DR. JUSTIN H BAUMANN (Orcid ID : 0000-0003-0113-0491)
MR. JOHN RIPPE (Orcid ID : 0000-0002-6243-0757)
MR. TRAVIS COURTNEY (Orcid ID : 0000-0002-1868-9630)

Article type : Primary Research Articles

Title: Nearshore coral growth declining on the Mesoamerican Barrier Reef System

Running Title: Declining extension of nearshore corals

Justin H. Baumann[1,2*], Justin B. Ries[3], John P. Rippe[1], Travis A. Courtney[1,3,4], Hannah E. Aichelman[1,5], Isaac Westfield[3], Karl D. Castillo[1,6]

[1]Department of Marine Sciences, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina

[2]Biology Department, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina
[3]Department of Marine and Environmental Sciences, Marine Science Center, Northeastern University, Nahant, Massachusetts
[4]Scripps Institution of Oceanography, University of California San Diego, La Jolla, California

[5]Department of Biological Sciences, Boston University, Boston Massachusetts

[6]Environment, Ecology, and Energy Program, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina

*Corresponding author: baumannj@live.unc.edu, (513) 307-1516

Keywords: reef-building coral; skeletal extension; ocean warming; *Siderastrea siderea; Pseudodiploria strigosa*, Caribbean coral reefs; climate change

Article type: Primary Research Article

ABSTRACT:

Anthropogenic global change and local stressors are impacting coral growth and survival worldwide, altering the structure and function of coral reef ecosystems. Here, we show that skeletal extension rates of nearshore colonies of two abundant and widespread Caribbean corals (*Siderastrea siderea, Pseudodiploria strigosa*) declined across the Belize Mesoamerican Barrier Reef System (MBRS) over the past century, while offshore coral conspecifics exhibited relatively stable extension rates over the same temporal interval. This decline has caused nearshore coral extension rates to converge with those of their historically slower-growing offshore coral counterparts. For both species, individual mass coral bleaching events were correlated with low rates of skeletal extension within specific reef environments, but no single bleaching event was correlated with low skeletal extension rates across all reef environments. We postulate that the decline in skeletal extension rates for nearshore corals is driven primarily

by the combined effects of long-term ocean warming and increasing exposure to higher levels of land-based anthropogenic stressors, with acute thermally-induced bleaching events playing a lessor role. If these declining trends in skeletal growth of nearshore *S. siderea* and *P. strigosa* continue into the future, the structure and function of these critical nearshore MBRS coral reef systems is likely to be severely impaired.

INTRODUCTION

Global climate change is impacting ecosystems worldwide (Walther *et al.*, 2002), causing range expansions (Elmhagen *et al.*, 2015), habitat contractions (Smale & Wernberg, 2013), decreased productivity (O'Reilly *et al.*, 2003), pest outbreaks (Kurz *et al.*, 2008), phase shifts (Connell & Russell, 2010), and alterations in ecosystem structure and function (Hoegh-Guldberg & Bruno, 2010, Knowlton, 2001). For example, sea surface temperatures (SST) in the Caribbean Sea have increased by up to 0.8°C over the past century (Glenn *et al.*, 2015, Rhein, 2013), impacting the health and viability of coral reef ecosystems. As tropical corals already live near their thermal limits (Fitt *et al.*, 2001, Jokiel & Coles, 1977), even small increases in ocean temperature can have dire consequences for their survival. Increased seawater temperature is the primary cause of widespread coral bleaching, a phenomenon describing the breakdown of the obligate coral-algal symbiosis for many reef-building scleractinian corals (Jokiel & Coles, 1990). Mass coral bleaching events have caused significant coral mortality across reef ecosystems globally (Hughes *et al.*, 2017), including within the Caribbean Sea (Eakin *et al.*, 2010, McWilliams *et al.*, 2005).

Rising seawater temperatures coupled with disease outbreaks have caused major reductions in coral cover on many Caribbean reefs since the 1980s (Gardner *et al.*, 2003), induced declines in the structural complexity of local reefs (Alvarez-Filip *et al.*, 2009), and led to a shift in coral dominance from large, fast-growing, and structurally complex species (e.g., *Acropora* sp.) to less structurally complex and more stress tolerant species that tend to be small and faster-growing (e.g., *Porites astreoides*)(Green *et al.*, 2008) or large and slower-growing, (e.g., *S. siderea*) (Alvarez-Filip *et al.*, 2013). If present warming trends continue, bleaching events on Caribbean coral reefs are predicted to increase in frequency, duration, and severity, potentially occurring every two years as soon as 2030 (Donner *et al.*, 2007) and annually by approximately 2040 (Van Hooidonk *et al.*, 2015), depending on the rate of coral adaptation (Logan *et al.*, 2014). This predicted increase in coral bleaching, triggered by exposure to more intense, frequent, and/or prolonged thermal stress, would negatively impact rates of coral growth and survival, even in thermally tolerant species (Berkelmans & Van Oppen, 2006, Hoegh-Guldberg *et al.*, 2007, Hughes *et al.*, 2010).

Coral growth and calcification rates are influenced by many processes, including seawater temperature, sedimentation, and nutrient concentrations (e.g, see complete discussion of the environmental drivers of coral growth in Castillo *et al.*, 2014, Courtney *et al.*, 2017, Jokiel & Coles, 1977, Pratchett *et al.*, 2015). Moderate increases in temperature (up to and slightly beyond a coral's thermal optimum) have been shown to increase coral growth rates (Castillo *et al.*, 2014, Courtney *et al.*, 2017, Jokiel & Coles, 1977, Marshall & Clode, 2004, Pratchett *et al.*, 2015), while temperatures surpassing this thermal optimum by more than a degree have been shown to impair coral growth (Jokiel & Coles, 1977, Lough & Cantin, 2014, Pratchett *et al.*, 2015).

Local impacts, such as increased sedimentation and nutrient loading associated with human development, have been shown to correlate with slower or declining coral growth rates (Carilli *et al.*, 2010, Cooper *et al.*, 2008, D'Olivo *et al.*, 2013). However, elevated nutrient and sediment loads can also lead to increased heterotrophy, which can offset negative impacts of environmental stress and increase coral resilience (Ferrier-Pages *et al.*, 2003, Grottoli *et al.*, 2006, Houlbreque & Ferrier-Pages, 2009, Mills *et al.*, 2004, Mills & Sebens, 2004). Meanwhile, observations of elevated growth rates relative to lower variability sites and increasing and/or stable growth rates through time on reefs exposed to higher degrees of environmental variability (e.g., temperature and/or nutrients) indicate that exposure to environmental variation may precondition coral populations (Carilli *et al.*, 2012, Carricart-Ganivet & Merino, 2001, Castillo *et al.*, 2012, Manzello *et al.*, 2015) potentially affording them greater resilience in the face of more frequent and/or more intense thermal stress events. Changing seawater chemistry (i.e., ocean acidification) may also lead to lower coral growth rates (e.g., Bove *et al.*, 2019, Chan & Connolly, 2013). Temporal trends in coral growth rates at any given location are dependent upon a complex network of factors due to the interactive nature of environmental variables known to influence calcification, (Courtney *et al.*, 2017, Jokiel & Coles, 1977, Pratchett *et al.*, 2015).

The stressors known to impact coral calcification can vary in intensity along environmental gradients, warranting comparisons of coral growth and resilience across reef environments (Baumann *et al.*, 2016, Cooper, 2008, Cooper *et al.*, 2007, Lirman & Fong, 2007, Manzello *et al.*, 2015). For example, coral reefs more proximal to the coast (i.e., nearshore reefs) generally experience more extreme environmental conditions than reefs more distal from the coast (i.e., offshore reefs), including greater thermal variability (Baumann *et al.*, 2016, Oliver & Palumbi, 2011) and land-based stressors, such as sedimentation and nutrients (Baumann *et al.*, 2016, Dodge *et al.*, 1974, Fabricius, 2005, Heyman & Kjerfve, 1999). However, environmental conditions on nearshore reefs are highly site-specific, potentially driving large spatial differences in coral growth response.

Here, we characterize reef-wide trends in skeletal extension over the past century for two abundant and widely distributed massive Caribbean reef-building corals, *Siderastrea siderea* and *Pseudodiploria strigosa*, across five reef environments that span a nearshore-to-offshore environmental stress gradient (Baumann *et al.*, 2016) throughout the Belize Mesoamerican Barrier Reef System (MBRS). Specifically, this study addresses the following research questions: (1) What are the trends in coral growth over the past century for two species of massive corals (*S. siderea*, *P. strigosa*) on the Belize MBRS? (2) Do temporal trends in coral growth vary between reef environments? (3) What are the effects of mass bleaching events on temporal trends in coral growth? The resulting reconstructions of historical coral extension will provide a framework for predicting the growth trajectories of these resilient coral species in response to future global change.

MATERIALS AND METHODS

Research sites

Research sites were located along the 300 km-long coast of the Belize portion of the Mesoamerican Barrier Reef System (MBRS)—a 1,200 km-long network of coral reefs in the western Caribbean Sea extending south from the tip of the Yucatán Peninsula in Mexico, traversing the entire coast of Belize and the Atlantic coast of Guatemala, and culminating in the Islas de la Bahía (Bay Islands) off the coast of Honduras (Fig. 1). Coral cores were obtained from five different reef environments (i.e., nearshore, backreef, forereef, atoll backreef, and atoll forereef) along a putative nearshore-offshore environmental stress gradient (Fig. 1). Nearshore coral cores were obtained from patch reefs within 10 km of the Belize coast. Backreef and forereef coral cores were obtained on the landward and seaward sides of the reef crest, respectively. Backreef, forereef, atoll backreef, and atoll forereef are referred to collectively as offshore reefs as they are located 30-60 km away from mainland Belize. Corals in nearshore habitats are exposed to higher summer temperatures, increased thermal variability (diurnal and seasonal), more days per year above the estimated bleaching threshold (Baumann *et al.*, 2016), elevated chlorophyll-a (used as a proxy for nutrient delivery and primary productivity) (Baumann *et al.*, 2016), and greater local anthropogenic stress (e.g., sedimentation, pollution) than offshore corals (backreef, forereef, atolls) due to their proximity to mainland Belize (Carilli *et al.*, 2010, Heyman & Kjerfve, 1999).

Coral core collection

A total of 124 coral cores (93 *S. siderea* and 31 *P. strigosa*) were collected from 19 sites along the Belize MBRS by SCUBA divers using a pneumatic core drill (Chicago Pneumatic CP 315) in 2009 and 2012 (Castillo *et al.*, 2011) or a hydraulic core drill (Chicago Pneumatic COR 5 in 2012 and CS Unitec model 2 1335 0010, 3.8 HP in 2015) equipped with a 5 cm diameter diamond tipped core bit (Castillo *et al.*, 2011) (Table S1). All of the *P. strigosa* cores (31 in total) and 37 of the *S. siderea* cores were collected in 2015. The remaining 56 *S. siderea* cores were collected in 2009 (13) and 2012 (43). All cores were extracted from colonies that appeared healthy (i.e., no bleaching, abnormalities, scarring, or disease). Cores were extracted parallel to the central growth axis of each colony. Overall, core lengths ranged from 10 to 100 cm. After extracting each core, a concrete plug was inserted into the drilled hole and the hole was sealed with *Z-spar* underwater epoxy to prevent bioerosion and promote re-growth of coral tissue. Cores were rinsed in ethanol, stored in PVC tubes, and transported to the University of North Carolina at Chapel Hill for analysis. Collection permits were obtained from the Belize Fisheries Department and all cores were collected and transported pursuant to local, federal, and international regulations. It should be noted that because cores were collected from apparently healthy corals, the results of this study may underestimate population-wide declines in coral growth rates over the historical study interval owing to the well-documented deleterious effects of coral diseases and growth anomalies on calcification rates (e.g., Peters, 2015 and references therein)

Coral computer tomography scanning

Coral cores collected in 2009 and 2012 were CT scanned on a Siemens Somatom Definition AS (120 kV, 300 mAs, 0.6 mm slice thickness) scanner at Wake Radiology Chapel Hill in 2013 using methods modified from Carilli et al. (2012). Cores collected in 2015 were scanned on a Siemens Biograph mCT (120 kV, 250 mAs, 0.6 mm slice thickness) at UNC Biomedical Research Imaging Center (BRIC). Images were reconstructed at 0.1 mm increments and exported as DICOM files.

Cores collected in 2009 and 2012 were scanned with the growth axis oriented perpendicular to the length of the CT table. Importantly, the perpendicular orientation of the cores on the CT scanning table was found to distort density readings slightly at the ends of each core through a phenomenon known as "beam hardening" (Brooks & Di Chiro, 1976). To rectify this issue, cores collected in 2015 were scanned in a parallel orientation relative to the CT table. However, all cores from 2009 and 2012 were slabbed and sampled for geochemical analysis before they could be re-scanned; thus, skeletal density could not be reliably measured from these cores. As a result, analyses in this study focus on annual linear extension rate as the principal growth parameter, which has been found to be a reliable proxy for annual coral calcification (Fig. 2; Supplementary Methods; Lough & Barnes, 2000), though the relative contribution of linear extension and density to calcification rate varies by species (Pratchett *et al.*, 2015).

Linear extension rates were measured by uploading all CT scans to the DICOM image viewing softwares OsiriX or Horos v2.0.2, which permitted visualization of annual density bands on 8-10 mm thick "digital slabs" of stacked 0.6 mm layers using "Mean" projection mode (i.e., displays mean density of each voxel within the digital slab). Annual high- and low-density band couplets were inspected visually as the distance from the top of a high density band to the bottom of the next low density band. Linear transects were then drawn parallel to the coral growth axis and within the exothecal space between corallite walls down the core using the "Length" tool in OsiriX/Horos. Density measurements were then extracted from linear transects and a custom *R* code was used to calculate the width of each annual pair of high- and low-density bands. Transects were performed in triplicate for each segment of the core in order to average out the spatial variability in linear extension within the annual growth bands. The entire length of the core was analyzed in this manner, or until it was no longer possible to resolve annual growth bands due to the effects of bioerosion and/or loss of seasonal density banding. Additional details on this methodology, including example images of coral CT scans, can be found in Figure S1 and in Rippe et al. (2018). Data for the individual cores analyzed in this experiment, including length of each growth record, are provided in Table S1.

Linear extension as a proxy for calcification rate

To validate the use of linear extension as a proxy of coral calcification in this study, skeletal density and calcification rate were also calculated for all cores collected and CT scanned in 2015 (n = 68 cores). Coral density standards of known mass and volume were obtained from coral cores with the same diameter as those used in the study and scanned alongside the corals to construct a standard curve for each scanning session that correlated Hounsfield unit values (CT scan output) to density (g/cm^3) (DeCarlo *et al.*, (2015), Rippe *et al.*, (2018). In this study, extension rate was well correlated with calcification rate (p <0.001, R^2 = 0.919 for *S. siderea* and p <0.001, R^2 = 0.598 for *P. strigosa*), while density is not (p <0.001, R^2 = 0.052 for *S. siderea* and p <0.001, R^2 = 0.002 for *P. strigosa*) (Fig. S2).

Belize sea surface temperature, population, and agricultural data

Hadley Centre Sea Surface Temperature (HadISST1, 1880–present) and NOAA Coral Reef Watch Degree Heating Weeks (DHW; 1994-present) data for Belize were obtained from the NOAA Environmental Research Division Data Access Program (ERDDAP) website (http://coastwatch.pfeg.noaa.gov/erddap/griddap/index.html) over the full available temporal. Sea surface temperature (SST) measurements from all 1° x 1° latitudinal-longitudinal grid cells within the Belize Exclusive Economic Zone were averaged annually, and linear regression was used to evaluate statistically significant changes in temperature over time.

Degree Heating Weeks (DHW) is a measure of accumulated thermal stress over a 12 week interval measured in °C weeks where 1°C week is equal to one week of temperatures 1°C over the estimated 29.7 °C regional coral bleaching threshold for Belize (Aronson *et al.*, 2002) over a 12 week interval (Liu *et al.*, 2006). Maximum annual DHW data at 5km resolution were obtained from NOAA ERDAAP for grid cells nearest each coring site. DHW data were averaged across reef environments to compare accumulated thermal stress between each environment during reported bleaching events.

Population data for the country of Belize from 1980-to-present and for major coastal cities in Belize (i.e., Belize City, San Pedro, Dangriga, Punta Gorda) from 2008-to-present were obtained from the Statistical Institute of Belize website (http://www.sib.org.bz/statistics/population). Agricultural land use statistics for Belize from 1960-to-present were obtained from the Food and Agricultural Organization of the United Nations (FAO) website (http://www.fao.org/faostat/). All parameters are plotted in Figure S3.

Statistical analyses

To evaluate long-term trends in linear extension rates across the Belize MBRS, a linear mixed-effects modeling framework was employed, which accounts for variability in individual *S. siderea* and *P. strigosa* core chronologies, rather than relying on a single master chronology (Castillo *et al.*, 2011). A linear regression of annual skeletal extension rates vs. year was obtained by fitting a set of mixed effects models that treated each individual core as a sampling unit and incorporated the inherent variability in core chronologies as random effects (both random slopes and random intercepts for each core chronology; Tables 1, S2). This mixed effects modeling approach was employed to address the inherent hierarchical nature of coral skeletal extension data. See Castillo *et al.* (2011) and Rippe *et al.* (2018) for further details on the advantage of this approach with respect to interpreting coral extension data.

Species	**Reef environment**	**Slope**	**Slope *p-value***	**Number of cores**
S. siderea	AFR	0.00024	0.599	9
	ABR	-0.00056	0.141	15
	BR	0.00013	0.591	33
	FR	-0.00030	0.182	23
	NS	-0.00108	**<0.001**	16
P. strigosa	FR	-0.00183	0.329	20
	NS	-0.00755	**<0.001**	15

Table 1: Slope of annual extension rate vs. year by species and reef environment from linear mixed effects models. Significant *p-values* ($p<0.05$) are in bold and indicate a statistically significant from zero slope for change in annual extension rate through time. 95% confidence intervals (CI) that do not overlap indicate significant differences between reef environments (see Figs. 2, 3, S3, S4). AFR, ABR, BR, FR, and NS represent atoll forereef, atoll backreef, backreef, forereef, and nearshore, respectively.

Linear mixed effects model selection

The central goal of the present study was to describe how annual skeletal extension of *S. siderea* and *P. strigosa* on the Belize Mesoamerican Barrier Reef System (MBRS) varied for each species throughout time (1814-present for *S. siderea* and 1950-present for *P. strigosa*). A model testing procedure was employed for each species (Table S2; Supplementary Methods) and Akaike Information Criterion (AIC) was used to identify the best-fit model (Burnham & Anderson, 2002). AIC provides a measure of the explanatory power of a model discounted by the number of parameters that contributed to its construction; a lower value indicates a better fitting model (Burnham & Anderson, 2002).

Statistical analyses were carried out using the nlme package (Pinheiro *et al.*, 2017) in *R* (R Core Team, 2017). Slopes and the variance of slopes were extracted from each linear mixed effects model for all reef environments. 50% and 95% confidence intervals (CI) were calculated for all reef environments within each species, with 95% CI that do not overlap indicating significant differences in the rate of change in annual extension between reef environments (Figs. 2, 3; Table S3, S4). *t*-tests and 95% confidence intervals were used to identify slopes that were significantly different from zero (Figs. 2, 3; Table S3, S4). This method has previously been utilized to analyze coral core data (Barkley & Cohen, 2016, Castillo *et al.*, 2011, Rippe *et al.*, 2018) and has been shown to be sensitive enough to assess significant differences between small slopes (on the order of 10^{-3} cm/year/year) and zero (Castillo *et al.*, 2011).

Reef-environment-averaged extension rates

To investigate differences in recent extension rates between reef environments, skeletal extension rates (cm/year) were averaged for all corals within a reef environment across five-year time bins from 1950-to-2014 (e.g., 1950-1954, 1955-1959, etc.) in order to smooth out year-to-year noise in coral growth associated with anomalous growth events caused by warming or local stressors. A two-way analysis of variance (ANOVA) and a TUKEY HSD test were used to determine significant differences (p<0.05) in average extension between reef environments within these five-year time bins (Figs. 2C, 3C; Table S3).

Extension anomaly vs. mass-bleaching events

To test whether reported coral bleaching events correlate with low annual extension rates, "low extension" years were identified as those with extension rates falling in the bottom 10th percentile of the core's full growth record for each core chronology. The fraction of cores registering low extension was determined for each year in which the sample size exceeded 5 in a given reef environment (1975-present for *P. strigosa;* 1920-present for *S. siderea*). Low extension anomalies within each reef environment were then compared with years in which max DHW ≥ 4, as DHW = 4 is the threshold at which significant bleaching is expected (Eakin *et al.*, 2010). These high DHW years were compared with reports of historical mass-bleaching events in the Caribbean region: 1995 (McField, 1999); 1997-1998 (Aronson *et al.*, 2002, Podesta & Glynn, 2001); 2005 (Donner *et al.*, 2007, Eakin *et al.*, 2010, LaJeunesse *et al.*, 2009); 2009-2010 (Alemu & Clement, 2014, Buglass *et al.*, 2016, Kemp *et al.*, 2014); and 2014-2016 (Eakin *et al.*, 2016). Years that directly preceded or followed a reported bleaching event, years containing bleaching events (DHW ≥ 4), and other years that had high numbers of cores exhibiting low extension were noted and included as explanatory variables in least squares regression, thereby identifying which years contained significantly higher fractions of cores exhibiting low extension within each reef environment. The fraction of cores exhibiting low extension was then averaged for bleaching and non-bleaching years for each reef environment. The percentage of cores exhibiting low extension was then compared between bleaching and non-bleaching years via two-way analysis of variance (ANOVA) and a TUKEY HSD test ($p<0.05$; Table S5).

RESULTS

Coral linear extension trends

The slopes of annual skeletal extension rates vs. time for nearshore *S. siderea* from the late 19th century to present (Table 1; Fig. 2A, B, S6) and nearshore *P. strigosa* from the mid-20th century to present (Table 1; Fig. 3A, B, S7) were significantly negative (Tables 1, S3), indicating declining rates of mean skeletal extension for both coral species on nearshore reefs across the Belize MBRS. In contrast, *S. siderea* and *P. strigosa* colonies from the backreef, forereef, atoll backreef, and atoll forereef (collectively defined as "offshore" because of their >30 km distance from mainland Belize) exhibited no net decrease in mean skeletal extension through time (Table 1; Fig. 2A, 2B, 3A, 3B). However, it is important to note that the extension rates vs. time slopes for individual cores for both species in each of the respective reef environments varies from positive to negative, indicating colony and site-level variability in growth responses through time (Fig. 2, 3). Skeletal extension trends that mirror these century scale trends are also seen when data are trimmed to include only the years 1980-present, an interval that includes at least 50% of all cores from each reef environment and a total of 66% of total cores (Fig S4, S5).

Nearshore *S. siderea* and *P. strigosa* exhibited higher skeletal extension rates than offshore conspecifics from at least 1990 to 2009 (Fig. 2C, 3C; Tables S3, S4; *p*-values <0.001). This trend is visually apparent as far back as 1965, but decreasing sample size further back in time may have diminished the statistical significance of this relationship (Fig. 2C, 3C; Tables S3, S4). After 2009, however, skeletal extension rates of nearshore *S. siderea* and *P. strigosa* converge with those of their offshore conspecifics (*p*-values: 0.986 and 0.186, respectively; Figs. 2C, 3C; Tables S3, S4) owing to both the decline in skeletal extension rates for the nearshore corals and the increase in skeletal extension rates for the offshore corals (Fig. 2C, 3C). Notably, nearshore and forereef linear extension rates also converge between 1950 and 1960. Earlier convergences of nearshore and forereef extension rates cannot be evaluated for *P. strigosa* due to the shorter temporal length of their nearshore growth record, but may have occurred.

Environmental parameters

The average SST across all reef environments of the Belize MBRS has increased by ca. 0.5 °C since 1880 ($p<0.01$; Fig. S3A). Additionally, human population densities in local coastal cities increased by 39% and regional agricultural land area increased by 100% from the mid-20th century to present (Figs. S3B-C).

Impacts of acute bleaching stress on coral linear extension

Mass coral bleaching was documented in the Caribbean in 1995, 1998, 2005, 2010, and 2014-2016 (see methods). Degree Heating Week (DHW) data for each reef environment indicates likely mass bleaching (DHW value ≥ 4; Liu *et al.*, 2006) at nearshore sites in 1998, 2010, and 2015, at back reef and forereef sites in 1998 and 2010, and at atoll backreef, and atoll forereef sites in 1998, 2005, 2009, 2010, and 2011 (Table 2). Nearshore, backreef, and forereef sites experienced the highest DHW values in 1998, while atoll backreef and atoll forereef experienced the highest DHW values in 2005 (Table 2). Notably, there is considerable variation in DHW values between sites within a single reef environment (Table 2). The skeletal extension data from the present study was evaluated to determine whether bleaching conditions (DHW ≥ 4) significantly impacted coral skeletal extension within each reef environment of the Belize MBRS. Overall, skeletal extension was significantly lower during years in which DHW ≥ 4 than during non-bleaching years for *S. siderea* (p<0.001; Table S5), but not for *P. strigosa*, although *P. strigosa* did exhibit significantly lower extension in the 2011 (i.e., DHW ≥ 4 in 2011) than during non-bleaching years (i.e., DHW < 4; Fig. 4; Table S6). In general, no reef environment was more likely than any other to experience lower extension rates during bleaching years than during non-bleaching years. However, skeletal extension was anomalously low for *S. siderea* on the forereef of the atolls following the 1995 bleaching event in spite of low DHW values (Table 2). Skeletal extension was also anomalously low for *S. siderea* on the forereef and backreef of the atolls during the 1997-1998 bleaching event and on the backreef of the atolls following the 2005 bleaching event (Fig. 4; Table S6), for nearshore *S. siderea* and *P. strigosa* following the 2010 bleaching event (Fig. 4; Table S6), and for nearshore *S. siderea* and forereef corals of both species in the 2014 bleaching year (Fig. 4; Table S6). Notably, anomalously low skeletal extension rates were also observed for some non-bleaching years in both species (e.g., in 1985 for nearshore *S. siderea* and in 1992 for nearshore *P. strigosa*; Fig. 4; Table S6), potentially due to other stressors [e.g., storms, human activity, or sedimentation (Hughes *et al.*, 2017, Pratchett *et al.*, 2015)] or unreported/small-scale bleaching.

Reef Environment	**Site**	1995	**1998**	2003	2004	**2005**	2008	2009	**2010**	2011	**2015**
Nearshore	**Average**	0.40 ± 0.18	**7.32 ± 0.22**	3.90 ± 0.58	2.46 ± 0.93	3.15 ± 0.55	3.86 ± 0.35	3.60 ± 0.51	**4.02 ± 0.26**	3.77 ± 0.51	**6.55 ± 0.75**
	Belize City	0.63	**6.71**	3.52	**5.84**	**4.81**	**4.42**	**5.2**	3.49	**5.09**	**4.49**
	Dangriga	0.15	**6.99**	**5.41**	2.9	3.76	3.94	**4.34**	3.53	**4.69**	**5.34**
	Placencia	0.31	**7.95**	**5.11**	1.82	3.27	**4.82**	3.29	**4.94**	3.86	**6.68**
	Port Honduras	0.47	**7.43**	2.86	0.8	2.03	3.09	2.59	3.93	2.58	**8.6**
	Snake Keys	0.48	**7.54**	2.59	0.93	1.89	3.04	2.59	**4.19**	2.64	**7.65**
Backreef	**Average**	0.82 ± 0.35	**6.45 ± 0.45**	3.07 ± 0.20	2.90 ± 0.69	3.52 ± 0.29	3.22 ± 0.14	3.63 ± 0.33	**4.04 ± 0.68**	3.71 ± 0.21	3.85 ± 0.82
	Belize City	1.11	**6.18**	2.67	**4.49**	3.58	3.45	**4.11**	2.67	**4.21**	2.87
	Dangriga	0.60	**5.67**	3.23	2.9	**4.09**	2.8	3.94	3.65	3.62	3.42
	Placencia	0.47	**7.34**	3.27	1.82	3.22	3.62	3.42	**6.23**	**4.22**	**4.5**
	San Pedro	1.28	**5.4**	2.55	**4.33**	**4.13**	3.07	**4.23**	2.72	3.27	1.82

	Sapodilla	0.63	**7.67**	3.61	0.95	2.57	3.17	2.43	**4.94**	3.25	**6.62**
Forereef	**Average**	0.73 ± 0.23	**6.30 ± 0.36**	3.29 ± 0.10	3.22 ± 0.68	3.72 ± 0.28	3.19 ± 0.09	3.88 ± 0.35	**4.032 ± 0.57**	3.81 ± 0.16	3.80 ± 0.62
	Alligator	0.75	**5.74**	3.65	3.96	3.7	3.1	**4.04**	3.31	3.76	3.81
	Belize City	0.77	**5.95**	2.92	**4.15**	**4.11**	3.36	**4.77**	2.78	**4.31**	2.69
	Dangriga	0.60	**5.67**	3.23	2.9	**4.09**	2.8	3.94	3.65	3.62	3.42
	Gladdens	0.7	**7.22**	3.22	1.81	3.31	3.41	3.52	**6.26**	**4.26**	**4.23**
	San Pedro	1.15	**5.62**	3.24	**5.52**	**4.53**	3.32	**4.62**	2.96	3.52	2.16
	Sapodilla	0.64	**7.6**	3.48	0.96	2.58	3.14	2.41	**5.23**	3.39	**6.51**
Atoll Backreef	**Average**	0.90 ± 0.20	**5.36 ± 0.38**	3.91 ± 0.05	3.08 ± 0.44	**5.62 ± 0.36**	3.44 ± 0.24	**4.24 ± 0.36**	**5.23 ± 0.68**	**4.34 ± 0.63**	3.82 ± 0.41
	Glovers	0.77	**5.77**	3.99	2.06	**4.86**	3.22	**4.13**	**6.3**	3.31	**4.28**
	Lighthouse	1.13	**4.63**	3.91	3.44	**6.33**	3.91	3.84	**5.01**	**4.65**	**4.17**
	Turneffe	0.8	**5.55**	3.82	3.58	**5.21**	3.2	**4.96**	**4.2**	**5.24**	3
Atoll Forereef	**Average**	0.85 ± 0.26	**5.32 ± 0.35**	3.91 ± 0.05	3.03 ± 0.49	**5.47 ± 0.44**	3.44 ± 0.23	**4.31 ± 0.34**	**5.17 ± 0.61**	**4.4 ± 0.57**	3.82 ± 0.41
	Glovers	0.62	**5.91**	**4**	2.21	**5.31**	3.2	3.93	**6.48**	3.14	**4.28**
	Lighthouse	1.13	**4.63**	3.91	3.44	**6.33**	3.91	3.84	**5.01**	**4.65**	**4.17**
	Turneffe	0.8	**5.55**	3.82	3.58	**5.21**	3.2	**4.96**	**4.2**	**5.24**	3

Table 2: Average maximum annual Degree Heating Weeks (DHW) for each reef environment and maximum DHW for each site within a reef environment for all years of the instrumental record in which DHW ≥ 4 for any site. Years in which mass bleaching was reported in the Caribbean region are bold. All DHW values ≥ 4 are bold. Average values are reported as average ± 1 standard error of the mean.

DISCUSSION

Declining skeletal extension rates for nearshore corals

We postulate that the observed declines in skeletal extension rates for nearshore *S. siderea* and *P. strigosa* corals may have been driven primarily by a combination increasing seawater temperatures (Carilli *et al.*, 2012, Pratchett *et al.*, 2015), ocean acidification, eutrophication, increasing sedimentation, coastal development, and/or land use change

(Fabricius, 2005, Hoegh-Guldberg *et al.*, 2007, Wiedenmann *et al.*, 2013). Additionally, nearshore reef environments historically supported higher skeletal extension rates than offshore reef environments, but recent declines in nearshore coral growth rates have caused nearshore coral growth rates to converge with offshore coral growth rates since 2010 (Tables 3, S3, S4; Fig. 2C, 3C, S4).

Sea surface temperature across all reef environments of the Belize MBRS has increased since 1880 (p<0.01; Fig. S3A), and average summer SST across this reef system has increased by approximately 0.5°C since 1985 (Castillo *et al.*, 2012). Analysis of satellite SST data for the region reveals that nearshore reefs on the Belize MBRS were exposed to between 54 and 78 days per year above the estimated regional bleaching threshold of 29.7 °C (Aronson *et al.*, 2002) over the years 2003-2012 (Baumann *et al.*, 2016). In contrast, offshore reef sites experienced only 20 to 40 days per year above the regional bleaching threshold during that same interval. Nearshore reefs also had warmer average annual temperatures (0.6-0.7°C warmer) as well as hotter summers than offshore reefs (Baumann *et al.*, 2016).

Although temperature increases up to and slightly beyond a coral's thermal optimum can increase coral skeletal growth rates (Castillo *et al.*, 2014, Courtney *et al.*, 2017, Jokiel & Coles, 1977, Pratchett *et al.*, 2015), and corals become locally adapted to warmer temperatures over time (Coles & Brown, 2003), temperatures surpassing the thermal optimum by more than a degree have been shown to negatively impact coral growth (Lough & Cantin, 2014, Pratchett *et al.*, 2015). This negative impact of elevated temperature on coral skeletal growth rate is driven not only by the magnitude of the warming, but also by its duration (Pratchett *et al.*, 2015). Century-scale and recent (1980-present) declines in skeletal extension rates of nearshore colonies along the Belize MBRS, combined with the absence of century-scale or recent (1980-present) declines in the mean extension rates of backreef and forereef colonies (Figs. 2, 3, S4, S5), suggest that a critical threshold of thermal stress (e.g., magnitude, frequency, and/or duration) may have been exceeded for nearshore *S. siderea* and *P. strigosa* corals, but not for forereef and backreef colonies.

However, localized drivers such as eutrophication and sedimentation may also play a role in the convergence of nearshore and offshore coral growth rates observed in this study. Previous work has demonstrated that high sediment and riverine nutrient loads (D'Olivo *et al.*, 2013) and increased turbidity (Fabricius, 2005) impair coral growth rates. Additionally, nutrient enrichment along with subsequent altering of nitrogen (N):phosphorus (P) ratio (Rosset *et al.*, 2017, Wiedenmann *et al.*, 2013) can increase bleaching susceptibility and lead to decreased growth rates (D'Olivo *et al.*, 2013, Dodge *et al.*, 1974). Coral calcification rates on nearshore reefs of the Great Barrier Reef are declining on multi-decadal timescales, while calcification rates on offshore reefs are increasing (D'Olivo *et al.*, 2013). This declining growth on nearshore reefs is attributed to the impacts of wet season river discharge of sediment and nutrients, a trend that is exacerbated by warming (D'Olivo *et al.*, 2013). As human population densities and agricultural land area have increased in Belize since the mid-20th century (Fig. S3B, C), runoff and eutrophication in the MBRS have also increased over time, with the greatest effects of these land-based changes occurring in the nearshore environments closest to the land-based runoff sources (Fig S2; Carilli *et al.*, 2009, Chérubin *et al.*, 2008, Heyman & Kjerfve, 1999, Prouty *et al.*, 2008). However, *S. siderea* and *P. strigosa* also metabolize N from ingested sediments and particulates (Mills *et al.*, 2004, Mills & Sebens, 2004). This N may augment coral nutrition during intervals of increased sedimentation and eutrophication, potentially mitigating some of the negative impacts of these processes. Thus, elevated nutrient and sediment loads on nearshore reefs may historically contribute to higher growth rates compared to offshore reefs, but continued nutrient and sediment loading associated with coastal development and increased runoff due to increasing human populations and/or land-use changes (Fig. S3 B,C) may have contributed to the observed decline in nearshore coral growth in recent years.

It is likely that increasing nutrient and sediment loading (Heyman & Kjerfve, 1999, Thattai *et al.*, 2003), coupled with increasing water temperatures and increasing duration of time that water temperatures exceed the species' bleaching threshold, are responsible for the decline in skeletal extension rates observed for nearshore colonies of the Belize MBRS in this study. This finding agrees with previous work documenting declining growth rates for *O. faveolata* corals nearest land-based impacts exhibit in the MBRS (Carilli *et al.*, 2010). The observed declines in nearshore extension rates and recent convergence of extension rates for nearshore and offshore colonies of *S. siderea* and *P. strigosa* (Fig. 2) suggests that the growth advantage that nearshore corals appear to have historically had over offshore corals has now been lost, perhaps due to the rate of warming surpassing the speed at which corals can locally adapt/acclimatize to it, coupled with eutrophication and sedimentation on nearshore reefs (Tables 3, S4; Figs. 2, 3;

Courtney *et al.*, 2017). If temperature and eutrophication continue to increase, nearshore coral growth rates should continue to decline—with offshore corals potentially following suit. Indeed, some offshore corals in southern Belize already exhibit declining growth rates, likely due to proximity to land-based stressors (Carilli *et al.*, 2010). Although there is metagenomic evidence that nearshore *S. siderea* have begun acclimatizing to these elevated temperatures (Davies *et al.*, 2018), the observation that skeletal extension rates have continued declining for both species up to present time in nearshore reefs of the MBRS suggest that such acclimatization is not sufficient to maintain stable rates of skeletal growth under present-day nearshore environmental conditions.

Recent bleaching events differentially impact corals across reef environments

Siderastrea siderea corals exhibited anomalously low linear extension rates during years in which DHW ≥ 4 (and the years directly following) while *P. strigosa* corals did not, indicating that growth rates of *S. siderea* may be more susceptible to acute bleaching stress (Fig. 4; Tables S5, S6;). *Siderastrea siderea* and *P. strigosa* are classified as stress-tolerant coral species (Darling *et al.*, 2012), but *S. siderea* are often among the first coral species to bleach during a thermal stress event (Banks & Foster, 2016, Hernández-Delgado *et al.*, 2006). While the early onset of bleaching for a stress-tolerant *S. siderea* appears to be a contradiction for life history expectations, the resilience of *S. siderea* to bleaching events may suggest that early onset bleaching is part of an adaptive strategy for this coral (Buddemeier & Fautin, 1993) under elevated thermal stress and warrants further investigation.

Anomalously low growth is observed in nearshore colonies of both species in 2011 following the 2010 bleaching event, during which DHW ≥ 4 (Table 2; Table S6; Fig. 4). Anomalously low growth is also observed in atoll backreef *S. siderea* during the 2005 bleaching year (DHW ≥ 4) and the year immediately following (2006) (Table 2; Table S6; Fig. 4). Average DHW for individual reef environments were ≥ 4 on 16 other occasions, yet anomalously low growth was not recorded during these years or during the years directly following them—including the year 1998, the only year in which every individual site was exposed to DHW ≥ 4 (Table 2). In fact, the only year in which anomalously low growth was observed across multiple reef environments was 2014, a year in which DHW was not greater than 4, highlighting the variability in how individual bleaching events impact skeletal extension across coral species and reef environments (Fig. S8). Importantly, nearshore, backreef, forereef, and atoll forereef corals did not exhibit anomalously low extension during the year in which they experienced the highest DHW (1998; Tables 2, S6), but atoll backreef *S. siderea* did (2005-2006; Tables 2, S6). Collectively, these results indicate differential growth responses to bleaching between reef environments and years and that the magnitude of acute thermal stress alone is likely not a reliable predictor of coral growth rate. This is likely due to spatial variation in warming across the MBRS, site- and depth-specific thermal variability that can reduce bleaching (Safaie *et al.*, 2018, Schramek *et al.*, 2018), as well as the ability of coral populations to modify their bleaching thresholds (Coles & Brown, 2003, Palumbi *et al.*, 2014).

Overall, growth rates of *S. siderea* appear more susceptible to the impacts of bleaching than *P. strigosa*. Additionally, as corals on nearshore reefs only exhibited anomalously low extension rates following one of three bleaching events (DHW ≥ 4 on nearshore reefs; 2010) (Table 2; Table S6; Fig. 4), the observed decline in skeletal extension rates on nearshore reefs of the Belize MBRS are not likely due to the increasing frequency of mass bleaching events in recent years. Instead, the steady nature of the decline in skeletal extension of the investigated species in nearshore reef environments suggests that it is related to the increase in seawater temperatures over the same interval, coupled with the increasing influence of land-based stressors, such as increased sedimentation and eutrophication. Nevertheless, the increasing frequency of the bleaching events may indeed be exacerbating the deleterious impacts of steady anthropogenic warming on skeletal extension rates in nearshore reef environments, especially for *S. siderea*.

Nearshore colonies of P. strigosa *on pace to cease growing by year 2110*

Although both coral species studied here are considered stress-tolerant (Darling *et al.*, 2012), linear extrapolation of extension trends observed here suggest that nearshore *P. strigosa* corals could cease growing by 2110 and *S. siderea* by 2370. These results suggest that coral growth on nearshore reefs along the Belize MBRS may decline substantially over the next century, even in the most stress-tolerant species, threatening reef complexity and leading to habitat loss (Alvarez-Filip *et al.*, 2013, Alvarez-Filip *et al.*, 2009).

These predicted declines in coral growth assume that the temporal trends in coral extension observed over the cored interval can be linearly extrapolated into the future, which is predicated on the assumptions that the primary coral stressors (e.g., warming, acidification, eutrophication, sedimentation, pollution) will continue changing at the same rate and that corals' responses to these stressors will be linear. However, continued improvement of local water quality and reduction in global CO_2 emissions (if achieved) have the potential to mitigate some of these projected growth decreases. For example, emissions scenarios lower than or on par with the commitments of the Paris Agreement have been projected to potentially increase or at least maintain stable growth rates for Bermudan corals assuming +0.1°C/decade acclimatization rates (Courtney *et al.*, 2017). Conversely, further deterioration of water quality and/or acceleration of warming and acidification beyond rates observed over the cored interval and/or development of synergistic impacts amongst stressors would accelerate future declines in coral extension.

Declining skeletal extension of nearshore corals may foretell decline of offshore corals on the MBRS

The results of the present study reveal a decline in historically elevated nearshore calcification rates in Belize MBRS *S. siderea* and *P. strigosa* corals to match calcification rates of their offshore conspecifics. Single mass bleaching events do not reliably correlate with coral extension rates—suggesting that the long-term decline in nearshore coral extension cannot be unequivocally attributed to the increasing frequency of mass bleaching events alone, although they may play a role. Instead, long-term increases in seawater temperature and local stressors (e.g., eutrophication and sedimentation), are the more likely drivers of the observed decline in nearshore coral growth. Any advantage historically conferred to corals by inhabiting the nearshore environment appears to have substantially diminished in recent decades. Importantly, as cores were only collected from apparently healthy corals, the results of this study are indicative of growth trends for well-performing corals within each reef environment. As such, these results likely underestimate declines in coral growth rates observed here. Further research on this subject should explore the intrinsic (e.g., adaptation and acclimatization) and extrinsic (e.g., environmental gradients) processes that lead to the observed variability in growth trends within and across reef environments. Continued protection, monitoring, and management of nearshore reef environments is essential to afford these corals on the Belize MBRS sufficient time to acclimatize to and, hopefully, survive this interval of rapid climate and oceanic change.

Competing Interests

The authors are not aware of any competing interests.

Authors' contributions

JB designed the study, carried out the research, carried out the statistical analysis, and wrote the manuscript; JBR conceived of the study, helped carry out the field component of the study, provided resources, and helped draft the manuscript; JR helped carry out the research, helped design the statistical analysis, and helped draft the manuscript; TC helped design the study, helped carry out the study, and contributed to statistical analysis; HA coordinated the field component of the study; IW helped carry out the field component of the study; KC conceived of the study, helped carry out the field component of the study, provided resources, helped draft the manuscript, and coordinated the study. All authors gave final approval for publication.

Acknowledgements

We thank K. Horvath, K. Cobleigh, C. Hines, A. Rash, Garbutt's Marine, and the Toledo Institute for Development and the Environment (TIDE) for field assistance, A. Foguel for development of the *RunningCoral* program for quantifying coral extension, and Wake Radiology and UNC Biomedical Research Imaging Center (BRIC) for assistance with coral CT scanning. We also thank the Belize Fisheries Department for issuance of the relevant research permits and for their continued support of our research efforts on the Belize MBRS. This research was funded by a Rufford Foundation grant to J. Baumann, NOAA grants NA11OAR431016 and NA13OAR4310186 to J. Ries and K. Castillo, and National Science Foundation grants to K. Castillo (OCE 1459522) and J. Ries (OCE 1437371).

Figure Captions

Figure 1: Map of reef sites on the Belize Mesoamerican Barrier Reef System where *Siderastrea siderea* and *Pseudodiploria strigosa* cores were extracted in 2009, 2012, and 2015. Circles and triangles represent core extraction sites for *S. siderea* and *P. strigosa*, respectively. Colors denote reef environment (nearshore = red, backreef = green, forereef = blue, atoll backreef = pink, and atoll forereef = yellow). Numbers denote total cores extracted for a particular species at a specific site.

Figure 2: (A) Results of linear model of extension rate (cm year^{-1}) vs. time for *S. siderea* by reef environment for the 1814-to-present interval. Gray lines are raw extension data, black lines are average linear models of extension for all *S. siderea* cores across all reef environments, blue lines are average linear models of extension for all *S. siderea* cores within each reef environment, and red lines are linear models of extension for individual *S. siderea* cores within reef environments. Raw (gray) and linearly modeled (red) extension chronologies highlight the variability in growth amongst colonies. (B) Slopes of linear models describing extension vs. time for each reef environment, with small points representing individual cores and large points representing average slopes of all cores within a reef environment (gray bars and colored bars are 50% and 95% confidence intervals (CI), respectively, of average slope for each reef environment). Slopes are significantly different from each other if their 95% CI do not overlap. Likewise, slopes are significantly different from zero if their 95% CI do not overlap with the vertical red dashed line centered on zero. (C) Five-year averages of skeletal extension rate by reef environment ± 1 SE. Asterisks indicate statistically significant differences ($p < 0.05$) between nearshore and forereef values.

Figure 3: Results of linear model of extension rate (cm year^{-1}) vs. time for *P. strigosa* by reef environment for the 1950-to-present interval. Gray lines are raw extension data, black lines are average linear models of extension for all *P. strigosa* cores across all reef environments, blue lines are average linear models of extension for all *P. strigosa* cores within each reef environment, and red lines are linear models of extension for individual *S. siderea* cores within reef environments. Raw (gray) and linearly modeled (red) extension chronologies highlight the variability in growth amongst colonies. (B) Slopes of linear models describing extension vs. time for each reef environment, with small points representing individual cores and large points representing average slopes of all cores within a reef environment [gray bars and colored bars are 50% and 95% confidence intervals (CI), respectively, of average slope for each reef environment]. Slopes are significantly different from each other if their 95% CI do not overlap. Likewise, slopes are significantly different from zero if their 95% CI do not overlap with the red dashed line centered on zero. (C) Five-year averages of skeletal extension rate by reef environment ± 1 SE. Asterisks indicate statistically significant differences ($p < 0.05$) between nearshore and forereef values.

Figure 4: Total number of cores analyzed for each reef environment per species per year (top panel) and fraction of cores within each reef environment exhibiting anomalously low extension rates (i.e., annual extension rate in lowest 10% of cores) per year (bottom panel). Higher values in bottom panel indicate greater proportion of cores within a reef environment exhibiting anomalously low extension within a given year. Black horizontal lines indicate time-averaged ratios for each reef environment (separated by species). Horizontal dashed lines indicate the 95% confidence interval for the time-averaged ratios for each reef environment. Peaks that exceed this confidence interval represent significantly ($p < 0.05$) higher percentages of corals exhibiting anomalously low extension rates in a given year. Vertical dashed lines indicate years in which DHW ≥ 4 for each reef environment (Table 2).

References

Alemu JB, Clement Y (2014) Mass coral bleaching in 2010 in the southern Caribbean. Plos ONE, **9**, e83829.

Alvarez-Filip L, Carricart-Ganivet JP, Horta-Puga G, Iglesias-Prieto R (2013) Shifts in coral-assemblage composition do not ensure persistence of reef functionality. Scientific reports, **3**. https://doi.org/10.1038/srep03486.

Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR (2009) Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. Proceedings of the Royal Society of London B: Biological Sciences, rspb20090339.

Aronson RB, Precht WF, Toscano MA, Koltes KH (2002) The 1998 bleaching event and its aftermath on a coral reef in Belize. Marine Biology, **141**, 435-447.

Banks S, Foster K (2016) Baseline Levels of Siderastrea siderea Bleaching under Normal Environmental Conditions in Little Cayman. Open Journal of Marine Science, **7**, 142.

Barkley HC, Cohen AL (2016) Skeletal records of community-level bleaching in Porites corals from Palau. Coral Reefs, **35**, 1407-1417.

Baumann JH, Townsend JE, Courtney TA, Aichelman HE, Davies SW, Lima FP, Castillo KD (2016) Temperature Regimes Impact Coral Assemblages along Environmental Gradients on Lagoonal Reefs in Belize. Plos ONE, **11**, e0162098. 10.1371/journal.pone.0162098.

Berkelmans R, Van Oppen MJ (2006) The role of zooxanthellae in the thermal tolerance of corals: a 'nugget of hope'for coral reefs in an era of climate change. Proceedings of the Royal Society of London B: Biological Sciences, **273**, 2305-2312.

Bove CB, Ries JB, Davies SW, Westfield IT, Umbanhowar J, Castillo KD (2019) Common Caribbean corals exhibit highly variable responses to future acidification and warming. Proceedings of the Royal Society B*,* **286**, 20182840.

Brooks RA, Di Chiro G (1976) Beam hardening in x-ray reconstructive tomography. Physics in medicine and biology*,* **21**, 390.

Buddemeier RW, Fautin DG (1993) Coral bleaching as an adaptive mechanism. BioScience*,* **43**, 320-326.

Buglass S, Donner SD, Alemu JB (2016) A study on the recovery of Tobago's coral reefs following the 2010 mass bleaching event. Marine Pollution Bulletin*,* **104**, 198-206.

Burnham KP, Anderson DR (2002) *Model selection and multimodel inference: a practical information-theoretic approach*, Springer Science & Business Media.

Carilli J, Donner SD, Hartmann AC (2012) Historical temperature variability affects coral response to heat stress. Plos ONE*,* **7**, e34418.

Carilli JE, Norris RD, Black B, Walsh SM, Mcfield M (2010) Century-scale records of coral growth rates indicate that local stressors reduce coral thermal tolerance threshold. Global Change Biology*,* **16**, 1247-1257.

Carilli JE, Prouty NG, Hughen KA, Norris RD (2009) Century-scale records of land-based activities recorded in Mesoamerican coral cores. Marine Pollution Bulletin*,* **58**, 1835-1842.

Carricart-Ganivet JP, Merino M (2001) Growth responses of the reef-building coral Montastraea annularis along a gradient of continental influence in the southern Gulf of Mexico. Bulletin of Marine Science*,* **68**, 133-146.

Castillo KD, Ries JB, Bruno JF, Westfield IT (2014) The reef-building coral Siderastrea siderea exhibits parabolic responses to ocean acidification and warming. Proceedings of the Royal Society of London B: Biological Sciences*,* **281**, 20141856.

Castillo KD, Ries JB, Weiss JM (2011) Declining coral skeletal extension for forereef colonies of Siderastrea siderea on the Mesoamerican Barrier Reef System, Southern Belize. Plos ONE*,* **6**, e14615.

Castillo KD, Ries JB, Weiss JM, Lima FP (2012) Decline of forereef corals in response to recent warming linked to history of thermal exposure. Nature Climate Change*,* **2**, 756-760.

Chan NCS, Connolly SR (2013) Sensitivity of coral calcification to ocean acidification: a meta-analysis. Global Change Biology*,* **19**, 282-290. 10.1111/gcb.12011.

Chérubin L, Kuchinke C, Paris C (2008) Ocean circulation and terrestrial runoff dynamics in the Mesoamerican region from spectral optimization of SeaWiFS data and a high resolution simulation. Coral Reefs*,* **27**, 503-519.

Coles SL, Brown BE (2003) Coral Bleaching-Capacity for Acclimatization and Adaptation. Advances in Marine Biology*,* **46**, 183-213.

Connell SD, Russell BD (2010) The direct effects of increasing CO2 and temperature on non-calcifying organisms: increasing the potential for phase shifts in kelp forests. Proceedings of the Royal Society B: Biological Sciences*,* **277**, 1409-1415. 10.1098/rspb.2009.2069.

Cooper TF (2008) Declining coral calcification in massive Porites in two nearshore regions of the northern Great Barrier Reef. Global Change Biology*,* **14**, 529-538, DOI: 510.1111/gcb.2008.1114.issue-1113.

Cooper TF, De'ath G, Fabricius KE, Lough JM (2008) Declining coral calcification in massive Porites in two nearshore regions of the northern Great Barrier Reef. Global Change Biology*,* **14**, 529-538.

Cooper TF, Uthicke S, Humphrey C, Fabricius KE (2007) Gradients in water column nutrients, sediment parameters, irradiance and coral reef development in the Whitsunday Region, central Great Barrier Reef. Estuarine, Coastal and Shelf Science*,* **74**, 458-470. http://dx.doi.org/10.1016/j.ecss.2007.05.020.

Courtney TA, Lebrato M, Bates NR *et al.* (2017) Environmental controls on modern scleractinian coral and reef-scale calcification. Science advances*,* **3**, e1701356.

D'olivo J, Mcculloch M, Judd K (2013) Long-term records of coral calcification across the central Great Barrier Reef: assessing the impacts of river runoff and climate change. Coral Reefs*,* **32**, 999-1012.

Darling ES, Alvarez-Filip L, Oliver TA, Mcclanahan TR, Côté IM (2012) Evaluating life-history strategies of reef corals from species traits. Ecology Letters*,* **15**, 1378-1386.

Davies SW, Ries JB, Marchetti A, Castillo KD (2018) Symbiodinium Functional Diversity in the Coral Siderastrea siderea Is Influenced by Thermal Stress and Reef Environment, but Not Ocean Acidification. Frontiers in Marine Science*,* **5**. https://doi.org/10.3389/fmars.2018.00150.

Decarlo TM, Cohen AL, Barkley HC *et al.* (2015) Coral macrobioerosion is accelerated by ocean acidification and nutrients. Geology*,* **43**, 7-10.

Dodge RE, Aller RC, Thomson J (1974) Coral growth related to resuspension of bottom sediments. Nature*,* **247**, 574-576.

Donner SD, Knutson TR, Oppenheimer M (2007) Model-based assessment of the role of human-induced climate change in the 2005 Caribbean coral bleaching event. Proceedings of the National Academy of Science*,* **104**, 5483-5488.

Eakin C, Liu G, Gomez A *et al.* (2016) Global coral bleaching 2014–2017: status and an appeal for observations. Reef Encounter*,* **31**, 20-26.

Eakin CM, Morgan JA, Heron SF *et al.* (2010) Caribbean corals in crisis: record thermal stress, bleaching, and mortality in 2005. Plos ONE*,* **5**, e13969.

Elmhagen B, Kindberg J, Hellström P, Angerbjörn A (2015) A boreal invasion in response to climate change? Range shifts and community effects in the borderland between forest and tundra. AMBIO*,* **44**, 39-50. 10.1007/s13280-014-0606-8.

Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Marine Pollution Bulletin*,* **50**, 125-146.

Ferrier-Pages C, Witting J, Tambutte E, Sebens KP (2003) Effect of natural zooplanton feeding on the tissue and skeletal growth of the scleractinian coral *Stylophora pistillata*. Coral Reefs*,* **22**, 229-240.

Fitt WK, Brown BE, E. WM, Dunne RP (2001) Coral bleaching: interpretation of thermal tolerance limits and thermal thresholds in tropical corals. Coral Reefs*,* **20**, 51-56.

Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. Science*,* **301**, 958-960.

Glenn E, Comarazamy D, González JE, Smith T (2015) Detection of recent regional sea surface temperature warming in the Caribbean and surrounding region. Geophysical Research Letters*,* **42**, 6785-6792.

Green D, Edmunds P, Carpenter R (2008) Increasing relative abundance of Porites astreoides on Caribbean reefs mediated by an overall decline in coral cover. Marine Ecology Progress Series*,* **359**, 1-10. 10.3354/meps07454.

Grottoli AG, Rodrigues LJ, Palardy JE (2006) Heterotrophic plasticity and resilience in bleached corals. Nature*,* **440**, 1186-1189. 10.1038/nature04565.

Hernández-Delgado EA, Toledo C, Claudio H *et al.* (2006) Spatial and taxonomic patterns of coral bleaching and mortality in Puerto Rico during year 2005. Satellite Tools and Bleaching Response Workshop: Puerto Rico and the Virgin Islands, 16.

Heyman WD, Kjerfve B (1999) Hydrological and oceanographic considerations for integrated coastal zone management in southern Belize. Environmental Management*,* **24**, 229-245.

Hoegh-Guldberg O, Bruno JF (2010) The Impact of Climate Change on the World's Marine Ecosystems. Science*,* **328**, 1523-1528. 10.1126/science.1189930.

Hoegh-Guldberg O, Mumby PJ, Hooten AJ *et al.* (2007) Coral Reefs Under Rapid Climate Change and Ocean Acidification. Science*,* **318**, 1737-1742.

Houlbreque F, Ferrier-Pages C (2009) Heterotrophy in Tropical Scleractinian Corals. Biological Reviews*,* **84**, 1-17. 10.1111/j.1469-185X.2008.00058.x.

Hughes TP, Graham NA, Jackson JB, Mumby PJ, Steneck RS (2010) Rising to the challenge of sustaining coral reef resilience. Trends in Ecology & Evolution*,* **25**, 633-642.

Hughes TP, Kerry JT, Álvarez-Noriega M *et al.* (2017) Global warming and recurrent mass bleaching of corals. Nature*,* **543**, 373-377.

Jokiel PL, Coles SL (1977) Effects of temperature on the mortality and growth of Hawaiian reef corals. Marine Biology*,* **43**, 201-208.

Jokiel PL, Coles SL (1990) Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. Coral Reefs*,* **8**, 155-162.

Kemp DW, Hernandez-Pech X, Iglesias-Prieto R, Fitt WK, Schmidt GW (2014) Community dynamics and physiology of Symbiodinium spp. before, during, and after a coral bleaching event. Limnology and Oceanography*,* **59**, 788-797.

Knowlton N (2001) The future of coral reefs. Proceedings of the National Academy of Sciences*,* **98**, 5419-5425.

Kurz WA, Dymond CC, Stinson G *et al.* (2008) Mountain pine beetle and forest carbon feedback to climate change. Nature*,* **452**, 987-990. http://www.nature.com/nature/journal/v452/n7190/suppinfo/nature06777_S1.html.

Lajeunesse TC, Smith RT, Finney J, Oxenford H (2009) Outbreak and persistence of opportunistic symbiotic dinoflagellates during the 2005 Caribbean mass coral 'bleaching'event. Proceedings of the Royal Society of London B: Biological Sciences*,* **276**, 4139-4148.

Lirman D, Fong P (2007) Is proximity to land-based sources of coral stressors an appropriate measure of risk to coral reefs? An example from the Florida Reef Tract. Marine Pollution Bulletin*,* **54**, 779-791.

Liu G, Strong AE, Skirving W, Arzayus LF (2006) Overview of NOAA coral reef watch program's near-real time satellite global coral bleaching monitoring activities. Proceedings of the 10th international coral reef symposium: Okinawa, 1783-1793.

Logan CA, Dunne JP, Eakin CM, Donner SD (2014) Incorporating adaptive responses into future projections of coral bleaching. Global Change Biology, **20**, 125-139.

Lough J, Barnes D (2000) Environmental controls on growth of the massive coral Porites. Journal of Experimental Marine Biology and Ecology, **245**, 225-243.

Lough JM, Cantin NE (2014) Perspectives on massive coral growth rates in a changing ocean. The Biological Bulletin, **226**, 187-202.

Manzello DP, Enochs IC, Kolodziej G, Carlton R (2015) Recent decade of growth and calcification of Orbicella faveolata in the Florida Keys: an inshore-offshore comparison. Marine Ecology Progress Series, **521**, 81-89.

Marshall AT, Clode P (2004) Calcification rate and the effect of temperature in a zooxanthellate and an azooxanthellate scleractinian reef coral. Coral Reefs, **23**, 218 - 224.

Mcfield MD (1999) Coral response during and after mass bleaching in Belize. Bulletin of Marine Science, **64**, 155-172.

Mcwilliams JP, Cote IM, Gill JA, Sutherland WJ, Watkinson AR (2005) Accelerating impacts of temperature-induced coral bleaching in teh Caribbean. Ecology, **86**, 2055-2060.

Mills MM, Lipschultz F, Sebens KP (2004) Particulate matter ingestion and associated nitrogen uptake by four species of scleractinian corals. Coral Reefs, **23**, 311-323.

Mills MM, Sebens KP (2004) Ingestion and assimilation of nitrogen from benthic sediments by three species of coral. Marine Biology, **145**, 1097-1106.

O'reilly CM, Alin SR, Plisnier P-D, Cohen AS, Mckee BA (2003) Climate change decreases aquatic ecosystem productivity of Lake Tanganyika, Africa. Nature, **424**, 766-768. http://www.nature.com/nature/journal/v424/n6950/suppinfo/nature01833_S1.html.

Oliver T, Palumbi S (2011) Do fluctuating temperature environments elevate coral thermal tolerance? Coral Reefs, **30**, 429-440.

Palumbi SR, Barshis DJ, Traylor-Knowles N, Bay RA (2014) Mechanisms of reef coral resistance to future climate change. Science, **344**, 895-898.

Peters EC (2015) Diseases of coral reef organisms. In: *Coral reefs in the Anthropocene.* pp Page., Springer.

Pinheiro J, Bates D, Debroy S, Sarkar D, Heisterkamp S, Van Willigen B, Maintainer R (2017) Package 'nlme'. Linear and nonlinear mixed effects models, 3-1.

Podesta GP, Glynn PW (2001) The 1997-98 El Nino event in Panama and Galapagos: an update of thermal stress indices relative to coral bleaching. Bulletin of Marine Science, **69**, 43-59.

Pratchett MS, Anderson KD, Hoogenboom MO *et al.* (2015) Spatial, temporal and taxonomic variation in coral growth—implications for the structure and function of coral reef ecosystems. Oceanography and Marine Biology: An Annual Review*,* **53**, 215-296.

Prouty N, Hughen K, Carilli J (2008) Geochemical signature of land-based activities in Caribbean coral surface samples. Coral Reefs*,* **27**, 727-742.

Rhein M (2013) Observations: Ocean in Climate Change 2013 The Physical Science Basis in Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (eds Stocker, TF et al.) 255–316. pp Page, Cambridge University Press.

Rippe JP, Baumann JH, De Leener DN, Aichelman HE, Friedlander EB, Davies SW, Castillo KD (2018) Corals sustain growth but not skeletal density across the Florida Keys Reef Tract despite ongoing warming. Global Change Biology*,* **24**, 5205-5217.

Rosset S, Wiedenmann J, Reed AJ, D'angelo C (2017) Phosphate deficiency promotes coral bleaching and is reflected by the ultrastructure of symbiotic dinoflagellates. Marine Pollution Bulletin*,* **118**, 180-187.

Safaie A, Silbiger NJ, Mcclanahan TR *et al.* (2018) High frequency temperature variability reduces the risk of coral bleaching. Nature communications*,* **9**. https://doi.org/10.1038/s41467-018-04074-2.

Schramek T, Colin P, Merrifield M, Terrill E (2018) Depth-Dependent Thermal Stress Around Corals in the Tropical Pacific Ocean. Geophysical Research Letters*,* **45**, 9739-9747.

Smale DA, Wernberg T (2013) Extreme climatic event drives range contraction of a habitat-forming species. Proceedings of the Royal Society B: Biological Sciences*,* **280**. https://doi.org/10.1098/rspb.2012.2829.

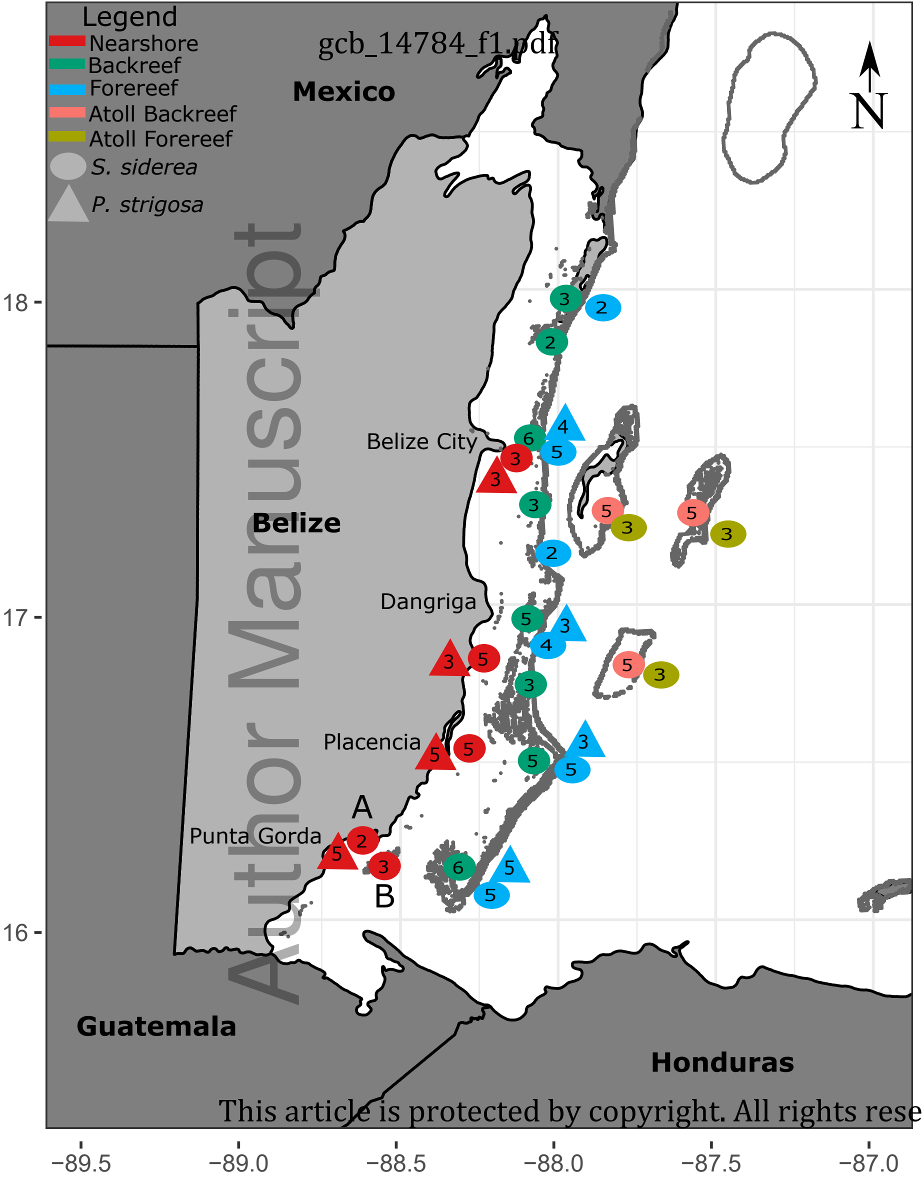
Team RC (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

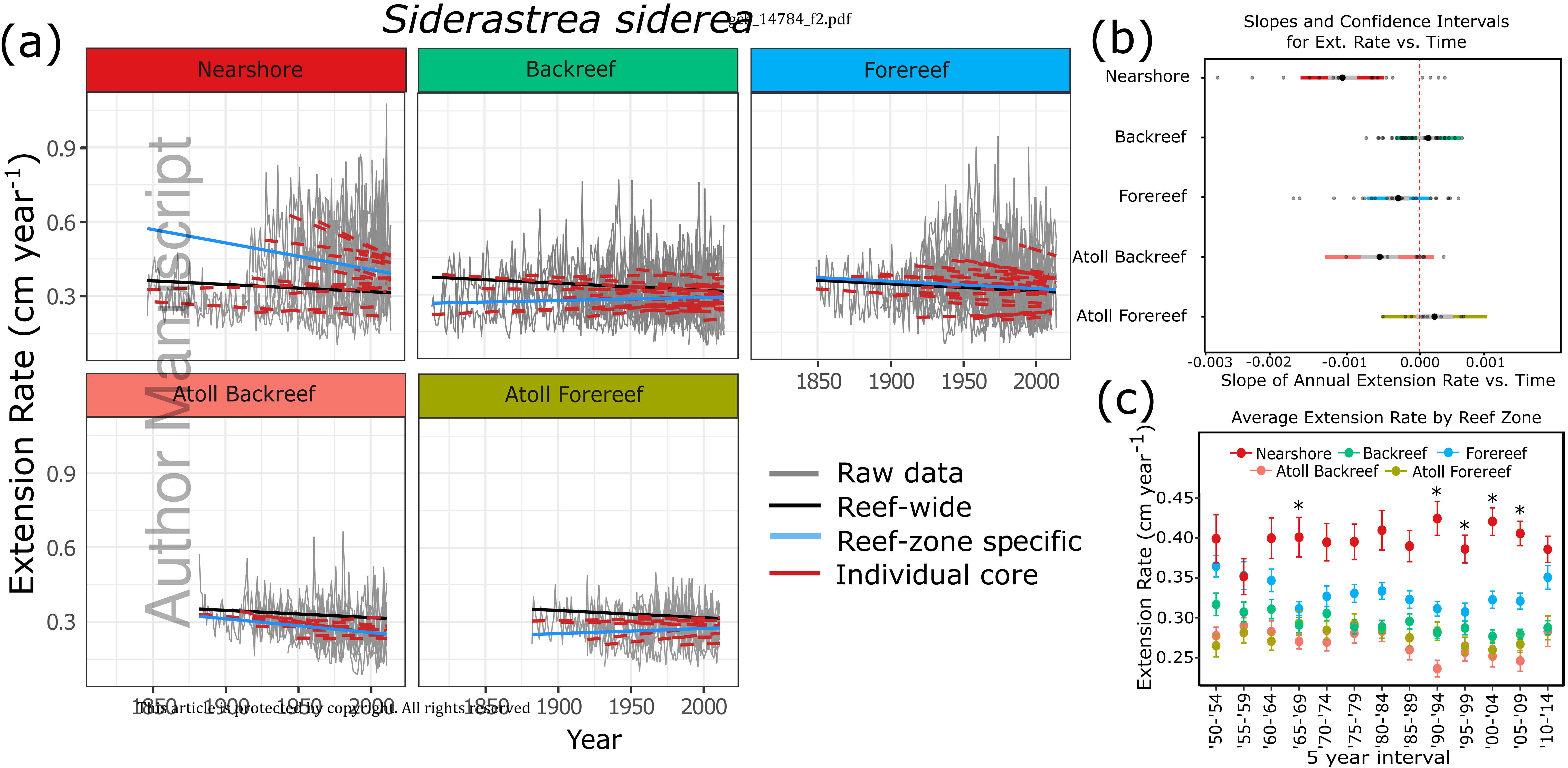
Thattai D, Kjerfve B, Heyman W (2003) Hydrometeorology and variability of water discharge and sediment load in the inner Gulf of Honduras, western Caribbean. Journal of Hydrometeorology*,* **4**, 985-995.

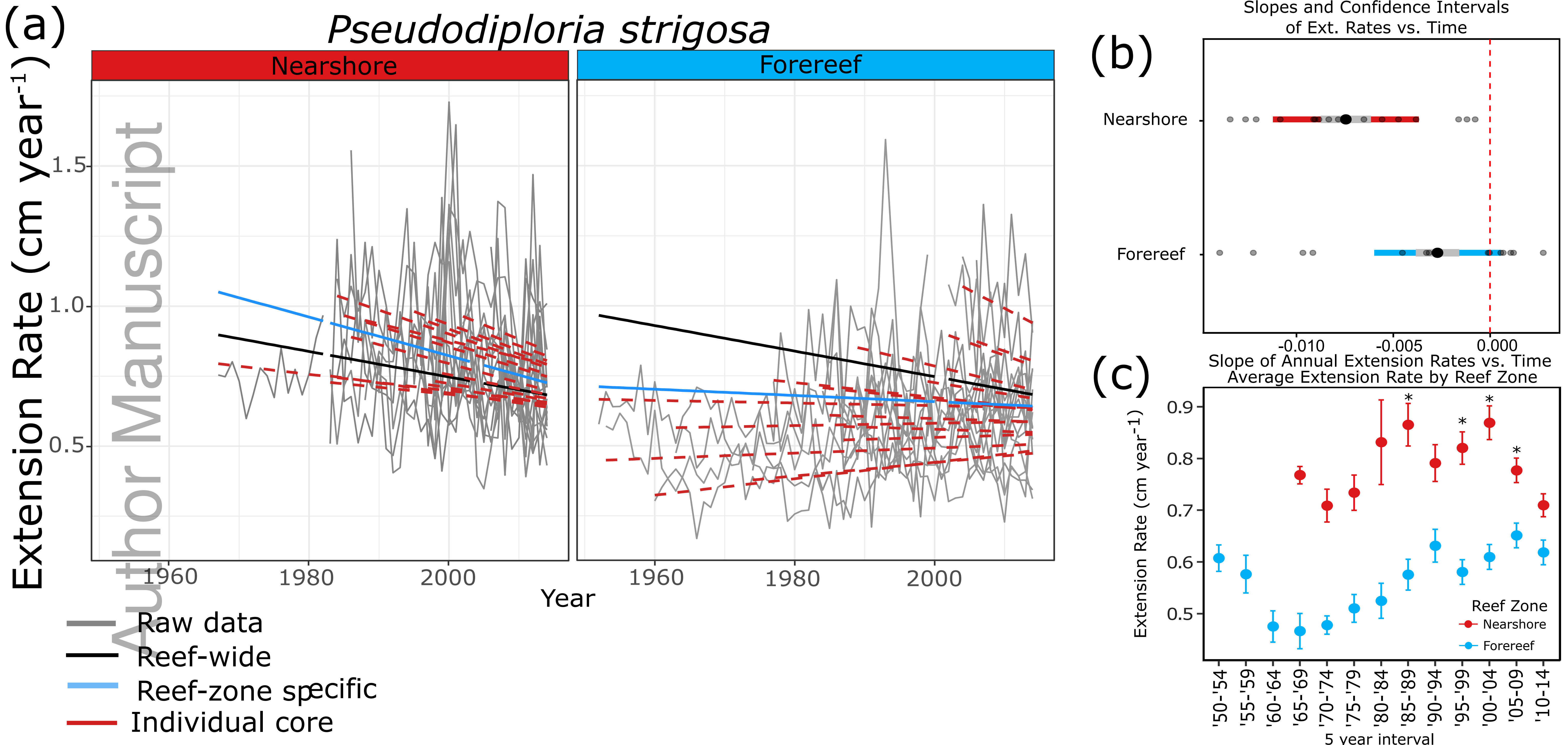
Van Hooidonk R, Maynard JA, Liu Y, Lee SK (2015) Downscaled projections of Caribbean coral bleaching that can inform conservation planning. Global Change Biology*,* **21**, 3389-3401.

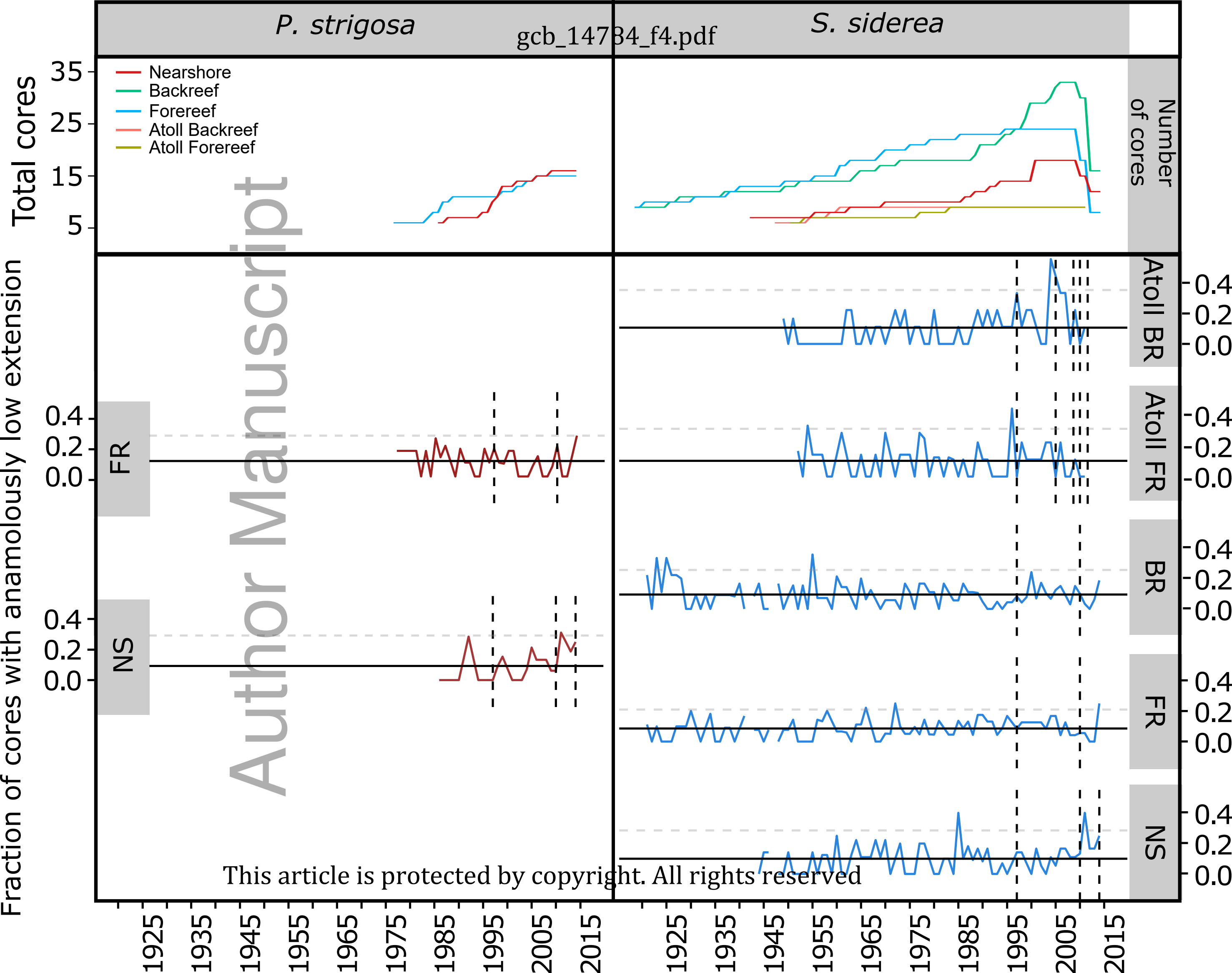
Walther G-R, Post E, Convey P *et al.* (2002) Ecological responses to recent climate change. Nature*,* **416**. https://doi.org/10.1038/416389a.

Wiedenmann J, D’angelo C, Smith EG, Hunt AN, Legiret F-E, Postle AD, Achterberg EP (2013) Nutrient enrichment can increase the susceptibility of reef corals to bleaching. Nature Climate Change, **3**, 160-164.


Legend
Nearshore
Backreef
Forereef
Atoll Backreef
Atoll Forereef
S. siderea
P. strigosa
Mexico
N
Belize City
Belize
Dangriga
Placencia
A
Punta Gorda
B
Guatemala
Honduras
18
17
16
−89.5
−89.0
−88.5
−88.0
−87.5
−87.0


Siderastrea siderea
(a)
Nearshore
Backreef
Forereef
Atoll Backreef
Atoll Forereef
Extension Rate (cm year^{-1})
0.3
0.6
0.9
1850
1900
1950
2000
Year
Raw data
Reef-wide
Reef-zone specific
Individual core
(b)
Slopes and Confidence Intervals for Ext. Rate vs. Time
Nearshore
Backreef
Forereef
Atoll Backreef
Atoll Forereef
-0.003
-0.002
-0.001
0.000
0.001
Slope of Annual Extension Rate vs. Time
(c)
Average Extension Rate by Reef Zone
Nearshore
Backreef
Forereef
Atoll Backreef
Atoll Forereef
Extension Rate (cm year^{-1})
0.25
0.30
0.35
0.40
0.45
*
'50-'54
'55-'59
'60-'64
'65-'69
'70-'74
'75-'79
'80-'84
'85-'89
'90-'94
'95-'99
'00-'04
'05-'09
'10-'14
5 year interval


(a)
Pseudodiploria strigosa
Nearshore
Forereef
Extension Rate (cm year^{-1})
1.5
1.0
0.5
1960
1980
2000
Year
Raw data
Reef-wide
Reef-zone specific
Individual core
(b)
Slopes and Confidence Intervals of Ext. Rates vs. Time
Nearshore
Forereef
-0.010
-0.005
0.000
(c)
Slope of Annual Extension Rates vs. Time
Average Extension Rate by Reef Zone
Extension Rate (cm year^{-1})
0.9
0.8
0.7
0.6
0.5
*
Reef Zone
Nearshore
Forereef
'50-'54
'55-'59
'60-'64
'65-'69
'70-'74
'75-'79
'80-'84
'85-'89
'90-'94
'95-'99
'00-'04
'05-'09
'10-'14
5 year interval


P. strigosa
S. siderea
Total cores
35
25
15
5
Nearshore
Backreef
Forereef
Atoll Backreef
Atoll Forereef
Number of cores
Fraction of cores with anamolously low extension
FR
NS
0.4
0.2
0.0
Atoll BR
Atoll FR
BR
FR
NS
1925
1935
1945
1955
1965
1975
1985
1995
2005
2015