Coral Reefs
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REPORT

Stress-tolerant corals of Florida Bay are vulnerable to ocean acidification

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Abstract In situ calcification measurements tested the hypothesis that corals from environments (Florida Bay, USA) that naturally experience large swings in pCO_2 and pH will be tolerant or less sensitive to ocean acidification than species from laboratory experiments with less variable carbonate chemistry. The pCO_2 in Florida Bay varies from summer to winter by several hundred ppm roughly comparable to the increase predicted by the end of the century. Rates of net photosynthesis and calcification of two stress-tolerant coral species, *Siderastrea radians* and *Solenastrea hyades*, were measured under the prevailing ambient chemical conditions and under conditions amended to simulate a pH drop of 0.1–0.2 units at bimonthly intervals over a 2-yr period. Net photosynthesis was not changed by the elevation in pCO_2 and drop in pH; however, calcification declined by 52 and 50 % per unit decrease in saturation state, respectively. These results indicate that the calcification rates of *S. radians* and *S. hyades* are just as sensitive to a reduction in saturation state as coral species that have been previously studied. In other words, stress tolerance to temperature and salinity extremes as well as regular exposure to large swings in pCO_2 and pH did not make them any less sensitive to ocean acidification. These two species likely survive in Florida Bay in part because they devote proportionately less energy to calcification than most other species and the average saturation state is elevated relative to that of nearby offshore water due to high rates of primary production by seagrasses.

Keywords Growth · Calcification · *Siderastrea radians* · *Solenastrea hyades* · Net photosynthesis · Climate change

Introduction

Atmospheric CO_2 has increased by over 100 ppm since the start of the industrial revolution principally as a result of the burning of fossil fuels. The world's oceans have absorbed ~33–50 % of this CO_2 (Sabine et al. 2004), which has in turn caused well-documented reductions in carbonate ion concentration and concomitant decreases in pH (Dore et al. 2009; González-Dávila et al. 2010). While studies and meta-analyses have shown varying organismal responses to ocean acidification (Ries et al. 2009; Hendriks et al. 2010; Kroeker et al. 2010), coral calcification is consistently negatively impacted with general declines of 20–30 % per unit change in aragonite saturation state (Langdon and Atkinson 2005; Kroeker et al. 2010). However, some studies suggest certain corals appear less sensitive to pCO_2 changes than others (Gattuso et al. 1998; Marubini et al. 2001, 2003; Reynaud et al. 2003). Furthermore, recent work has shown factors such as feeding can mitigate the negative effects of pCO_2 on calcification (Cohen and Holcomb 2009). Altogether, these studies indicate corals have varying responses to pCO_2, but little is known about the nature of this variance.

In addition to ocean acidification, climate change is expected to increase sea surface temperatures (SSTs) past corals' thermal optimums. The dual stressors of higher temperatures and changing ocean chemistry are expected to have compounding negative effects on net reef growth

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(Hoegh-Guldberg 2005; Silverman et al. 2009). A study by Reynaud et al. (2003) illustrates these compounded effects, where calcification of *S. pistillata* declined by −38 % at elevated temperature and pCO_2 compared to −5 % as a result of pCO_2 alone. The 3 °C temperature increase that these corals experienced is within the annual (and diurnal) temperature range of many reefs. Consequently to understand coral responses to ocean acidification, calcification must be measured under a range of conditions that represent the conditions that corals experience in nature and that are associated with future climate change.

Florida Bay as a natural laboratory

Florida Bay, bordered by the Everglades to the north and the Florida Keys to the south and east (Fig. 1), consists of a series of shallow, compartmentalized basins whose chemistry is dominated by carbonate sediment precipitation and dissolution (Ginsburg 1956; Kerr 1972; Yates et al. 2007). The relative isolation and shallow basins subject Florida Bay to more extremes in temperature and salinity (Montague and Ley 1993; Boyer et al. 1997, 1999; Millero et al. 2001). Mass seagrass dieoff and chronic ecosystem degradation beginning in the summer of 1987 have been attributed to such extremes in temperature and salinity (Fourqurean and Robblee 1999; Porter et al. 1999; Zieman et al. 1999; Koch et al. 2007). Because the depth is shallow (<3 m), ambient air temperatures affect SSTs in the bay to a greater degree than offshore waters. Winter cold fronts traveling southward over the Florida peninsula cause cold spells (Roberts et al. 1982; Duever et al. 1994), whereas summer temperatures typically raise bay temperatures over 30 °C for extended periods (Fig. 2). Two different processes heavily influence salinity variations in the bay: Everglades runoff in the northeast and evaporation/precipitation in the southwest (Swart and Price 2002).

With respect to carbonate chemistry and ocean acidification, Florida Bay acts as a natural laboratory for changing pCO_2, with seasonal pCO_2 of 325–725 µatm (Millero et al. 2001), and diurnal swings of 100–200 µatm pCO_2 (Yates et al. 2007). Variability in pH values in Florida Bay reflects those reported in other nearshore systems (Wootton et al. 2008; Hofmann et al. 2011). Diurnal changes in carbonate chemistry of Florida Bay are driven by biogenic sediment precipitation and dissolution (Yates et al. 2007), which in turn are driven by photosynthesis and respiration effects on pCO_2 and pH (Yates and Halley 2006). Seasonal variability is also biologically driven through calcification and photosynthesis (Millero et al. 2001), as well as by oxidation of organic matter and by the exchange with marine water (Swart et al. 1996a, 1999). Because of this natural variation in pCO_2, in situ measurements of calcification in Florida Bay throughout the year can be used to predict coral calcification responses to future increases in atmospheric CO_2.

Stress-tolerant corals

Corals are not widely found throughout Florida Bay, principally as a result of the lack of suitable hard substrate.

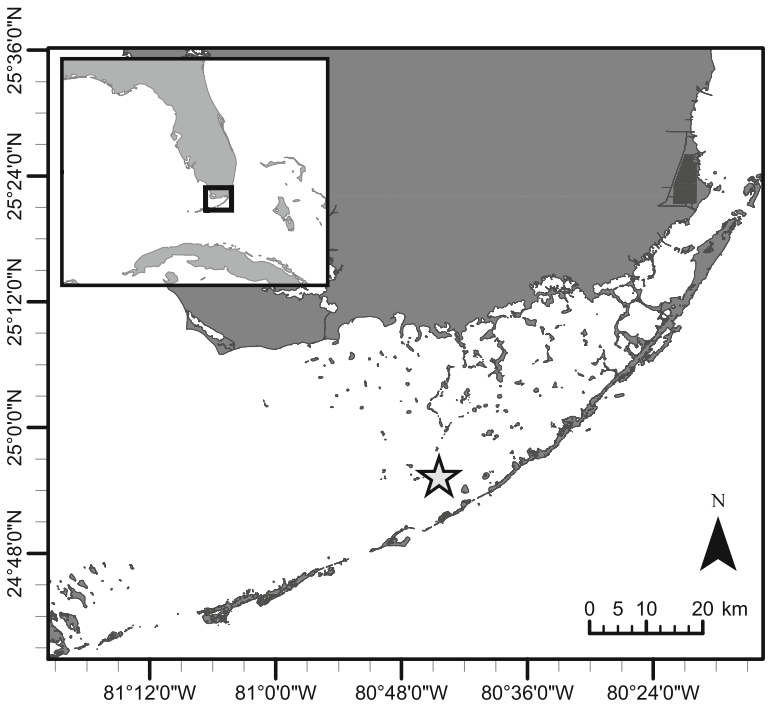

Fig. 1 The field site, denoted by a *star*, is located just north of Peterson Keys in Florida Bay

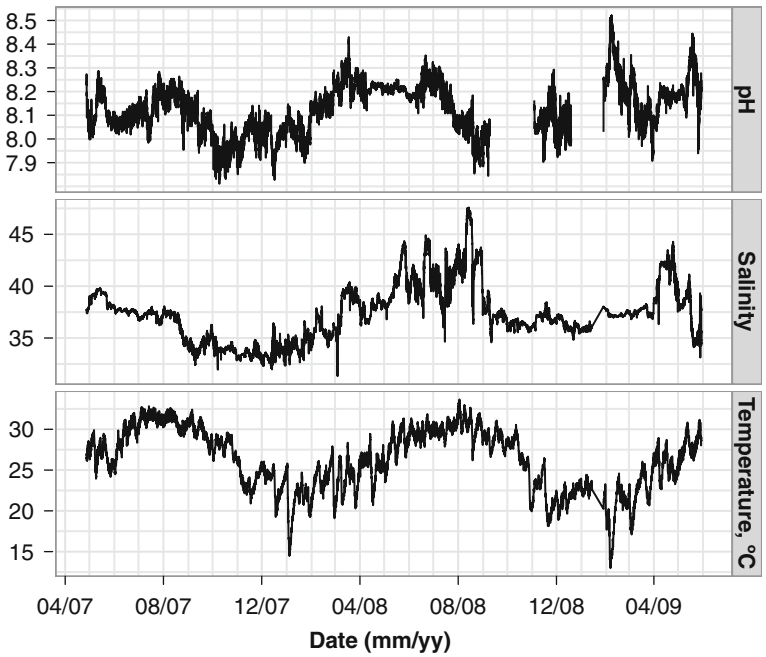

Fig. 2 Water quality parameters over the course of the study period. This portion of Florida Bay regularly experiences hypersalinity, summer temperatures in excess of 30 °C, and winter cold spell temperatures below 15 °C. The pH rarely falls below 8.0. Gaps in the pH record were due to sensor malfunctions

Where there is bare rock on which they can attach, corals appear healthy despite the variable pCO_2. These corals might therefore represent CO_2-resistant scleractinians. Three species of corals occur in the study area: *Siderastrea radians* (Pallas 1776), *Solenastrea hyades* (Dana 1846), and *Porites divaricata* (LeSuer 1821). Given the ability of these species to tolerate stress and marginal or disturbed habitats (Vaughan 1913; Yonge 1936; Macintyre and Pilkey 1969; Lewis 1989; Rice and Hunter 1992; Lirman et al. 2002, 2003; Macintyre 2003; Chartrand et al. 2009; Lirman and Manzello 2009), they may also have the ability to tolerate changing pCO_2 levels, that is, maintain constant calcification rates even in high pCO_2 conditions. Such corals would provide model organisms for studying how other taxa might cope with ocean acidification and physiological mechanisms that determine pCO_2 resistance. In addition, the two tropical corals examined in this study, *Siderastrea radians* and *Solenastrea hyades*, have been observed in temperate waters as far north as North Carolina, USA (Macintyre and Pilkey 1969; Macintyre 2003).

Methods and materials

Field site

Eleven specimens of *Siderastrea radians* and nine specimens of *Solenastrea hyades* were collected near Peterson Keys (Fig. 1; 24.926°N, 80.740°W) in Florida Bay and epoxied to plastic tiles, which were attached to a platform of cinderblocks at the collection site. Surface areas of *Siderastrea radians* and *Solenastrea hyades* were 45 ± 17 and 138 ± 43 cm^2 (mean $\pm$ standard deviation), respectively.

Environmental loggers (Yellow Springs Instruments) recorded conductivity, temperature, pressure, dissolved oxygen and pH from April 2007 to November 2010 at 30-min intervals. Between deployments, the loggers were calibrated against standards (Yellow Springs Instruments) and discrete water samples collected during field trips. Light was measured with Onset HOBO Temperature/Light Data Loggers in units of lux, which does not have an exact conversion to photosynthetically active radiation (PAR) but was approximated using a lux-PAR conversion factor of lux/50 = PAR. While light readings were not obtained for all visits, light levels ranged from 100 to 600 µmol photons m^{-2} s^{-1}, with differences due to water quality, that is, turbidity.

Chemical measurements

Total alkalinity (TA) was determined in duplicate using an automated Gran titration (Dickson et al. 2007), and accuracy was checked against certified seawater reference material (A. Dickson, Scripps Institute of Oceanography). The pH on the total scale (Dickson et al. 2007) was determined at 25.0 °C using an Orion Ross combination pH electrode calibrated against Tris buffer prepared in synthetic seawater (Nemzer and Dickson 2005). Concentrations of CO_3^{2-}, Ca^{2+}, and saturation state (Ω_{arag}) were computed from TA, pH, temperature, and salinity using the program CO2SYS (Lewis and Wallace 1998; Pierrot et al. 2006) and dissociation constants for carbonate from Mehrbach et al. (1973) as refit by Dickson and Millero (1987) and for boric acid from Dickson (1990). The pH is reported on the total scale, the

scale on which K1 and K2 were determined in the Gran functions. Dissolved oxygen (DO) was determined by Winkler titration using an automated titrator that utilized amperometric endpoint detection (Langdon 2010). Salinity was measured on a Guildline 8410A Salinometer.

Incubations

At approximately bi-monthly intervals from May 2007 to March 2009, a random subset of corals from the sample population were detached from the platform that held them in place between trips and incubated in situ in 2-L chambers (Fig. 3) for approximately 90 min. Under this sampling regime, certain individuals were measured multiple times over the course of the experiment. Battery-powered magnetic stirrers in the bases provided circulation within the chambers. Individual corals were incubated twice during each visit: once with the chamber filled with ambient seawater and once with the seawater in the chamber modified to simulate mid- to end-of-century projections of pCO_2, that is, 100–200 µatm above ambient conditions. The order of incubations was randomized such that half the corals were incubated under ambient conditions first, while the other half under elevated pCO_2 conditions. The incubations were performed between 1000 and 1400 hrs when daily solar insolation peaked, assuming photosynthesis would be saturating (Langdon and Atkinson 2005). Light levels were equal for both incubations. Laboratory tests indicated no reduction in light across the clear polycarbonate chamber tops. Incubations with an empty chamber were made to account for any non-coral changes to the water chemistry, which were found to be negligible. Chambers that malfunctioned during the incubation and samples that were lost were excluded from the analyses. Water samples were withdrawn using syringes fitted to a valved port on the incubation chambers. The chambers themselves acted as large syringes, with the clear tops sliding over the bases to account for changes in volume from sampling while maintaining the separation of outside water from the inner incubation water. Water samples were then poisoned with $HgCl_2$ for TA or pickled Winkler reagents for DO.

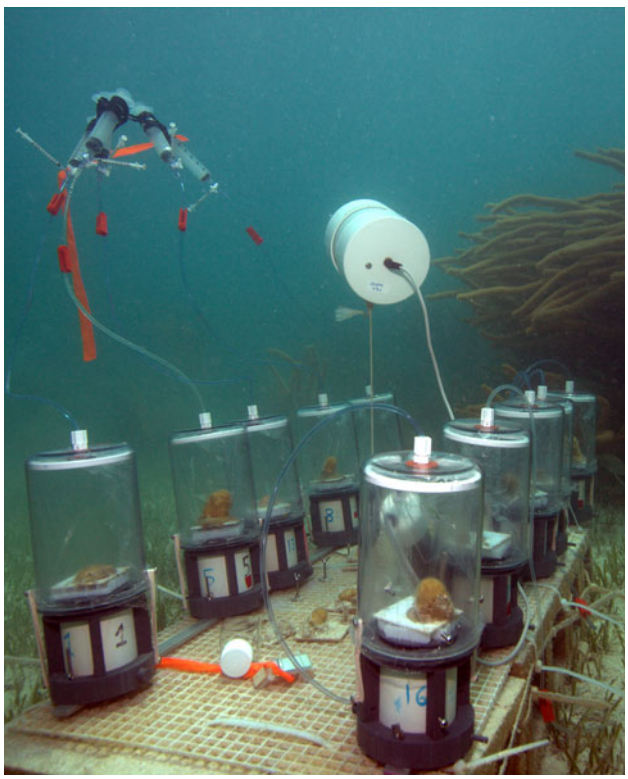

Fig. 3 Corals were placed in incubation chambers to measure calcification and net photosynthesis. The pCO_2 levels were elevated above ambient conditions by equimolar additions of $NaHCO_3$ and HCl through a sampling port. Water samples were drawn from the same port. Photo credit: Evan D'Alessandro

CO_2 treatments

A two-part chemical injection of $NaHCO_3$ followed by HCl was used to elevate pCO_2 in the treatment incubations. This procedure was necessary for these underwater, in situ incubations and is chemically identical to bubbling with pCO_2 (Gattuso et al. 2010). The addition of $NaHCO_3$ causes an increase in dissolved inorganic carbon (DIC), while the HCl cancels the increase to TA caused by the addition of the Na^+ ions. The net result is an increase in DIC and no change in TA that closely simulates what would happen if the seawater was bubbled with CO_2 until the desired pCO_2 was achieved. Calculation of the amounts of $NaHCO_3$ and HCl needed to achieve the desired chemical conditions in the 2-L chambers were computed as follows. First, present-day pCO_2 and average Florida Bay TA were used to compute present-day DIC using CO2SYS. Second, future DIC was computed holding TA constant and choosing a target pCO_2 of 750 ppm. The addition of $NaHCO_3$ is the desired increase in DIC and is given by Eq. 1.

$$V_{\text{spike}} = \frac{\Delta\text{DIC} \times V_{\text{chamber}}}{N_{\text{spike}}} \quad (1)$$

where V_{spike} is the volume of $NaHCO_3$ solution added to the chambers, ΔDIC is the difference in DIC between simulated future and present-day conditions (µmol L^{-1}), V_{chamber} is the volume of the incubation chamber (2 L), and N_{spike} is the normality of the $NaHCO_3$ solution. Since the addition of $NaHCO_3$ increases the DIC and the TA equally, Eq. 1 also gives the volume of the HCl spike.

The actual achieved pCO_2 varied due to differences in ambient conditions and generally ranged from 500 to 800 ppm, which in turn resulted in a variable decrease in Ω_{arag}. Sample sizes for each field trip are listed Table 1.

Biological variables

Changes in TA and DO were used to calculate calcification and net photosynthesis. Carbonate parameters and dissolved oxygen were measured as described above. Rates were normalized to coral surface area, determined from morphometric measurements. Biological variables were calculated from the following equations: Calcification:

$$G = \frac{-0.5\rho\Delta\mathrm{TA} \times V}{t \times \mathrm{SA}} \quad (2)$$

where G is calcification, ρ is seawater density, ΔTA is the change in total alkalinity (μmol kg^{-1} seawater), V is chamber volume, t is the incubation time, and SA is the coral surface area. Net photosynthesis:

$$\mathrm{NP} = \frac{\Delta\mathrm{DO} \times V}{t \times \mathrm{SA}} \quad (3)$$

where NP is net photosynthesis, ΔDO is the change in dissolved oxygen over the incubation period. Coral responses to high CO_2 treatments were calculated as the change in calcification or photosynthesis between ambient and high CO_2 treatments normalized to the ambient treatment rate:

$$R_{\mathrm{calcif}} = \left(\frac{G_{\mathrm{ambient}} - G_{\mathrm{CO_2}}}{G_{\mathrm{ambient}}}\right) \quad (4)$$

$$R_{\mathrm{photosyn}} = \left(\frac{\mathrm{NP_{ambient}} - \mathrm{NP_{CO_2}}}{\mathrm{NP_{ambient}}}\right) \quad (5)$$

Table 1 Physical parameters measured during field trips

Date (m/d/yr)	Time (hh:mm)	T (°C)	Sal.	O_2 (μM)	pH_t	TA (μmol kg^{-1} SW)	TCO_2 (μmol kg^{-1} SW)	Ω_{arag}	pCO_2 (ppm)	Sample size (A = ambient, T = treatment)			
										S. radians		*S. hyades*	
										A	T	A	T
4/27/07	15:00	26.5	37.7	224	8.21	2,267	1,821	4.7	237	–	–	–	–
5/4/07	11:15	28.3	39.1	178	7.99	2,407	2,027	3.8	465	3	–	1	–
7/11/07	11:00	30.6	37.4	163	8.05	2,206	1,822	4.1	360	–	–	–	–
7/23/07	11:30	30.8	36.5	224	8.12	2,159	1,693	4.4	293	–	–	–	–
9/12/07	11:30	29.6	33.1	203	8.00	2,212	1,884	3.5	437	4	4	1	1
9/12/07	14:45	29.9	33.5	208	8.02	2,222	1,878	3.6	422				
11/19/07	11:30	22.2	33.4	237	8.12	2,505	2,168	3.9	358	3	1	–	–
11/19/07	13:55	22.5	33.4	235	8.11	2,495	2,163	3.8	368				
12/12/07	11:15	23.9	32.2	214	8.07	2,676	2,338	4.1	447	2	2	3	3
12/12/07	14:00	24.2	32.3	224	8.08	2,653	2,309	4.2	430				
1/30/08	10:30	19.5	35.3	239	8.11	2,711	2,370	3.8	396	4	4	5	4
1/30/08	13:00	19.9	35.4	237	8.10	2,715	2,369	3.8	406				
4/9/08	11:00	25.8	36.6	204	8.12	2,308	1,935	4.1	316	–	–	–	–
4/9/08	13:00	26.3	36.6	217	8.14	2,271	1,885	4.2	293				
4/28/08	11:00	25.1	38.0	216	8.23	2,201	1,759	4.9	234	4	3	5	5
4/28/08	14:00	25.7	37.9	212	8.22	2,223	1,777	4.9	239				
6/9/08	11:00	28.1	39.7	191	8.20	2,174	1,711	5.0	244	4	4	3	3
6/9/08	14:00	28.4	39.5	200	8.20	2,177	1,714	5.1	248				
8/12/08	11:00	29.9	46.5	131	8.03	2,187	1,781	3.9	366	4	4	5	5
8/12/08	13:30	30.1	47.2	131	8.07	2,179	1,733	4.1	317				
11/3/08	11:30	22.7	36.3	229	8.14	2,466	2,096	4.1	326	5	5	5	5
11/3/08	13:00	23.0	36.4	231	8.14	2,456	2,083	4.1	323				
1/28/09	10:45	21.8	38.0	235	8.23	2,895	2,421	5.4	297	4	4	3	3
1/28/09	12:45	22.2	37.9	241	8.26	2,870	2,361	5.7	268				
3/31/09	10:50	25.7	37.3	197	8.05	2,396	2,057	3.8	415	4	4	2	2
3/31/09	12:45	26.3	37.3	212	8.08	2,378	2,012	4.0	375				

Sample sizes refer to the total number of corals measured on a particular date

Dividing Eq. 4 for R_{calcif} by the change in saturation ($\Delta\Omega$) state between ambient and high CO_2 treatments yields the change in calcification per unit change in saturation state, a useful metric for comparing coral growth responses across studies (Langdon and Atkinson 2005; Kleypas and Langdon 2006; Hendriks et al. 2010).

Chemical environment

The diurnal pH range was calculated from the difference between the maximum and minimum recorded value for every day from April 2007 through April 2009. Saturation state was estimated for a typical year based on pH values recorded from the environmental logger and TA values reported in this study, Millero et al. (2001), and Yates and Halley (2006). TA generally shows low interannual variation relative to seasonal variation. Monthly values were extrapolated for missing months using adjacent dates.

Statistical analyses

Each fieldtrip measured a subset of corals from the same experimental pool, necessitating a multilevel model that could account for repeated measures, unbalanced data, and missing-at-random corals (i.e., not every coral was measured on every trip). Coral calcification and photosynthesis responses to high CO_2 treatments were analyzed as a function of pCO_2 treatment, temperature, salinity, coral, and date. The baseline null model grouped response by individual corals:

$$R_{ij} = \beta_0 + \mu_{0j} + \varepsilon_{ij} \quad (6)$$

where R_{ij} is the calcification or photosynthesis response for the ith measurement of the jth coral, β_0 is the overall mean calcification or photosynthesis response, μ_{0j} is the residual between the individual and the overall calcification or photosynthesis response, assumed to have a mean of zero with variance σ^2_{u0}, and ε_{ij} is the residual difference between the average jth coral response and ith measured response for that coral. Explanatory variables were individually forward-stepped into the model and evaluated against the simpler nested model with likelihood ratio (LR) tests. If they improved the model fit, they were retained and the next variable was added. The treatment variable $\Delta\Omega$ was first added to the null model as a fixed effect because it was the only treatment imposed on the corals:

$$R_{ij} = \beta_0 + \beta_1 \Delta\Omega_{ij} + \mu_{0j} + \varepsilon_{ij} \quad (7)$$

with slope term β_1 for $\Delta\Omega$. Median-zeroed time, temperature, and salinity were subsequently forward-stepped into the model as random effects with diagonal covariance structures:

$$R_{ij} = \beta_0 + \beta_1 x_{1ij} + \mu_{1j} x_{1ij} + \beta_2 x_{2ij} + \mu_{2j} x_{2ij} + \cdots + \beta_k x_{kij} + \mu_{kj} x_{kij} + \mu_{0j} + \varepsilon_{ij} \quad (8)$$

where β_2 through β_k are slopes for each explanatory variable x_2 to x_k. The error terms μ_{2j} to μ_{kj} for the random variables 2 to k are assumed to follow a zero-centered normal distribution with σ^2_{2j} to σ^2_{kj} variance. Equation 8 shows the full model with all explanatory variables though the final model would not necessarily contain all variables. Models were fit with maximum likelihood estimates of parameters. Model residuals were examined for normality. Bayesian highest probability density (HPD) 95 % confidence intervals were calculated from Markov chain Monte Carlo samples of posterior distributions of the fixed effect parameters.

Statistical analyses were performed using the software program R, version 2.14.1 (R Development Core Team 2011). The statistical packages 'stats' and 'lme4' (Bates et al. 2011) within R were used for the curve-fitting and multi-level modeling, respectively. Significance thresholds were set at $\alpha = 0.05$.

Results

Field conditions

Conditions recorded in Florida Bay exhibit large-scale diurnal and seasonal variability (Table 1; Fig. 2). Over the 3-yr deployment of the environmental loggers, temperature ranged diurnally 1.4 ± 0.5 °C (n = 1,297 d) with more extreme values of approximately 4 °C d^{-1}. Seasonally, temperature varied approximately 15 °C from summer to winter (Fig. 2). The average diurnal salinity range was 1.0 ± 1.4 (n = 1,297 d). The most extreme daily salinity ranges were 10, the same as the seasonal variation. Average diurnal pH range was 0.09 ± 0.05 (n = 1,297 d) with more extreme ranges of 0.2–0.3 d^{-1}. Seasonally, pH ranged from approximately 7.9 to 8.3 (Fig. 2). Ambient

Table 2 Pooled calcification (G) and net photosynthesis (NP) measurements for *Siderastrea radians* and *Solenastrea hyades*

	S. radians	*S. hyades*
$G_{ambient}$	5.2 ± 3.2 (41)	3.1 ± 1.8 (33)
G_{CO_2}	2.7 ± 5.6 (35)	2.0 ± 2.7 (31)
$NP_{ambient}$	18.7 ± 12.3 (41)	9.1 ± 4.3 (33)
NP_{CO_2}	20.1 ± 12.1 (35)	10.0 ± 5.6 (31)
$G{:}NP_{ambient}$	0.29 ± 0.12 (40)	0.37 ± 0.20 (33)

Subscripts 'ambient' and 'CO_2' indicate control and elevated pCO_2 conditions, respectively. Values are reported as mean ± standard deviation (sample size)

pCO_2 averaged 350 ± 70 ppm ($n = 11$ incubation dates). Treatment pCO_2 conditions were 480 ± 100 ppm ($n = 11$).

Calcification and photosynthesis

Pooled ambient calcification rates for *Siderastrea radians* were 5.24 ± 3.17 mmol $CaCO_3$ m^{-2} h^{-1} over the study period, while calcification rates for *Solenastrea hyades* were 3.07 ± 1.81 $CaCO_3$ m^{-2} h^{-1} (Table 2; Fig. 4). Pooled net photosynthesis was 18.70 ± 12.29 mmol O_2 m^{-2} h^{-1} and 9.10 ± 4.28 for *Siderastrea radians* and *Solenastrea hyades*, respectively (Table 2; Fig. 4). Ambient calcification to net photosynthesis (G:NP) ratios were 0.26 ± 0.12 for *Siderastrea radians* and 0.37 ± 0.20 for *Solenastrea hyades* (Table 2). Calcification rates tracked changes in temperature, light, and pH that are known to affect growth, but calcification was best explained as a function of net photosynthesis. Pooled calcification data were linearly correlated with net photosynthesis for both species. However, for *Siderastrea radians,* calcification was better fit to a hyperbolic tangent function ($G = 14.59$ tanh(NP/46.34)) than linear regression (AIC scores of 161.0 and 164.9, respectively) (Fig. 5). Traditionally, hyperbolic tangent functions have been used to describe calcification or photosynthesis as a function of irradiance (Chalker 1981). Multiple linear regressions with physical data did not yield significant models for predicting calcification or net photosynthesis, suggesting interactions with other unmeasured variables such as feeding or flow rates may influence these processes (Kinsey and Davies 1979; Dennison and Barnes 1988; Houlbrèque et al. 2003).

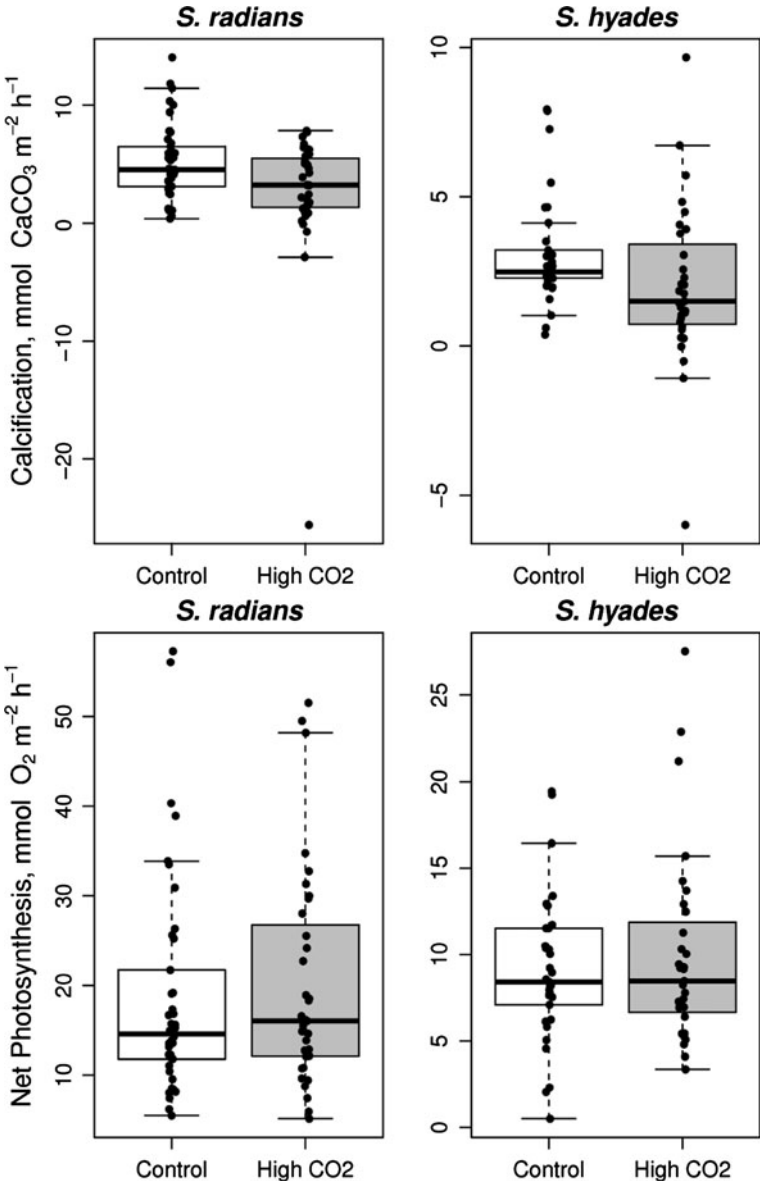

Fig. 4 Boxplots of pooled calcification and net photosynthesis data

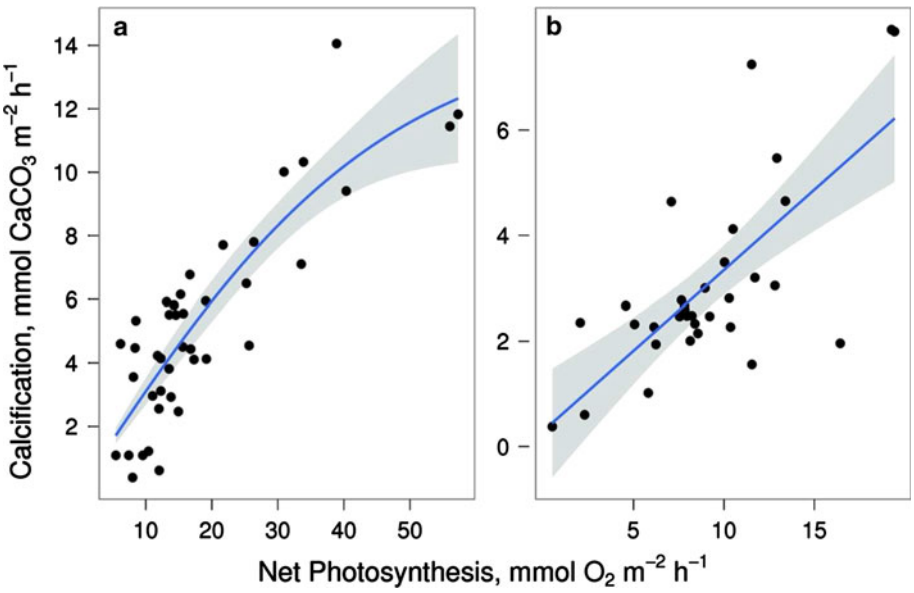

Fig. 5 Calcification (G) correlated with net photosynthesis (NP) for pooled data of **a** *Siderastrea radians* and **b** *Solenastrea hyades*. *Lines* represent best fit models, while *shaded regions* represent 95 % CI. *Siderastrea radians* is fitted to the hyperbolic tangent function: $G = 14.59 \tanh(\mathrm{NP}/46.34)$. *Solenastrea hyades* is fitted to linear regression parameters: $G = 0.305\ \mathrm{NP} + 0.292$

Table 3 Multilevel model comparisons of the only observed significant calcification response variable, change in saturation state, against a null model accounting only for coral

	S. radians		*S. hyades*	
	Null model	Model 1	Null model	Model 1
Fixed effects				
Intercept	0.414 (0.111)	−0.073 (0.244)	0.370 (0.130)	−0.156 (0.202)
ΔΩ		0.516 (0.234)		0.502 (0.160)
Random effects				
Coral	0	0	0	0
Residual	0.427	0.375	0.526	0.399
Log likelihood	−34.776	−32.498	−34.016	−29.73
HDP 95 % CI				
ΔΩ		(0.013–0.997)		(0.157–0.832)
n coral	10		7	
n observations	35		31	

Calcification and net photosynthesis responses

Multilevel models of calcification responses found both species responded to ΔΩ, with calcification decreasing 52 % (1–100 % HPD 95 % CI) and 50 % (16–83 % HPD 95 % CI) per unit change in saturation state for *Siderastrea radians* and *Solenastrea hyades*, respectively (Table 3; Null model vs model 1, fixed effects ΔΩ: *S. radians* $\mathrm{LR}_1 = 4.6$, $p = 0.03$, *S. hyades* $\mathrm{LR}_1 = 8.6$, $p = 0.003$). Date, temperature, salinity, and initial saturation state did not improve model fits and were therefore not considered in the final model. Estimates of zero variance suggest that grouping by corals did not help explain overall variability in the data, that is, there is insufficient evidence that individual corals had unique responses. The coral calcification responses to increased pCO_2 observed here are greater than the range of 5–40 % for other species summarized by Kleypas and Langdon (2006). None of the variables of increased pCO_2/decreased saturation state, initial saturation state, date, temperature, and salinity had detectable effects on photosynthetic responses of either species of corals.

Discussion

The calcification rates reported here are lower than other corals and reef communities (Chave et al. 1972; Kinsey 1983; Davies 1990; Meesters et al. 1994; Ohde and van Woesik 1999; Bates et al. 2001; Langdon and Atkinson 2005). The low G:NP ratios of <0.4 reported here relative to other studies (Jacques and Pilson 1980; Dennison and Barnes 1988; Swart et al. 1996b; Furla et al. 2000; Gattuso et al. 2000; Houlbrèque et al. 2003; Al-Horani et al. 2005; Schneider and Erez 2006) suggest Florida Bay corals' photosynthate provides energy for processes other than

calcification, possibly for coping with temperature and salinity extremes or large swings in pH. *Siderastrea radians* and *Solenastrea hyades* have historically populated disturbed areas (Yonge 1936; Lewis 1989; Sorauf and Harries 2009), and the extremes in temperature and salinity posed by Florida Bay are more immediate and threatening to survival than extremes in pCO_2. As a result, these corals have most likely developed survival strategies that favor stress-tolerant mechanisms and have possibly prioritized them over calcification processes.

Another possible explanation for the relatively low G:NP ratios is that zooxanthellae may be hoarding photosynthate and thereby slowing coral calcification. This explanation assumes calcification is driven mainly by energy from translocated photosynthate instead of the direct chemical effects of increased pH from photosynthesis. This explanation is not favored because it contradicts many studies that indicate calcification is chemically linked to photosynthesis (Furla et al. 2000; McConnaughey et al. 2000; Al-Horani et al. 2003).

Calcification–photosynthesis curves offer insight into the nature of this relationship. A linear relationship supports a direct inorganic chemical response, whereas an asymptotic curve indicates some biological constraint, such as enzyme saturation. Calcification rates of *S. radians* fit better to an asymptotic hyperbolic tangent curve than a simple linear curve, indicating possible limits to photosynthesis-stimulated calcification (Fig. 5). The mechanisms underlying this restriction are unknown, but may include limitations in H^+ transport from the calcification site (Ries 2011; McCulloch et al. 2012). This relationship may be species-specific as *Solenastrea hyades* calcification data were linearly correlated with photosynthesis. Further studies on this relationship would better elucidate the effects of photosynthesis on calcification.

Two aspects of the calcification response findings are noteworthy: (1) Both species exhibited high variability in calcification responses, with some individuals exhibiting positive responses to increased pCO_2 on some dates, and (2) calcification rates for both species are not, on average, CO_2 resistant. Such variability in calcification responses could serve as an adaptive mechanism to increasing ocean acidification where over time colonies whose calcification rates are resistant to CO_2 increase in abundance relative to CO_2-susceptible conspecifics. However, positive responses to acidification were not consistent by coral or any other measured parameter, and no such resistant individuals were observed in this study.

Furthermore, calcification is an energy-intensive process (Chalker and Taylor 1975; Chalker 1976; Fang et al. 1989; Tambutté et al. 1996), and the hypothetically resistant corals may maintain calcification at the expense of other processes such as tissue repair or gamete production. Comparably, Wood et al. (2008) showed echinoderms that increased calcification during ocean acidification suffered muscle wastage and increased metabolic costs. The Florida Bay corals appear to exhibit the opposite pattern, where calcification decreases because of ocean acidification and is superseded by other metabolic demands. Furthermore, corals exhibited consistent declines in calcification under high pCO_2/low pH treatments despite experiencing diurnal swings in pH of 0.08 ± 0.04 units in their natural environment. This response suggests short-term variability in pH will not mask the negative effects of incremental, long-term declines in pH on coral calcification. More studies are needed to determine how corals prioritize resource allocation and whether they might face tradeoffs between calcification and other processes.

Role of the environment

The persistence of *Siderastrea radians* and *Solenastrea hyades* in Florida Bay initially seems counterintuitive given their skeletal growth susceptibility to low saturation states and the bay's low winter saturation states (Millero et al. 2001). However, over the course of this study saturation state at the field site remained high relative to oceanic waters ($\Omega_{arag} = 4.27 \pm 0.57$ vs oceanic $\Omega_{arag} = 3.6$). The pH remained above 8.0 for 88 % of the time during the study (Fig. 2). An annual composite of aragonite saturation state created from recorded pH and discrete TA samples over a 3-yr period extending from 2007 to 2010 indicates aragonite saturation state would remain above 3.6 for 80 % of the year (Fig. 6). Consequently, the environment augments the low calcification rates of *Siderastrea radians* and *Solenastrea hyades* (relative to other species), while its extremes preclude other less stress-tolerant coral species. With its low average annual pCO_2, Florida Bay could potentially serve as a refuge against ocean acidification (Manzello et al. 2012), if not for the frequent phytoplankton blooms, persistent turbidity, and extremes in temperature and salinity (Boyer et al. 1999, 2009; Fourqurean and Robblee 1999). However, seagrass areas and other highly productive habitats should be included in any management plan to deal with ocean acidification due to their ability to reduce ambient pCO_2 levels.

Future research should decouple these corals from their chemically favorable environment to better evaluate their calcification-pCO_2 responses. If these corals direct a large portion of their resources toward survival in Florida Bay's marginal conditions, then under more benign oceanic conditions they may have more robust pCO_2 responses than observed in this study. Comparing these corals with conspecifics from the nearby reef tract might elucidate how individuals and their environments interact to affect pCO_2 responses.

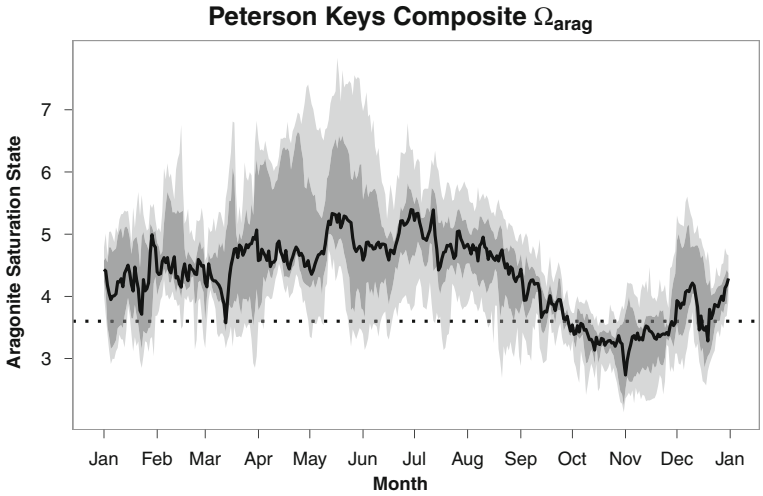

Fig. 6 Composite monthly saturation state based on pH recorded at the field site and discrete monthly total alkalinity (TA) samples from 2007 to 2010. CO2SYS was used to calculate saturation state as discussed in the methods section. *Black line* represents median aragonite saturation state (Ω_{arag}), *dark shaded* region represents the middle 50 % of composite values, *light shaded* region represents the full range of composite estimates of Ω_{arag}. *Dotted horizontal line* represents the modern-day oceanic average saturation state of 3.6. Saturation states in Florida Bay were generally closer to pre-industrial levels of 4.6 for most of the year. As a result, Florida Bay is a chemically favorable environment for calcification

Potential mechanisms for calcification resistance to pCO_2

The means by which corals might achieve CO_2-resistant calcification are unknown. Many researchers have shown calcification is a linear function of saturation state (Langdon et al. 2000; Leclercq et al. 2000, 2002; Marubini et al. 2001; Ohde and Hossain 2004; Langdon and Atkinson 2005), which is directly proportional to carbonate ion concentration. As more CO_2 dissolves in the ocean, $[CO_3^{2-}]$ decreases while $[HCO_3^-]$ increases, causing saturation state reductions and depressed calcification (Langdon et al. 2000; Schneider and Erez 2006; Marubini et al. 2008). Hence, one possible mechanism of calcification resistance could involve corals switching from CO_3^{2-} to HCO_3^- as the primary substrate used for calcification. If corals were able to utilize ambient bicarbonate, they would have more substrate available for calcification under ocean acidification scenarios. To date, only *Madracis auretenra* has been shown to utilize bicarbonate instead of carbonate for calcification (Jury et al. 2010). This study did not support this hypothesis because bicarbonate levels increased under elevated pCO_2 conditions while calcification decreased. Furthermore, multiple models of calcification posit Ca^{2+}-ATPase proton pumps drive pH gradients that create favorable calcification conditions (Adkins et al. 2003; Al-Horani et al. 2003; McConnaughey 2003; Cohen and Holcomb 2009). Reduced ambient seawater pH would increase the metabolic cost of maintaining these pH gradients, countering any gains made from switching to bicarbonate as the primary substrate.

Another potential CO_2-calcification resistance mechanism is the stimulation of photosynthesis by increased pCO_2. Increased CO_2 concentrations could reduce photorespiration in symbiotic dinoflagellates' form II Rubisco leading to a more efficient Calvin cycle or indirectly reduce the metabolic costs of operating a carbon-concentrating mechanism (CCM) (Leggat et al. 1999; Bertucci et al. 2010). Increased photosynthesis might then boost calcification (Gattuso et al. 1999; Furla et al. 2000; Marubini et al. 2001; Al-Horani et al. 2003, 2005; Allemand et al. 2004), likely through (1) the production of CO_3^{2-} as carbonic anhydrase dehydrates HCO_3^- to supply CO_2 for photosynthesis, (2) removal of CO_2 elevating pH and essentially countering ocean acidification, and (3) additional photosynthates for calcification. The basis for this mechanism requires photosynthetic stimulation in higher pCO_2, for which evidence is equivocal: some researchers have shown potential CO_2 fertilization (Marubini et al. 2008), while others, including this study, have not (Langdon et al. 2003; Reynaud et al. 2003; Schneider and Erez 2006). Whether or not CO_2 fertilizes photosynthesis, photosynthesis generally does not buffer calcification declines from increased CO_2 (Kroeker et al. 2010).

Despite experiments showing the importance of heterotrophy in reducing the negative effects of ocean acidification on calcification (Cohen and Holcomb 2009) and increasing photosynthesis (Borell et al. 2008), heterotrophy may not be enough to buffer coral calcification under predicted future climate conditions. It is possible that the limited positive responses of calcification rates to increased pCO_2 observed here could be due to feeding or increased

nutrient uptake by corals, which were not measured in this study. However, positive responses were not consistent for individual corals or time. Additionally, the corals in this study were kept in their natural environment and had ample opportunity to feed, yet their calcification responses were more sensitive those from many laboratory studies summarized in Kleypas and Langdon (2006).

In conclusion, increased frequency of bleaching as a result of climate change and increased local stress from growing human populations will probably favor more stress-tolerant corals on reefs. For example, *Montastraea* sp. increased in prominence with respect to *Acropora cervicornis* following the decline of *A. cervicornis* in the early 1980s (Gardner et al. 2003), and *Porites astreoides* in general have increased in abundance throughout the Caribbean relative to other species (Green et al. 2008). However, the ability of reefs to cope with future warming by supporting more stress-tolerant species will be undermined whether those species are vulnerable to ocean acidification. This study found that the calcification rates of two stress-tolerant corals, *Siderastrea radians* and *Solenastrea hyades,* are just as sensitive to elevated pCO_2 as other corals previously studied, which suggests a limited ability of corals to adjust to ocean acidification. The corals from this study appear uniquely adapted to the marginal environment of Florida Bay, with their low calcification rates augmented by the environment's generally high saturation state and their physiologies adapted to frequent extremes in water quality. As a result, calcification appears to be a secondary priority compared to survival in Florida Bay. The sensitivity of calcification rates of *Siderastrea radians* and *Solenastrea hyades* to pCO_2 discounts the notion that reefs can adjust to climate change by shifting to eurytopic species.

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