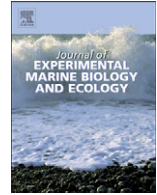




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Coral growth patterns of *Montastraea cavernosa* and *Porites astreoides* in the Florida Keys: The importance of thermal stress and inimical waters



Derek P. Manzello^{a,*}, Ian C. Enochs^{a,b}, Graham Kolodziej^{a,b}, Renée Carlton^{a,b}

^a Atlantic Oceanographic and Meteorological Laboratories (AOML), NOAA, 4301 Rickenbacker Cswy., Miami, FL 33149, United States

^b Cooperative Institute for Marine and Atmospheric Studies, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Cswy., Miami, FL 33149, United States

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ABSTRACT

The calcification and extension rates of two species of scleractinian coral (*Montastraea cavernosa*, *Porites astreoides*) were measured in corals experimentally transplanted to paired inshore and offshore locations in the Upper, Middle, and Lower Florida Keys from 2010 to 2011. Growth rates were compared with respect to 1) shelf location, 2) species, 3) region, and 4) temperature. Transplanted corals on inshore reefs generally calcified less than those at paired offshore sites, but these differences were only significant in a few cases. This difference in growth is likely because of two thermal stress events that occurred inshore, but not offshore, as growth records from cores of *P. astreoides* revealed significantly higher extension and calcification inshore from 2001–2013. The core data confirmed that the years 2010–2012 were a period of depressed growth inshore. Calcification and extension rates of the experimental corals were not statistically different between *M. cavernosa* and *P. astreoides* within a given site. The only exceptions were that calcification was higher in *M. cavernosa* at the Middle Keys inshore site. The Middle Florida Keys sites had the lowest rates of calcification, supporting the hypothesis that the influence of Florida Bay waters in this region contributes to poor reef development. Mean calcification rates negatively correlated with metrics of cold stress in *M. cavernosa* and heat stress in *P. astreoides*. The lack of a significant correlation between heat stress and mean calcification in *M. cavernosa* may help explain this species persistence on today's reefs. Maximum calcification and mean extension, however, were negatively correlated with maximum running 30-day mean temperature, showing that the growth of *M. cavernosa* is not completely insensitive to warm water stress. The 'weedy' life-history strategy of *P. astreoides* may compensate for the sensitivity of calcification rates to heat stress reported here, allowing this species to maintain the stable populations that have been observed throughout Florida and the wider Caribbean.

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1. Introduction

The greatest reef development of the Florida Reef Tract, excluding the Dry Tortugas, occurs offshore of the Upper Florida Keys while the poorest reef development occurs in the Middle Keys (Ginsburg and Shinn, 1964; Marszalek et al., 1977; Shinn et al., 1977, 1989). The poor reef development of the Middle Keys was hypothesized to be due to the exchange of Florida Bay waters through the wide channels in this region, thought to be inimical to reef growth (Ginsburg and Shinn, 1964). There is indeed a net outflow from Florida Bay through these channels to the reefs offshore and these waters have high turbidity, variable temperature and salinity, and elevated nutrient concentrations (Shinn, 1966; Hudson, 1982; Szmant and Forrester, 1996; Porter et al., 1999; Lee and Smith, 2002).

Despite the 'inimical water hypothesis' being more than 50 years old, only a few studies have directly addressed the impact of inimical

waters on coral fitness. Kuffner et al. (2013) found that exposure to Florida Bay waters had little impact on calcification rates of *Siderastrea siderea*, but was correlated with a significant elevation in net calcification of crustose coralline algae. High temperatures alone and in combination with high salinity mimicking those found in the outflow of Florida Bay waters caused a complete collapse of photosynthesis and mortality in *Orbicella* (formerly *Montastraea*) *faveolata* after 12 and 36 h of exposure, respectively (Porter et al., 1999). Cook et al. (2002) observed that *O. faveolata* skeletal density and calcification declined with nearness to shore, but extension rates were maintained.

The coral reefs of the Florida Keys have undergone a rapid, recent decline in coral cover, much like the entire Caribbean region, since the 1980s (Dustan and Halas, 1987; Porter and Meier, 1992; Gardner et al., 2003). Coral disease, warm water bleaching, hurricanes, declining water quality, and overfishing have all been implicated as important factors causing this degradation (Pandolfi et al., 2005; Precht and Miller, 2007). Present-day coral cover in the Florida Keys is about 5%, except on inshore patch reefs, where percent cover ranges from 15% to >40% (Lirman and Fong, 2007; Somerfield et al., 2008; Ruzicka

* Corresponding author.

E-mail address: Derek.Manzello@noaa.gov (D.P. Manzello).

et al., 2013). The persistence of high coral cover inshore is puzzling as these reefs are exposed to extremes in environmental variables classically thought to be restrictive to coral reef growth and development, including greater temperature variance, turbidity, sedimentation, and nutrients (Shinn, 1966; Hudson, 1982; Lirman and Fong, 2007).

Multiple studies spanning the Atlantic and Pacific Oceans have observed a similar cross-shelf gradient in coral skeletal density (Dodge and Brass, 1984; Risk and Sammarco, 1991; Scoffin et al., 1992; Carricart-Ganivet and Merino, 2001; Cook et al., 2002; Manzello et al., 2015). This trend, termed ‘stretch-modulation’ by Carricart-Ganivet and Merino (2001), describes the process whereby corals inshore respond to declines in cross-shelf water quality by extending their skeleton at the same or greater rates as corals offshore, generally at the expense of skeletal density. This reduced density nearshore has been attributed to increased nutrients, sedimentation, and lower light availability (Risk and Sammarco, 1991; Carricart-Ganivet and Merino, 2001; Cook et al., 2002).

Temperature, light, and those variables that affect light attenuation such as turbidity, are the most important factors controlling the rates of coral growth (Goreau and Goreau, 1959; Glynn, 1977; Tomascik and Sander, 1985). More recently it has been appreciated that coral calcification rates are also a function of aragonite saturation state (Ω_{arag}), but considerable inter-species differences in sensitivity to changes in Ω_{arag} have been reported (McCulloch et al., 2012; Chan and Connolly, 2013). Temperature exhibits a strong and often overriding control on coral growth and calcification in the field (e.g., Lough and Barnes, 2000; Cooper et al., 2012). The relative role of the other variables is difficult to discern from field studies. This is because these variables tend to co-vary across natural gradients, making inferences about the attribution of one particular variable challenging (Manzello et al., 2014). Field studies can also yield seemingly paradoxical results when considered alongside laboratory results. At volcanically acidified, low Ω_{arag} seeps in Papua New Guinea, coral calcification in massive *Porites* is no different than what occurs at control sites (Fabricius et al., 2011). In the Galápagos Islands, extension and calcification rates of massive *Porites* corals are greater than what occurs at other Indo-Pacific locations with comparable temperatures despite high nutrients and low Ω_{arag} (Manzello et al., 2014). These field studies, however, do provide real-world context into environmental versus biological controls on coral growth and how corals acclimatize to suboptimal physico-chemical conditions.

We assessed coral calcification and extension rates for two species of reef-building coral (*Montastraea cavernosa* and *Porites astreoides*) at six sites from 2010–2011 in the Florida Keys using the buoyant weight approach (Jokiel et al., 1978). These sites spanned an inshore-to-offshore gradient in the Upper, Middle, and Lower Florida Keys. Growth was measured annually from 2010–2011 and during the summer of 2011. Growth rates were compared with respect to 1) shelf location, 2) species, 3) region, and 4) temperature. Small coral cores of *P. astreoides* were collected from inshore and offshore reef sites in the Upper Florida Keys to examine long-term trends in growth of un-manipulated corals.

2. Materials and methods

2.1. Sites

Paired inshore and offshore sites were selected in the Upper, Middle, and Lower Florida Keys (Fig. 1). For simplicity, these sites are hereafter abbreviated as follows: UKO, Upper Keys Offshore (Little Conch Reef); UKI, Upper Keys Inshore (Tavernier Rocks); MKO, Middle Keys Offshore (Tennessee Reef); MKI, Middle Keys Inshore (Channel 5); LKO, Lower Keys Offshore (Looe Key); LKI, Lower Keys Inshore (Marker 50A). These sites were chosen following the previously established convention for dividing the Florida Keys into regions with different oceanographic characteristics that impact reef development (Ginsburg and Shinn, 1964; Marszalek et al., 1977). Depth was constrained (4–6 m)

during site selection to minimize variance due to depth-associated influences on coral growth (Huston, 1985). Lirman and Fong (2007) defined inshore as <4.5 km and offshore as >4.5 km from shore and this was used as a guide for site determination.

2.2. Coral growth measurements

In the Lower Keys, corals were collected for the buoyant weight studies at LKI and transplanted to LKI and LKO (Fig. 1). For the Upper and Middle Keys sites, coral collections were made at UKO (Fig. 1, Little Conch Reef). The 2010 cold water event had little impact on the reefs offshore of the Upper Keys (Min temp = 15.9 °C, number of hours < 16 °C = 1: Lirman et al., 2011; Kemp et al., 2011; Colella et al., 2012), thus we expect that there was limited residual stress occurring in these corals. Growth rates in *O. faveolata* were not impacted at this site (UKO, Little Conch reef) providing evidence that there was limited impact from the cold water event (Manzello et al., 2015). The corals collected at LKI likely experienced some cold-water stress, but there were no visible signs of stress during collection and the 2010 cold-water stress event had the least impact in the Lower Keys (Lirman et al., 2011). *P. astreoides* at LKO displayed the highest calcification and extension rates of all sites and these corals were collected from LKI, showing that there was little lingering impact and that the rates documented were largely a result of proximal environmental conditions.

Coral fragments (9–16 cm²) were obtained with hammer and chisel from healthy parent colonies. One to two fragments were collected per parent colony. Twenty fragments of each species were collected at UKO and LKI. After collection, corals were transferred back to shore where they were kept in well-aerated, large coolers and then affixed to previously constructed cement plugs using All-Fix epoxy. After allowing the epoxy to set for 1 h, the corals were buoyant weighed to the nearest milligram. The maximum distance from the bottom of the cement plug to top of the coral colony was measured to the nearest 0.1 mm using calipers. Ten individual corals per species were deployed at each site following weighing. Corals were secured to the seafloor on PVC frames that were approximately 1 m L × 0.5 m W × 0.5 m H. PVC frames were affixed to rebar that had been hammered into the reef framework substrate. The initial coral collections and measurements took place on 14 and 16 June 2010 for the Lower and Middle Keys sites, respectively.

Corals deployed at UKO were originally collected and deployed on 26 May 2009. The 2010 cold-water event killed all the corals at UKI with the exception of *M. cavernosa*, whereas those corals at UKO did not suffer any mortality. As a result, a new collection of corals was made at UKO on 24 August 2010. These corals were brought back to shore along with the existing corals at UKO, affixed to plugs, weighed, measured, and redeployed.

After 336 (Lower and Middle Keys sites) and 268 (Upper Keys sites) days, the corals were collected from the field between 16–19 May 2011, carefully cleaned of all non-coral flora and fauna, and then re-weighed following the buoyant weight methodology (Jokiel et al., 1978). This time period was used to estimate annual rates of growth. These same corals were subsequently redeployed at the same sites and collected again after 146 days (all sites) from 10–13 October 2011. This second time period was used to estimate rates of growth during the summer period of 2011.

Calcification rate was determined as percentage increase in weight gain from the initial weight and linear extension was calculated as the change in maximum distance from the bottom of the cleaned coral plug to the top of coral tissue. Colonies exhibiting any mortality, bleaching/paling, competitive overgrowth (e.g., *Millepora*, bryozoan, and bivalve), or infauna (e.g., *Spirobranchus*) were not used for growth calculations. When negative extension was measured, these values were not used. This occurred infrequently as only four of the 86 colonies measured during the annual interval had negative extension and were not used. Calcification and extension are expressed as monthly rates

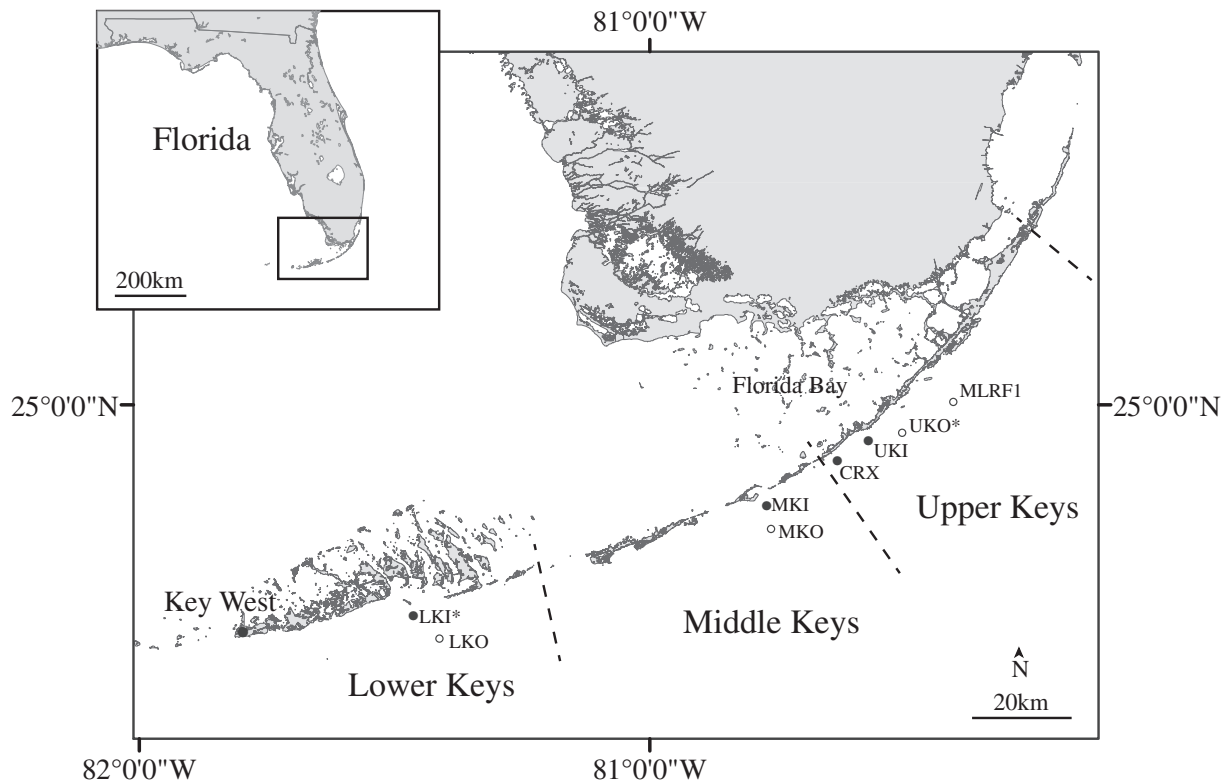


Fig. 1. Sites in Florida Keys where growth measurements were obtained. Open circles are offshore sites, whereas closed are inshore. Abbreviations, MLRF1, Molasses Reef; UKO, Upper Keys Offshore; UKI, Upper Keys Inshore; MKO, Middle Keys Offshore; MKI, Middle Keys Inshore; LKO, Lower Keys Offshore; LKI, Lower Keys Inshore; CRX, Cheeca Rocks. Asterisk indicates location of coral collections.

to compare all sites and time periods. Control plugs without corals were deployed at LKI and LKO.

Small coral cores (5 cm diameter, 10 cm length) were collected from colonies of *P. astreoides* at similar depths (4–6 m) from UKO, as well as Cheeca Rocks, which is an inshore patch reef of the Upper Keys, from 21–22 July 2014 (Fig. 1). The methodology of collection and analysis was previously published (Manzello et al., 2015). In brief, coral cores were collected by divers using a pneumatic drill and scanned with a micro-CT. The distance between annual high density peaks in the coral cores was used as annual linear extension, which was multiplied by the integrated average of skeletal density between peaks to obtain calcification. Extension, density, and calcification data from eight core samples from UKO and Cheeca Rocks are presented spanning the years 2001–2013.

2.3. Temperature data

Coincident with all coral growth periods, seawater temperature was measured in situ every 30 min using HOBO Pro V2 thermistors (Onset Corp.) that were directly attached to the coral frames. Hourly sea temperature data from the Molasses Reef Coastal Marine Automated Network (C-MAN) station (hereafter referred to as MLRF1, approx. 1 m depth) are available nearly continuously since 1988 (www.ndbc.noaa.gov) (Fig. 1). The seasonal cycle, or climatology, for MLRF1 was determined as previously described (Manzello et al., 2007).

Bleaching thresholds were previously estimated for the C-MAN sites located on offshore reefs in the Florida Keys (Fig. 1) (Manzello et al., 2007). The bleaching threshold for Molasses Reef and Sand Key was equal to a monthly mean sea temperature of 30.4 °C. The Sombra Reef site, which is influenced by the exchange of Florida Bay waters, had a higher threshold of 30.9 °C. To determine if the thresholds

estimated for the offshore C-MAN sites were exceeded at the six sites studied here, we calculated the running 30-day mean sea temperature at each site.

Multiple metrics of in situ sea temperature variability were calculated to compare to the coral growth measurements. Metrics included overall mean, standard deviation, minimum, maximum, range, minimum and maximum daily average temperature, maximum running 30-day mean temperature, and the number of days sea temperatures were >31, 31.5, 32, 32.5 and <20, 18, 17, and 16 °C. These variables were categorized as temperature variance (standard deviation, range), cold stress (Min, Daily Avg. Min, days <20, 18, 17, 16 °C), and heat stress (Max, Daily Avg. Max, Max 30-day running mean, days >31, 31.5, 32, 32.5 °C).

2.4. Statistical analysis

One-way ANOVA was used to compare rates of calcification and extension between more than two groups. A non-parametric Kruskal–Wallis test was used when data failed to meet the assumption of normality or homoscedasticity. Post-hoc Tukey t-tests were used to compare differences between two measurements when ANOVA indicated significant differences. T-tests were used when comparing two groups (e.g. inshore vs offshore). A Mann–Whitney *U*-test was used when data were not normal or variances unequal.

Correlation analysis was run for all growth parameters and all temperature parameters over the period that both growth and temperature were measured simultaneously (2010–2011). Pearson correlation was used when data conformed to the assumption of normality, according to a Shapiro–Wilk's test. When data were not normal, a Spearman correlation analysis was run. When significant correlations were found, linear regression was used to find the best-fit temperature metric

explaining growth patterns. All statistical analysis was performed using the computer software SigmaPlot 12.

3. Results

3.1. Growth of experimental corals

Calcification and extension were generally greater at the offshore sites in the experimental corals (Fig. 2), though high variance caused this trend to only be significant in a few instances (Table 1). Mean weight gain and linear extension of the control plugs were not statistically different (t-tests) inshore vs. offshore during the annual and summer deployments (Tables 1, 2). Rates of calcification and extension were higher in summer than the annual period (Fig. 2, Table 2). However, this greater calcification and extension during summer was only significant in *M. cavernosa* at MKO and LKI ($p < 0.05$, t-tests for extension, Mann–Whitney for calcification). Extension of *M. cavernosa* at UKI was also significantly greater in summer ($p < 0.001$, t-test). For *P. astreoides*, calcification was greater in summer at all sites except UKI where bleaching occurred ($p < 0.05$, t-test). Only UKO and LKI had significantly higher extension in the summer for *P. astreoides* ($p < 0.05$, t-tests).

Calcification and extension rates were not statistically different between species within a given site (Fig. 2), with the exception of greater calcification in *M. cavernosa* at MKI during the annual deployment. Furthermore, rates of calcification and extension were similar within species when compared across the three inshore and offshore sites, with the exception of the notable depression in calcification at the Middle Keys sites (Fig. 2, Table 3).

The lowest calcification rates for both species inshore and offshore occurred at the Middle Keys sites (Fig. 2). The only exception was for *P. astreoides* during bleaching. During both time periods the greatest extension for *M. cavernosa* occurred at MKO, but calcification was depressed relative to the other offshore sites (Table 4). A similar trend occurred in *P. astreoides* in the summer such that the MKO site had the greatest extension of all offshore sites, but lowest calcification. Despite the elevated extension, calcification of *M. cavernosa* at MKO was similar to the inshore sites other than MKI in summer. The ‘inimical waters’ of the Middle Florida Keys had a greater impact on *P. astreoides* (Fig. 2). The calcification rates over the annual deployment were similar for *P. astreoides* both inshore and offshore in the Upper and Lower Keys, but depressed in the Middle Keys (Fig. 2B, Table 3).

3.2. Temperature and 2011 bleaching event

The inshore sites were warmer in summer and colder in winter than the offshore sites, but all sites had similar seasonal patterns (Fig. 3). During the summer of 2010 and 2011, all six sites met or exceeded the 30.4 °C MLRF1 bleaching threshold, whereas five of the six sites reached the higher 30.9 °C threshold. Bleaching occurred in *P. astreoides*, but not *M. cavernosa* at UKI in 2011; the maximum running 30-day mean temperature at UKI during bleaching was 31.8 °C (data reported in Manzello, in review). The max 30-day mean temperature at the other inshore sites in 2010 and 2011 was 31.7 °C. This may indicate a monthly mean bleaching threshold for these inshore sites of 31.8 °C, but this is not clear because very high short-term temperatures occurred in 2011 that did not occur in 2010. Temperatures measured every 30 min

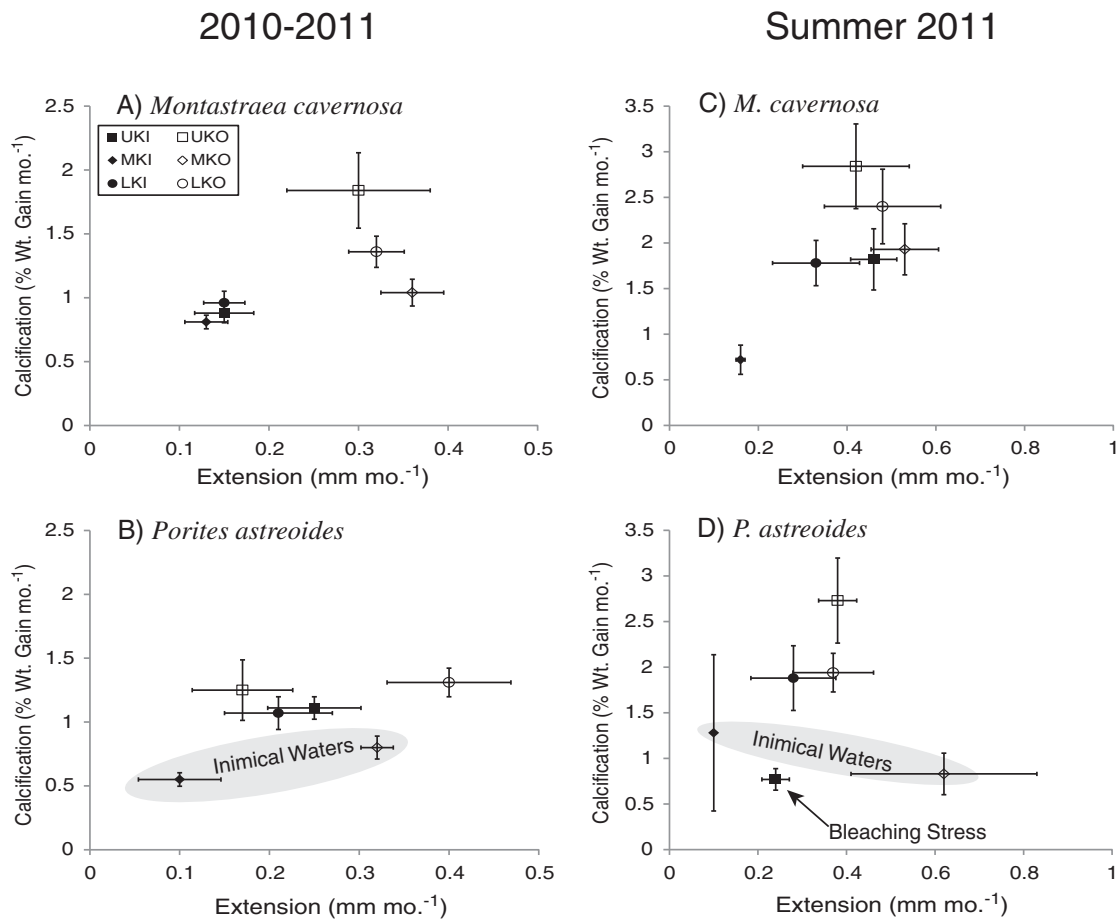


Fig. 2. Coral calcification (y-axis) and extension (x-axis) at Inshore and Offshore sites in the Upper, Middle, and Lower Florida Keys. (A) *Montastraea cavernosa*, (B) *Porites astreoides* for June/Aug 2010–May 2011. (C) *M. cavernosa*, (D) *P. astreoides* for May–Oct 2011. Values plotted are means \pm standard error of the mean (SEM). Note, bleaching observed in *P. astreoides* at the inshore Upper Keys site in the summer of 2011 upon measurement of corals in October 2011.

Table 1
Coral Calcification and Extension at Inshore and Offshore sites in the Upper, Middle, and Lower Florida Keys, June/Aug 2010–May 2011. Data are means \pm standard error of the mean (SEM) normalized to monthly rates for comparison. Range is minimum and maximum values. Upper Keys, UK; Middle Keys, MK; Lower Keys, LK. Species abbreviations: MC, *Montastraea cavernosa*; PA, *Porites astreoides*; CO, Control plugs without corals. Asterisk indicates significantly greater value.

Region	Spp.	Inshore						Offshore					
		% wt. gain month ⁻¹			Linear extension (mm month ⁻¹)			% wt. gain month ⁻¹			Linear extension (mm month ⁻¹)		
		N	Mean (SEM)	Range	N	Mean (SEM)	Range	N	Mean (SEM)	Range	N	Mean (SEM)	Range
UK	MC	7	0.88 (0.076)	0.62–1.15	6	0.15 (0.033)	0.06–0.26	8	*1.84 (0.295)	0.36–3.18	7	0.30 (0.080)	0.08–0.65
	PA	10	1.11 (0.088)	0.74–1.63	9	0.25 (0.052)	0–0.46	5	1.25 (0.237)	0.22–1.73	5	0.17 (0.056)	0.02–0.48
MK	MC	10	0.81 (0.053)	0.59–1.14	9	0.13 (0.024)	0.02–0.24	9	1.04 (0.105)	0.68–1.68	9	*0.36 (0.035)	0.22–0.55
	PA	3	0.55 (0.053)	0.46–0.64	3	0.10 (0.046)	0.01–0.15	3	0.80 (0.090)	0.69–0.98	2	*0.32 (0.018)	0.30–0.34
LK	MC	9	0.96 (0.091)	0.63–1.31	9	0.15 (0.023)	0.02–0.25	8	*1.36 (0.122)	0.90–1.77	8	*0.32 (0.031)	0.21–0.45
	PA	6	1.07 (0.128)	0.82–1.50	6	0.21 (0.060)	0.01–0.37	8	1.31 (0.112)	0.61–1.66	8	0.40 (0.069)	0.16–0.74
	CO	3	0.49 (0.113)	0.36–0.71	3	0.01 (0.018)	–0.02–0.04	3	0.40 (0.019)	0.37–0.43	3	0.02 (0.045)	–0.04–0.11

peaked at 33.9 °C at UKI in 2011, which was 0.4 °C and 1.2 °C higher than the maximum temperatures at MKI and LKI, respectively.

Fifty percent of the *P. astreoides* on the growth racks bleached and only the colonies that were not visibly bleached or pale were measured. Rates of calcification in *P. astreoides* were significantly depressed at UKI relative to UKO even in those colonies that did not visibly bleach (*t*-tests, $p < 0.05$; Fig. 2, Table 2). Thermal stress impacted calcification more than extension (Fig. 2). The growth of *M. cavernosa* did not exhibit any notable impacts during this period of thermal stress (Fig. 2).

3.3. Coral core growth data

Extension and calcification rates measured in the *P. astreoides* cores were significantly greater inshore from 2001–2013 (*t*-test comparisons of annual means: extension: $t = 3.72$, $df = 24$, $p < 0.001$; calcification: $t = 4.18$, $p < 0.001$) (Fig. 4, Table 4). None of the growth parameters for *P. astreoides* offshore were ever significantly greater than inshore during any individual year, even during the two periods when the inshore site was impacted by thermal stress that did not occur offshore (2009–10, 2011–12). Skeletal density was greater inshore, and this was significant from 2005–13 ($t = 4.18$, $df = 16$, $p < 0.001$), but not from 2001–13. The latter time period coincides with the analysis of core data from *O. faveolata* from the same sites (Manzello et al., 2015).

The extension rates for *P. astreoides* in the experimental corals ranged from 0.12–0.3 cm yr⁻¹ at the inshore sites and 0.2–0.48 cm yr⁻¹ offshore (Table 1). Mean extension rates in the cores from un-manipulated control corals were 0.43 cm yr⁻¹ inshore and 0.35 cm yr⁻¹ offshore (Table 4). Extension in the cores from 2010–2011 was 0.39 cm inshore and 0.42 cm offshore. The extension rates of the experimental corals offshore were similar to the core data, but the inshore experimental corals had lower rates.

3.4. Correlations between experimental coral growth and temperature

Mean calcification and extension rates of *M. cavernosa* were negatively correlated with the standard deviation of temperature and cold

stress during the annual deployment, but positively related to minimum temperature (Table 5). Minimum temperature provided the best fit when regressed with mean calcification for *M. cavernosa* ($r^2 = 0.686$, $p < 0.05$, $n = 6$, Fig. 5A), followed by temperature range ($r^2 = 0.663$, $p < 0.05$). When the outlier UKO was excluded, the fit improved for both minimum temperature ($r^2 = 0.964$, $p < 0.01$, Fig. 5B) and temperature range ($r^2 = 0.830$, $p < 0.05$). Note that UKO was not an outlier for *P. astreoides* and exclusion of this data point had no impact on correlations for that species. Mean linear extension could also be explained by cold water exposure as the best fit was found for number of days < 20 °C ($r^2 = 0.946$, $p < 0.01$). Unlike calcification, mean extension was negatively correlated to warm water exposure, being negatively related to the maximum running 30-day mean sea temperature ($r^2 = 0.864$, $p < 0.01$). Maximum calcification negatively correlated to maximum running 30-day mean, indicating a depression of maximum rates with warm water exposure that wasn't reflected in the mean values. Thus, extension rate in *M. cavernosa* correlated with cold-water metrics, just like calcification, but was also related to cumulative high temperature exposure. During the summer deployment, there were no significant correlations for mean calcification or extension with any variable likely because of some additional unmeasured variable led to depressed growth at MKI (see Discussion). Temperature variance and heat stress did exhibit relationships with minimum and maximum extension during summer (Table 5).

Mean calcification of *P. astreoides* negatively correlated with temperature range, maximum temperatures, and the heat stress metrics of days > 32 and 32.5 °C during the annual deployment (Table 6). These heat stress metrics also correlated with maximum calcification. Temperature range provided the best fit with mean calcification ($r^2 = 0.714$, $p < 0.05$) followed by maximum daily average temperature ($r^2 = 0.677$, $p < 0.05$). Minimum and maximum extension correlated with cold and warm water stress, but mean extension was not correlated with any variable (Table 6). During the summer of 2011, the best fit for mean extension was a negative relationship with number of days > 31 °C ($r^2 = 0.731$, $p < 0.05$). Calcification did not correlate with any variable.

Table 2
Coral calcification and extension at inshore and offshore sites in the Upper, Middle, and Lower Florida Keys, May–October 2011. Data are means (\pm SEM) normalized to monthly rates for comparison. Range is minimum and maximum values. Upper Keys, UK; Middle Keys, MK; Lower Keys, LK. Species abbreviations: MC, *Montastraea cavernosa*; PA, *Porites astreoides*; CO, Control plugs without corals. *, indicates significant difference between inshore and offshore sites in that species. Asterisk indicates significantly greater value.

Region	Spp.	Inshore						Offshore					
		% wt. gain month ⁻¹			Linear extension (mm month ⁻¹)			% wt. gain month ⁻¹			Linear extension (mm month ⁻¹)		
		N	Mean (SEM)	Range	N	Mean (SEM)	Range	N	Mean (SEM)	Range	N	Mean (SEM)	Range
UK	MC	12	1.82 (0.335)	0.20–3.30	14	0.46 (0.052)	0.02–0.74	10	2.84 (0.464)	0.39–5.31	9	0.42 (0.120)	0.06–1.27
	PA	3	0.77 (0.118)	0.53–0.90	2	0.24 (0.031)	0.21–0.27	6	*2.73 (0.466)	1.23–4.07	6	0.38 (0.043)	0.23–0.53
MK	MC	6	0.72 (0.160)	0.30–1.29	3	0.16 (0.010)	0.04–0.36	7	*1.93 (0.280)	0.99–3.15	6	*0.53 (0.076)	0.27–0.82
	PA	2	1.28 (0.856)	0.43–2.14	1	0.10 (N/A)	N/A	3	0.83 (0.228)	0.38–1.10	3	0.62 (0.210)	0.29–1.01
LK	MC	7	1.78 (0.248)	0.83–2.76	6	0.33 (0.098)	0.05–0.74	8	2.40 (0.409)	1.28–3.95	8	0.48 (0.131)	0.08–1.11
	PA	6	1.88 (0.355)	0.60–2.89	5	0.28 (0.096)	0.02–0.60	5	1.94 (0.212)	1.56–2.72	5	0.37 (0.091)	0.12–0.68
	CO	3	0.00 (0.086)	–0.17–0.09	3	–0.01 (0.083)	–0.14–0.14	3	–0.02 (0.460)	–0.21–0.10	3	–0.02 (0.153)	–0.06–0.04

Table 3

One-way ANOVA of calcification and extension rates by species across inshore and offshore Florida Keys sites. Upper Keys, UK; Middle Keys, MK; Lower Keys, LK. Species abbreviations as follows: MC, *Montastraea cavernosa*; PA, *Porites astreoides*. Asterisk shows significance of ANOVA with indication of significant site differences shown as indicated by post-hoc tests, **p* < 0.05, ***p* < 0.01, ns is non-significant. IN, inshore; OFF, offshore.

Time Period	IN/OFF	Growth variable	Species	
			MC	PA
Annual	IN	Calcification	ns	*, MK < UK + LK
		Extension	ns	ns
	OFF	Calcification	*, MK < UK + LK	ns
		Extension	ns	ns
Summer 2011	IN	Calcification	** , MK < LK	ns
		Extension	*, MK < UK	ns
	OFF	Calcification	ns	*, MK < UK + LK
		Extension	ns	ns

4. Discussion

4.1. The role of inimical waters on coral calcification

The lowest rates of extension and calcification, both inshore and offshore, occurred in the Middle Keys for both species, supporting the hypothesis that the efflux of Florida Bay waters limits reef development (Ginsburg and Shinn, 1964). This contrasts with the findings of Kuffner et al. (2013) who assessed calcification in *S. siderea* over approximately the same time period and found little difference in calcification between sites in the Middle and Upper Keys. This may be a result of the high thermal tolerance of *S. siderea*, which is more resistant to thermal stress than the two species studied here (Lirman et al., 2011; Kemp et al., 2011; Colella et al., 2012).

M. cavernosa was less impacted by the inimical Florida Bay water relative to *P. astreoides* (Fig. 2), but the combination of warm water thermal stress and some unmeasured property of the inimical waters during the summer of 2011 led to very depressed growth at MKI (Fig. 2). This suggests that while *M. cavernosa* can tolerate high temperatures that cause bleaching in other species without large depressions in growth as seen at UKI in summer 2011, it cannot tolerate such high temperatures in combination with additional stressors associated with Florida Bay waters. Previous research has shown negative physiological responses in *O. faveolata* to high temperature and high salinity waters, mimicking that found in the outflow of Florida Bay (Porter et al., 1999). Additionally, Coles and Jokiel (1978) showed that deviations of salinity from optimal values reduced the thermal tolerance of corals. The Middle Keys have significantly higher nutrient levels than the Upper and Lower Keys (Szmant and Forrester, 1996), which may also be contributing to the inimical water effect. Cook et al. (2002) found limited evidence for a nutrient effect, however, in *O. faveolata* in the Middle Keys at inshore and offshore sites.

We observed hypersaline waters at MKI in May 2011 that was presumably exiting Florida Bay through channel #5. This water mass was stratified with an inverted thermocline and visible with the naked eye as a turbid, warm layer that was yellowish in color. Salinity values at the surface of MKI were 36.75–37.16 practical salinity units (psu) over two days (salinity data presented in Manzello et al., 2012). At 4 m depth adjacent to the coral frames, salinity was 39.55 psu when the

Table 4

Mean linear extension (cm yr⁻¹), skeletal density (g cm⁻³), and calcification (g cm⁻² yr⁻¹) of *Porites astreoides* at Cheeca Rocks and Little Conch Reef from 2001 to 2013. SEM is standard error of the mean; n, number of cores.

Site	n	Linear Extension	Density	Calcification
		Mean (±SEM)	Mean (±SEM)	Mean (±SEM)
Cheeca Rocks	8	0.43 (0.015)	1.61 (0.013)	0.69 (0.025)
Little Conch	8	0.35 (0.014)	1.58 (0.022)	0.55 (0.020)

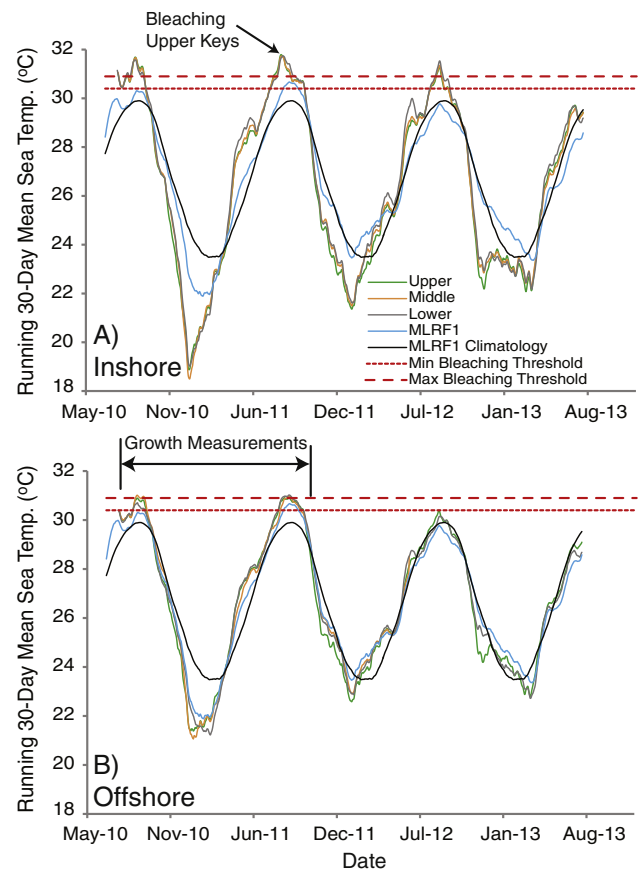


Fig. 3. Running 30-day mean sea temperatures (°C) for the three inshore (A) and offshore (B) Florida Keys sites. Also shown is data from nearby Molasses Reef (MLRF1), the climatology for Molasses Reef (MLRF1 Climatology), and the locally-derived bleaching thresholds.

surface value was 37.16. This water mass extended to MKO, where salinity values at 5 m depth were 37.55–38.18 psu over the same two days. Values at the surface were 36.46 psu when values at depth were 37.55. This dense water mass was noticeably warmer than the surface, but the gradient was not measured as the thermistors were deployed next to the benthos, on the coral frames. Sea temperatures inshore at this time were 27.7–27.8 °C and, counterintuitively, about a half a degree warmer offshore at 28.2 °C. It has been hypothesized that the transport of these hot, dense, and salty waters from Florida Bay in the summer has contributed to reef decline in the Keys, and that this phenomenon is either new or exacerbated as a result of the interruption of the natural freshwater flow from the Everglades into Florida Bay (Porter et al., 1999). The interaction of high temperature and salinity may have resulted in the very low calcification of *M. cavernosa* at MKI in the summer of 2011, but further study is needed.

4.2. Thermal stress and coral growth

Minimum temperatures and cold stress (days < 20 °C) correlated with mean calcification and extension of *M. cavernosa*, respectively. Conversely, heat stress (days > 32 °C) and maximum temperatures correlated with calcification of *P. astreoides*. Both *M. cavernosa* and *P. astreoides* are more tolerant than other Caribbean species to high temperatures, but among the least tolerant to cold waters (Fitt and Warner, 1995; Wagner et al., 2010; Lirman et al., 2011; Miller et al., 2011). *M. cavernosa* is known to be less sensitive to warm water bleaching than *P. astreoides* (Wagner et al., 2010; Lirman et al., 2011) and the data here agree with this trend. Half of the experimental *P. astreoides* colonies bleached in the summer of 2011 and those that weren't

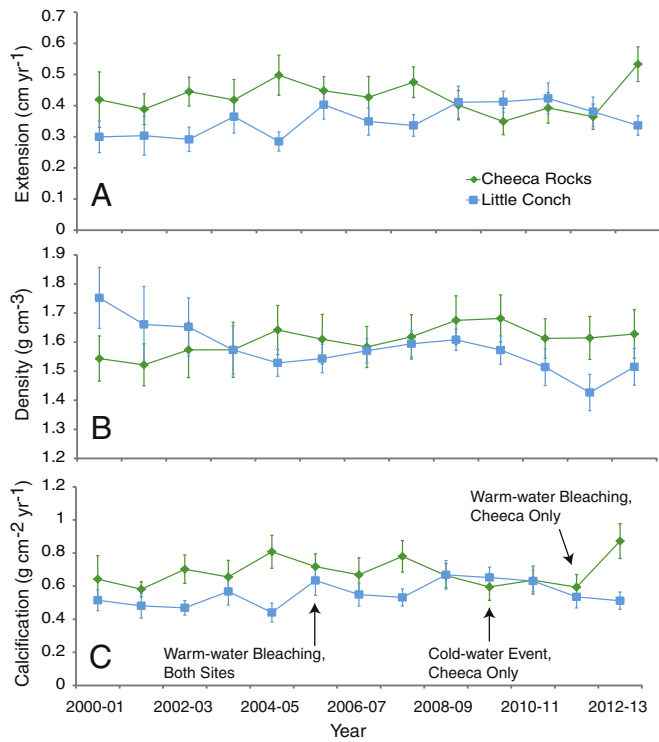


Fig. 4. (A) Mean Linear extension, (B) skeletal density, and (C) calcification rate per year from 2001–2013 for *Porites astreoides* at Cheeca Rocks and Little Conch Reef. Error bars are standard error of the mean.

bleached had significantly depressed growth. *M. cavernosa* did not bleach and growth was not notably impacted. The negative correlation between mean calcification and heat stress for *P. astreoides*, but not *M. cavernosa* further supports these observations. Carricart-Ganivet et al. (2012) have also shown a marked sensitivity to high temperature in the rates of calcification for *P. astreoides*.

The core data from 2000–2013 suggest that the growth of *P. astreoides* is less sensitive to thermal stress than *O. faveolata* (Manzello et al., 2015). Extension and calcification of *P. astreoides* actually increased during the 2005 bleaching event offshore relative to the previous year, whereas there was only a slight decline inshore (Fig. 4). Both extension and calcification declined at a similar magnitude, while density increased in *O. faveolata* inshore and offshore during the 2005 bleaching event (Manzello et al., 2015). Furthermore, the three growth parameters were no different than the previous two years for *P. astreoides* during the 2011 inshore bleaching (Fig. 4). Thus, the data

Table 5
Correlation of *Montastraea cavernosa* growth metric averages by site with temperature variables. Value is correlation coefficient, $p < 0.05$ unless underlined, then $p < 0.01$. Temperature terms: SD, std. deviation; Min, minimum temperature; DAVG, daily average temperature; No. of days is number of days daily average temperature was $>$ or $<$ listed value in degrees Celsius; Max 30D, maximum value of running 30-day mean temperature. Calc., calcification; Ext., extension.

Time period		Mean	SD	Range	Min	DAVG	Min	Cold stress					Heat stress						
								#days <20	<18	<17	<16	Max	DAVG Max	Max 30D	#days >31	>31.5	>32	>32.5	
Annual	Calc.	Mean	ns	−0.85	−0.81	0.83	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
		Min	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
		Max	ns	ns	−0.94	ns	0.89	ns	ns	−0.94	−0.88	ns	ns	ns	−0.87	ns	ns	ns	ns
	Ext.	Mean	ns	−0.84	ns	ns	0.92	−0.84	−0.95	−0.95	ns	ns	ns	−0.93	ns	ns	ns	ns	ns
		Min	ns	ns	ns	ns	0.85	−0.93	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
		Max	ns	ns	−0.91	ns	ns	ns	ns	−0.89	ns	ns	ns	ns	ns	ns	ns	ns	ns
Summer 2011	Calc.	Mean	ns	ns	ns	ns	N/A	N/A	N/A	N/A	ns	ns	ns	ns	ns	ns	ns	ns	
		Min	ns	ns	ns	ns	0.84	N/A	N/A	N/A	N/A	ns	ns	ns	ns	ns	ns	ns	
		Max	ns	ns	ns	ns	ns	N/A	N/A	N/A	N/A	ns	ns	ns	ns	ns	ns	ns	
	Ext.	Mean	ns	ns	ns	ns	ns	N/A	N/A	N/A	N/A	ns	ns	ns	ns	ns	ns	ns	
		Min	ns	ns	−1.0	−1.0	ns	N/A	N/A	N/A	N/A	ns	ns	ns	ns	ns	−0.83	−0.94	
		Max	ns	ns	ns	ns	ns	N/A	N/A	N/A	ns	ns	ns	ns	ns	ns	ns	−0.83	

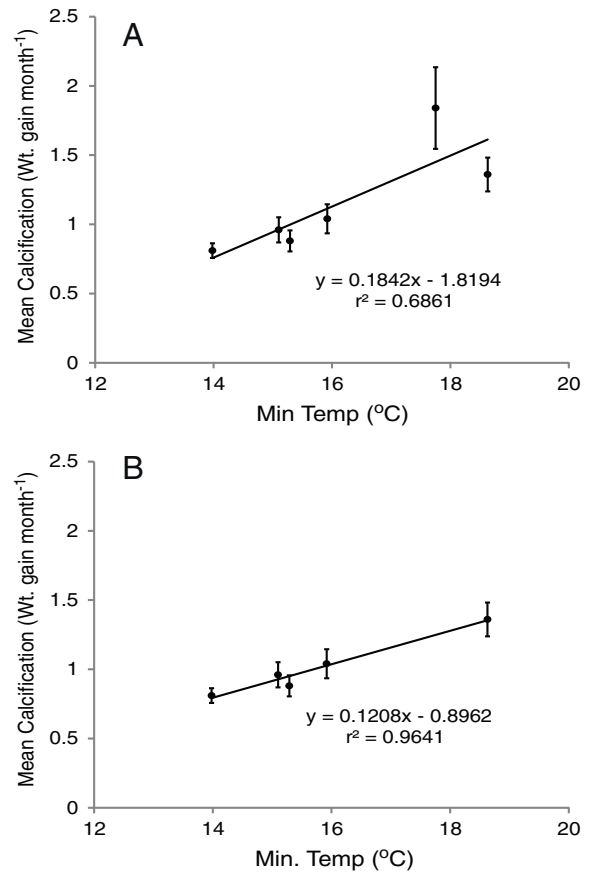


Fig. 5. (A) Mean annual calcification rate (\pm SEM) of *Montastraea cavernosa* regressed against minimum temperature by site. (B) Same regression, with high outlier removed.

presented here suggest that the sensitivity in growth to acute warm water stress is greatest in *O. faveolata*, followed in order by *P. astreoides* and *M. cavernosa*.

Despite the sensitivity to thermal stress in *O. faveolata*, Helmle et al. (2011) did not observe any trends in extension and calcification in this species from 1937–1996 in the Florida Keys. One possible reason is that recent warming in the Florida Keys accelerated in the mid-1990s (Kuffner et al., 2014; Manzello, in review). On the Great Barrier Reef, extension and calcification of massive *Porites* actually increased up until 1990, likely due to warming that did not exceed thermal tolerances, and then rapidly declined from 1990–2005 (De'ath et al., 2009). In contrast to our results, Carricart-Ganivet et al. (2012) report that the

Table 6

Correlation of *Porites astreoides* growth metric averages by site with temperature variables. Value is correlation coefficient, $p < 0.05$. Temperature terms: SD, std. deviation; Min, minimum temperature; DAVG, daily average temperature; Number (#) of days is number of days daily average temperature was $>$ or $<$ listed value; Max 30D, maximum value of running 30-day mean temperature. Calc., calcification; Ext., extension.

Time period		Mean	SD	Range	Min	DAVG	Min	Cold stress						Heat stress							
								#days <20	<18	<17	<16	Max	DAVG Max	Max 30D	#days >31	>31.5	>32	>32.5			
Annual	Calc.	Mean	ns	ns	−0.85	ns	ns	ns	ns	ns	ns	ns	−0.82	−0.82	ns	ns	ns	−0.88	−0.88		
		Min	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	
		Max	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	−0.88	−0.88	
	Ext.	Mean	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	
		Min	ns	ns	ns	ns	ns	ns	−0.88	−0.91	ns	ns	ns	ns	−0.83	ns	ns	ns	ns	ns	
		Max	ns	ns	−0.91	0.89	ns	ns	ns	ns	ns	−0.82	ns	ns	ns	ns	ns	ns	−0.88	−0.88	
Summer 2011	Calc.	Mean	ns	ns	ns	ns	ns	N/A	N/A	N/A	N/A	ns	ns	ns	ns	ns	ns	ns	ns	ns	
		Min	ns	ns	ns	ns	ns	ns	N/A	N/A	N/A	N/A	ns	ns	ns	ns	ns	ns	ns	ns	ns
		Max	ns	ns	ns	ns	ns	ns	N/A	N/A	N/A	N/A	ns	ns	ns	ns	ns	ns	ns	ns	ns
	Ext.	Mean	−0.82	−0.85	ns	ns	ns	ns	N/A	N/A	N/A	N/A	ns	ns	ns	ns	−0.86	ns	ns	ns	−0.88
		Min	ns	ns	ns	ns	ns	ns	N/A	N/A	N/A	N/A	ns	ns	ns	ns	ns	ns	ns	ns	ns
		Max	ns	−0.85	−0.87	0.83	ns	ns	ns	N/A	N/A	N/A	ns	ns	ns	ns	ns	ns	ns	ns	−0.83

growth of *P. astreoides* was more sensitive to warm temperatures than *O. faveolata* on the Mesoamerican Barrier Reef. These results were based on the relationship between regional annual calcification and annual sea surface temperature, whereas the inferences reported herein are based on site-specific responses to individual bleaching events. The magnitude of decline in growth and rate of recovery due to bleaching and thermal stress, as well as the response to annual temperatures will be key determinants to the net long-term growth of corals moving forward. These data suggest that the growth response of *P. astreoides* and *O. faveolata* to acute versus chronic thermal stress may differ.

Thermal stress that elicits coral bleaching is known to cause reduced rates of growth (Goreau and Macfarlane, 1990; Leder et al., 1991), but we understand far less about the impacts of thermal stress on growth when obvious bleaching does not occur. In their seminal study, Jokiel and Coles (1977) showed that growth declined once the normal summertime maximum temperature was exceeded, even without any noticeable bleaching or stress. The growth rates in the core data were highest for both *P. astreoides*, as well as *O. faveolata*, over the annual interval 2012–2013, which is when the coolest summer temperatures since 1996 occurred at MLRF1 (Manzello et al., 2015; Manzello, in review). Lirman and Fong (2007) showed higher rates of growth at inshore versus offshore reefs and their measurements spanned the period from 2001–2002. This too was a period when summer temperatures remained below average (Manzello, in review). It is intriguing that this elevation in growth in 2012–13 was less pronounced offshore for *O. faveolata* and did not occur for *P. astreoides*.

4.3. Cross-shelf patterns in coral growth

The higher inshore calcification rates and their quick recovery after thermal stress are likely an important factor in the persistence of high coral cover at inshore patch reefs versus those offshore (Manzello et al., 2015). We hypothesized in our previous work that the elevated inshore calcification rates were a result of an increased capacity for acclimatization/adaptation to thermal stress or stimulation in growth from elevated nutrients and/or the relatively high aragonite saturation states (Ω_{arag}). Nutrients can stimulate extension and calcification, but at the expense of skeletal density (Edinger et al., 2000; Dunn et al., 2012; Manzello et al., 2014). Density was depressed inshore for *O. faveolata*, but not *P. astreoides*. If thermal acclimatization plays a role in this phenomenon, it is puzzling that the corals at the inshore sites in the Upper and Lower Keys had similar rates of growth given that those in the Upper Keys were collected offshore, but those in the Lower Keys were collected inshore. This suggests they were responding more to the environmental conditions than preconditioning or genetic factors. The elevated rates of inshore growth in 2012–2013 for both

P. astreoides and *O. faveolata* coincident with cooler than average temperatures at MLRF1 suggests that elevated growth inshore may only occur below certain temperatures.

The inshore–offshore trend in the *P. astreoides* coral core data differed from the usual ‘stretch-modulation’ sensu Carricart-Ganivet and Merino (2001) as extension, density, and calcification were all elevated inshore. *O. faveolata* collected at the same sites did have decreased density inshore, but calcification and extension were greater than offshore (Manzello et al., 2015). This too was slightly different than stretch-modulation because the depression in density usually translates into lower rates of calcification even when extension is similar or greater inshore. The elevated inshore calcification in *O. faveolata* and *P. astreoides* in the Florida Keys, as well as increased density for *P. astreoides*, could be a result of the significantly higher Ω_{arag} (Manzello et al., 2012). The elevated density for *P. astreoides* inshore is particularly unique, as multiple other studies in both the Atlantic and Pacific have always, to our knowledge, reported decreases in density with increasing proximity to shore (e.g., Dodge and Brass, 1984; Risk and Sammarco, 1991; Scoffin et al., 1992; Carricart-Ganivet and Merino, 2001; Cook et al., 2002). Further study is needed to reconcile the role of elevated Ω_{arag} on coral growth patterns on inshore reefs in the Florida Keys versus the other co-varying factors such as elevated nutrients, depressed light, and variable temperatures. The degree of autotrophy-to-heterotrophy inshore and offshore may also be important, but the data obtained to-date for *O. faveolata* and *P. astreoides* were inconclusive (Teece et al., 2011).

5. Conclusions

M. cavernosa and *P. astreoides* are more stress and heat tolerant than other Caribbean genera like *Acropora* and *Orbicella*, which have undergone drastic declines over the past 35 years (Aronson and Precht, 2001; Edmunds and Elahi, 2007). Increasing anthropogenic CO_2 is causing warming and declining Ω_{arag} , termed ‘ocean acidification’ (Hoegh-Guldberg et al., 2007). This is negatively impacting coral reefs and is expected to further impact coral calcification, as well as reef health in general. Despite some interesting cases (e.g., Cooper et al., 2012), recent declines in coral growth and calcification have been documented across the globe (Edmunds, 2007; Bak et al., 2009; De’ath et al., 2009; Tanzil et al., 2009; Manzello, 2010; Manzello et al., 2014).

P. astreoides has significantly increased in relative abundance in the Caribbean (Green et al., 2008), whereas the absolute and relative cover of *M. cavernosa* has not significantly changed in Florida or across the wider Caribbean (Ruzicka et al., 2013; Edmunds et al., 2014). The ability of *M. cavernosa* to maintain calcification at high temperature may help contribute to the stable populations of this species. Maximum calcification and mean extension, however, did negatively correlate with cumulative high temperature exposure, showing that this species

is not completely insensitive to warm water stress. *P. astreoides* is a weedy species characterized by small colony sizes and high reproductive output, which has helped it persist and increase in relative abundance on highly disturbed Caribbean reefs (Green et al., 2008). The mean calcification rates of *P. astreoides* were negatively correlated with heat stress while *M. cavernosa* were not, thus the life-history traits of *P. astreoides* may be able to compensate for its depressed growth during warm water stress.

The Florida Keys represent a highly dynamic ecosystem with multiple interacting stressors. The inimical waters from Florida Bay led to significantly reduced rates of calcification in *M. cavernosa* and *P. astreoides*. The Comprehensive Everglades Restoration Plan was created to restore natural freshwater inputs into Florida Bay (USACE and SFWMD, 1999). As such, the impacts to calcification that were observed may be altered by Everglades restoration. Nevertheless, the efflux of Florida Bay waters has impacted reef development in the Florida Keys over geologic time (Ginsburg and Shinn, 1964), thus a continued depression in calcification in the Middle Keys after natural freshwater flows are restored would not be unexpected. Further research is needed to integrate the effects of climate change, local anthropogenic stressors, and natural phenomenon like inshore–offshore gradients on the growth, reproduction, and survivorship of corals in the Florida Keys to maximize management effectiveness in an era of large-scale coral reef decline.

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