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REPORT

Relative sensitivity of five Hawaiian coral species to high temperature under high-pCO_2 conditions

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Abstract Coral reef ecosystems are presently undergoing decline due to anthropogenic climate change. The chief detrimental factors are increased temperature and increased pCO_2. The purpose of this study was to evaluate the effect of these two stressors operating independently and in unison on the biological response of common Hawaiian reef corals. Manipulative experiments were performed using five species (*Porites compressa*, *Pocillopora damicornis*, *Fungia scutaria*, *Montipora capitata*, and *Leptastrea purpurea*) in a continuous-flow mesocosm system under natural sunlight conditions. Corals were grown together as a community under treatments of high temperature (2 °C above normal maximum summer temperature), high pCO_2 (twice present-day conditions), and with both factors acting in unison. Control corals were grown under present-day pCO_2 and at normal summer temperatures. *Leptastrea purpurea* proved to be an extremely hardy coral. No change in calcification or mortality occurred under treatments of high temperature, high pCO_2, or combined high temperature–high pCO_2. The remaining four species showed reduced calcification in the high-temperature treatment. Two species (*L. purpurea* and *M. capitata*) showed no response to increased pCO_2. Also, high pCO_2 ameliorated the negative effect of high temperature on the calcification rates of *P. damicornis*. Mortality was driven primarily by high temperature, with a negative synergistic effect in *P. compressa* only in the high-pCO_2–high-temperature treatment. Results support the observation that biological response to temperature and pCO_2 elevation is highly species-specific, so generalizations based on response of a single species might not apply to a diverse and complex coral reef community.

Keywords Coral calcification · Ocean acidification · Interactive effects · Synergy · Antagonistic · Climate change

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Introduction

Coral reefs have immense biological wealth and provide economic and environmental services (e.g., tourism, fisheries, wave protection, food production) for millions of people. However, reefs throughout the world are undergoing significant ecological change due to anthropogenic climate change (Hoegh-Guldberg 1999; Pandolfi et al. 2011). A major concern is the decrease in the pH of the ocean due to increasing uptake of anthropogenic atmospheric pCO_2, a process referred to as ocean acidification (OA) (Hoegh-Guldberg et al. 2007; Erez et al. 2011). Ocean acidity has increased by approximately 25 % (decrease of 0.1 pH units) since pre-industrial times (Lacis et al. 2010) and has resulted in severe negative effects on calcifying marine organisms (Smith and Buddemeier 1992; Kleypas et al. 2006; Jokiel et al. 2008; Erez et al. 2011; Gattuso and Hansson 2011; Kroeker et al. 2013). The calcification rate of reef-building corals is predicted to decrease by 40 % with increasing pCO_2 concentrations by the end of the century (Gattuso et al. 1999; Kleypas et al.

1999; Langdon et al. 2000; Marubini et al. 2001, 2003; Müller et al. 2004; Langdon and Atkinson 2005; Kleypas and Langdon 2006; Hofmann et al. 2010; Erez et al. 2011). Experimental and field studies show that the impact of increased pCO_2 on calcification rates varies among species (Gattuso et al. 1998; Marubini et al. 2001, 2003; Reynaud et al. 2003; Edmunds et al. 2012; Comeau et al. 2013b). These variations in OA sensitivities may lead to differences in coral and algal species composition and therefore modify habitat complexity in the future (Fabricius et al. 2014; Comeau et al. 2015).

Along with OA, excessive ocean warming is predicted to negatively affect corals through increased thermal bleaching, reduced calcification, and increased coral mortality (Jokiel and Coles 1977, 1990; Glynn and D'Croz 1990; Lesser et al. 1990; Brown 1997; Erez et al. 2011). Prolonged exposure to elevated sea surface temperatures (SST) (+2 °C above upper lethal maximum) decreases photosynthesis and photosynthetic efficiency in the algal symbionts (Brown 1997); therefore, photosynthesis-to-respiration ratio decreases with increasing temperatures (Coles and Jokiel 1977). Calcification declines sharply above peak summer temperature with bleaching and eventual death of corals under future temperature scenarios (Hoegh-Guldberg et al. 2007; Buddemeier et al. 2008; Hoeke et al. 2011). The occurrence and severity of mass coral bleaching has increased dramatically over the last two decades with almost every reef region in the world suffering extensive coral stress and mortality (Jokiel and Brown 2004; Buddemeier et al. 2008; Bahr et al. 2015b). The isolated subtropical coral reef communities of Hawai'i, which contain high proportions of marine endemic species (>25 % in most taxa), have only recently begun to suffer from conditions that have ravaged coral reef communities in other areas of the world (Bahr et al. 2015b).

Increases in SST and pCO_2 operating independently have been shown to be detrimental to corals, but less is known about their effect when operating in unison. Therefore, it is essential to assess direct impacts of multiple stressors and determine whether the combine effects exceed (synergism) or are less than (antagonism) the sum of their individual effects. Moreover, the biological response of calcifying organisms to these climate change stressors may be species-specific, which may explain conflicting results regarding coral response to OA and multiple climate change stressors (Ban et al. 2014). The objectives of this study were to characterize the relative biological response (calcification and partial mortality) of Hawaiian reef-building corals under elevated temperatures and high pCO_2 and to describe the interactive effect (synergism or antagonism) when both factors operate in unison. Five abundant Hawaiian scleractinian corals—*Porites compressa*, *Montipora capitata*, *Fungia scutaria*, *Leptastrea purpurea*, and *Pocillopora damicornis*—were studied. These corals show a wide range of skeletal morphologies, tissue structure, documented stress tolerance levels, and reproductive strategies (Bahr et al. 2015a). The goal of the present study was to evaluate the direct and interactive effects of elevated temperature and acidification on the biological response of these corals in order to improve our ability to forecast future changes in species composition for Hawaiian reefs under projected global climate change conditions.

Materials and methods

Experimental system

This research was conducted at University of Hawai'i, Hawai'i Institute of Marine Biology (HIMB) at Moku o Lo'e, Kāne'ohe Bay, Hawai'i. The experiment was conducted in an outdoor continuous-flow experimental facility that mimics the physical, chemical, and biological conditions on the adjacent reef flat under projected conditions of climate change (Jokiel et al. 2008, 2014a). Carbonate chemistry within the mesocosms was manipulated through direct bubbling of CO_2 (Jokiel et al. 2014a), and temperature was controlled using titanium heaters (Finnex, TH-800, 800 W) (Table 1).

The stressors of acidification and temperature were manipulated within 500-L mesocosms to test each factor independently and provide a pairwise comparison of these variables during the summer months of June through August 2013. The experimental mesocosms were located in full sunlight (Fig. 1; Table 2) and allowed for natural diurnal fluctuations in seawater chemistry under present and future climate change projections (Jokiel et al. 2014a) (Fig. 2). Unfiltered seawater was pumped from 2 m offshore of the adjacent reef. Flow rate through the mesocosms was maintained at a rate of 8 L min^{-1} resulting in a seawater turnover rate of 45 min.

Experimental design

The biological response (calcification and partial mortality) of five common Hawaiian coral species (*P. compressa*, *M. capitata*, *F. scutaria*, *L. purpurea*, and *P. damicornis*) to acidification and temperature acting alone and in unison was examined over an 8-week (56-d) experimental period. Adult colony fragments of comparable size and morphology within each species were collected from the reef flat surrounding Moku o Lo'e at a depth of ~1 m. Corals were labeled for identification and 20 colonies of each species (<8 cm) were randomly assigned to one of the four experimental treatments. The experimental units were pseudoreplicated within each tank (Hurlbert 1984), but colonies of all five species

Table 1 Environmental and chemical conditions for each treatment during the 56-d experimental period

Treatment	Temperature (°C)			pCO_2 (µatm)	DO (%)	pH_T	TA (µmol kg^{-1})
	Mean ± SE	Minimum	Maximum	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
Ambient	27.4 ± 0.01	25.7	29.9	460 ± 13	108.9 ± 1	8.01 ± 0.01	2181 ± 9
Acidified	27.4 ± 0.01	25.7	29.6	990 ± 86	106.9 ± 2	7.74 ± 0.03	2180 ± 11
Heated	29.7 ± 0.01	26.4	31.6	475 ± 12	109.9 ± 1	8.04 ± 0.01	2191 ± 9
Acidified heated	29.5 ± 0.01	26.4	31.8	1000 ± 76	111.9 ± 1	7.72 ± 0.03	2168 ± 9

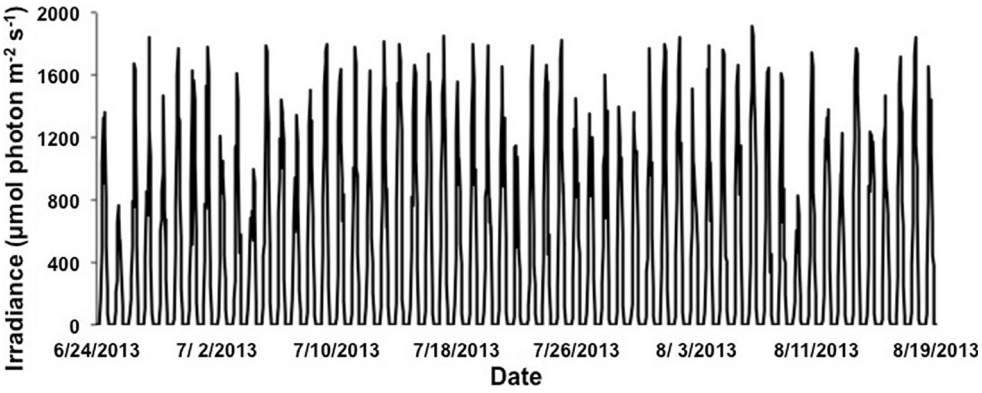

Fig. 1 Hourly irradiance levels measured continuously by cosine-corrected quantum sensor over a 56-d experimental period. Corals received maximum irradiance levels of 1914 µmol photon m^{-2} s^{-1} and mean net daily irradiance fluxes of 375.8 ± 8.8 mol photons m^{-2} d^{-1} (see Table 2)

Table 2 Irradiance characteristics for the 56-d experimental period

Maximum flux (µmol photons m^{-2} s^{-1})	Maximum daily flux (mol photons m^{-2} d^{-1})	Minimum daily flux (mol photons m^{-2} d^{-1})	Mean daily flux (mol photons m^{-2} d^{-1})
1914.0	498.5	176.1	375.8 ± 8.8

were randomly placed and each colony experienced the same conditions. The individual corals were functionally independent because the aggregated biomass (1 kg) was relativity small compared to the volume of seawater (500 L) and high turnover rates (8 L s^{-1}). We embrace the argument presented by Putnam and Edmunds (2011) that the coral fragments were not sufficiently large to change the water chemistry. In any event, all of the colonies within a treatment experienced the same physical, chemical, and biological conditions, so comparisons between species are valid.

The experimental treatments consisted of two pCO_2 levels: present-day Kāne'ohe Bay levels of 460 ± 13 µatm (mean ± SE) and double the present-day levels (990 ± 85 µatm), crossed with two temperature regimes of summer ambient 27.4 ± 0.01 °C and heated to 29.5 ± 0.01 °C (Table 1).

Chemical analyses

Midday water parameters [pH_{NBS}, salinity (‰), dissolved oxygen (% saturation), and temperature (°C)] were measured daily to confirm desired environmental and chemical conditions (Table 1). Measurements of pH_{NBS} were taken daily using an Accumet AP72 pH/mV/temperature meter (accuracy ±0.01 pH and ±0.02 mV) and confirmed spectrophotometrically twice a week using *m*-cresol purple dye (Sigma-Aldrich #857890) according to SOP 7 (Dickson et al. 2007). Total alkalinity (TA) was measured independently twice a week using an automatic titrator (Ttitrino Plus 877, Metrohm) with pH glass electrode (9101 Herisau, Metrohm) to verify the accuracy and precision of the pCO_2 manipulation mechanism (Jokiel et al. 2014a). Desired precision of the automatic titrator was confirmed with certified reference materials (Batch 127 from A. Dickson Laboratory, Scripps Institution of Oceanography) twice a week. Temperature, TA, pH_{Total}, and salinity were used to calculate pCO_2 in CO2SYS (Pierrot et al. 2006) with the stoichiometric dissociation constants (K1, K2) defined by Mehrbach et al. (1973) and refit by Dickson and Millero (1987). Daily irradiance reaching the corals within the mesocosms was measured using a cosine-corrected quantum sensor (LI-250A meter,

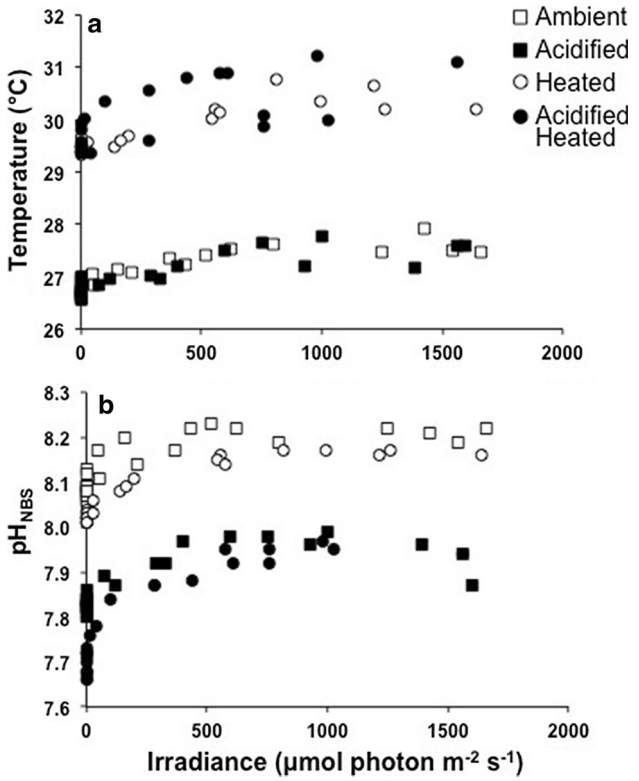

Fig. 2 **a** Temperature (°C) and **b** pH_{NBS} as a function of irradiance (µmol photon m^{-2} s^{-1}) in each experimental mesocosm: ambient (*open squares*), acidified (*solid squares*), heated (*open circles*), and acidified heated (*solid circles*)

LI-7792 sensor). Onset Hobo temperature loggers (UA-001-64, accuracy ±0.53 °C) were placed into each treatment, recording at 10-min intervals for the duration of the experiment. Additionally, diurnal variability in environmental parameters [pH_{NBS}, salinity (‰), dissolved oxygen (% saturation), and temperature (°C)] among treatments were confirmed by placing a YSI sonde (model 6920V2-S) in each mesocosm for a 24-h period programmed at 5-min intervals (Fig. 2; Electronic Supplementary Material, ESM, Table S1).

Calcification

Coral calcification rates (mm d^{-1}) were measured throughout the 56-d experimental period using the buoyant weight method (Jokiel et al. 1978). This technique is a nondestructive and sensitive measurement of the skeletal mass, which allows for multiple measurements over time. Corals ($n = 400$) were weighed every 2 weeks for 56 d. The initial and final buoyant weights were converted to dry skeletal weight for each species (Jokiel et al. 1978). These data were expressed as the mean solid radius, which uses cube-root approximation to compute a one-dimension linear estimate (Maragos 1978). Therefore, the calcification rate is expressed as a change in length of the radius rather than the weight change. This transformation permits comparison of colony calcification independent of corallum sizes and morphology (Maragos 1978).

Partial mortality

Partial mortality was defined as percentage of dead skeletal area on each coral colony. Partial mortality was scored in bins of 5 % twice per week. Values ranged from zero (no mortality) through various amounts of tissue loss (partial mortality) to 100 % (whole-colony mortality) (Baird and Marshall 2002). To reduce observer variability, two experienced investigators conducted repeated measures until estimated tissue loss was <5 %.

Statistical treatment of data

Coral calcification and partial mortality were measured throughout the 56-d experimental period. Mortality began after 42 d of exposure to the experimental treatments and proceeded rapidly. Therefore, coral calcification rates (mm d^{-1}) were analyzed at 42 d (no mortality) and at the end of the experiment (56 d). A two-way ANOVA model with fixed factors of pCO_2 and temperature by species was used to analyze the 42-d calcification data. Coral calcification at the end of the experiment was analyzed using a general linear model (GLM). Corals with high levels of partial mortality (>50 % tissue loss) at the end of the 56-d experiment were removed from the GLM calcification analysis. Type III sums of squares were used to estimate the main effect of the squared differences of the unweighted marginal means.

Mortality was analyzed at the end of the full 8-week experimental stress period. Because data were percentages, partial mortality data were adjusted using an arcsine cube-root transformation and subsequently analyzed using a two-way ANOVA model with fixed factors of temperature and pCO_2 by species. Assumptions of normal distribution and homoscedasticity were assessed through graphical analyses of the residuals. Descriptive and statistical analyses were conducted using JMP Pro 11 (SAS Institute Inc., USA).

Among the response variables, interactions between stressors were described as additive, synergistic, or antagonistic within each species (Schmidt et al. 2014). If both individual factors were significant and the interaction was not, the combined effects of the stressors were equal to the sum of the individual effects; therefore, the interaction was considered additive. In cases where the statistical model indicated a significant interaction between the stressors, the combined effects were assessed by the percentage change between the responses of the corals in the treatment (least squared means) compared with the response of the corals in

the control (27.4 °C, 460 µatm) within each species. If the combined effect exceeded the sum of the individual effects, the interaction was considered to be synergistic. Conversely, if the combined effect of the stressors was less than the sum of the individual effects, the interaction was considered to be antagonistic (Table 3).

Results

Treatment conditions

During the experiment, the corals received full natural solar radiation at midday maximum irradiance levels of 1914 µmol photons m^{-2} s^{-1} and mean net daily irradiance fluxes of 375.8 ± 8.8 mol photons m^{-2} d^{-1} (Fig. 1; Table 2). Manipulative treatments of temperature (one-way ANOVA; $F_{(3,187)} = 100.35$; $p = 0.6660$) and acidification (one-way ANOVA; $F_{(3,43)} = 34.02$; $p = 0.4746$) were not significantly different among mesocosms.

Calcification

Compared to control treatment (27.4 °C), increased temperatures (29.5 °C) significantly reduced calcification rates (pooled among pCO_2; $n = 80$, mean difference ± SE) in *P. damicornis* (−58 %; −0.20 ± 0.05 mm d^{-1}; $p < 0.0001$), *M. capitata* (−55 %; −0.15 ± 0.05 mm d^{-1}; $p < 0.0001$), and *P. compressa* (−89 %; −0.27 ± 0.05 mm d^{-1}; $p < 0.0001$) after 42 d of exposure (Fig. 3; ESM Table S2). Elevated temperatures did not have a significant effect on calcification of *F. scutaria* ($p = 0.108$) or *L. purpurea* ($p = 0.7114$). Increased pCO_2 to double the present-day levels significantly reduced calcification (pooled among temperature; $n = 80$) in *P. damicornis* (−28 %; −0.08 ± 0.03 mm d^{-1}; $p = 0.019$) and *P. compressa* (−92 %; −0.28 ± 0.05 mm d^{-1}; $p < 0.0001$) when compared to control corals (Table 3). The calcification rates of *F. scutaria* ($p = 0.070$), *L. purpurea* ($p = 0.279$), and *M. capitata* ($p = 0.056$) were not significantly suppressed under acidified conditions. Elevated temperatures and increased pCO_2 revealed an antagonistic interaction on the calcification response of *P. damicornis* with an average decline of 66 % (−0.28 ± 0.03 mm d^{-1}) (Table 3). Temperature and pCO_2 did not have a combined effect on the other tested species (Fig. 2; Table 3).

Over the 56-d exposure to experimental treatments, elevated temperature significantly reduced calcification rates (pooled among pCO_2) in *P. damicornis* (−69 %; −0.022 ± 0.003 mm d^{-1}; $n = 63$; $p < 0.0001$), *F. scutaria* (−23.9 %; −0.015 ± 0.004 mm d^{-1}; $n = 80$; $p = 0.0391$), and *M. capitata* (−67.4 %; −0.019 ± 0.002 mm d^{-1}; $n = 64$; $p < 0.0001$) (ESM Fig. S1; ESM Table S2). Increased pCO_2 significantly reduced calcification (pooled among temperature) in *P. damicornis* (−38.6 %; −0.009 ± 0.003 mm d^{-1}; $n = 63$; $p = 0.0372$) and *F. scutaria* (−26.4 %; −0.013 ± 0.004 mm d^{-1}; $n = 80$; $p = 0.0196$) (ESM Fig. S1; ESM Table S2). Statistical analysis of the 56-d calcification period revealed no significant interactions between elevated temperature and pCO_2 among tested species.

Table 3 Summary of the individual and combined effects of increased temperature and acidification stress on the biological responses of the tested coral species based on the statistical models given in ESM Table S1

Biological response	Summary of linear model results			Fractional changes compared to control			Additive interaction prediction	
Species	Temp	pCO_2	Temp × pCO_2	Temp	pCO_2	Temp × pCO_2	A + B − (A × B)	Combined effect
Calcification (mm d^{-1}) 42 d								
Pocillopora damicornis	**<0.0001**	**0.019**	**0.029**	−0.576	−0.289	−0.662	−1.031	Antagonistic
Fungia scutaria	0.180	0.070	0.293	n.a.	n.a.	n.a.	n.a.	n.a.
Leptastrea purpurea	0.416	0.279	0.073	n.a.	n.a.	n.a.	n.a.	n.a.
Montipora capitata	**<0.0001**	0.056	0.095	−0.549	n.a.	n.a.	n.a.	Only temp effect
Porites compressa	**<0.0001**	**<0.0001**	0.196	−0.892	−0.919	n.a.	n.a.	Additive
Partial Mortality (% dead skeletal area)								
Pocillopora damicornis	**<0.0001**	0.752	0.058	1.825	n.a.	n.a.	n.a.	Only temp effect
Montipora capitata	**<0.0001**	0.118	0.283	0.675	n.a.	n.a.	n.a.	Only temp effect
Porites compressa	**<0.0001**	**<0.0001**	**0.012**	0.649	0.715	2.543	0.900	Synergy

Interpretation of combined effects is based on calculated predicted additive inhibition based on the fractional changes of treated corals compared with control corals. N.A. indicates that the single factor and/or interaction terms are not significant. Significant p values ($p < 0.05$) are shown in bold type. There were no significant interactions between elevated temperature and pCO_2 among tested species, except in partial mortality of *P. compressa*

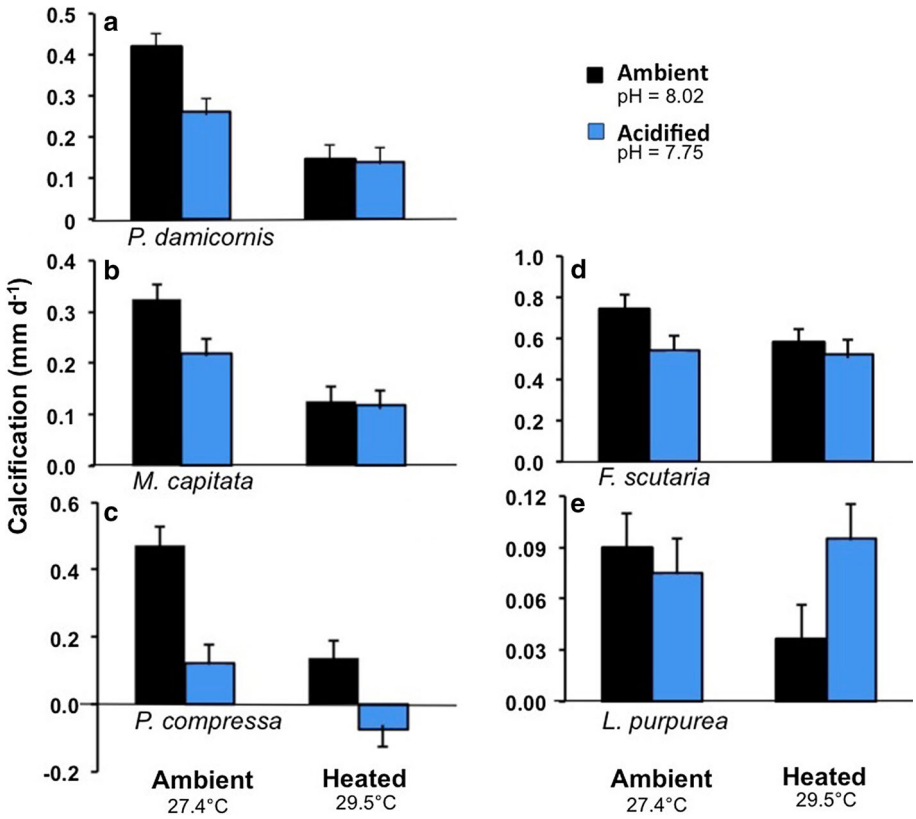

Fig. 3 Calcification (mm d^{-1}) of **a** *Pocillopora damicornis*, **b** *Montipora capitata*, **c** *Porites compressa*, **d** *Fungia scutaria*, and **e** *Leptastrea purpurea* after 42-d exposure to ambient (ambient, 27.4 ± 0.01 °C) and elevated temperatures (heated, 29.5 ± 0.01 °C) and ambient (*black bars*; pH 8.02 ± 0.01) and high pCO_2 (acidified; *blue bars*; pH 7.75 ± 0.03) conditions. *Error bars* represent standard error of mean ($n = 20$)

Partial mortality

At the end of the 56-d experimental period, mortality was not observed in *F. scutaria* ($n = 80$) or *L. purpurea* ($n = 80$). Elevated temperature caused high rates of tissue loss leading to significant increases in exposed dead skeleton (pooled among pCO_2; $n = 80$) in *P. damicornis* (183 %), *M. capitata* (67 %), and *P. compressa* (65 %) (Fig. 3; Table 3). Elevated pCO_2 (pooled among temperature; $n = 80$) increased dead skeletal area of *P. compressa* (71 %) (Table 3). Temperature and pCO_2 interacted synergistically in *P. compressa* ($p = 0.012$), increasing dead skeletal area by over 254 % in comparison with control corals (Fig. 4; Table 3). Elevated temperature and pCO_2 did not have a combined effect on the other species.

Discussion

Results of this experiment support observations that biological response of calcifying organisms to temperature and pCO_2 elevation is highly variable and species-specific (Rodolfo-Metalpa et al. 2010; Erez et al. 2011; Edmunds et al. 2012; Comeau et al. 2013b; Schmidt et al. 2014). In this study, increased temperature was the dominant factor controlling reef coral calcification and mortality, with increased pCO_2 playing a lesser role. Coral species' responses to pCO_2 and elevated temperatures acting independently and in unison varied across tested species. The synergistic effect between high temperature and high pCO_2 was weak or nonexistent among the five species tested. The interaction of elevated temperature and increased acidification showed a reduced effect on calcification rates of *P. damicornis* suggesting that acidification may ameliorate the effects of high temperature on this species. Conversely, the calcification rate of *M. capitata* was suppressed by high temperature and was not influenced by acidification. The individual effects of temperature and acidification suppressed calcification rates in *P. compressa*, but the effects were not further exacerbated by their interaction. Similarly, long-term exposure (56 d) to elevated temperature and acidification independently suppressed calcification rates in *F. scutaria*, but the response was not observed after 42 d of exposure. Mortality was mainly driven by high temperature, but interacted synergistically with pCO_2 in *P. compressa*. Elevated temperature and increased pCO_2 and their interaction did not influence the biological response of *L. purpurea*.

Thus, the combined effects of acidification and increased seawater temperatures revealed antagonistic, synergistic, and additive effects. A variety of interactive effects of temperature and pCO_2 have been reported for

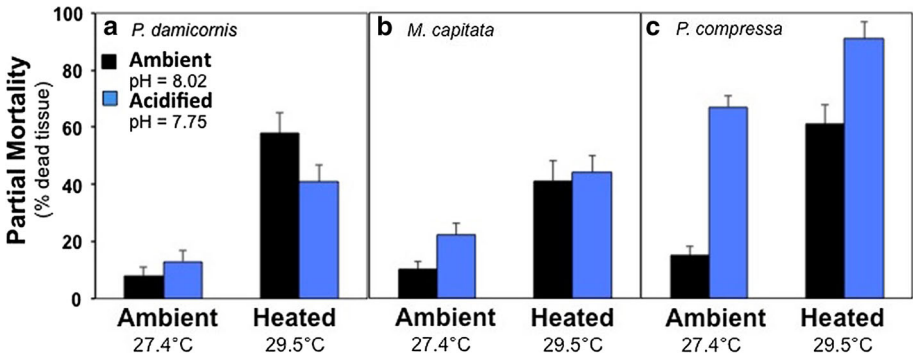

Fig. 4 Partial mortality (percent dead tissue) of **a** *Pocillopora damicornis*, **b** *Montipora capitata*, and **c** *Porites compressa* at the end of the 56-d experiment under ambient (ambient; 27.4 ± 0.01 °C) and elevated temperatures (heated; 29.5 ± 0.01 °C) and ambient (*black bars*; pH 8.02 ± 0.01) and high pCO_2 (acidified; *blue bars*; pH 7.75 ± 0.03) conditions. Mortality was not observed in *Fungia scutaria* or *Leptastrea purpurea*. *Error bars* represent standard error of mean ($n = 20$)

different species. For example, Reynaud et al. (2003) and Anlauf et al. (2011) showed negative synergistic effects of increased temperatures under acidification on *Stylophora pistillata* and *Porites panamensis*.

Increases in mortality resulted in unbalanced 56-d calcification data in *M. capitata*, *P. compressa*, and *P. damicornis*. This may lead to multicollinearity, therefore reducing the power of the design and making it possible to overlook the effects of the factors (Shaw and Mitchell-Olds 1993). Thus, we have focused on the interpretation of the 42-**d** calcification analyses for these species. No mortality was observed in *L. purpurea* or *F. scutaria*. Elevated temperature and acidification had no influence on the calcification rates of *L. purpurea* regardless of the length of exposure. Conversely, reductions in calcification were observed in *F. scutaria* after long-term exposure to elevated temperature and pCO_2.

The species responses observed in this study and others can be attributed to differences in properties of both the coral host and symbiont (Baird et al. 2009). These differences may include holobiont metabolism, heterotrophic carbon contribution capability (Grottoli et al. 2006), tissue composition and thickness (Hoegh-Guldberg 1999; Loya et al. 2001), mass-transfer rates (Nakamura and Van Woesik 2001), physiological and photosynthetic differences among the symbionts (Rowan and Powers 1991; Iglesias-Prieto and Trench 1994; Warner et al. 1996; Stimson et al. 2002; Baker 2003), species morphology (Loya et al. 2001), or other environmental and physiological conditions.

Branched corals appear to be more susceptible to thermal stress than massive and encrusting forms (Loya et al. 2001). For example, the hardy encrusting coral, *L. purpurea*, is found in extreme environments (e.g., tide pools, ship harbors, reef flats) (Coles et al. 1999; Bahr et al. 2015a) and has been shown to survive and increase in relative abundance during reoccurring thermal events (Loya et al. 2001; van Woesik et al. 2013). In addition, *P. damicornis* was susceptible to previous bleaching events in Hawai'i (Jokiel and Brown 2004; Bahr et al. 2015b) and prolonged exposure to high temperatures led to high mortality levels within 2 weeks (Mayfield et al. 2013). Elevated temperatures decrease the ratio of photosynthesis to respiration (Coles and Jokiel 1977). *Fungia scutaria* has higher ratios of photosynthesis to respiration, higher lethal temperatures, and higher rates of heterotrophy than *M. capitata* and *P. damicornis* (Coles and Jokiel 1977). *Montipora capitata* and *P. compressa* exhibited different lipid compositions and lipid depletion rates following a bleaching event (Grottoli et al. 2006). *Montipora capitata* was better able to support daily metabolic energy requirements by its relatively low respiration rate and heterotrophic carbon contribution capability in comparison with *P. compressa*. Additionally, *F. scutaria* completely bleached during this experiment and was only significantly affected after long-term exposure to elevated temperature or increase pCO_2. Recovery of *F. scutaria* was observed within 60 d after the stressors were removed. Therefore, in corals with low respiration rates and high heterotrophic capability, lipid reserves may be able to offset energetic costs of high temperature.

High pCO_2 may reduce calcification through increased metabolic cost and photochemical impairment (Edmunds 2012). Therefore, faster growing corals may be more vulnerable to acidification (Jokiel 2011; Comeau et al. 2013a; Jokiel et al. 2014b). The faster growing corals (*P. damicornis*, *P. compressa*) in this experiment were more susceptible to acidification stress and temperature stress. *Montipora capitata*, *F. scutaria*, and *L. purpurea* showed low sensitivity to high pCO_2, which agrees with results reported for other species including additionally fed massive *Porites* spp. (Edmunds 2012), the temperate coral

Cladocora caespitosa (Rodolfo-Metalpa et al. 2010), and *Stylophora pistillata* (Reynaud et al. 2003). Lack of sensitivity in a species may be attributed to higher heterotrophic capability, lower respiration rates, and lower calcification rates, which are more dependent on temperature. Coral species with these attributes (high rates of heterotrophy and lower respiration rates) may have an ecological advantage over other species under these conditions. Coral populations that have the ability to feed heterotrophically, compile large lipid reserves, and reduce their metabolic rate may display high resistance and resilience to climate change stressors (Grottoli et al. 2006; Cohen and Holcomb 2009). This may lead to a species composition shift on future reefs (Grottoli et al. 2006).

Variation in the biological response to temperature and pCO_2 stressors may lie in regulation of material fluxes between the coral boundary layers as well as energy allocation and storage. Environmental variability may also influence conflicting results among experiments. Irradiance has been shown to interact with temperature as well as pCO_2 to produce variability in the biological response of corals (Jokiel and Coles 1977; Dufault et al. 2013; Suggett et al. 2013). Therefore, further experimentation is needed to test the interactive effects of temperature, pCO_2, and irradiance in combination. Conclusions on the biological response of corals to future climate change conditions drawn from manipulative experiments with unnatural physical and chemical water conditions may be misleading (Edmunds et al. 2012). It is therefore important to consider the extent of the experimental manipulations, degree of manipulation, the duration of the experiment, and irradiance regimes in biological responses to climate change stressors.

In general, increased seawater temperatures played the dominant role in influencing coral calcification and mortality among the tested Hawaiian species. The overall response of this five-species mixed coral community was negative as shown by decreased calcification and increased mortality among many of the species. Biological response to temperature and pCO_2 elevation is highly species-specific, so care must be taken when applying generalizations based on response of a single species to diverse and complex coral reef communities.

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