1999, 2000-
138 2006, 2007-2010, 2011-2015). Number of growth increments in each epoch is 1470, 1421, 1486,
139 and 1824, respectively. We conducted two GAMM analyses – a spatial model and a spatio-

140 temporal model – to explore the importance of spatio-temporal interaction. In GAMM analyses,
141 each covariate is conditioned on all other covariates. For example, any differences in CL of
142 turtles in different regions or different years would be accounted for in assessments of spatial or
143 temporal effects.

144 The R code for the spatio-temporal model is: `mgcv(data.gam <- gam(grow.rate ~ diet +`
145 `cl.type + s(mean.size) + s(mean.year, k=4) + s(duration) + te(lon, lat, by=decade, bs="ds",`
146 `m=c(1,.5)) + s(project, bs="re"), family=scat(link="identity"), method="REML")`.

147 Annualized mean growth rates are expressed as standardized values ([Annual value -
148 mean of annual values]/SD of annual values) to allow direct comparison among the three sea
149 turtle species. To evaluate whether the significant region-wide effect of mean year on growth
150 rates was related to the two drivers proposed for the Atlantic ERS beginning in the mid-1990s
151 (ENSO and ocean heating), we related annualized mean growth rates generated from our GAMM
152 analysis to the MEI and SST. We selected the MEI to represent ENSO because it is currently
153 considered the most representative index (Mazzarella *et al.*, 2013) and reflects ecological
154 changes well because it integrates six variables in the eastern tropical Pacific Ocean as a proxy
155 for the ENSO: SST, surface air temperature, sea-level pressure, two components of surface
156 winds, and total cloudiness of the sky (Mazzarella *et al.*, 2013). Climate teleconnection between
157 the Pacific and Atlantic is strong with the ENSO affecting Atlantic SST, rainfall, and associated
158 regional-scale ocean-atmosphere anomalies in our study region (Giannini *et al.*, 2001; Spillman
159 *et al.*, 2011; Gouirand *et al.*, 2014) and Atlantic warming possibly triggering ENSO events in the
160 Pacific (Ham *et al.*, 2013).

161 We sourced MEI bimonthly data from 1950 to present
162 (<http://www.esrl.noaa.gov/psd/enso/mei/table.html>) and annualized the bimonthly index to an

163 annualized index. We then ran a GAMM with autoregressive (AR1) error to reveal any
164 underlying annual trend since 1950 and lag plotted the GAMM trend MEI against annualized
165 mean growth rates for 0- to 11-yr lags with *astsa* package for R (Stoffer, 2014). We followed a
166 similar approach with SST data. Because of the variation in temporal and spatial coverage of our
167 growth data, rather than use the SST values for the entire region, we used mean SST values from
168 625 km² around three sites (Bermuda; Inagua, The Bahamas; and Fernando de Noronha, Brazil)
169 (Fig. 1). These three sites represent 53% of the growth increments in our study, 100% of the
170 temporal range, and the latitudinal range of 93% of our study sites. SST data were sourced from
171 NOAA OISST (Optimum Interpolation Sea Surface Temperature) AVHRR (Advanced Very
172 High Resolution Radiometer) satellite data (25-km x 25-km (1/4 degree)
173 <https://www.ncdc.noaa.gov/oisst>). SST data begin in 1982 when the satellite started recording
174 data.

175 We also explored the relationship between somatic growth rates and MEI using a
176 statistical forecasting approach. For instance, does an environmental driver such as MEI
177 improve the forecasting performance of expected somatic growth rates for West Atlantic green
178 turtles? A common test of this forecasting performance is Granger-causality analysis (Enders,
179 1995; Triacca, 2005). This analysis in no way assesses true causality and refers only to forecast
180 ability while also assuming a linear dependence between the response variable and the predictor
181 (Mariusz, 2015). See Appendix S1 (Supporting Information) for details of the Granger-causality
182 analysis.

183

184 **Results**

185 *Dataset and GAMM results*

186 Green turtles were sampled in mixed stock foraging aggregations that include turtles from all
187 five Atlantic regional management units (Bjorndal & Bolten, 2008; Wallace *et al.*, 2010). Our
188 initial dataset ($n = 9690$) with a 60 d minimum duration for growth increments was revised to a
189 dataset with durations from 330 to 1640 d. Our final dataset has 6201 growth increments for
190 3958 individual green turtles. Number of growth increments for individual turtles varies from 1
191 to 10 with a mean \pm SD of 1.6 ± 1.1 . Growth rates from all growth increments vary from -0.9
192 to 11.9 cm/yr with a mean \pm SD of 3.4 ± 2.0 cm/yr. Green turtles were captured from 1973
193 through 2015, and mean year of growth increments is from 1974 through 2015. SCLnt values
194 from all turtle captures ($n = 12,402$) vary from 23.2 to 117.0 cm, and mean SCLnt values for all
195 growth increments ($n = 6201$) range from 24.6 to 117.0 cm. Mean CL of growth increments did
196 not change over time (linear regression, $n = 6201$, $P = 0.289$).

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

204 Mean CL is a significant fixed effect ($P < 0.0001$; Fig. 2a). Growth rates initially
205 increase from 25 to ~ 40 cm SCLnt, probably as a result of increased nutrient gain as new recruits
206 improve foraging behavior, diet selection, and digestive processing. Growth rates then decline to
207 a size of about 90 cm SCLnt at which size green turtles approach maturity and growth rates slow
208 as resource allocation is shifted from growth to reproduction. The slope of the decline becomes

209 substantially steeper around 70 cm SCLnt, perhaps because of changes in habitat, diet selection,
210 and food intake with increasing body size. A graph of predicted growth rates (cm/yr) plotted
211 against mean CL is presented in Fig. S2-2 (in Appendix S2 Supporting Information). For
212 discussion of size-specific growth dynamics see Appendix S3 Supporting Information.

213 Mean year of the growth increment also has a significant effect ($P < 0.0001$; Fig. 2b).
214 Growth rates increase from 1974 to 1999, although the 95% confidence interval is broad until
215 ~1985. After 1999, growth rates exhibit a steady decline. This decline is not a result of changes
216 in CL because, as noted above, covariates in the GAMM are conditioned on each other and mean
217 CL values do not change over years. See Fig. S2-3 (in Appendix S2 Supporting Information) for
218 a graph of predicted growth rates (cm/yr) plotted against mean year.

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

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

232 plots presented here would probably present different patterns.

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

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

240 *Drivers of mean year effect*

241 Annualized mean growth rates increase to a high value in 1999 and then decline by 26% to 2015
242 (Fig. 3a). The correlation of this pattern with SST values from 1982 to 2015 is moderate ($r = -$
243 0.43 to -0.54 with 0 to 11 yr lags; Fig. S2-4 in Appendix S2 Supporting Information).

244 Correlation improves greatly when data are restricted to years with stable and declining growth
245 starting in 1997 ($r = -0.94$ for 0-yr lag; Fig. 4). There is an apparent threshold temperature
246 between 25.9 °C and 26.0 °C below which growth rates tend to increase with increasing SST and
247 above which growth rates decline as SST increases.

248 Annualized mean growth rates for all years (1974 to 2015) correlate strongly ($r = 0.74$)
249 with annualized MEI with 2- to 4-yr distributed lags (Fig. 5). An inverse-precision weighted
250 GAMM (Fig. S2-5 in Appendix S2 Supporting Information) with 3-yr lagged MEI accounts for
251 ~52% of the variance in the annualized mean growth rates. We found a statistically significant
252 2-year lag between annualized MEI and annualized somatic growth rates using the Granger-
253 causality test [VAR($p = 2$) model was best fit for p ranging from 1:10, F-test = 93.1, $df = c(1,66)$,
254 $P < 0.0001$]. Forecasting performance declined rapidly with increasing lags 3-10. Thus,

255 including MEI from 2 years prior significantly improves the forecast performance of predicting
256 current somatic growth above and beyond just simply using the growth rates themselves. This
257 finding is consistent with the simpler lagged plot approach (Fig. 5). Our results indicate that
258 green turtle growth rates decrease with increasing SST above a threshold between 25.9 and 26.0
259 °C (Figs. 3a,b, 4) and increase with increasing MEI (Figs. 3a,c, 5 and Fig. S2-5 in Appendix S2
260 Supporting Information).

261

262 **Discussion**

263 *Region-wide drivers of sea turtle growth declines*

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

279 Based on the similar growth dynamics among three sea turtle species across a trophic
280 spectrum and on strong correlations with MEI and SST, we conclude that the declining growth
281 trajectories are most likely a result of the ERS that occurred in the late 1990s. The ERS is
282 believed to be a result of the synergistic effect of two strong thermal processes: abrupt warming
283 during the strong ENSO event of 1997/1998 and the intensification of warming rate over the last
284 two to three decades (Martinson *et al.*, 2008; Reid & Beaugrand, 2012; IPCC, 2014; Beaugrand
285 *et al.*, 2015; Wijffels *et al.*, 2016). During this ERS, abrupt ecological changes occurred in the
286 Atlantic from the North Sea to the Antarctic shelf, including substantial loss of Antarctic sea ice,
287 extreme global bleaching event of corals, and shifts in distribution and phenology in populations
288 of phytoplankton, zooplankton, molluscs, echinoderms, fish, and seabirds (Hoegh-Guldberg,
289 2007; Martinson *et al.*, 2008; Luczak *et al.*, 2011; Beaugrand *et al.*, 2013, 2015; Ortega *et al.*,
290 2013).

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

298 The decline in hawksbill growth rates was also strongly correlated with warming SST in
299 the Caribbean and declining MEI values, with a better fit with the latter (Bjorndal *et al.*, 2016).
300 The MEI and SST effects were attributed to indirect negative effects of rising temperatures on
301 foraging habitats (primarily coral reefs) and prey organisms. Similar explorations of climatic

302 indices were not conducted in the loggerhead growth study although water temperature was
303 suggested as a primary driver for the decline in growth rates (Bjorndal *et al.*, 2013).

304 *Multiple Stressors*

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

316 In our study, 63% and 22% of growth increments are for turtles with primary diets of
317 seagrasses (most commonly *Thalassia testudinum*) and seagrass/algae, respectively. Many
318 reports exist of seagrasses living near their thermal maxima for both temperate and tropical
319 species (Collier & Waycott, 2014; Thomson *et al.*, 2015; Pedersen *et al.*, 2016). Increasing
320 temperatures can have direct effects on physiological functions such as photosynthesis and
321 reproduction (Bulthuis, 1987; Short & Neckles, 1999). Optimal temperatures for maximum
322 productivity of *T. testudinum* range from 28 to 31 °C (Lee *et al.*, 2007), and the threshold for *T.*
323 *testudinum* under sustained exposure is ~33 °C (Koch *et al.*, 2007). Direct thermal effects on *T.*
324 *testudinum* may seem unlikely with high values of monthly SST at 30 °C in our study region.

325 However, *T. testudinum* meadows often grow in shallow, protected waters that may experience
326 water temperatures well above regional monthly SST and above the optimal thermal zone of the
327 seagrass, especially at low tides (Collier & Waycott, 2014). Many indirect effects of increased
328 temperatures on productivity, mortality, abundance, and distribution of seagrasses have been
329 identified, including decrease in light penetration resulting from thermal-induced eutrophication,
330 changes in salinity, and increased epiphytic algae, water depths, phytotoxins, and incidence of
331 diseases (Short & Neckles, 1999; Koch *et al.*, 2007).

332 Sea turtle foraging habitats are negatively impacted by many anthropogenic effects in
333 addition to rising temperatures (Rees *et al.* 2016). The great increase in human populations in
334 coastal areas (Norström *et al.*, 2016) brings a plethora of threats to sea turtles and their habitats
335 on continental shelves. Net human migration to coastal areas both globally and in areas of coral
336 reefs remained constant in the 1970s and 1980s and increased greatly in the 1990s by factors of
337 2.7 and 5, respectively (Norström *et al.*, 2016). The timing of this migration fits with the
338 initiation of declines in sea turtle growth rates in the late 1990s and the dramatic decline in
339 seagrass pastures. Annual rates of loss of seagrass pastures have increased over the past decades,
340 resulting in the loss of substantial seagrass area since the 1990s (Waycott *et al.*, 2009; Mcleod *et*
341 *al.*, 2011). These are global seagrass losses, but within our study region seagrass loss has been
342 substantial (Short & Wyllie-Echeverria, 1996). A network of 52 seagrass (primarily *T.*
343 *testudinum*) sampling sites across the Greater Caribbean was monitored by CARICOMP from
344 1993 to the present (van Tussenbroek *et al.*, 2014). Of the 35 sites that allowed longterm
345 monitoring, 15 (43%) had clear trends indicating environmental deterioration and 25 (71%)
346 exhibited at least one of the six indicators of environmental deterioration (van Tussenbroek *et al.*,
347 2014).

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

362 Anthropogenic degradation of foraging grounds of hawksbills and loggerheads are also
363 well documented. Hawksbills are closely associated with coral reefs, and extent and health of
364 reef habitats in the West Atlantic have suffered serious declines (references in Jackson *et al.*,
365 2014). Coral bleaching, acidification, and diseases interact synergistically with local stressors
366 such as sedimentation, eutrophication, and overfishing to extend the effects of the ERS
367 (Ateweberhan *et al.*, 2013). Loggerheads are the most generalist of sea turtle species (Bolten,
368 2003) and occupy many habitats including seagrass pastures, hard bottom and soft bottom
369 habitats. Although diverse habitat use makes loggerheads less vulnerable to habitat destruction,
370 they are not immune. Trawl fisheries and loggerhead foraging areas often overlap; trawl fishing

371 drastically degrades bottom habitats and removes loggerhead prey (Bjorndal, 1997; National
372 Research Council, 2002). All sea turtle habitats are also seriously degraded by accumulation of
373 anthropogenic debris. Ingestion of marine debris by sea turtles has increased in the last few
374 decades (Nelms *et al.*, 2015) and can decrease nutrient gain in sea turtles through nutrient
375 dilution which decreases growth rates (McCauley & Bjorndal, 1999).

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

392 We conclude that the declining growth rates in sea turtles are most likely a result of an
393 ERS that occurred in the late 1990s and exacerbated by the cumulative impacts of ongoing

394 anthropogenic degradation of foraging habitats in the region. Determining the relative
395 importance of individual stressors on growth rates is not possible at this time and deserves
396 further research. Regardless of the mechanisms, the summary conclusion that productivity of sea
397 turtles is lower at warmer temperatures is not good news in an age of warming seas.

398

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416

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608

609 **Figure Legends**

610 Fig. 1: Location of study sites based on dataset with recapture durations ≥ 330 d and ≤ 1644 d (n
611 = 6201). 1 = Bermuda ($n = 845$); 2 – 5 = Florida East Coast, USA ($n = 878$); 6 = Dry Tortugas,
612 Florida, USA ($n = 53$); 7 = St. Joseph Bay, Florida, USA ($n = 64$); 8 = Mansfield Channel,
613 Texas, USA ($n = 14$); 9 = Laguna Madre, Texas, USA ($n = 15$); 10 = Campeche, México ($n =$
614 17); 11 = Akumal, México ($n = 80$); 12 = Cayman Islands ($n = 9$); 13 – 16 = Bahamas North &
615 Central ($n = 1111$); 17 = Great Inagua, Bahamas ($n = 1119$); 18 = Turks and Caicos Islands ($n =$
616 15); 19 – 20 = Puerto Rico ($n = 284$); 21 = British Virgin Islands ($n = 7$); 22 – 23 = US Virgin
617 Islands ($n = 95$); 24 = Pearl Cays, Nicaragua ($n = 7$); 25 = Panama ($n = 36$); 26 = Bonaire ($n =$
618 191); 27 = Fernando de Noronha, Brazil ($n = 1206$); 28 = Atol das Rocas, Brazil ($n = 89$); 29 =
619 Praia do Forte, Brazil ($n = 39$); 30 = Uruguay ($n = 27$).

620

621 Fig. 2. Graphical summary of GAMM analysis. The response variable (mean annual growth
622 rate) is shown on the y -axis as a centered smoothed function scale to ensure valid pointwise 95%
623 confidence bands and allow direct comparisons of effect strength among covariates. The
624 covariate is shown on the x -axis: mean SCL (straight carapace length, cm) (a); mean year (b);
625 diet (S is seagrass, S/A is seagrass and algae, A is algae, O is omnivorous) (c); duration (yr) (d);
626 CL (carapace length) measurement type (SNT is straight CL notch to tip, CNT is curved CL
627 notch to tip, SNN is minimum straight CL, CNN is minimum curved CL, see Appendix S1 in
628 Supporting Information) (e). Solid curves are the smoothing spline fits conditioned on all other
629 covariates. Dashed lines are pointwise 95% confidence curves around the fits. All covariates are
630 significant except duration and CL type. Rug plot indicates smaller sample sizes at large body
631 size.

632

633 Fig. 3. Annualized mean growth rates (standardized) for green turtles (a); annualized sea surface
634 temperature (SST, °C) (b); annualized Multivariate El Niño Southern Oscillation Index (MEI)
635 (c); annualized mean growth rates for hawksbills (standardized), modified from Bjorndal *et al.*
636 (2016) (d); annualized mean growth rates (standardized) for loggerheads, modified from
637 Bjorndal *et al.* (2013) (e); and loggerhead growth rates with centered smoothed GAMM function
638 scale on the y -axis, modified from Avens *et al.* (2015) (f). For growth rates (a,d,e,f) solid lines
639 are smoothing spline fits conditioned on all other covariates and dashed lines are pointwise 95%
640 confidence curves around the fits. For SST and MEI (b,c) solid lines are annualized values and
641 dashed lines are from GAMM analyses showing underlying annual trend; MEI data from 1950 to
642 1974 are not shown so that x -axes are consistent among graphs.

643

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

648

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

653

654 **Supporting information**

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

656 **Appendix S1.** Supplemental Methods

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

661 **Appendix S2.** Supplemental Results

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

672 **Appendix S3.** Supplemental Discussion

673 **Appendix S4.** Acknowledgements for individual projects