Species-specific responses to climate change and community composition determine future calcification rates of Florida Keys reefs

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ABSTRACT

Anthropogenic climate change compromises reef growth due to increasing temperatures and ocean acidification. Scleractinian corals vary in their sensitivity to these variables, suggesting species composition will influence how reef communities respond to future climate change. However, most studies that model future reef growth rely on uniform scleractinian calcification sensitivities to temperature and ocean acidification because data are lacking for many species. In order to address this knowledge gap, calcification of twelve common and understudied Caribbean coral species was measured for two months under crossed temperatures (27°C, 30.3°C) and CO_2 partial pressures (pCO_2) (400, 900, 1300 µatm). Mixed effects models of calcification for each species were then used to project community-level scleractinian calcification using Florida Keys reef composition data and IPCC AR5 ensemble climate model data. Three of the four most abundant species, *Orbicella faveolata, Montastraea cavernosa,* and *Porites astreoides*, had negative calcification responses to both elevated temperature and pCO_2. In the business-as-usual CO_2 emissions scenario, reefs with high abundances of these species had projected end-of-century declines in scleractinian calcification of >50% relative to present-day rates. *Siderastrea siderea*, the other most-common species, was insensitive to both temperature and pCO_2 within the levels tested here. Reefs dominated by this species had the most stable end-of-century growth. Under more optimistic scenarios of reduced CO_2 emissions, calcification rates throughout the Florida Keys declined <20% by 2100. Under the most extreme emissions scenario, projected declines were highly variable among reefs, ranging 10 to 100%. Without considering bleaching, reef growth will likely decline on most reefs, especially where resistant species like *S. siderea* are not already dominant. This study demonstrates how species composition influences reef community responses to climate change and how reduced CO_2 emissions can limit future declines in reef calcification.

INTRODUCTION

Coral reefs are diverse ecosystems that vary in their coral species composition. This in turn shapes the underlying habitat and the species they support (Cheal *et al.*, 2008, Hixon & Beets, 1993). As a result of the 2 Tt of anthropogenic CO_2 emissions since the start of the Industrial Revolution (Le Quere *et al.*, 2015), oceans are experiencing unprecedented rates of pH decline ("ocean acidification") (Hönisch *et al.*, 2012) and increased temperatures (Domingues *et al.*, 2008). These changes deleteriously influence coral growth and cover through unfavorable chemistry and a disruption of the algal-coral symbiosis ("bleaching") (Hoegh-Guldberg *et al.*, 2007). Declining coral cover and calcification (Perry *et al.*, 2013) reduce the architectural complexity of reefs (Alvarez-Filip *et al.*, 2009) and cause cascading negative effects on habitat, diversity, and biomass (Paddack *et al.*, 2009, Rogers *et al.*, 2014, Wilson *et al.*, 2006).

Most studies conclude reef growth will slow significantly by the end of the century (Chan & Connolly, 2013, Hoeke *et al.*, 2011, Kleypas *et al.*, 1999, Kleypas & Yates, 2009, Langdon *et al.*, 2000) or even cease by mid-century (Silverman *et al.*, 2009). Assumed uniform coral responses to increased temperature and partial pressure of CO_2 (pCO_2) are often used in these modeling exercises (Buddemeier *et al.*, 2008, Evenhuis *et al.*, 2015, Silverman *et al.*, 2009) because data on species-level responses are limited. In general, calcification has been measured as a Gaussian function of temperature (Jokiel & Coles, 1977, Marshall & Clode, 2004) at the organismal level, and a linear function of temperature across latitude (Lough & Barnes, 2000). Bleaching often sets the upper thermal limit to calcification by depriving corals of photosynthate, a key energy source. Bleaching thresholds are usually within 1-2°C of summertime means (Coles *et al.*, 1976, Jokiel & Coles, 1977). With respect to pCO_2, calcification is often fit as a linear or power law function $k(\Omega_{arag} - 1)^n$ of aragonite saturation state (Ω_{arag}), a carbonate chemistry

parameter inversely proportional to pCO_2. However, compilations and meta-analyses have shown the slope of the calcification- Ω_{arag} relationship varies across published literature (Chan & Connolly, 2013, Kleypas & Langdon, 2006, Langdon & Atkinson, 2005). These differences can be attributed to both species and the experimental methods though species-specific responses have been measured within the same study where methods and conditions were consistent (Comeau *et al.*, 2013). Variation in Ω_{arag} sensitivity among species and the ability of corals to regulate the chemistry within the calcifying space (McConnaughey, 2003) indicate species composition will determine how reefs respond to climate change. Predictions based on uniform constants therefore may not reflect future $CaCO_3$ precipitation of individual reefs.

Underscoring how reefs may vary in their responses to climate change, recent studies of reefs under elevated pCO_2 have documented stable states ranging from reduced growth (Fabricius *et al.*, 2011, Manzello, 2010) to tolerance (Shamberger *et al.*, 2014, Shamberger *et al.*, 2011) to phase shifts to macroalgae-dominated systems (Enochs *et al.*, 2015). Furthermore, temperature often exerts a larger measurable influence on growth than Ω_{arag} (Carricart-Ganivet *et al.*, 2012, Helmle *et al.*, 2011, Venti *et al.*, 2014). This pattern is not surprising when the relative sensitivities of coral growth to temperature and Ω_{arag} are compared to the annual variation of each parameter. In the Florida Keys, mean monthly temperature and Ω_{arag} range from 23 to 30°C and 3.1 to 4.6 units, respectively (Fig. S1) (Kuffner *et al.*, 2015, Sutton *et al.*, 2014). Beyond this 7°C temperature range coral growth slows and eventually ends with mortality (Jaap, 1984, Vaughan, 1916, Vaughan & Wells, 1943).In contrast, the 1.5 unit Ω_{arag} range would only affect calcification by 23% (assuming a uniform 15% Ω_{arag}^{-1} sensitivity from Chan and Connolly (2013)). Future increases in temperature could increase net annual calcification over certain timescales depending on corals' thermal optima (Jokiel & Coles, 1977). However, sustained

elevated temperatures can acutely stress corals and eventually induce bleaching and mortality. Conversely, decreased Ω_{arag} will chronically depress calcification year-round. These different timescales and effect sizes highlight the need for studies testing coral responses to both increased temperature and pCO_2.

The first goal of this experiment was to assay calcification of twelve common Caribbean species under elevated temperature crossed with elevated pCO_2 in the same experimental conditions (seasonality, duration, feeding, light, etc.). The control temperature of 27°C was chosen as representing the thermal optimum for these species in this region (Carricart-Ganivet *et al.*, 2012, Kennedy *et al.*, 2013) and is near the present-day mean annual temperature in the Florida Keys, where these species were collected. The elevated treatment temperature was set at 30.3°C, near the 30.5°C bleaching threshold for the Florida Keys based on NOAA's climatological bleaching model (Manzello *et al.*, 2007). The study species were *Acropora cervicornis*, *Agaricia agaricites*, *Dichocoenia stokesii*, *Montastraea cavernosa*, *Orbicella faveolata*, *Porites astreoides*, *Porites divaricata*, *Pseudodiploria clivosa*, *Pseudodiploria strigosa*, *Siderastrea siderea*, *Siderastrea radians,* and *Solenastrea hyades*. These species were chosen because of their current or historic abundance and/or because data are sparse on their growth responses to increased temperature and pCO_2. The second goal was to test whether reef-building species composition is important in determining potential changes in overall reef calcification. Empirical growth responses were coupled with benthic cover and climate model data to project end-of-century scleractinian community calcification at 43 reefs in the Florida Keys. Only two temperatures were tested to allow for a wider range in pCO_2 levels, and therefore intra-annual sinusoidal temperature variation was not examined. Rather, the study focuses on

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calcification responses to shifts in mean annual temperatures, which are expected to increase steadily this century (IPCC, 2014).

MATERIALS AND METHODS

Experimental corals

Coral colonies were collected from sites in the Florida Keys (Table S1) in the summer of 2011 and brought to the University of Miami's Climate Change facility. Branching colonies were trimmed to approximately 5 cm long fragments. Non-branching colonies were cored into flat, circular 2.5 cm diameter fragments. Coral fragments (hereafter referred to as corals) were glued to labeled ceramic plugs (Boston Aqua Farms) and allowed to recover at 27°C and ambient pCO_2 for at least one month before the experiment. Corals showed polyp extension as well as tissue growth over cut scars. Total number of corals per species ranged from 20 to 152 (Table S1). Coral surface areas were measured with ImageJ software (Abràmoff *et al.*, 2004) using planar surface for mounding corals and cylindrical approximations for *P. divaricata*. The surface area of *A. cervicornis* was measured using 3D imaging at NOAA AOML's Ocean Chemistry and Ecosystems Division (Enochs *et al.*, 2014).

Experimental system

Experiments were conducted at the University of Miami Corals and Climate Change Laboratory from October to December 2011. Three pCO_2 treatments of 400, 900, and 1300 µatm were crossed with two temperatures of 27 and 30.3°C. Mass flow controllers (Sierra Instruments Model 810C) mixed pure CO_2 with ambient air to achieve the treatment pCO_2 levels. A pCO_2 equilibrator coupled to a LICOR LI-820 gas analyzer was rotated across tanks to monitor tank pCO_2 levels. Temperatures were maintained by Omega Engineering temperature controllers (Model CN7833) coupled with 1.5 kW heating elements and cooling coils.

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Each tank consisted of a 60 L holding tank coupled to its own 200 L sump tank for a total volume of 260 L. Venturi injectors bubbled the sump tanks with the gas mixtures. In each tank, seawater was pumped from the sump to the holding tank where it gravity-fed back into the sump. Tanks were supplied with a steady 30 mL min^{-1} input of 10 μm-filtered seawater from Bear Cut, Virginia Key. Bulk seawater exchanges associated with coral feeding and tank cleaning were >120 L week^{-1}. Nutrients were not monitored in this study, but source water dissolved inorganic nitrogen is <1 μM and phosphate is 0.1 μM (Devlin, 2015). HOBO U30 data loggers (Onset

Computer) recorded temperatures in each tank every five minutes along with light from a centrally-located photosynthetically active radiation (PAR) sensor. Light levels were adjusted with window screen such that average peak sunlight was 327 ± 14 μmol quanta m^{-2} s^{-1} (mean $\pm$ standard error, n=66) and total light exposure was 3.7 ± 0.2 mol quanta m^{-2} d^{-1} (n=66).

Water samples were collected weekly from each tank to document chemical conditions. Total alkalinity (TA) was measured in duplicate on an automated Gran titrator and dissolved inorganic carbon (DIC) in duplicate using a coulometer (UIC, Inc). Tris synthetic seawater buffer (Nemzer & Dickson, 2005) was used to calibrate the titrator pH sensor (Orion) on the total scale (pH$_t$). Salinity (S) was measured on a Guildeline 8410A Salinometer. Total alkalinity and DIC were used to characterize carbonate parameters using the *seacarb* package v3.0.11 (Gattuso *et al.*, 2015) in R v3.2.4 revised (R Core Team, 2016), using dissociation constants from Lueker *et al.* (2000), Perez and Fraga (1987), and Dickson (1990).

Procedure

The six treatments were each randomly distributed across twelve experimental tanks (two replicate tanks per treatment). Corals were then distributed among treatments using a stratified randomization based on parent colony. Treatments were ramped up from 27°C and ambient 400

µatm pCO_2 (control treatment) to target levels at rate of ~0.3ºC d^{-1} and 100-200 µatm pCO_2 d^{-1}. The buoyant weights of corals were recorded every two weeks with Sargent Welch SWT-403 and Mettler PB303-S balances (readability 1 mg). Growth rates, relative to surface area, were calculated as dry weight gain (Davies, 1989) between the last recorded weighing and the first weighing after the treatment ramping period, nominally six weeks. Corals were fed twice weekly a diet of live rotifers (~10 rotifers L^{-1}) and larval feed (AP brand) composed of ~6 mg L^{-1} each of <100 µm particles and 250-450 µm particles. Aquarium pumps with diffusers kept food suspended in the feeding bins. Corals were fed starting late afternoon to early night (~ 4 h), after which the feeding water was discarded and bulk seawater replenishment was approximately 60 L.

Every two weeks, the treatments were randomly reassigned to tanks to account for any potential tank effects. The tank shuffling occurred while corals were isolated during feeding, with water changes of ~100 L and tank sumps rapidly equilibrating to new treatments during the four-hour feeding period. After feeding, corals were returned to the newly-assigned tanks containing their treatment. Twice during the experiment, corals were randomly reassigned within-treatments/between-tanks to account for potential cohort effects. In other words, treatments did not covary with tanks or cohorts.

Growth analyses and projections

Calcification rates (G_{ij}) for coral i in colony j were fit by restricted maximum likelihood to linear mixed effects models for each species with temperature (T) and Ω_{arag} (A) as fixed effects (β_T and β_A, respectively), random intercepts by colony (μ_{0j}), and a cohort grouping random effect (μ_{0g}):

Growth responses of Caribbean coral species

$$G_{ij} = \beta_0 + \beta_T T_{ij} + \beta_A A_{ij} + \mu_{0j} + \mu_{0g} + \varepsilon_{ij} \tag{1}$$

where $\begin{pmatrix} \mu_{0j} \\ \mu_{0g} \end{pmatrix} \sim N \begin{pmatrix} \sigma_1^2 & 0 \\ 0 & \sigma_2^2 \end{pmatrix}$ and residual $\varepsilon_{ij} \sim N(0, \lambda^2)$. The cohort grouping is the unique

combination of tank assignments for each coral. It combines cohort, time, and tank to account for

the periodic random shuffling of corals and tanks within treatments. Temperature and Ω_{arag} were

treated as additive linear effects because 1) temperature was limited to two treatments, 2)

previous studies indicate linear relationships between calcification and Ω_{arag} (Chan & Connolly,

2013, Langdon & Atkinson, 2005, Langdon $et\ al.$, 2000), and 3) observed interactions between

temperature and Ω_{arag} were limited or insignificant (Langdon & Atkinson, 2005). If calcification

did not appear to vary as a linear function of Ω_{arag}, then calcification rates were fit to a

generalized additive mixed model with Gaussian error distribution and identity link function,

replacing the $\beta_A A_{ij}$ term with a smoothing function of Ω_{arag} based on cubic regression splines.

Model fits were evaluated from visual inspection of residuals (Fig. S3). The significance of

linear mixed model fixed effects was evaluated from profile likelihood 95% confidence intervals.

Significance of general additive mixed model terms was evaluated from p-values based on Wald

tests. Equation (1) was compared against models with a temperature-Ω_{arag} fixed effect interaction

term or colony-location random intercept (Supporting Information). To test for tank effects,

longitudinal versions of Equation (1) with and without tanks as random intercepts (Supporting

Information) were evaluated with likelihood ratio tests. Models were fit using the $lme4$ v1.1-11

(Bates $et\ al.$, 2011) and $gamm4$ v0.2-3 (Wood & Scheipl, 2014) packages in the software

program R v3.2.4 revised (R Core Team, 2016).

Growth rates for Florida Keys reefs were projected to 2100 based on 1) the mixed effects

models from this experiment, 2) Florida Keys reef composition data from the Coral Reef

Evaluation and Monitoring Project (CREMP) (CREMP, 2013, Ruzicka *et al.*, 2013), and 3)

temperature and Ω_{arag} inputs from regridded Intergovernmental Panel on Climate Change (IPCC)

AR5 climate model data (van Hooidonk *et al.*, 2014). Projections for each Representative

Concentration Pathway (RCP) scenario (van Vuuren *et al.*, 2011) were based on the temperature

and Ω_{arag} data from the 1° x 1° cell located at the center of the Florida Keys. The most recent

CREMP estimates of coral cover from 2013 were averaged across stations within each reef. Six

out of 49 reefs were omitted because none of the study species were present, leaving 43 reefs for

projections. Reefs were categorized as patch, offshore shallow (3-6 m) and offshore deep (10-20

m) reefs. The CREMP data combined benthic cover for certain groupings of corals: *Agaricia*

agaricites/Undaria agaricites complex, *Orbicella annularis* complex, and *Porites porites*

complex. Growth for these complexes was estimated by this experiment's mixed effect models

for *A. agaricites, O. faveolata,* and *P. divaricata*, respectively. The coral calcification projections

only apply to the portion of reefs covered by the study species, which was generally over three-

quarters of the total scleractinian cover (Table S4). To facilitate intercomparisons across sites,

calcification rates were scaled to the first year in the climate dataset (2006). Standard uncertainty

of prediction was calculated by summing in quadrature the standard uncertainty in model

coefficients and standard uncertainty due to colonies.

RESULTS

Experimental conditions

  Experimental tank conditions (Table 1) exhibited slight diurnal patterns in temperature

and pCO_2. Temperatures increased approximately 0.2°C from morning to the mid-afternoon peak

as ambient heat energy outpaced the tank cooling mechanism while pCO_2 concentrations

decreased by approximately 50-200 µatm from morning to mid-afternoon due to photosynthesis.

Diurnal variations in temperature and pCO_2 based on Cheeca Rocks MAPCO2 data are approximately 0.4-1°C and 20-80 µatm for comparison (Fig. S2). One tank from the high temperature, high pCO_2 treatment experienced a system failure towards the end of the experiment, and therefore, the penultimate weighing was used to calculate calcification for its corals. Tank chemistry was stable despite biological activity from coral fragments and physical processes like evaporation because of the seawater replenishment from steady feeds and periodic bulk exchanges.

Table 1. Treatment conditions. Mean temperatures are from the monitoring system (n = 12 h^{-1}). Chemistry measurements (mean ± SD, n = 12-14) are from weekly discrete water samples for each treatment, inclusive of two replicate tanks. Three water samples are missing at random.

Treatment	T (°C)	pCO_2 (µatm)	pH_t	TA (µmol kg^{-1} SW)	DIC (µmol kg^{-1} SW)	Ω_{arag}	S
1	27.0 ± 0.1	400 ± 60	8.06 ± 0.05	2377 ± 41	2057 ± 43	3.8 ± 0.3	33 ± 1
2	27.1 ± 0.1	899 ± 211	7.78 ± 0.10	2422 ± 47	2246 ± 41	2.3 ± 0.5	33 ± 1
3	27.0 ± 0.1	1343 ± 207	7.62 ± 0.06	2442 ± 33	2336 ± 33	1.7 ± 0.2	33 ± 1
4	30.4 ± 0.5	399 ± 49	8.06 ± 0.04	2406 ± 47	2052 ± 38	4.3 ± 0.4	33 ± 1
5	30.4 ± 0.5	946 ± 196	7.77 ± 0.09	2460 ± 52	2268 ± 54	2.5 ± 0.5	33 ± 1
6	30.3 ± 0.5	1292 ± 247	7.64 ± 0.08	2447 ± 77	2311 ± 77	2.0 ± 0.4	33 ± 1

Calcification

Calcification rates ranging from 0 to 2 mg $CaCO_3$ cm^{-2} d^{-1} (Fig. 1). The highest growth rates in control conditions were 1.0-1.5 mg $CaCO_3$ cm^{-2} d^{-1} for *A. agaricites, O. faveolata,* and *S. siderea*. Calcification responses to elevated temperature and pCO_2 varied by species. *Orbicella faveolata* was evaluated with a general additive mixed effects model (Table S3, Fig. S4) because mean calcification was near zero in the elevated temperature, mid-pCO_2 treatment. *Acropora cervicornis* experienced early mortality, with no growth measurements in the high temperature,

highest pCO_2 treatment. Significant negative responses to temperature were observed for *D. stokesii*, *M. cavernosa*, *O. faveolata*, *P. astreoides,* and *P. clivosa,* ranging from -0.18 ± 0.09 to -0.05 ± 0.01 mg $CaCO_3$ cm^{-2} d^{-1} $°C^{-1}$ (β_T ± standard error, SE) (Fig. 2, Table S2). However, when two influential data points were excluded from *P. clivosa,* β_T changed to a statistically insignificant -0.08 ± 0.07 mg $CaCO_3$ cm^{-2} d^{-1} $°C^{-1}$. Two species, *S. radians* and *S. hyades*, exhibited positive β_T responses to elevated temperature of 0.03 ± 0.01 and 0.07 ± 0.01 mg $CaCO3$ cm^{-2} d^{-1} $°C^{-1}$, respectively. Calcification was proportional to Ω_{arag} for *A. agaricites, M. cavernosa, P. astreoides, S. radians,* and *S. hyades,* with growth responses ranging 0.04 ± 0.02 to 0.19 ± 0.08 mg $CaCO_3$ cm^{-2} d^{-1} Ω_{arag}^{-1} (β_A ± SE). Coral colonies accounted for 20-70% of random effects variance, while cohort grouping accounted for 0-30%. *Acropora cervicornis* was the exception to this pattern, with cohort grouping accounting for almost all of the random effects variance. This is expected given corals came from mostly unique colonies. The temperature-Ω_{arag} interaction and colony-location random intercept terms did not improve model fits (Supplemental Information). No tank effect was observed based on likelihood ratio tests of the nested longitudinal models ($X^2_{df=1} < 0.1$, p ~ 1 for all species).
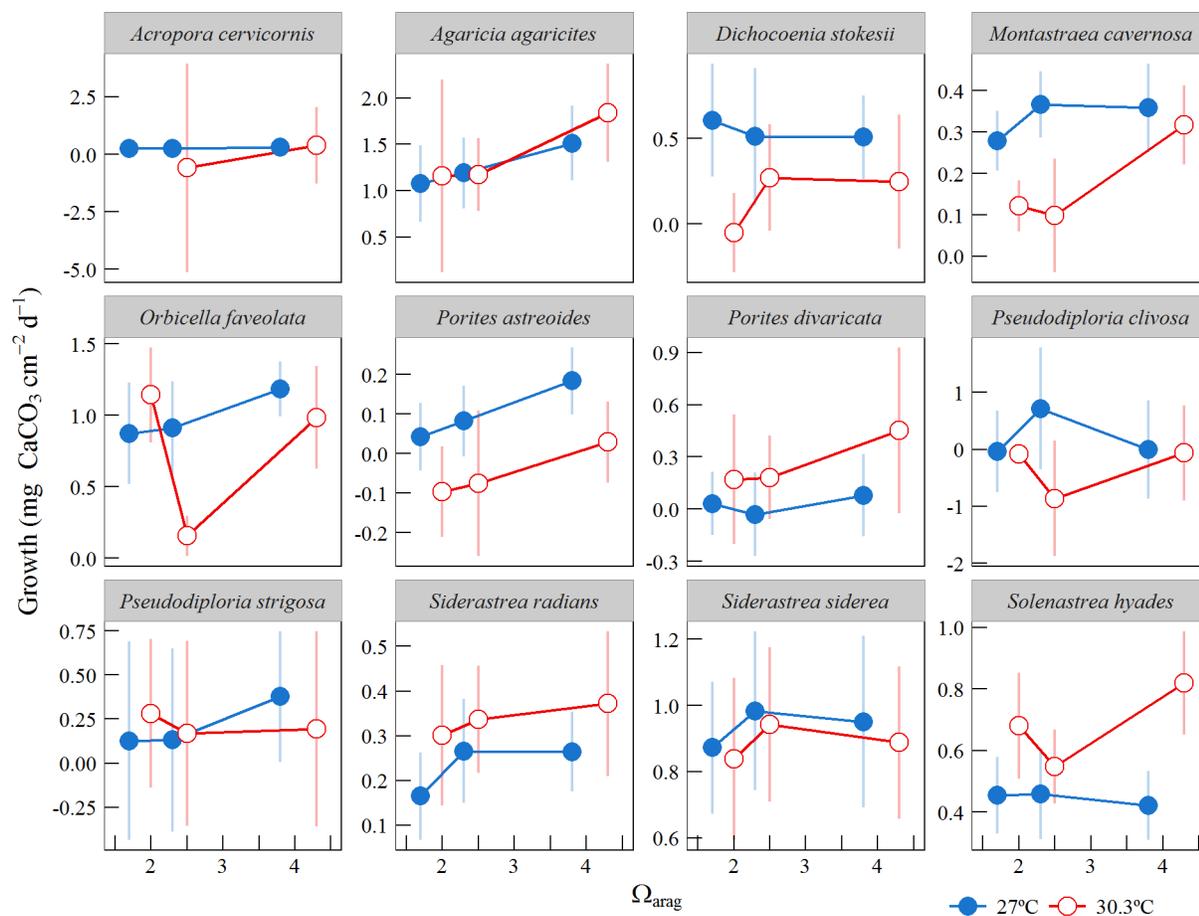
Fig. 1. Coral growth rates (mean ± 95% confidence interval) across control (solid blue) and elevated temperature (open red) treatments.
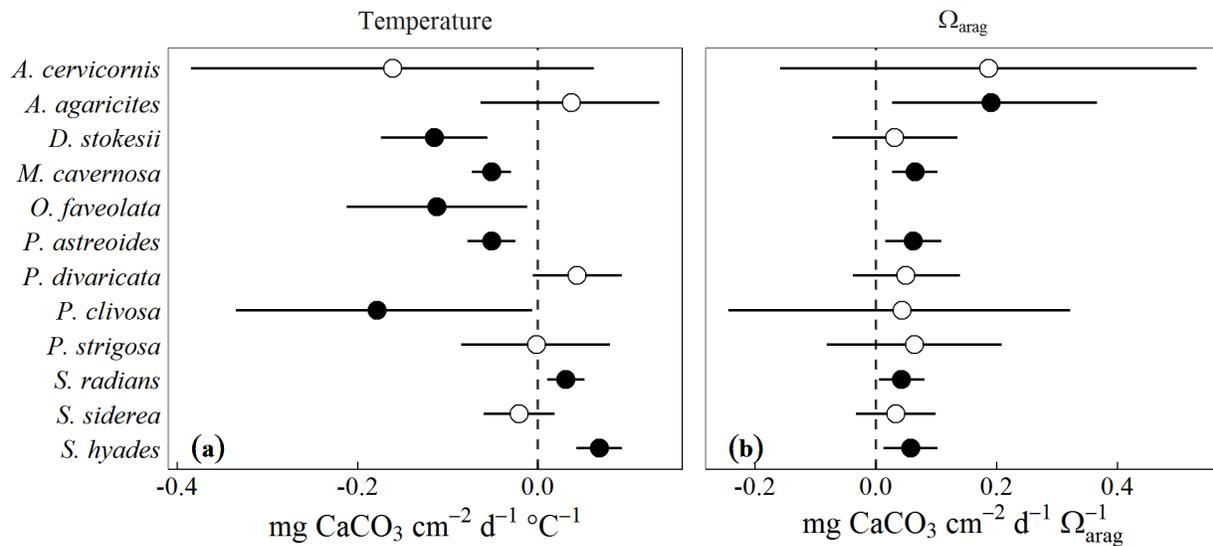
Fig. 2. Fixed effects linear coefficients for (a) temperature and (b) Ω_{arag} with 95% confidence intervals from likelihood profiles. Closed symbols indicate coefficients with confidence intervals that do not overlap zero. Model data are summarized in Table S2.

Growth projections

The IPCC AR5 ensemble climate models predict end-of-century temperature increases in the Florida Keys from present-day 26.7°C to 27.1°C under the optimistic RCP 2.6 and 29.6°C under business-as-usual RCP 8.5 (Fig. S5). The annual range in temperature is 6°C. Mean annual Ω_{arag} decreases from present-day 4.0 to 3.9 units (RCP 2.6) and 2.7 units (RCP 8.5) over the same time period. The annual range in Ω_{arag} is 0.1-0.2 units. Standard deviations in temperature and Ω_{arag} among climate models are 0.3-0.7°C and 0.1-0.4 units, respectively, depending on year and RCP.

Scleractinian coral cover in the Florida Keys in 2013 ranged from <1% to 41% across 43 sites (Table S4). The twelve species from this study comprised 82 ± 16% (43), mean ± SD (n reefs), of the total scleractinian coral cover. The most abundant of these species were *Siderastrea siderea* (11-42% interquartile range (IQR)), *Orbicella annularis* complex (0-23% IQR), *Porites astreoides* (3-17% IQR), and *Montastraea cavernosa* (1-11% IQR). Most of the other species

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contributed ≤10% relative coral cover at any given site. Applying laboratory-measurements to species composition results in a baseline Florida Keys coral calcification rate of 0.25 ± 0.09 g $CaCO_3$ cm^{-2} y^{-1}. This value is likely a lower estimate of coral calcification because it is constrained to the study species.

Ensemble mean scleractinian calcification rates in year 2100 were $96 \pm 2\%$ and $84 \pm 8\%$ (ensemble mean $\pm$ SD, n = 43) of present day for RCP 2.6 and 4.0 respectively (Fig. 3a,b, Table S4). End-of-century ensemble scleractinian calcification rates were $69 \pm 18\%$ and $55 \pm 24\%$ of present-day rates for RCP 6.0 and RCP 8.5, respectively. The median standard uncertainty in model coefficients was $\pm16\%$ and the median standard uncertainty of prediction was $\pm46\%$. Reefs with the largest projected declines in relative growth of 80 to 90% in RCP 8.5 (Fig. 3d) predominately consisted of *O. annularis* complex, *P. astreoides,* and *M. cavernosa*. These reefs included Eastern Sambo (shallow), Looe Key (shallow), Jaap, Black Coral Rock, Grecian Rocks, and Wonderland, where benthic coral cover is 5-40%. Reefs with higher relative proportions of *S. siderea* had projected calcification rates that were relatively unchanged across all emissions scenarios. These relatively unaffected sites include the patch reefs Dustan Rocks, Rawa, Thor, and West Turtle Shoal, as well as the deeper Molasses and Sombrero reefs (Fig. S6).
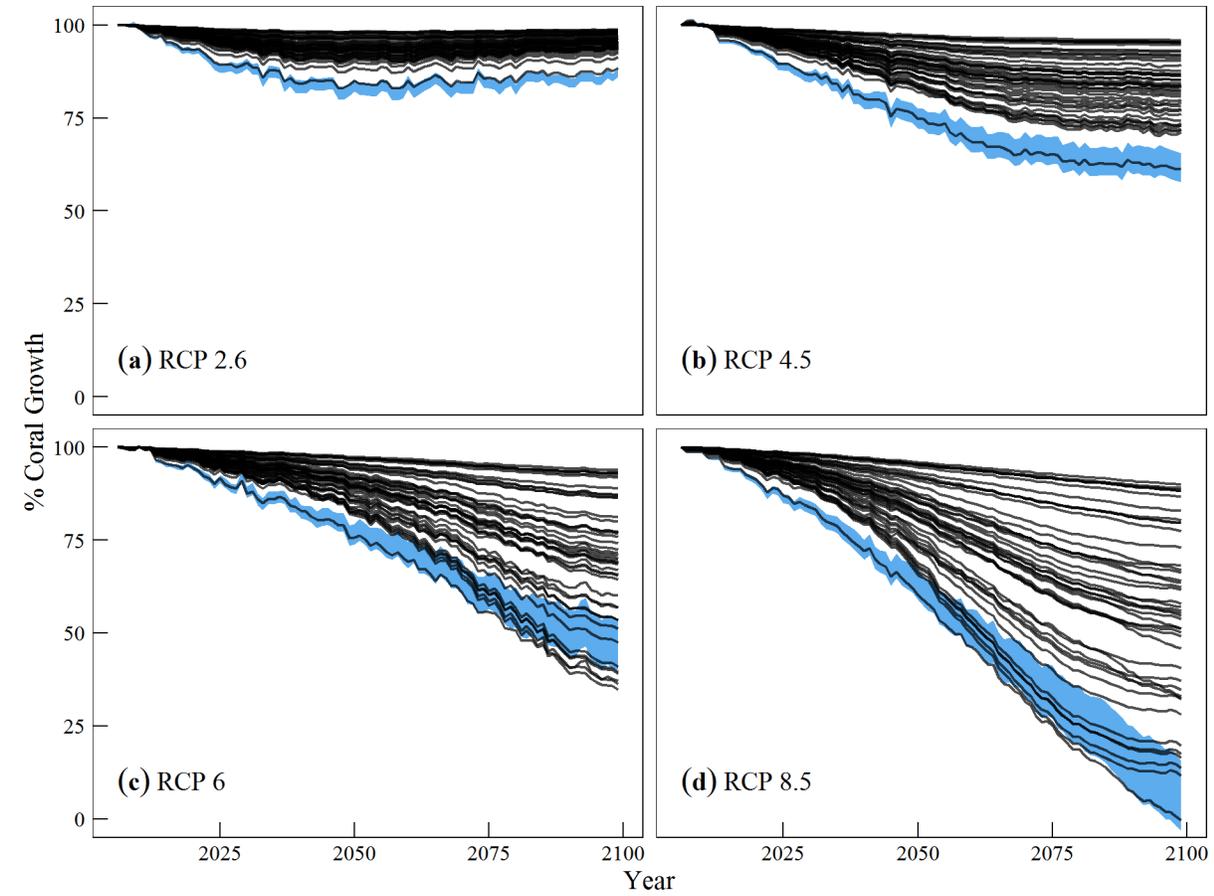
Fig. 3. Projected coral growth of Florida Keys reefs relative to the baseline year (2006) under four Representative Concentration Pathway (RCP) CO₂ emission scenarios. Projections were based on mixed effects models of experimentally-measured calcification, annual average temperature and aragonite saturation state (Ω_{arag}) from ensemble climate model data, and species composition data for 43 sites across the Florida Keys. The blue shaded region represents the projection for all reefs using uniform additive linear sensitivities to temperature and Ω_{arag}. The sensitivity coefficients are -24% °C^{-1} for temperatures greater than the thermal optimum (mean response of Al-Horani *et al.* (2005), Carricart-Ganivet *et al.* (2012), Clausen and Roth (1975), Coles and Jokiel (1978), Houck *et al.* (1977), Marshall and Clode (2004), Reynaud-Vaganay *et al.* (1999)) and 10% to 25% Ω_{arag}^{-1} (Chan & Connolly, 2013).

DISCUSSION

Growth responses to elevated temperature and Ω_{arag} varied among species (Fig. 1) with

reef-builders such as *O. faveolata, M. cavernosa, P. clivosa, A. agaricites, D. stokesii,* and *P.*

astreoides calcifying at decreased rates under treatment conditions. Two species, *S. radians* and

S. hyades, had calcification rates that increased with increasing temperature but decreased with

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decreasing Ω_{arag}. In contrast, *S.siderea, A. cervicornis, P. strigosa,* and *P. divaricata* did not show detectable responses to either temperature or Ω_{arag}. The varied responses of these twelve species under the same experimental conditions suggest calcification is not solely an abiotic function of ambient temperature and chemical conditions.

Of the twelve study species, only the calcification rates of *A. cervicornis* and *S. siderea* have been tested in similar laboratory settings (i.e. including feeding) under climate change scenarios (increased temperature and pCO_2) (Table 2). Fed *A. cervicornis* corals maintained calcification under elevated pCO_2 (Towle *et al.*, 2015). Although this study corroborates those prior results, *A. cervicornis* experienced increased mortality at elevated temperatures. Due to the protected status of this species, colonies were obtained from a sheltered coral nursery (Schopmeyer *et al.*, 2012) and therefore may be less thermally robust than conspecifics from other sites. Unlike this study, *Siderastrea siderea* corals exhibited mixed, though not incompatible, responses to elevated temperature and pCO_2 in two experiments (Castillo *et al.*, 2014, Horvath *et al.*, 2016). The corals from those studies were collected from the same location and the experiments were conducted under similar conditions but different treatment levels. Other laboratory experiments on coral growth under elevated pCO_2 but constant temperature have documented null (Bedwell-Ivers *et al.*, 2016) to negative (Enochs *et al.*, 2014, Renegar & Riegl, 2005) pCO_2 respones for *A. cervicornis,* negative responses for *P. divaricata* (Bedwell-Ivers et al., 2016), and negative responses for *P. astreoides* juveniles (Albright & Langdon, 2011, Albright *et al.*, 2008, de Putron *et al.*, 2011). The present study measured no growth for *O. faveolata* in the intermediate 2.5 Ω_{arag}, 30°C treatment, which may indicate an enzymatic "deadzone" for this species (Wooldridge, 2008).

This study attempted to replicate general Florida Keys reef conditions at 10 m depth, but this approach carries inherent tradeoffs. Coral species do not occupy the same niche and therefore the control treatment could be less optimal for some species than others. This appears to be the case for *S. radians* and *S. hyades*, which were mostly collected from Florida Bay where annual temperature maximums are regularly ≥2°C higher than the Florida Reef Tract (Okazaki *et al.*, 2013). These species exhibited positive responses to temperature from 27-30°C. Beyond this range, calcification would eventually decrease as temperatures near these corals' upper thermal limits. These species also appeared less sensitive to increased pCO_2 in the laboratory setting than in the field (Table 2).

Simultaneously testing multiple species in a mixed assemblage has numerous advantages in comparison to meta-analyses, which are challenged to combine studies that differ in seasonality, duration, conditions, and methods. The mixed assemblage can be considered representative of actual reef environments. A multispecies approach is valuable for reducing potential publication bias (Møller & Jennions, 2001) from not reporting species with null responses (the "file drawer effect") because it facilitates comparisons among species. Despite the robust evidence showing decreasing calcification under elevated pCO_2, prior meta-analyses have found evidence for publication bias in ocean acidification research (Chan & Connolly, 2013, Kroeker *et al.*, 2010).

The growth responses from these common but understudied Caribbean coral species can be used to refine estimates of reef $CaCO_3$ precipitation based on species abundance (Perry *et al.*, 2012) and to model changes in coral calcification of reefs over time. With respect to the latter, emissions scenarios and community composition determine the trajectories of scleractinian calcification. These trajectories were relatively stable under the optimistic RCP 2.6 and RCP 4.5

scenarios with <20% declines relative to present day (Fig. 3a,b). Under more realistic and extreme emissions scenarios of RCP 6 and RCP 8.5 where temperature increases by 1.5-3°C and Ω_{arag} decreases by 1-1.3 units, more pronounced differences in reef trajectories are a result of species composition (Fig. 3c,d). The most abundant corals in terms of benthic cover were *M. cavernosa*, *O. faveolata*, *P. astreoides*, and *S. siderea*. Consequently, their calcification rates and responses to treatments were the most influential on the projections (Table S4). Of these four species, calcification of *S. siderea* was unaffected by the temperature and pCO_2 levels tested here. Reefs with relative scleractinian cover consisting of >40% *S. siderea* generally were the most stable. These reefs tended to be patch reefs or deeper (10-20 m) offshore reefs (Fig. S6). *Siderastrea siderea* is already noted for its tolerance to extreme temperatures (Lirman *et al.*, 2011) and high relative abundance on the Florida Reef Tract (Lirman & Fong, 2007).

In comparison, uniform scleractinian sensitivity coefficients for temperature and Ω_{arag} yield end-of-century calcification of 16% to -3% (net dissolution) relative to present-day under RCP 8.5 (blue shaded region in Fig. 3). These projections are based on additive, linear scleractinian calcification changes of 10 to 25% Ω_{arag}^{-1} (Chan & Connolly, 2013) and a mean -24% °C^{-1} for temperatures above the thermal optimum (Al-Horani *et al.*, 2005, Carricart-Ganivet *et al.*, 2012, Clausen & Roth, 1975, Coles & Jokiel, 1978, Houck *et al.*, 1977, Marshall & Clode, 2004, Reynaud-Vaganay *et al.*, 1999). These declines based on uniform constants are steeper and more homogenous than the declines of 0% to 90% based on species-specific responses (Fig. 3d; Table S1). These results clearly show the importance of community composition in determining reef-wide calcification responses to climate change. However, in the absence of data on species sensitivities and reef composition, uniform assumptions/constants are

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still valuable for predicting aggregate, regional calcification trajectories, especially if they are based on the dominant coral species.

Several caveats must be considered with the projections. While calcification responses to elevated temperature and pCO_2 were mostly negative, variability among colonies, communities, and climate models all contribute uncertainty to predictions at a given reef. Therefore, efforts to measure baseline calcification rates and long-term monitoring of colonies at multiple sites are important (Kuffner et al., 2013). This experiment may also underestimate compensatory mechanisms that might allow corals to calcify at rates faster than measured here due to long-term acclimation or adaptation to these conditions over several decades (Wall et al., 2016). Only twelve of the ~70 coral species in the Caribbean were tested in this experiment, and calcification responses of the remaining species could influence the projected outcomes. Projections are also based only on scleractinian corals, which represent <8% benthic cover in the Florida Keys (Ruzicka et al., 2013). They do not consider non-scleractinian $CaCO_3$ precipitation and dissolution processes which may contribute significantly to reef $CaCO_3$ budgets (Perry et al., 2014).

The projections are likely conservative because they do not account for processes that are expected to reduce coral cover. Increased bleaching and mortality with increasing temperatures (Hoegh-Guldberg, 1999) will severely cripple or halt calcification (van Hooidonk et al., 2014). To illustrate the importance of high-temperature stress, simulated coral cover in Hawaii over the next century was stable or increased when bleaching and mortality effects were ignored (Hoeke et al., 2011). The adverse effects of increased temperature and pCO_2 on reproduction and recruitment (Albright, 2011, Anlauf et al., 2011, Chua et al., 2013, Hendriks et al., 2010, Kroeker et al., 2010) are expected to further reduce coral cover but they have not been well-

quantified at the community-scale. Finally, actual CO_2 emissions have consistently increased faster than the IPCC's most extreme scenarios (Peters *et al.*, 2013), and therefore future changes in temperature and Ω_{arag} may be greater than predicted. Including all of these processes would likely result in more depressed calcification, but the focus of this study was calcification at sub-lethal temperatures.

Despite these caveats and conservative assumptions, the underlying pattern is lower, less stable growth from critical reef framework builders. In addition to bleaching, Caribbean reefs have already experienced large declines in scleractinian coral cover from reductions in herbivory, nutrient pollution, and disease (Aronson & Precht, 2001, Gardner *et al.*, 2003, Kuffner & Toth, 2016). Current levels of coral cover are already associated with static reef growth or dissolution (Perry *et al.*, 2013). Coupled with the prospect of more frequent bleaching and reduced aragonite saturation state driven by increasing anthropogenic atmospheric CO_2, reefs are likely to experience continued declines. The species-specific responses measured here indicate that forecasts must take into account community composition. In addition to limiting pollution and overfishing (Kennedy *et al.*, 2013, Wooldridge & Done, 2009), another local strategy for mitigating climate change is focusing management efforts on reefs with corals capable of resisting high temperatures and low Ω_{arag}. However, this approach may amount to no more than a triage strategy for minimizing further losses. Alternatively, the growth projections under the different RCPs illustrate how reducing global CO_2 emissions has the potential to benefit all reefs throughout the Florida Reef Tract.

1 **Table 2. Elevated pCO_2 experiments conducted on the study species. Methods include pCO_2 bubbling (pCO_2), chemical**
2 **additions (HCl, HCl/NaOH + Na_2CO_3/$NaHCO_3$), and natural variation (none). Methods of measuring calcification (G) include**
3 **buoyant weighing (BW), x-ray analysis (x-ray), image analysis (image), alkalinity anomaly (AA), and computerized**
4 **tomography (CT). Some parameters are not disclosed (ND) or not applicable (NA). Light is reported as net daily radiation**
5 **assuming 12 h d^{-1} of light. Calcification responses have been simplified to pairwise comparisons of pCO_2 treatments and**
6 **extrapolated relative to a baseline, pre-industrial Ω_{arag} of 4.6. Italicized calcification responses were not determined to be**
7 **significant in the original study.**

species	CO_2 treatment	Calcification metric	setting	n corals	n colonies	Ω_{arag}	T (°C)	S	light (mol m^{-2} d^{-1})	nutrition	recovery time	ramping time
A. cervicornis	pCO_2	BW	lab	20	ND	2.9-4.0	30	ND	ND	not fed[1]	5 d	0 d
A. cervicornis	pCO_2	BW	lab	64	4	2.5-3.9	28	32	4.0-15.6	ND	7 d	9 d
A. cervicornis	pCO_2	BW	lab	192	ND	1.2-3.5	25	36	NS	ND	ND	0 d
A. cervicornis	pCO_2	BW	lab	80	8	2.2-4.1	26-30	33	5.8	fed & not fed	4 weeks	0 d
O. faveolata	none	x-ray	field	7	7	4-4.5	ND	ND	NS	*in situ*	NA	NA
P. astreoides	pCO_2	image	lab	102	102	2.3-3.9	28	36	ND	not fed	NA	0 d
P. astreoides	HCl	image	lab	35	35	2.2-3.2	25	35	<0.4	not fed	NA	0 d
P. astreoides	HCl/NaOH + Na_2CO_3	BW; AA	lab	80	80	2.1-3.9	28-30	35	17-22	not fed[1]	24 d	0 d
P. astreoides	none	CT	field	14	14	0.8-4.2	28	34	ND	*in situ*	NA	NA
P. astreoides	HCl; pCO_2	DW	lab	ND	ND	0.1-4.2	29	37-38	2.6	not fed	NA	NA
P. astreoides	none	AA; x-ray	field	9	9	2.8-3.5	19-28	36-37	7.4-55.5	*in situ*	6 mo	0 d
P. divaricata	pCO_2	BW	lab	20	ND	2.9-4	30	ND	ND	not fed[1]	5 d	0 d
P. strigosa	none	AA; x-ray	field	9	9	2.8-3.5	19-28	36-37	7.4-55.5	*in situ*	6 mo	0 d
S. radians	HCl + $NaHCO_3$	AA	field	10	10	1.1-5.7	20-31	32-47	3.5-50.0	*in situ*	NA	NA

Growth responses of Caribbean coral species

S. siderea	pCO$_2$	BW	lab	216	18	1.1-4.0	28	35	10.8	fed	30 d	15 d
S. siderea	pCO$_2$	BW	lab	144	18	2.7-6.8	28-32	35	10.8	fed	30 d	14 d
S. hyades	HCl + NaHCO$_3$	AA	field	7	7	1.1-5.7	20-31	32-47	3.5-50.0	in situ	NA	NA
A. cervicornis	pCO$_2$	BW	lab	20	16	1.7-4.3	27-30	33	3.7	fed	4 weeks	10 d
A. agaricites	pCO$_2$	BW	lab	54	22	1.7-4.3	27-30	33	3.7	fed	4 weeks	10 d
D. stokesii	pCO$_2$	BW	lab	59	5	1.7-4.3	27-30	33	3.7	fed	4 weeks	10 d
M. cavernosa	pCO$_2$	BW	lab	145	9	1.7-4.3	27-30	33	3.7	fed	4 weeks	10 d
O. faveolata	pCO$_2$	BW	lab	130	17	1.7-4.3	27-30	33	3.7	fed	4 weeks	10 d
P. astreoides	pCO$_2$	BW	lab	152	10	1.7-4.3	27-30	33	3.7	fed	4 weeks	10 d
P. divaricata	pCO$_2$	BW	lab	115	71	1.7-4.3	27-30	33	3.7	fed	4 weeks	10 d
P. clivosa	pCO$_2$	BW	lab	43	6	1.7-4.3	27-30	33	3.7	fed	4 weeks	10 d
P. strigosa	pCO$_2$	BW	lab	42	9	1.7-4.3	27-30	33	3.7	fed	4 weeks	10 d
S. radians	pCO$_2$	BW	lab	146	44	1.7-4.3	27-30	33	3.7	fed	4 weeks	10 d
S. siderea	pCO$_2$	BW	lab	138	30	1.7-4.3	27-30	33	3.7	fed	4 weeks	10 d
S. hyades	pCO$_2$	BW	lab	138	22	1.7-4.3	27-30	33	3.7	fed	4 weeks	10 d

8   [1]Coral nutrition assumed from water changes. [2]Data fit to parabolic response. [3]Data fit to general additive model.

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14 **Acknowledgements**

27 **Supporting Information**

28   Figure S1. Cheeca Rocks annual composite SST, fCO_2, and Ω_{arag}.
29   Figure S2. Cheeca Rocks diurnal ranges of SST, fCO_2, and Ω_{arag} by month.
30   Table S1. Colony collection sites and sample sizes.
31   Appendix S1. Additional information on methods.
32   Table S2. Linear coefficients of mixed effects models.
33   Table S3. General additive mixed effects model results for *O. faveolata.*
34   Figure S3. Fitted general additive mixed effects model for *O. faveolata.*
35   Figure S4. Mean annual Florida Keys temperature and Ω_{arag} under four RCP emissions scenarios.
36   Table S4. Growth projection outputs and species composition by reef.
37   Figure S5. Projected growth under RCP 8.5 by habitat and most-abundant species.
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