


Corals sustain growth but not skeletal density across the Florida Keys Reef Tract despite ongoing warming

John P. Rippe¹  | Justin H. Baumann¹ | Daphne N. De Leener¹ |
Hannah E. Aichelman^{1,2} | Eric B. Friedlander³ | Sarah W. Davies^{1,2} | Karl D. Castillo^{1,4}

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

²Department of Biology, Boston University, Boston, Massachusetts

³Department of Statistics and Operations Research, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina

⁴Curriculum for Environment and Ecology, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina

Correspondence

John P. Rippe, Department of Marine Sciences, University of North Carolina at Chapel Hill, Chapel Hill, NC.
Email: jpr6mg@gmail.com

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Abstract

Through the continuous growth of their carbonate skeletons, corals record information about past environmental conditions and their effect on colony fitness. Here, we characterize century-scale growth records of inner and outer reef corals across ~200 km of the Florida Keys Reef Tract (FKRT) using skeletal cores extracted from two ubiquitous reef-building species, *Siderastrea siderea* and *Pseudodiploria strigosa*. We find that corals across the FKRT have sustained extension and calcification rates over the past century but have experienced a long-term reduction in skeletal density, regardless of reef zone. Notably, *P. strigosa* colonies exhibit temporary reef zone-dependent reductions in extension rate corresponding to two known extreme temperature events in 1969–1970 and 1997–1998. We propose that the subtropical climate of the FKRT may buffer corals from chronic growth declines associated with climate warming, though the significant reduction in skeletal density may indicate underlying vulnerability to present and future trends in ocean acidification.

KEYWORDS

calcification, Caribbean, climate change, coral reef, Florida keys, global warming, ocean acidification, sclerochronology

1 | INTRODUCTION

As the most thoroughly monitored coral reef ecosystem in the wider Caribbean, the Florida Keys Reef Tract (FKRT) has unfortunately become a paradigm for the severe decline of coral reefs across the region throughout the last four decades. Following the near extirpation of acroporids in the 1970s and 1980s, a further decline in stony coral cover on the order of 40% since 1996 has driven an ecological shift on the FKRT toward greater dominance of octocorals, macroalgae, and sponges (Miller, Bourque, & Bohnsack, 2002; Ruzicka et al., 2013; Somerfield et al., 2008). This deterioration of the stony coral community has been attributed primarily to chronically warming waters (Causey, 2001; Manzello, 2015), acute high and low temperature stress events (Colella, Ruzicka, Kidney, Morrison, & Brinkhuis, 2012; Kemp et al., 2011; Lirman et al., 2011), and widespread disease (Porter et al., 2001; Precht, Gintert, Robbart, Fura, & Van Woesik, 2016).

Yet, sustained reductions in coral cover have been unevenly skewed toward outer reef environments, highlighting a unique cross-shelf distinction on the FKRT (Ruzicka et al., 2013). Inner patch reefs along the seaward boundary of Hawk Channel, a 10-m-deep channel running 2–3 km offshore of the Florida Keys archipelago, maintain 15%–17% stony coral cover despite their proximity to the highly variable water conditions associated with Florida Bay (Ruzicka et al., 2013). By comparison, outer reef sites, which are bank-barrier reefs located 8–9 km offshore along the edge of the shelf predominantly immersed in the clear waters of the Florida Current, have been reduced to ≤5% coral cover and continue to experience significant mortality of important reef-building coral species (Ruzicka et al., 2013).

Depending on geographic context, two theories are often proposed to explain differences in ecology and resilience of corals at inner versus outer reef sites. In some cases, observations of higher coral cover (Lirman & Fong, 2007; Thomson & Frisch, 2010), greater

colony size and growth rates (Manzello, Enochs, Kolodziej, & Carlton, 2015; Soto, Muller Karger, Hallock, & Hu, 2011), elevated bleaching resistance (Barshis et al., 2013; Palumbi, Barshis, Traylor-Knowles, & Bay, 2014), and stable growth trajectories (Carilli, Donner, & Hartmann, 2012; Castillo, Ries, Weiss, & Lima, 2012) on nearshore reefs suggest that consistent exposure to a highly variable environment preconditions resident coral populations to better cope with ocean warming and the increasing frequency of high-temperature stress events. However, conflicting reports of reduced coral cover (De'ath & Fabricius, 2010), degraded thermal tolerance (Carilli, Norris, Black, Walsh, & McField, 2010), and slower coral growth rates (Cooper, De'ath, Fabricius, & Lough, 2008) suggest that exposure to high levels of suspended sediments and nutrients associated with local human development reduces the fitness of nearshore corals. It is more likely that the evolutionary or acclimatory advantage gained by living in a variable thermal environment co-occurs with the negative impacts of terrestrial runoff, and the balance of these factors determines the relative condition of the reef community.

Sclerochronology, or the use of coral skeletal cores to examine historic trends in growth, provides a useful tool in diagnosing reef health in space and time and therefore can reveal differences in the sensitivity of sampled reef areas to their changing environments. Early studies from the upper Florida Keys report long-term growth trends of the *Orbicella* species complex, drawing qualitative comparisons between skeletal extension rates and anthropogenic factors related to human development in south Florida (Hudson, 1981; Hudson, Hanson, Halley, & Kindinger, 1994). More recent analysis of *Orbicella faveolata* from the same region reveals that opposing trends in skeletal density and extension rates over time correlate significantly with the Atlantic Multidecadal Oscillation index (Helmle, Dodge, Swart, Gledhill, & Eakin, 2011). Additionally, baseline calcification rates were found to be significantly greater at an inner reef site of the upper Florida Keys relative to a nearby outer reef site (Manzello et al., 2015). These findings support the premise that there may be a physiological growth advantage for corals living in inner patch reef environments of the FKRT (Anthony, 2006).

Notably, the long-term stability of extension and calcification rates reported for *O. faveolata* on the FKRT (Helmle et al., 2011) deviates from coral growth trends on other reef systems. In the Pacific, Southeast Asia, and Red Sea, for example, calcification rates of *Porites* spp. and *Diploastrea heliophora* have declined alongside rising ocean temperatures over the past three decades (Cooper et al., 2008; De'ath, Lough, & Fabricius, 2009; Tanzil et al., 2013; Tanzil, Brown, Tudhope, & Dunne, 2009).

Similarly, multiple studies on the Belize Mesoamerican Barrier Reef System (MBRS) have revealed long-term declines in the extension rates of *Siderastrea siderea* and *Pseudodiploria strigosa*, although the trend in this case varied based on proximity to shore and the spatial scale of investigation (Baumann et al., 2018; Castillo et al., 2012). Along a single inner–outer reef transect on the southern MBRS, forereef colonies of *S. siderea* were found to exhibit a long-term decline in extension rates, while those from nearshore and backreef environments maintained stable growth trajectories (Castillo

et al., 2012; Castillo, Ries, & Weiss, 2011). Carilli et al. (2010) also observed long-term declines in the extension rate of *O. faveolata* at nearby reefs in southern Belize and Honduras, but not at offshore atolls or in eastern Honduras. The authors of these studies suggest that the trends may arise due to local water quality dynamics or due to lower resilience of forereef corals to rising ocean temperatures. However, further investigation of *S. siderea* and *P. strigosa* conducted at the scale of the entire Belize MBRS revealed a contrasting pattern in which declining extension rates were observed only for colonies at nearshore sites, but not for colonies farther from shore (Baumann et al., 2018). Such complexity of coral growth trajectories throughout the MBRS reflects the delicate balance between the historical advantage of residing in a variable nearshore environment and the deteriorating conditions associated with terrestrial runoff and continual ocean warming.

Here, we assess growth trajectories of two abundant and ubiquitous Caribbean reef-building coral species (*Siderastrea siderea* and *Pseudodiploria strigosa*) from four inner–outer reef transects spanning ~200 km of the FKRT. Comparing long- and short-term patterns in extension, density, and calcification, we demonstrate that these two coral species have largely sustained extension and calcification rates throughout the FKRT, but have experienced a chronic reduction in skeletal density over the past century. These results suggest that a subtropical climate may buffer corals on the FKRT from warming-induced declines in extension and calcification rates, as is observed in other reef systems, but we propose that declining density may indicate underlying vulnerability to changing carbonate chemistry on the FKRT.

2 | MATERIALS AND METHODS

2.1 | Study design

In May 2015 and 2016, skeletal cores were collected from colonies of the reef-building corals, *Siderastrea siderea* and *Pseudodiploria strigosa*, from four pairs of inner–outer reef sites spanning the Florida Keys Reef Tract (FKRT; Figure 1). From south to north, inner reef sites include W Washerwoman (WW), Cheeca Rocks (CR), Basin Hill Shoals (BH), and Bache Shoals (BS). Outer reef sites include E Sambo (ES), Alligator Reef (AR), Carysfort Reef (CF), and Fowey Rocks (FR). In total, 39 *S. siderea* cores and 31 *P. strigosa* cores were collected from 3 to 7.5 m depth (Table S1). Cores were extracted using a CS Unitec Model 2 1335 0010 hydraulic drill affixed with hollow extension rods and a 5-cm-diameter wet diamond core bit. At each of the eight sites, five healthy colonies of each species were selected randomly for coring. Health was assessed qualitatively by visual inspection, and only colonies without evidence of significant mortality were sampled. In some cases, less than five colonies of *S. siderea* and *P. strigosa* were sampled, either because the dive team was unable to locate five colonies of sufficient size at certain sites or because coring efforts were halted due to inclement weather. Notably, large colonies of *P. strigosa* were relatively rare at the four outer reef sites, whereas colonies of *S. siderea* were ubiquitous across the entire reef tract (Table 1).

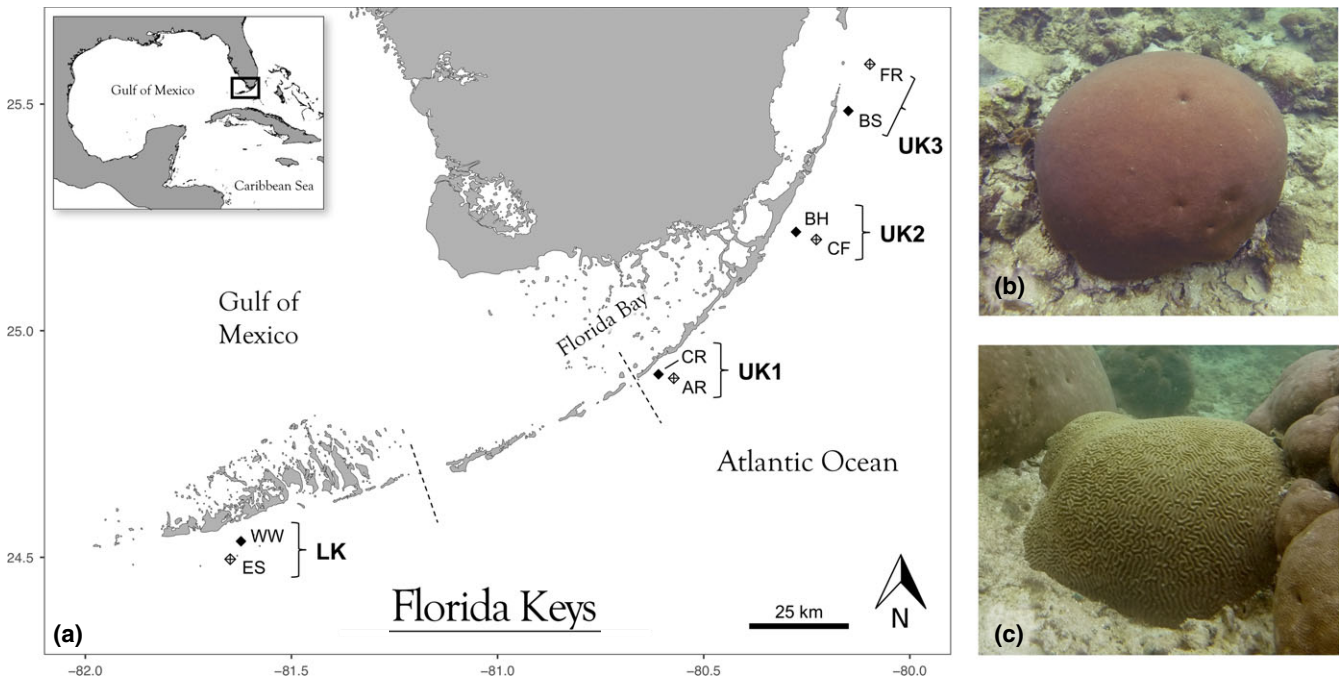


FIGURE 1 Map of sampling sites (a) and study species (b, c). Solid and crosshatch diamonds represent inner and outer reef sites, respectively. Dashed lines depict the approximate boundaries between the lower, middle, and upper Keys. Site and transect abbreviations are as follows: lower Keys (LK)—West Washerwoman (WW), Eastern Sambo (ES); upper Keys 1 (UK1)—Cheeca Rocks (CR), Alligator Reef (AR); upper Keys 2 (UK2)—Basin Hills (BH), Carysfort Reef (CF); and upper Keys 3 (UK3)—Bache Shoals (BS), Fowey Rocks (FR). The two study species are pictured on the right: *Siderastrea siderea* (top) and *Pseudodiploria strigosa* (bottom)

TABLE 1 Summary of growth parameters for *Siderastrea siderea* (top) and *Pseudodiploria strigosa* (bottom)

Site	N	Size (cm)	Age (year)	Extension (cm/year)	Density ($\text{g cm}^{-3} \text{ year}^{-1}$)	Calcification ($\text{g cm}^{-2} \text{ year}^{-1}$)
<i>Siderastrea siderea</i>						
W Washerwoman	5	24.0	56.4	0.38 (± 0.01)	1.34 (± 0.01)	0.51 (± 0.01)
E Sambo	5	49.8	82.8	0.36 (± 0.01)	1.35 (± 0.01)	0.48 (± 0.01)
Cheeca Rocks	5	58.4	106.8	0.36 (± 0.01)	1.38 (± 0.01)	0.50 (± 0.01)
Alligator Reef	4	23.8	45.5	0.34 (± 0.02)	1.46 (± 0.02)	0.49 (± 0.02)
Basin Hills	5	38.9	91.2	0.34 (± 0.01)	1.45 (± 0.01)	0.48 (± 0.01)
Carysfort Reef	5	32.3	61.0	0.38 (± 0.01)	1.49 (± 0.02)	0.57 (± 0.01)
Bache Shoals	4	35.3	52.5	0.36 (± 0.01)	1.38 (± 0.01)	0.50 (± 0.02)
Fowey Rocks	5	19.7	34.4	0.38 (± 0.02)	1.42 (± 0.02)	0.54 (± 0.02)
<i>Pseudodiploria strigosa</i>						
W Washerwoman	5	20.7	34.2	0.38 (± 0.02)	1.26 (± 0.04)	0.46 (± 0.02)
E Sambo	0	–	–	–	–	–
Cheeca Rocks	4	41.2	57.3	0.53 (± 0.02)	1.12 (± 0.03)	0.58 (± 0.02)
Alligator Reef	3	25.2	39.3	0.55 (± 0.023)	1.05 (± 0.04)	0.56 (± 0.02)
Basin Hills	5	36.2	53.0	0.49 (± 0.02)	1.14 (± 0.02)	0.55 (± 0.02)
Carysfort Reef	4	29.8	48.0	0.45 (± 0.01)	1.24 (± 0.02)	0.56 (± 0.01)
Bache Shoals	5	34.3	56.6	0.45 (± 0.01)	1.26 (± 0.03)	0.55 (± 0.01)
Fowey Rocks	3	17.7	18.7	0.46 (± 0.02)	1.42 (± 0.07)	0.64 (± 0.03)

Note. Site-wide averages of colony size (estimated by core length), record age, annual extension rate, density and calcification rate (\pm SE).

Cores were extracted from the vertical growth axis of each colony and were between 12 and 70 cm in length, encompassing 16–137 and 14–89 years of growth for *S. siderea* and *P. strigosa*,

respectively (Table S2). After extraction, a concrete plug was inserted and secured in the drilled hole with Z-Spar® underwater epoxy to protect the colony from erosion and further physical

damage. The collected cores were then stored in capped PVC tubes filled with 100% ethanol (EtOH) and transported to the University of North Carolina at Chapel Hill where they were air-dried in preparation for sclerochronology development.

2.2 | Sclerochronology development

To assess coral skeletal growth histories, we use a procedure adapted from Castillo et al. (2011). All cores were scanned using X-ray computed tomography (CT) on a Siemens Biograph CT scanner at the Biomedical Research Imaging Center, University of North Carolina at Chapel Hill. Coral cores were oriented lengthwise in rows of 4 to 5 on the scanning table, and equipment parameters were set to 120 kV, 250 mAs, and 0.6 mm slice thickness with images reconstructed at 0.1 mm increments using the H70h “Very Sharp Spine” window. All images were exported from the scanner as DICOM files, which were then three-dimensionally reconstructed using the open-access Horos v2.0.2 medical image viewing software. High- and low-density bands were visualized using a 10-mm thick “Mean” projection oriented as a rectangular prism through the center of each core (Figure S1).

All boundaries between semiannual density bands were delineated manually, and three sets of linear transects were drawn down the length of the cores using the Region of Interest (ROI) tool in Horos (Figure S1). Each set of transects was drawn within the exothecal space between corallite walls in order to standardize density measurements and to avoid aberrant density spikes in areas where the transect may otherwise have crossed a high-density corallite wall. Density and calcification measurements are therefore lower than would be expected if all features of the skeletal architecture were taken into account. In cases of nonlinear growth axes, transects were drawn in shorter segments that traced the central axis of corallite growth. A custom R script was then used to patch the segments together into three continuous growth records, which were averaged together to create the final chronology. Transects were drawn to avoid all areas of bioerosion, and whenever growth discontinuities were encountered (e.g., broken or fractured core), if necessary, the average extension rate of the 5 years before and 5 years after the discontinuity was used to estimate the number of years to be skipped in the chronology.

By-pixel density measurements were extracted from resulting linear transects and average density was calculated for each semiannual high- and low-density band. Following previously established protocol (DeCarlo et al., 2015), nine coral standards of known density were included in every scanning session to convert density measurements from CT Hounsfield units to g/cm^3 . Average density of each standard was assessed in Hounsfield units using Horos, and a standard curve was created for all cores scanned in the corresponding session (Figure S2). Linear extension was measured in Horos as the width of each annual density band couplet, and calcification (g/cm^2) was calculated as the product of density and linear extension.

Importantly, it has been shown that individual colonies may vary in their timing of high- and low-density band deposition due to intraspecific differences in tissue thickness and morphology (Barnes & Lough, 1993, 1996; Carricart-Ganivet, Vásquez-Bedoya, Cabanillas-Terán, & Blanchon, 2013; Taylor, Barnes, & Lough, 1993). Thus, to approximate a consistent time standard between cores, we begin all chronologies at the top of the first fully deposited high- or low-density band beneath the band of terminal growth. Additionally, because cores were collected in subsequent years, the most recent year of growth (2015) was not included for cores collected in 2016 in order to keep the beginning of chronologies uniform throughout the study.

2.3 | Statistical analysis

The following section describes the suite of statistical analyses undertaken to evaluate the patterns by which each growth parameter (i.e., extension, density, and calcification) varies spatially across the FKRT and temporally throughout the last century.

Mean growth parameters were calculated for each coral species within each site by averaging annual measurements of extension, density, and calcification across time. Additionally, as a coarse representation of colony size, the physical length of each core sample was measured and averaged within sites.

Variability in annual extension, density, and calcification within and between individual coral colonies was evaluated using two complementary methods. First, the coefficient of variation (CV) was calculated for each colony to determine the scale at which each growth parameter varied between years. CV is measured as the ratio of the standard deviation to the mean ($CV = s/\bar{x} * 100\%$). Additionally, spatial autocorrelation was calculated to assess similarity in growth patterns between coral colonies in close geographic proximity (i.e., within the same site). Positive values indicate significant correlation between colonies within specified distance classes. Spatial autocorrelation was evaluated using a permutation-based Mantel test ($n = 1,000$), and the resulting correlogram was fitted with a nonparametric correlation spline and 95% confidence interval determined by bootstrapping ($n = 1,000$). The Mantel test was conducted using an increment of 10 km to create 13 uniformly spaced pairwise distance classes. Analyses of spatial autocorrelation were performed in the *ncf* package in R (Bjornstad, 2009; R Core Team, 2017). In this analysis, we employ a 30-year threshold in order to compare sufficiently long-term chronologies while also retaining a large majority of sampled cores. Only cores longer than 30 years were included in the spatial autocorrelation analysis (58 of 67 samples).

To determine whether the overall “shape” (or multidimensional characteristics) of coral growth records differed between inner and outer reef zones, we used the concept of object-oriented data analysis, which treats each growth record as a multidimensional data object (see An et al. (2016) for a detailed description). Within this framework, similar to principal component analysis (PCA), the annual growth measurements of each chronology exist in d -

dimensional space, where d is the number of years included in the analysis. In this case, rather than finding the coordinate axes which represent the maximum amount of overall variation within the data, as in PCA, a method known as distance weighted discrimination (DWD) was used to compute the vector which best separates the two specified classes of corals (i.e., inner and outer reef) (Marron, Todd, & Ahn, 2007). Since the data exist in such high dimension, we expect there to be a direction which separates the two classes almost perfectly regardless of whether a difference actually exists. To remedy this, we conducted a Direction-Projection-Permutation (*DiProPerm*) statistical test (Wei, Lee, Wichers, & Marron, 2016) to evaluate whether the vector separating the two groups appears to be better than one would expect solely due to the high dimensionality of the data. The test is conducted by randomly relabeling the class of each core sample (i.e., inner and outer reef) and refitting the DWD direction 1,000 times. A p -value is then calculated as the percentage of iterations that are separated better than the DWD direction of the original data. Note, as with the analysis of spatial autocorrelation, only the most recent 30 years of growth are compared, and all shorter cores are not included in this analysis for the reasons described above.

Lastly, temporal trends in growth were assessed in two steps: first, using linear mixed effect (LME) modeling, generally following the statistical protocol of Castillo et al. (2011); and second, using generalized additive modeling to capture short-term fluctuations in growth. For both approaches, in order to account for the hierarchical nature of the dataset, mean-standardized annual values of linear extension, density, and calcification measured within each core were treated as the units of observation, while the cores themselves were treated as sampling units and were incorporated as random effects. Consistent with Castillo et al. (2011), the variable *Year* in all LME models was centered to minimize correlation between random slopes and intercepts, and the residual correlation structure of individual cores was described using an autoregressive moving-average model of order (p, q). An interaction term between *Reef Zone* and *Year* is included as a model predictor in order to compare linear trends in growth between reef zones (Appendix S1).

Basic generalized additive models (GAM) for extension, density, and calcification were implemented in the *mgcv* package in R (R Core Team, 2017; Wood, Pya, & Säfken, 2016), incorporating an adaptive smoothing spline of *Year* as a fixed effect predictor and *Core* as a random effect. Adaptive smoothing allows the degree of smoothing to vary with the covariates to be smoothed and is therefore well suited to capture rapid fluctuations in growth. The smoothing basis ($k = 25$) was selected following the protocol recommended by Wood (2017), whereby k was increased progressively ($k = 5, 10, 15, 20, 25$) until the effective degrees of freedom stabilized at a value sufficiently lower than $k - 1$. Once the models were fitted to the data, time intervals of significant change were computed using the first derivative of the fitted trend spline, following the methods of Benning, Simpson, and Goldsmith (2015). In short, a finite difference approximation of the first derivative is calculated at fixed time points along the model prediction with an associated 95% confidence

interval. Where the confidence interval of the derivative curve excludes 0 (i.e., zero slope), we conclude that significant change in growth is observed at that time point. These intervals of significant change are indicated on all GAM plots as thick green (increasing) and red (decreasing) segments.

3 | RESULTS

3.1 | Mean growth and variability within sites

To compare baseline growth parameters between all sampling sites, we calculated site-wide mean rates of extension, density, and calcification for each species (Table 1). On average, extension and calcification rates were significantly greater for *Pseudodiploria strigosa*, and skeletal density was greater for *Siderastrea siderea* throughout the FKRT ($p < 0.001$ for each parameter). Mean extension of *S. siderea* was relatively consistent across all sites on the FKRT, while extension of *P. strigosa* was greatest at the two sites within the middle upper Keys transect (UK2; i.e., Cheeca Rocks and Alligator Reef) and lowest at W Washerwoman (lower Keys). Between inner and outer reef sites within each transect, skeletal density of both species was generally greater on the outer reef with only one exception—within the southern upper Keys transect (UK1), density of *P. strigosa* colonies was greater on the inner reef (Cheeca Rocks; 1.124 ± 0.030) than on the outer reef (Alligator Reef; 1.049 ± 0.042). Similar to extension, site-wide averages of annual calcification rates were relatively consistent for *S. siderea*, but varied considerably between sites with no discernible pattern for *P. strigosa*. Mean calcification of *P. strigosa* was greatest at Fowey Rocks (0.637 ± 0.034) and lowest at W Washerwoman (0.461 ± 0.019).

Annual extension and calcification rates were found to vary substantially within and between all sampled colonies, regardless of their geographic proximity. Average interannual coefficients of variation (CV) in extension for each core were 20.5% (10.7%–33.0%) and 18.0% (9.8%–33.9%) for *S. siderea* and *P. strigosa*, and in calcification were 20.1% (11.6%–35.0%) and 18.6% (11.1%–29.7%) for *S. siderea* and *P. strigosa*, respectively. By comparison, interannual variability in density was considerably lower, with an average CV of 6.8% (3.2%–17.1%) and 12.1% (5.1%–20.2%) for *S. siderea* and *P. strigosa*, respectively (Figure S3). Additionally, spatial autocorrelation between standardized annual extension, density, and calcification of both species was assessed for the most recent 30 years of data (i.e., 1985–2014). Between the three growth parameters, no Mantel r statistics calculated for any of the 13 distance classes spanning the FKRT were found to be significant after Bonferroni correction, suggesting no evidence of spatial correlation between nearby colonies (Figure S4).

3.2 | Coral growth trajectories on the Florida Keys Reef Tract

Long-term linear trends reveal that skeletal density of both species significantly decreases through time, while extension and

calcification rates are neither increasing nor decreasing (Figure 2). We find no evidence to suggest that temporal patterns in extension, density, or calcification differ significantly between inner and outer reef sites at the scale of the FKRT ($p > 0.05$ for all parameters; Figure 2; Figure S5). Generalized additive model results also demonstrate little apparent difference in long- or short-term trends between reef zones in either species and, in fact, highlight the considerable colony-level variation in growth through time (Figure 3). Even accounting for short-term fluctuations, model predictions explain only 5.58% and 4.70% of the deviance in the chronologies of annual extension rate for *S. siderea* and *P. strigosa*, respectively.

Note, although a declining long-term trend in density and stable extension rates could be expected to cause a corresponding decline in calcification based on the direct relationship of the parameters, we find that the variation in calcification rates is driven primarily by variation in extension for these two species (Figure S6). Therefore, despite the slope estimates of calcification trending negative, we cannot conclude at the 95% confidence level

that calcification rates have declined over our period of investigation.

We also compared growth chronologies of each species between the four inner–outer reef site pairs, highlighting the along-shore variability in coral growth trends along the FKRT (Figure S7). The extension rate of both species declined significantly in the lower Keys transect (LK) during the 1997–1998 mass bleaching event and had still not fully recovered by 2014. Declining extension of *S. siderea* at the northern upper Keys transect (UK3) drives a corresponding reduction in calcification since 2001. Additionally, calcification of *P. strigosa* at the middle upper Keys transect (UK2) has declined significantly since 1980.

3.3 | Extreme temperature events differentially impact *Pseudodiploria strigosa*

Generalized additive model results reveal the short-term response of *P. strigosa* to two documented extreme temperature events on the

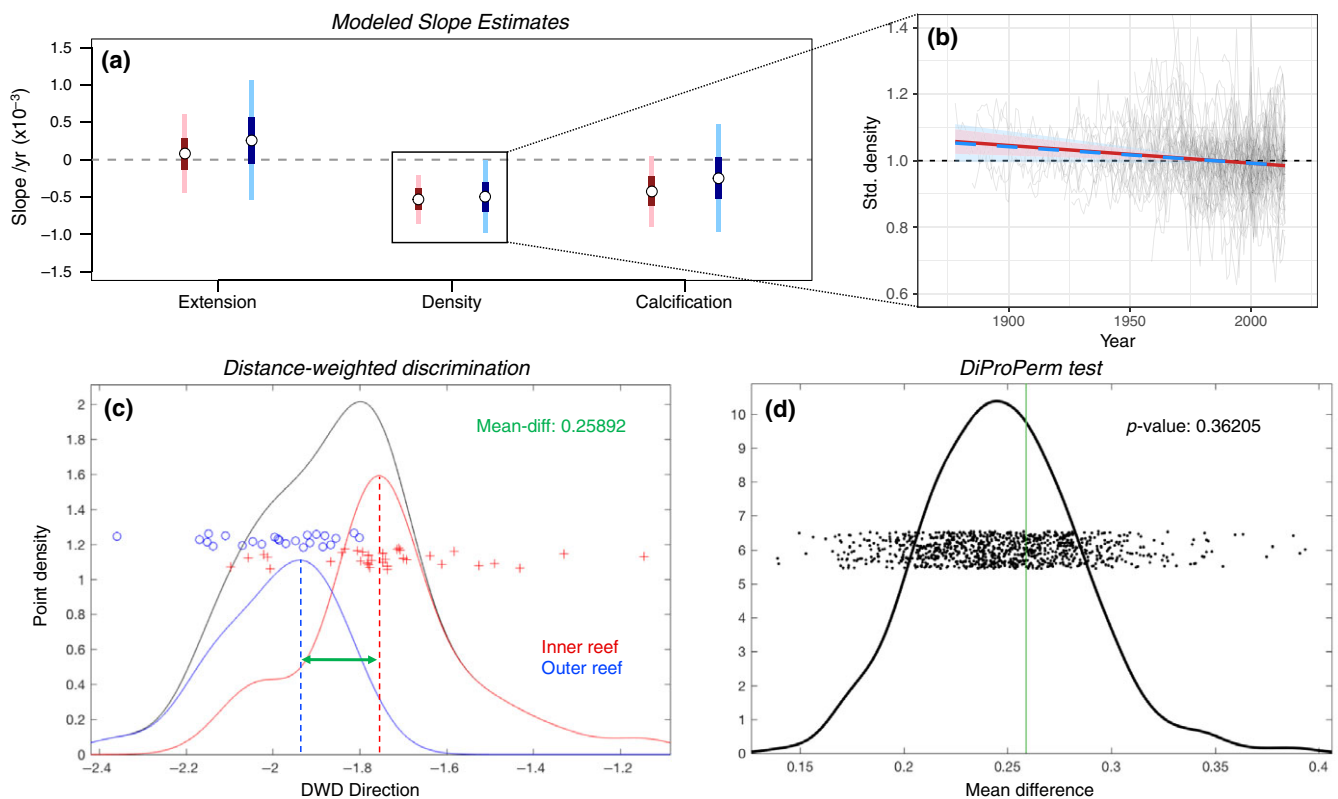


FIGURE 2 Long-term growth patterns do not differ between reef zones. (a) Modeled estimates of linear trends in extension, density and calcification for the inner (red) and outer reef (blue). Dark- and light-colored bars represent 50% and 95% confidence intervals, respectively. (b) Modeled linear trends with 95% confidence intervals overlaying individual chronologies of mean-standardized skeletal density (gray). Line colors correspond to inner and outer reef slope estimates displayed in Panel (a). (c) Extension chronologies of inner and outer reef cores were also compared using distance weighted discrimination (DWD). Red crosses (inner reef) and blue circles (outer reef) represent the relative position of each core chronology along the DWD axis, and the mean difference between the two groups was calculated. (d) The significance of the difference between the inner and outer reef cores along the DWD axis was evaluated using a DiProPerm test. Each point signifies a mean difference calculation after each of 1,000 permutations of randomly relabeling the data and refitting the DWD direction. The green line denotes the mean difference between the true groups (inner and outer reef) in the data. Curves in Panels (c) and (d) represent the density of points along the x-axes. All analyses pictured were performed on the full dataset including mean-standardized annual measurements of both study species together

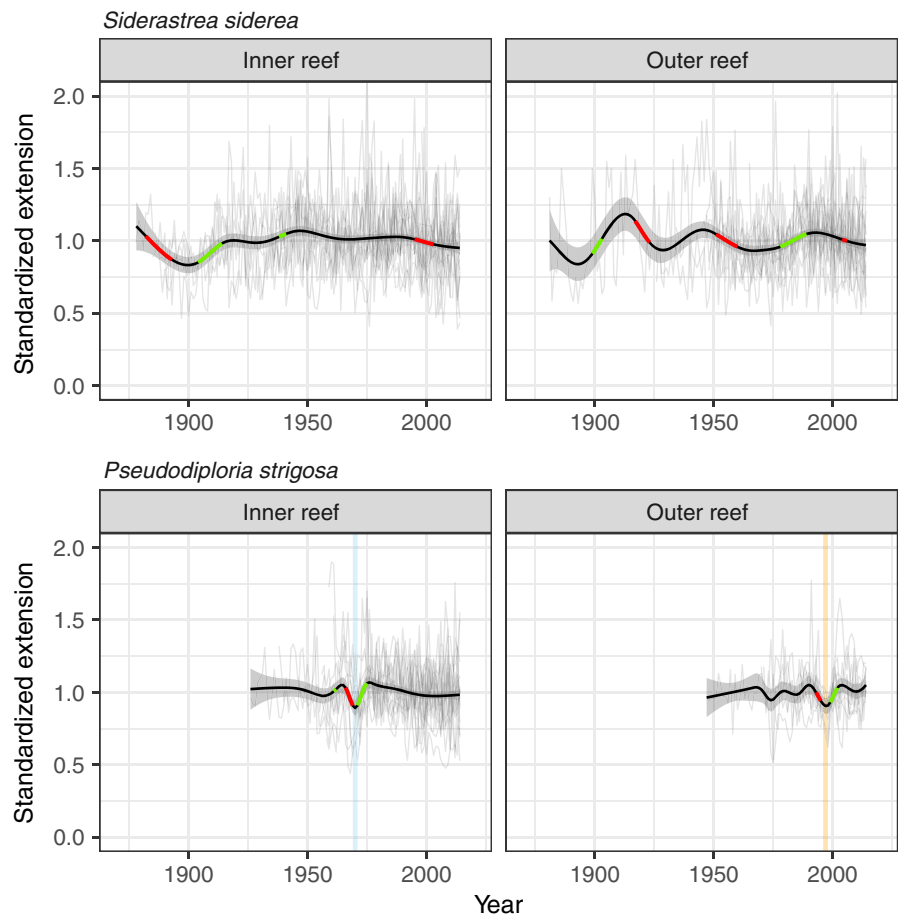


FIGURE 3 Sensitivity to extreme thermal events differs between species and reef zones. Generalized additive model predictions (± 2 SE) overlay individual core chronologies of mean-standardized annual extension (light gray), organized by reef zone and species. Green and red segments denote regions of the curve that are significantly increasing and decreasing, respectively. The light blue and orange vertical lines indicate two previously reported major bleaching events in the FL Keys: 1969–1970 cold water (blue) and 1997–1998 warm water (orange)

FKRT. In 1969–70, the extension rates of inner reef *P. strigosa* were depressed in association with a cold-water bleaching event (Hudson, Shinn, Halley, & Lidz, 1976). Similarly, in 1997–98, the extension rates of outer reef *P. strigosa* were depressed in association with a Caribbean-wide warm-water bleaching event (Causey, 2001). *Siderastrea siderea* did not demonstrate the same reduction in extension in association with extreme temperature events at the scale of inner and outer reef zones (Figure 3).

4 | DISCUSSION

This study reveals that the contrasting trends in coral cover and resilience previously observed between inner and outer reefs of the Florida Keys Reef Tract (FKRT) do not translate to clear reef zone differences in long-term growth for *Siderastrea siderea* and *Pseudodiploria strigosa* at the scale of the entire FKRT system. Rather, linear modeling indicates that long-term trends of all growth parameters are virtually indistinguishable between inner and outer reef colonies. Multidimensional DWD and DiProPerm analyses corroborate this result, offering no evidence that annual growth differs significantly between reef zones in the most recent 30 years (Figure 2).

The long-term growth trends observed here largely reflect those previously reported for *Orbicella faveolata* from the upper Keys, with extension and calcification remaining stable and density declining

significantly over time (Figure 2; Helmle et al., 2011). However, the lack of reef zone differences contradicts previous observations from the Belize MBRS, which demonstrate variable declines in extension rates based on proximity to shore (Baumann et al., 2018; Castillo et al., 2012). As hypothesized by Helmle et al. (2011), it is possible that the disparity between growth patterns on the FKRT and the MBRS may be attributed to the subtropical nature of the Florida Keys, in that mean temperature conditions on the FKRT have not yet crossed a critical optimum that would lead to extended declines in coral growth on a reef zone scale.

Previous research has shown that coral extension and calcification rates are correlated with temperature in a parabolic fashion. At moderate temperatures, coral growth accelerates with increasing temperature (Lough & Barnes, 2000); however, once a thermal optimum is reached, calcification declines with further warming (Castillo, Ries, Bruno, & Westfield, 2014; Jokiel & Coles, 1977). Recent theory supports the existence of such an optimum based on physiological factors known to regulate biomineralization (Wooldridge, 2013). Moreover, a comprehensive record of *Porites* growth rates from the Great Barrier Reef reflects this pattern temporally, with an extended period of increasing calcification until 1990 followed by a drastic decline throughout the modern era of climate warming (De'ath et al., 2009).

Historical in situ measurements of seawater temperature on the FKRT show that conditions have warmed $\sim 0.8^{\circ}\text{C}$ over the course of

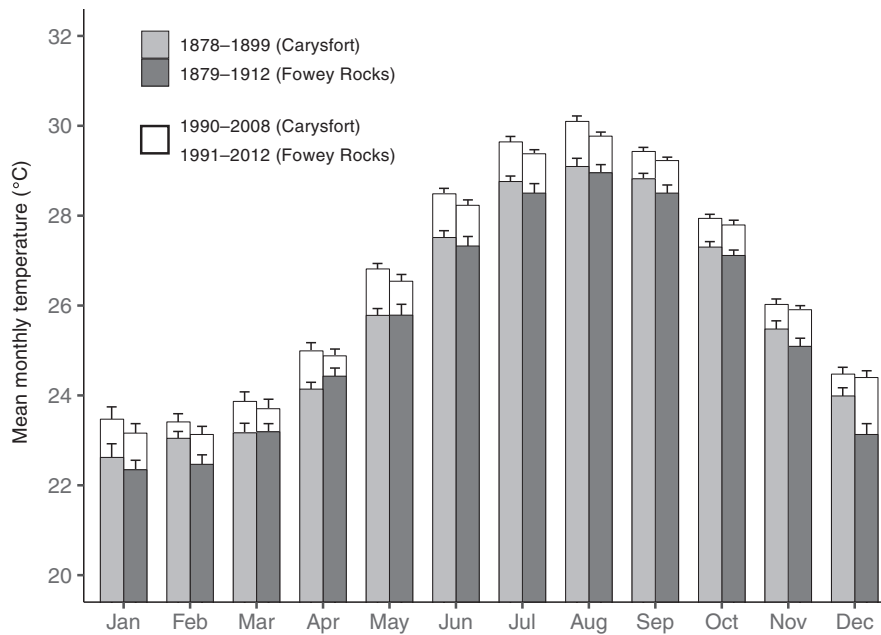


FIGURE 4 Century-scale warming on the FKRT. Stacked bar plots depict the difference between current and historic in situ temperatures at Carysfort Reef and Fowey Rocks on the FKRT. White bars reflect the increase in mean monthly temperatures from the late 1800s (colored bars) to modern day. Historic temperatures were documented by lighthouse keepers at each site and represent the oldest temperature records from the FKRT. Recent temperatures were recorded by fixed loggers as part of two large-scale monitoring efforts in the region. This figure has been adapted from Kuffner et al. (2015) with permission from the authors

the last century (see Figure 4; Kuffner, Lidz, Hudson, & Anderson, 2015), which is in line with the estimated global ocean warming rate of 0.11°C per decade since 1970 (Rhein et al., 2013). Mean annual temperatures, however, remain considerably cooler, and recent warming trends (1985–2009) are slower on the FKRT than on reefs in more tropical regions of the wider Caribbean (Chollett, Müller-Karger, Heron, Skirving, & Mumby, 2012; Chollett, Mumby, Müller-Karger, & Hu, 2012). In a broad-scale analysis of the physical environment throughout the Caribbean basin, Chollett, Mumby, et al. (2012) show that the mean annual temperature of high-latitude regions (including the FKRT, Bahamas, and western Cuba banks) was 26.05°C from 1993 to 2008. Conversely, coastal waters around Belize, Panama, and the Lesser Antilles had mean annual temperatures of 27.60 , 27.01 , and 27.15°C , respectively, during this period.

Notably, the warming trend on the FKRT, and throughout the Caribbean, is especially pronounced in summer months, which has led to more days per year spent above extreme temperature thresholds (Kuffner et al., 2015; Manzello, 2015). Tropical and subtropical reef environments also differ in the degree, frequency and duration of these extreme temperature events, which are factors known to weaken coral health and increase the likelihood of bleaching (Manzello, Berkemans, & Hendee, 2007). Using the Belize MBRS for comparison, previous work has shown that outer reef sites experienced 20.0–40.1 days per year of recorded average temperatures above the local bleaching threshold of $>29.7^{\circ}\text{C}$ between 2003 and 2012 (Aronson, Precht, Toscano, & Koltes, 2002; Baumann et al., 2016). During the same time period, a permanent monitoring station at Molasses Reef (MLRF1), an outer reef site on the FKRT, recorded

only 13.2 days per year with average temperatures $>29.7^{\circ}\text{C}$ (National Data Buoy Center). Moreover, if we consider the metric found to correlate best with bleaching occurrence specifically on the FKRT (i.e., number of days annually $>30.5^{\circ}\text{C}$; Manzello et al., 2007), we find that MLRF1 recorded on average only 7.3 days per year above this locally derived bleaching threshold during the same time period of comparison.

As global ocean temperatures continue to rise in the future, coral reefs will be faced with the combined effects of warmer average conditions and the increased frequency of high-temperature events (Van Hooidonk, Maynard, & Planes, 2013). At present, however, high-latitude reefs that currently experience less frequent extreme summer temperatures and relatively cooler annual temperatures may still fall beneath the thermal optimum beyond which coral growth is expected to decline. In accordance with this notion, previous work from western Australia found that *Porites* colonies from two southern sites (i.e., highest latitudes) have exhibited an increase in calcification rates with warming over the last century, while those from more tropical regions have shown no change (Cooper, O'Leary, & Lough, 2012). In addition, a recent study conducted in Bermuda, the northernmost reef system in the Atlantic basin, predicts that calcification rates of two dominant corals may in fact increase with moderate increases in ocean temperature over the next century, though only under conservative warming scenarios (Courtney et al., 2017). Similarly, *S. siderea* and *P. strigosa* colonies sampled here appear able to sustain baseline extension and calcification rates through present day, regardless of their reef zone origin and despite persistent warming on the FKRT (Kuffner et al., 2015; Manzello, 2015).

However, exceptions to this pattern occur when extreme temperature events punctuate the prevailing subtropical climate on the FKRT. As has been reported extensively, anomalously warm SSTs are increasing in frequency worldwide, causing more frequent recurrence of major coral bleaching events (Van Hooidonk et al., 2013). Moreover, corals on the FKRT are occasionally faced with intrusions of anomalously cold water from the neighboring Florida Bay. Florida Bay is a wide, shallow embayment extending south from the mainland peninsula of Florida and west behind the shelter of the Florida Keys (Figure 1). Bay waters are subjected to extreme seasonal fluctuations in temperature and salinity, as well as elevated suspended sediment and nutrient concentrations associated with freshwater outflow from the Everglades ecosystem (Boyer, Fourqurean, & Jones, 1999). Under average weather conditions, tidal water exchange from Florida Bay has a relatively marginal impact on reefs beyond the boundary of the Middle Keys (Szmant & Forrester, 1996). However, during severe winter cold fronts that draw polar air masses across the region, pulses of bay water can reach surrounding inner reef areas of the upper Keys and, in some cases, cause catastrophic mortality in the reef community (Colella et al., 2012; Kemp et al., 2011; Lirman et al., 2011).

The coral growth records presented here indicate that two particular extreme temperature events induced short-term reductions in extension rates of *P. strigosa* at the scale of entire reef zones (Figure 3b). The first instance was a cold-water bleaching event in 1969–1970, which reportedly caused 80%–90% coral mortality at Hens and Chickens Reef, an inner patch reef in the upper Keys (Hudson et al., 1976). Long-term growth trends indicate the impact of this event spanned inner reef sites across the FKRT, causing a significant drop in the extension rate of *P. strigosa* colonies at these sites. A similar growth response is observed in association with the severe 1997–1998 warm-water bleaching event, during which extension rates of *P. strigosa* colonies at outer reef sites were significantly depressed. This pattern suggests that, although extensive bleaching was reported throughout the FKRT in 1997–1998, outer reef areas were particularly impacted by this event, echoing the continued decline of stony coral communities on the outer reef since 1998 (Ruzicka et al., 2013). Some have shown that higher turbidity associated with inner reef areas acts to attenuate UV radiation through the water column, thereby reducing coral susceptibility to bleaching (Morgan, Perry, Johnson, & Smithers, 2017). Additionally, a number of coral genera have demonstrated capacity to mitigate the negative effects of thermal stress via heterotrophy (Grottoli, Rodrigues, & Palardy, 2006). One or both of these factors may have lessened bleaching severity or accelerated the recovery of inner reef corals.

Interestingly, a number of other major bleaching events are not evident in the long-term growth records, namely the 2004–2005 warm-water and 2009–2010 cold-water events, both of which caused extensive coral bleaching and mortality on the FKRT (Colella et al., 2012; Manzello et al., 2007; Wagner, Kramer, & Van Woessik, 2010). The absence of clear reductions in extension rate at the reef zone scale suggests that the impact of these events may not have been as widespread or as severe as the 1969–1970 or 1997–1998

events. Alternatively, inherent spatial variation in bleaching susceptibility and impact may hinder reliable correlation of acute stress events with long-term growth records. However, as extreme temperature anomalies become more frequent on the FKRT (Manzello, 2015), repeated exposure to these thermal stress events may begin to push conditions beyond their thermal optima and lead to future reductions in coral extension rates.

The long-term decline in skeletal density observed for both species throughout the FKRT highlights the complexity of the coral growth response to the impacts of climate change. Together, skeletal density and extension control the rate of calcification, or the annual amount of skeleton accreted by the coral, which is important in determining whether coral reefs are in a state of net framework construction or erosion (Eyre et al., 2018). Small changes to reef-wide calcification budgets can have direct implications on habitat function and viability; however, growing evidence indicates that density and extension are affected independently by different parameters of environmental change (Lough & Barnes, 2000; Mollica et al., 2018).

Early research revealed variations in density based on hydraulic energy of the reef setting, such that denser skeletons strengthened coral colonies exposed to higher wave activity (Scoffin, Tudhope, Brown, Chansang, & Cheeney, 1992). Reduced skeletal density has also been attributed to elevated nutrients and poor water quality associated with heavy influence from nearby human development (Carricart-Ganivet & Merino, 2001; Dunn, Sammarco, & LaFleur Jr, 2012; Edinger et al., 2000). Accordingly, we find that average density of both species is significantly lower at inner reef sites at all but one of the cross-shore transects across the FKRT (Table 1), implying that these factors may limit baseline coral density. However, we have no reason to believe that hydraulic energy on the FKRT has increased significantly over the past century, and in fact, water quality has improved throughout the FKRT since 1995 (reduced turbidity and organic carbon; Briceño & Boyer, 2014), which would be expected to stimulate an increase in skeletal density through time.

Rather, we hypothesize that the long-term reduction in coral density may reflect changing carbonate chemistry on the FKRT over the past century. Recent analysis of *Porites* growth from the central Pacific reveals a strong sensitivity of skeletal density, but not extension, to aragonite saturation state (Ω_{arag}) and ocean acidification (Mollica et al., 2018; Tambutté et al., 2015). Likewise, density has been shown to decrease from high to low Ω_{arag} along a natural pH gradient in Puerto Morelos, Mexico, and in Milne Bay, Papua New Guinea (Crook, Cohen, Rebolledo-Vieyra, Hernandez, & Paytan, 2013; Fabricius et al., 2011). Our findings also reflect those of Helmle et al. (2011), which demonstrated significant correlation between declining trends in skeletal density of *O. faveolata* on the FKRT and modeled Ω_{arag} .

In situ monitoring efforts are beginning to unravel the complex biogeochemical mechanisms driving daily and seasonal fluctuations in carbonate chemistry on the FKRT, revealing, in particular, that inner reef areas are elevated in Ω_{arag} relative to outer reef areas in the upper Keys, but depleted by comparison in the lower Keys (Manzello, Enochs, Melo, Gledhill, & Johns, 2012). Independently, we

would expect this to cause an associated *increase* in mean skeletal density at inner reef sites in the upper Keys, rather than the reduction observed here. However, within the local setting of elevated nutrients and suspended particulate matter in inner reef areas, coral growth patterns likely reflect the interaction of these factors, which in this instance, may have opposing effects on skeletal density.

Importantly, while we hypothesize that the observed density decline may reflect long-term acidification, some have found that scleractinian corals are able to regulate the internal pH conditions at the site of calcification at relatively low energetic cost (McCulloch, Falter, Trotter, & Montagna, 2012; Ries, Cohen, & McCorkle, 2009). This suggests that corals may be able to maintain calcification rates at current levels of acidification, although it is argued that this physiological buffering capacity is dependent on the ability of corals to adapt simultaneously to increasing temperature stress (McCulloch et al., 2012). Here, corals on the FKRT have been able maintain calcification despite a long-term reduction in density, but to truly elucidate the cause of the observed growth trends, continued research, and long-term records of Ω_{arag} in the nearshore reef environment are necessary.

Site-wide averages of growth parameters suggest that the baseline calcification rate for *P. strigosa* is greatest at the northernmost outer reef site (i.e., Fowey Rocks); however, the sampled colonies at this site were the smallest in size (Table 1). During the course of sampling, the dive team encountered numerous larger, older colonies of *P. strigosa* (100+ years) throughout the sampling site, but all had experienced recent mortality and were virtually extirpated, presumably during the 2014–2015 bleaching event (*pers. obs.*). It is possible that the colonies which were able to survive this event may be especially well adapted and productive in their environment and are therefore able to maintain comparably high calcification rates.

This finding, however, highlights a critical implication regarding the use of coral cover versus growth rates as indices of overall reef health. Because only living colonies were sampled for this analysis, the growth trends reported here represent only those individuals that have survived the major mortality events occurring over the past several decades and are therefore distinctly resilient to environmental change. Additionally, in comparison with other species, it is important to note that *S. siderea* is particularly robust to thermal stress, allowing the species to persist ubiquitously throughout the Caribbean basin and as far north as Onslow Bay, North Carolina (34.5°N; Macintyre & Pilkey, 1969). Its resilience to both cold- and warm-water stress has allowed it to become one of the most abundant species on the FKRT (Florida Fish & Wildlife Conservation Commission, 2016) and explains why the bleaching-associated growth rate reductions observed in *P. strigosa* are not reflected for *S. siderea*. Consequently, coral growth trends do not reflect the health of the entire coral reef community. Subtler environmental changes that may have significant consequences for more susceptible individuals or species might not be fully captured in the skeletal growth records of the sampled colonies.

Overall, this study provides a comprehensive assessment of past and current growth dynamics of two important reef-building species that are ubiquitous across the FKRT. In particular, we find that:

- *S. siderea* and *P. strigosa* have been able to sustain baseline rates of extension and calcification despite recent bleaching events and chronic ocean warming.
- *P. strigosa* has experienced two significant, acute reductions in extension associated with major coral mortality events.
- Skeletal density of both species has declined significantly over the past century.

The complex growth dynamics observed here highlight the importance of measuring each component of coral growth to fully understand the past and future trajectories of coral reefs in the modern era of climate change. Stable calcification rates suggest that the local climate may buffer corals from chronic growth declines associated with climate warming, such as those observed on other Caribbean reefs and globally. Furthermore, we posit that declining density may point to the susceptibility of corals to changing carbonate chemistry on the FKRT and suggest that corals may experience further skeletal weakening in the future. Additional investigation of coral growth trends for other, perhaps more susceptible species, coupled with targeted analysis of environmental correlates is encouraged to test this hypothesis and provide a more comprehensive understanding of the trajectory of the reef community as a whole.

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AUTHOR CONTRIBUTIONS

KDC conceived and designed this study. JPR, JHB, HEA, SWD, and KDC collected core samples in the field. Data analysis was performed by JPR with valuable input from KDC, JHB, DND, and EBF. JPR prepared the manuscript with all authors contributing to its final form.

DATA ACCESSIBILITY

Data tables including all annual measurements of extension rate, density and calcification rate included in this analysis are made available via the BCO-DMO Digital Repository, <https://www.bco-dmo.org/project/635863>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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