



Seasonal and annual calcification rates of the Hawaiian reef coral, *Montipora capitata*, under present and future climate change scenarios

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The response of corals to future conditions of global warming and ocean acidification (OA) is a topic of considerable interest. However, little information is available on the seasonal interaction between temperature, $p\text{CO}_2$, and irradiance under ecologically relevant experimental conditions. Controlled experiments were performed in continuous-flow mesocosms under full solar radiation to describe the direct and interactive effects of temperature, irradiance, and $p\text{CO}_2$ on growth of a Hawaiian reef building coral (*Montipora capitata*) over an annual cycle. Corals were subjected to 12 experimental treatments consisting of two $p\text{CO}_2$ levels (present-day levels, $2 \times$ present), two temperature regimes (ambient, heated $+2^\circ\text{C}$), and three conditions of irradiance (ambient, 50 and 90% reduction). A multiple polynomial regression model with full factorial fixed factors (temperature, $p\text{CO}_2$, irradiance) was developed. Temperature and irradiance were the primary factors driving net calcification (G_{net}) rates of *M. capitata*, with $p\text{CO}_2$ playing a lesser role. G_{net} showed a curvilinear response to irradiance and temperature, which defines thresholds at the end members. Also, high irradiance regimes under elevated temperatures showed a negative synergistic effect on G_{net} . Therefore, decreasing irradiance penetration resulting from greater depth and/or higher turbidity will lower the impact of ocean warming on *M. capitata*. Results suggest that under future climate conditions, the interaction of environmental parameters may shift seasonal patterns in G_{net} and timing of growth optima for *M. capitata*. Ocean warming in shallow water environments with high irradiance poses a more immediate threat to coral growth than acidification for this dominant coral species. In the future, increased temperature and the interaction between high irradiance and high temperature will be the main factors controlling G_{net} with OA playing a less important role. This observation is congruent with other reports that high temperature combined with high irradiance is the main cause of high coral mortality during mass bleaching events.

Keywords: climate change, coral reefs, irradiance, ocean acidification, ocean warming.

Introduction

One of the greatest contemporary ecological, social, and economic issues is the problem of climate change. Increasing levels of carbon dioxide (CO_2) in the atmosphere from the burning of fossil fuels is a major cause of increasing global temperatures. Approximately one-third of the CO_2 resulting from combustion of fossil carbon dissolves in the ocean, creating more acidic conditions and leading to a process known as ocean acidification (OA). Ocean acidity has increased by $\sim 25\%$ (decrease of 0.1 pH units) since preindustrial times (Lacis *et al.*, 2010) and has resulted in severe negative effects on calcifying organisms (Kleypas *et al.*, 2005; Jokiel *et al.*, 2008;

Erez *et al.*, 2011; Kroeker *et al.*, 2013). Additionally, increased production of anthropogenic gases and the “greenhouse effect” is responsible for large-scale thermal bleaching throughout the world (Hoegh-Guldberg, 1999; Pittock, 1999). Sea surface temperatures have increased by 0.7°C over the past several decades on various coral reefs throughout the world (Fitt *et al.*, 2001). Temperatures have increased 1.15°C in offshore waters of Hawai'i over the past 58 years, making these corals more vulnerable to elevated temperature stress (Bahr *et al.*, 2015). Changes in these environmental parameters that influence coral calcification rates will have serious implications on the abundance and distribution of coral reefs in the future.

Coral reef calcification rate is predicted to decrease by 20–60% by 2100, relative to preindustrial levels (Kleypas *et al.*, 1999; Müller *et al.*, 2004) due to increases in OA and global warming. Calcification rates of Hawaiian corals increase with increasing seawater temperature to an optimal temperature of 27°C (Jokiel and Coles, 1977), with rapidly decreasing growth above the optimum temperature. At temperatures 1–2°C above optimum, corals lose their algal symbionts through a process termed bleaching, which results in decreased calcification and increase mortality (Coles *et al.*, 1976). 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 (Bahr *et al.*, 2015). Further increases in CO₂ production and subsequent increases in sea surface temperatures will lead to more frequent, extensive, and severe bleaching events in the future (Buddemeier *et al.*, 2004; Jokiel and Brown, 2004; Hoegh-Guldberg *et al.*, 2007; Bahr *et al.*, 2015). As sea surface temperatures and *p*CO₂ increase simultaneously, future light availability to reefs will change as the physical nature of reef environments is altered by enhanced river run-off and sedimentation, sea level rise (Baker *et al.*, 2008), and cloud cover (Wild *et al.*, 2011). Reef coral calcification is fundamentally limited by light availability (Kleypas *et al.*, 1999; Yentsch *et al.*, 2002; Suggett *et al.*, 2012). Solar irradiance has been shown to interact with temperature as well as OA to produce variability in the biological response of corals (Jokiel and Coles, 1977; Suggett *et al.*, 2012; Dufault *et al.*, 2013). However, the importance of the interaction between irradiance, elevated temperatures, and increasing OA warrants further investigation (Suggett *et al.*, 2012). During a recent coral bleaching event in Hawai'i, corals in higher irradiance environments were observed to be more susceptible to bleaching (Bahr *et al.*, 2015). Conversely, corals in deeper water or under turbid conditions showed lower levels of bleaching. Therefore, it has been suggested that deeper coral ecosystems may provide a refuge from temperature–irradiance stress, as well as act as a buffer from several human and natural disturbances that predominantly affect shallow reefs (Bridge *et al.*, 2013). Nevertheless, more experimental data are needed.

Consequently, it is essential to assess direct impacts of multiple stressors (ocean warming, OA, and irradiance) to determine if the combined effects of high irradiance, increased temperature, and decreased pH exceed (i.e. are synergistic) or are less than (i.e. are antagonistic) the sum of their individual effects. The objective of this study was to describe the direct and interactive effects of temperature, irradiance, and *p*CO₂ on the net calcification (G_{net}) of a Hawaiian reef building coral, *Montipora capitata*, across seasonal and temporal scales that consider past, present, and future conditions. Extensive controlled multifactorial growth experiments were undertaken over a period of 2 years to unravel the interactions between these important environmental factors and to allow for the development of a biological model of coral response to changing ocean climate.

Methods

Experimental system

This research was conducted at University of Hawai'i's Hawai'i Institute of Marine Biology (HIMB) at Moku o Lo'e, Kāne'ohe Bay, Hawai'i (21.4°N, 157.8°W) in a mesocosm system that mimics the physical, chemical, and biological conditions on a reef under present and projected conditions of climate change (Jokiel *et al.*, 2008, 2014; Kuffner *et al.*, 2008). Experiments were conducted in

1 × 1 × 0.5 m fiberglass mesocosms, located in full natural sunlight and supplied with unfiltered seawater pumped continuously from 3 m depth in Kāne'ohe Bay. Flow was maintained at a rate of 8 l min⁻¹ resulting in a seawater turnover rate of 45 min. The seawater inflow configuration allows for a uniform and well-mixed system as documented with measurements of chemical and environmental parameters (Andersson *et al.*, 2009). The continuous-flow experimental system duplicates the natural diurnal and seasonal fluctuations in seawater chemistry that occur on the adjacent inshore reef.

Experimental design

The experimental design of this study aimed to quantify net calcification (G_{net}) under realistic seasonal conditions at present and under mid-century RCP 8.5 “worse case scenario projections” (Stocker *et al.*, 2013). The experimental treatments assumed that future conditions during each season can be represented by simply heating the water by +2°C throughout the year and doubling *p*CO₂ compared with ambient present-day conditions (Table 1). To account for seasonal changes in other parameters (e.g. daylength, cloud cover, irradiance, temperature, salinity, nutrient, etc.) the manipulated conditions were always conducted alongside reference treatments, which were always the present-day conditions in Kāne'ohe Bay. This approach embraces the extensive seasonal variation inherent in all environmental factors and thus requires an extremely large sample size to statistically identify the direct and indirect effects of temperature, irradiance, and *p*CO₂ on G_{net} .

Colonies of the Hawaiian reef coral, *M. capitata*, were collected from the adjacent reef flat and subjected to 12 experimental regimes consisting of 2 temperature levels (ambient and +2°C), 2 *p*CO₂ regimes (ambient and 2 × ambient), and 3 ambient irradiance conditions (ambient, 50% reduction, and 90% reduction) (Table 1). The split-plot experimental design consisted of four mesocosms with two elevated temperature and two acidified regimes (whole-plot factor). Within each mesocosm, three irradiance regimes were established using neutral density filters (split-plot factor; Jones and Nachtshiem, 2009). Ten corals were grown under each split-plot factor with the mean G_{net} ($n = 10$ corals) determined for each treatment. Corals were acclimated to the experimental conditions for 2 weeks before initiating the measurements. The experiment was replicated in time (seven replicates) to describe seasonality in G_{net} at present-day and future climate change scenarios. Coral growth (G_{net}) was measured twice a month during each 28-d experimental period using the buoyant weighing method (Jokiel *et al.*, 1978). The initial buoyant weight was subtracted from and final buoyant weight and divided by days of growth for the measure of increase dry skeletal weight (Jokiel *et al.*, 1978).

Experimental treatments

Carbonate chemistry within the mesocosms was manipulated through direct bubbling of CO₂ (Jokiel *et al.*, 2014) and temperature was controlled using titanium heaters (Finnex[®], TH-800, 800 W). Irradiance (split-plot factor) was manipulated using neutral density screen covering, in which shade cloths covered part of each temperature–*p*CO₂ tank (whole-plot factor) so that organisms under each shade regime experienced the same temperature and *p*CO₂ but with different irradiance levels.

Daily mid-day (11:00–13:00 h) water parameters [*p*H_{NBS}, salinity (‰), dissolved oxygen (% saturation), and temperature (°C)] were measured to confirm desired environmental and chemical

Table 1. Environmental and chemical parameters for each experiment conducted during August 2012–September 2014.

Experiment	Season	Treatment	Temperature (°C) Mean ± s.e.	pCO ₂ (µatm) Mean ± s.e.	Irradiance (µmol photon m ⁻² s ⁻¹)		
					Ambient Mean ± s.e.	50% reduction Mean ± s.e.	90% reduction Mean ± s.e.
1	Summer	AT, ACO ₂	27.60 ± 0.02	520.10 ± 10.93	468.79 ± 14.86	234.40 ± 7.43	37.50 ± 2.41
		HT, ACO ₂	30.36 ± 0.02	548.80 ± 13.19			
		HT, HCO ₂	30.00 ± 0.01	1288.80 ± 50.15			
2	Winter	AT, ACO ₂	23.53 ± 0.01	545.24 ± 13.02	219.25 ± 15.47	109.63 ± 7.73	17.54 ± 2.54
		AT, HCO ₂	23.54 ± 0.01	863.25 ± 77.47			
		HT, ACO ₂	24.99 ± 0.02	599.69 ± 13.43			
3	Winter	HT, HCO ₂	25.26 ± 0.02	994.70 ± 114.94	354.20 ± 17.15	177.10 ± 8.57	28.34 ± 3.15
		AT, ACO ₂	22.72 ± 0.01	552.78 ± 35.95			
		AT, HCO ₂	22.69 ± 0.01	1141.95 ± 144.79			
4	Winter	HT, ACO ₂	25.32 ± 0.02	580.89 ± 22.72	366.12 ± 24.84	183.06 ± 12.42	29.29 ± 2.38
		HT, HCO ₂	24.88 ± 0.02	1689.69 ± 225.96			
		AT, ACO ₂	23.92 ± 0.02	491.56 ± 16.69			
5	Summer	AT, HCO ₂	24.05 ± 0.01	1068.47 ± 73.62	414.92 ± 16.37	207.46 ± 8.18	33.19 ± 1.31
		HT, ACO ₂	26.74 ± 0.02	593.92 ± 21.52			
		HT, HCO ₂	26.48 ± 0.01	1152.7 ± 183.96			
6	Summer	AT, ACO ₂	27.37 ± 0.01	574.37 ± 19.11	397.32 ± 19.10	198.66 ± 9.36	31.79 ± 2.17
		AT, HCO ₂	27.04 ± 0.01	985.62 ± 87.71			
		HT, ACO ₂	30.49 ± 0.02	525.15 ± 51.79			
7	Summer	HT, HCO ₂	30.71 ± 0.02	1229.45 ± 149.11	386.38 ± 11.00	193.19 ± 5.26	30.91 ± 1.07
		AT, ACO ₂	27.09 ± 0.01	497.68 ± 41.65			
		AT, HCO ₂	27.15 ± 0.01	951.78 ± 81.27			
		HT, ACO ₂	29.05 ± 0.01	484.69 ± 43.32			
		HT, HCO ₂	29.07 ± 0.01	1142.58 ± 117.63			
		AT, ACO ₂	28.87 ± 0.01	559.40 ± 17.94			
		AT, HCO ₂	28.83 ± 0.01	1378.90 ± 187.92			
		HT, ACO ₂	30.71 ± 0.02	611.91 ± 9.25			
		HT, HCO ₂	30.65 ± 0.02	1493.40 ± 222.03			

Treatments included: ambient temperature, ambient pCO₂ (AT, ACO₂); ambient temperature, high pCO₂ (AT, HCO₂); high temperature, ambient pCO₂ (HT, ACO₂); high temperature, high pCO₂ (HT, HCO₂).

conditions. Desired pCO₂ regimes were confirmed daily by an Accumet[®] AP72pH/mV/temperature meter (pH_{NBS}) and twice a week spectrophotometrically (pH_{Total}) using *m*-cresol purple dye (Sigma-Aldrich[®] #857890) according to SOP 7 (Dickson *et al.*, 2007). Total alkalinity was measured independently twice a week using an automatic titrator (Titrimo[®] Plus 877, Metrohm) with pH glass electrode (9101 Herisau, Metrohm[®]). The precision of the automatic titrator was confirmed with certified reference materials (CRM) (Batch 127 from A. Dickson Laboratory, Scripps Institution of Oceanography) twice a week. Temperature, total alkalinity, pH_{Total}, and salinity were used to calculate pCO₂ in CO2SYS (Pierrot *et al.*, 2006) with the stoichiometric dissociation constants (K_1 , K_2) defined by Mehrbach (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, LI-7792 sensor). Onset[®] Hobo temperature loggers (UA-001-64, accuracy ± 0.53°C) were placed into each treatment, recording at 15 min intervals for the duration of the experiment.

Statistical approach

This study embraced a full factorial split-plot design in which the whole-plot (mesocosm) and split-plot (irradiance) factors were completely randomized. Ten small colonies (~8 cm diameter) were grown under each experimental treatment for a 28-d period. Different coral colonies were used and randomly assigned to each experimental treatment. The treatments were repeated seven times

throughout the various seasons characterized by different ambient temperatures, pCO₂, and irradiance regimes ($n = 810$ corals). The mean coral response ($n = 10$) in each treatment was used to calculate the mean G_{net} for each treatment ($n = 81$) to avoid within-treatment pseudoreplication. The mean G_{net} for each treatment was analysed with a multiple polynomial regression model that included interaction terms. The model encompassed a full factorial of fixed factors (i.e. temperature, pCO₂, irradiance) and their interactions as well as quadratic terms for temperature and irradiance designed to model curvature of the line fitted to the data (Table 2). The tank effect was dropped from the analyses because it was not significant at $p > 0.250$ (Quinn and Keough, 2002). Non-significant terms were also dropped from the model. All terms were continuous variables. Assumptions of normal distribution, homoscedasticity, and multivariate normality were assessed through graphical analyses of the residuals. A mean-centred regression was used to reduce multicollinearity among predictor variables. All statistical analyses were processed using JMP Pro 11 software (SAS Institute Inc., Cary, NC, USA).

The regression model output was used to generate *M. capitata* G_{net} under past (1945–1960), present, and future conditions. G_{net} values were generated by the polynomial regression analysis using baseline parameters from 1945 to 1960 for historical mean monthly temperature values (US Department of Commerce, 1970) and mean monthly environmental parameters for present values in Kane'ohe Bay. Future values were estimated using projected RCP 8.5 scenarios.

Results

Multiple polynomial regression analyses were conducted to examine the influence of temperature, irradiance, and $p\text{CO}_2$ on G_{net} . Table 2 summarizes the descriptive statistics and analysis results. The full factorial multiple polynomial regression model included the predictor

terms (temperature, irradiance, and $p\text{CO}_2$) as well as the quadratic terms for temperature and irradiance [$R^2 = 0.734$, $F_{(9,71)} = 21.79$, $p < 0.0001$; Table 2]. The effect of $p\text{CO}_2$ acting alone and/or with other predictors did not contribute to the multiple regression model (Table 2). Therefore, G_{net} of *M. capitata* is best predicted by

Table 2. Multiple regression model analysis of the mean G_{net} response of *M. capitata* to multifactorial treatments of temperature and irradiance.

Factor	Estimate	s.e.	t	p-value	R^2
Intercept	6.056	0.7800	7.98	<0.0001	0.719
Temperature	-0.1542	0.0288	-5.20	<0.0001	
Irradiance	0.0056	0.0005	10.60	<0.0001	
Temperature \times irradiance	-0.0006	0.0002	-3.10	0.0020	
Temperature ²	-0.082261	0.012587	-6.48	<0.0001	
Irradiance ²	-2.232E-05	4.37E-06	-5.20	<0.0001	

Factors including $p\text{CO}_2$ were not significant and were removed from the final model. Full model is located in Supplementary material. Significant effects at the level of $\alpha < 0.05$ are in bold.

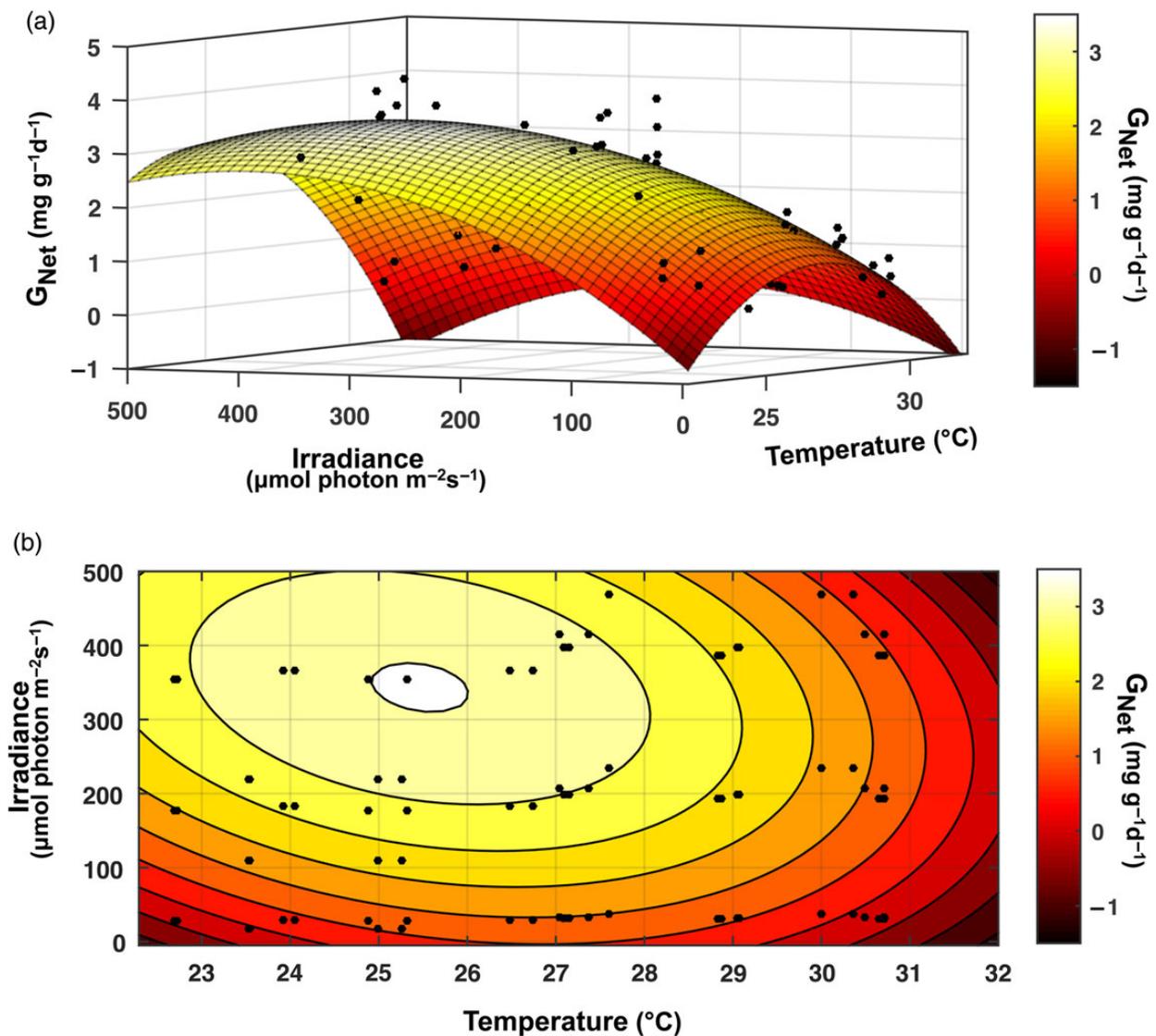


Figure 1. (a) Surface plot of net calcification (G_{net}) of *M. capitata* as a function of temperature ($^{\circ}\text{C}$) and irradiance ($\mu\text{mol photon m}^{-2}\text{s}^{-1}$). (b) Contour curve representation of the functional response of net calcification (G_{net}) of *M. capitata* (color map) at predicted combination of temperature and irradiance regimes. The colormap indicates positive and negative G_{net} by light and dark hues, respectively. Residual values are indicated by black dots. This figure is available in black and white in print and in colour at ICES Journal of Marine Science online.

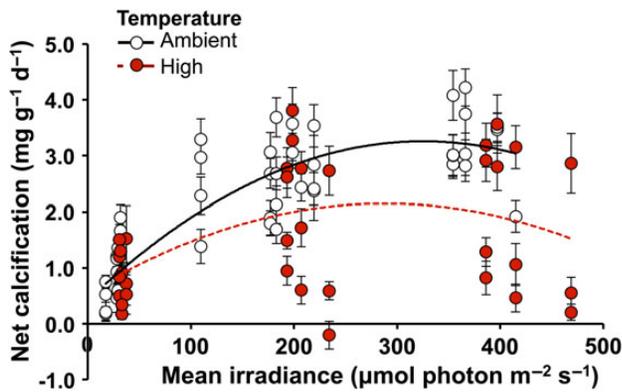


Figure 2. Net calcification (G_{net}) of *M. capitata* vs. mean irradiance at optimal ambient temperatures (23–27°C, open circle) and suboptimal high temperatures (27–31°C, solid circles) under ambient $p\text{CO}_2$ regimes. The mean irradiance measured at 1 h intervals between 6 a.m. and 6 p.m. Error bars represent \pm s.e. of the mean. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

the interaction of temperature and irradiance as well as their quadratic terms [$R^2 = 0.719$, $F_{(5,75)} = 38.29$, $p < 0.0001$; Table 2; Figure 1].

Temperature ($p < 0.0001$) and irradiance ($p < 0.0001$) showed a significant negative curvilinear relationship with G_{net} (Table 2). The highest G_{net} rates defined the optimal temperature and irradiance levels, while lower G_{net} rates occurred under the extreme end-member conditions (Figure 1).

Temperature and irradiance interacted synergistically on G_{net} ($p < 0.0001$), indicating a significant reduction at elevated temperatures under high irradiance regimes (Table 2; Figure 2). The significant polynomial terms of temperature and irradiance indicate the effect of changing the predictor varies depending on the value of that predictor. Similarly, the significant interaction term between irradiance and temperature indicates that the effect of each predictor on G_{net} depends on the value of the other predictor. The multiple regression analysis did not include mortality because mortality did not occur in these experiments.

Calcification response to temperature revealed a parabolic response that increased from 23 to 26°C, reached a maximum at 26.5°C and then decreased at temperatures above 26.5°C. This relationship varied under the irradiance regimes and was slightly suppressed ($p = 0.1066$) under high $p\text{CO}_2$ conditions (Figure 1). Maximum G_{net} occurred at 350 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ under ambient temperatures and 250 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ under elevated (ambient +2°C) temperatures (Figure 2).

Discussion

Results of this experiment reveal temperature and irradiance to be the primary factors driving G_{net} of *M. capitata*, with $p\text{CO}_2$ playing a lesser role. G_{net} showed a curvilinear response to irradiance and temperature, which defined thresholds at the extremes. High irradiance regimes under elevated temperatures produced a negative synergistic effect on G_{net} . Therefore, lower light penetration resulting from increasing depth and/or higher turbidity will lower the impact of ocean warming on *M. capitata*. These observations agree with the results of Castillo *et al.* (2014) who showed that both acidification and temperature produce a parabolic response in the G_{net} of *Siderastrea siderea* corals and that ocean warming

poses a more immediate threat to corals than OA. Their work did not consider interactions with irradiance.

The regression model output reveals shifts in optimum growth conditions of *M. capitata* across irradiance regimes under past, present, and future conditions (Figure 3). The model parameters show that historical (1945–1960) G_{net} was suppressed during winter with higher growth in summer. The model indicates that recent increases in sea surface temperatures have increased present-day G_{net} in winter; however, increases in G_{net} during summer have not occurred apparently due to the negative synergy between irradiance and temperature. The model projects that under RCP 8.5 scenarios G_{net} of *M. capitata* at mid-century and end of century will be hindered during summer and increased in winter. Studies of coral growth banding have become an essential ecological and paleo-ecological tool (Knutson *et al.*, 1972; Buddemeier *et al.*, 1974). This model suggests a shift in seasonal growth patterns in *M. capitata* will occur under future climate change scenarios, which may reverse high- vs. low-density seasonal coral banding patterns. G_{net} values produced in this experiment focused on the physiological growth response over a 28-d exposure. Mortality did not occur. However, from an ecological point of view, prolonged high temperature anomalies during summer will impact coral mortality as well as growth and thereby ultimately control coral distribution and abundance (Buddemeier *et al.*, 2008; Hoeke *et al.*, 2011). Buddemeier *et al.* (2008) emphasized the importance of both seasonal and inter-annual sea surface temperature variability. Coral growth is controlled by temperature in these models. However, the probability of bleaching events with massive coral mortality increases with prolonged exposure to elevated temperature. Such high-temperature events are not well constrained or readily predicted, but will increase in frequency and severity with consequent major impacts on coral survival.

Water temperatures in Hawai'i during winter were suboptimal (below 27°C) prior in the past century. These low temperatures limited coral growth. Warming of waters in this century has enhanced growth across irradiance levels (Figure 3). The primary factor controlling coral populations in the future will be coral mortality caused by short-term high-temperature excursions (i.e. bleaching events). The presented model does not account for such mortality. Therefore, if taken out of context, these results could imply that future warming will be beneficial to coral growth in Hawai'i because growth increase in winter will offset high-temperature reduction in summer. The growth response is curvilinear, so shifting temperature upwards across all 12 months will increase growth rate during months below the temperature optimum (27°C) while further decreasing growth for months above the optimum (Figure 3). Note that differences in monthly growth patterns occur at different irradiance levels. The most interesting observation is that resulting annual coral growth increases under future scenarios of warming at low irradiances, but corals grown at 50 and 90% reductions showed curvilinear response with temperature and decreasing growth under future scenarios (Figure 4). The results in Figures 3 and 4 must be viewed with caution. The primary effect of global warming on coral populations is the massive coral mortality during high-temperature mass bleaching events as predicted by the COMBO model (Buddemeier *et al.*, 2008) and as observed in Hawai'i (e.g. Jokiel and Brown, 2004; Bahr *et al.*, 2015). Therefore, the growth data presented here can be misleading if we do not take into account future anomalously high-temperature excursions and associated coral mortality that will greatly influence mortality, especially at high-irradiance regimes.

Results of this work are consistent with the classic observation that the distribution of reef corals in the ocean is controlled

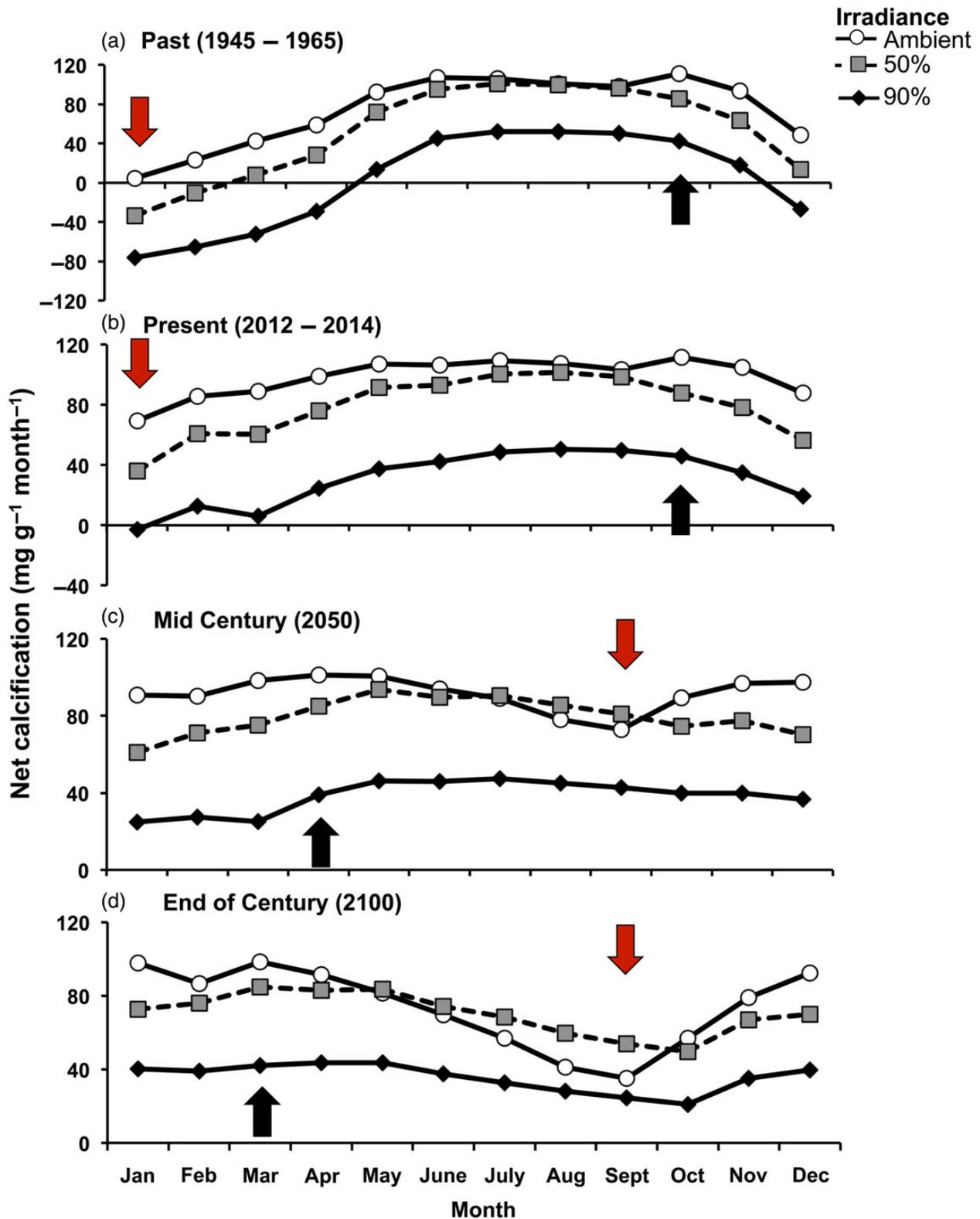


Figure 3. Net calcification (G_{net}) for *M. capitata* in Kāneʻohe Bay, Hawaiʻi, under past (a), present (b), and under projected climate change scenarios for mid-century (c) and end of the century (d) under ambient (open circles), 50% (shaded squares) and 90% (solid diamonds) reduction in irradiance. Maximum G_{net} values are indicated by black arrows and minimum G_{net} values are indicated by a red arrow. G_{net} values were generated by the multiple polynomial regression analysis using baseline parameters from 1945 to 1960 for past values and mean monthly environmental parameters for present values. Future values were estimated using projected RCP 8.5 scenarios. This figure is available in black and white in print and in colour at ICES Journal of Marine Science online.

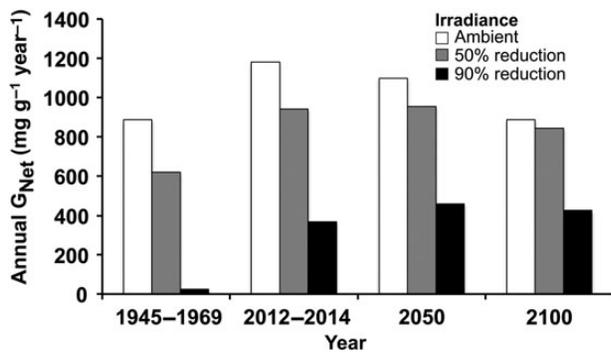


Figure 4. Annual net calcification budget for *M. capitata* at ambient (open bars), 50% reduction (shaded bars), and 90% reduction (solid bars) irradiance attenuated regimes under past (1945–1969), present (2012–2014), and under projected climate change scenarios for mid-century (2050) and end of the century (2100).

primarily by temperature and irradiance (Wells, 1957). Failure to recognize the curvilinear relationship between temperature and G_{net} can lead to spurious conclusions. McNeil *et al.* (2004) published a model based on the assumption that calcification increases linearly with increasing temperature and predicted an increase in G_{net} reef calcification rate of 35% by the year 2100. This model assumed that physical chemistry drives calcification and did not consider the curvilinear response of G_{net} that declines sharply above peak summer temperature due to physiological limitations with bleaching and eventual death of corals under future temperature scenarios (Kleypas *et al.*, 2005). In another example, a model of G_{net} based on enhanced thermal kinetics of calcification has been proposed (McCulloch *et al.*, 2012). This model describes the effect of increased temperature on abiotic processes in the calcifying fluid located in the space between calicodermis and the skeleton. The authors concluded that the increase in calcification due to global warming will accelerate chemical reactions in the calcifying fluid which in turn will outweigh the negative effects of declining $[\text{CO}_3^{2-}]$. They acknowledged that extensive biological experimental and observational data do not support their model, and concluded that the fate of corals will ultimately depend on biochemical processes. The results of our work are in agreement with others (Cox, 1971; Clausen and Roth, 1975; Jokiel and Coles, 1977; Marshall and Clode, 2004; Buddemeier *et al.*, 2008; Cantin *et al.*, 2010; Castillo *et al.*, 2014) which show a parabolic rather than a linear response of G_{net} to temperature.

Future projections of the impacts of climate change on coral reefs are inconsistent (Jokiel, 2016). Modelling future reefs should consider interactions between climate change stressors and other abiotic (e.g. dissolved oxygen, UV radiation, water flow) and biotic factors (e.g. competition and predation) as well as anthropogenic influences (e.g. sedimentation, dredging, sunscreen, oil spills, etc.) that may positively or negatively influence corals (Van Katwijk *et al.*, 1993; Torres, 2001; Fabricius, 2005; Jones, 2005; Langdon and Atkinson, 2005; Haapkylä *et al.*, 2007; Anthony *et al.*, 2008; Danovaro *et al.*, 2008; Jokiel *et al.*, 2008). Additionally, seasonality in environmental parameters (i.e. temperature and irradiance) will directly influence calcification rates. Moreover, the biological response of calcifying organisms to elevated temperature and CO_2 is highly variable and species-specific (Rodolfo-Metalpa *et al.*, 2010; Erez *et al.*, 2011; Edmunds *et al.*, 2012; Comeau *et al.*, 2013; Schmidt *et al.*, 2014; Bahr *et al.*, 2016). Calcium carbonate dynamics

(i.e. dissolution) and other ecosystem processes may also influence calcification rates and account for additional inconsistencies among experimental and field observations (Pandolfi *et al.*, 2011; Jokiel, 2016). A more unified model that includes thermal specialization, resource allocation trade-offs, and adaptations to local environments using experimental and observational data may give realistic insights to response of corals in the changing ocean climate (Evenhuis *et al.*, 2015).

Coral reefs are threatened by a multiple anthropogenic stresses, including overfishing, pollutants from sewage and agriculture, invasive species, sedimentation and run-off, dredging, and mechanical damage from dynamite fishing and recreational activities. However, these threats and endangerments are magnified by additional stress from climate change. Thus, it must be emphasized to understand current and future reef development in our changing ocean climate and identify the factors that influence G_{net} rates of corals and how these factors interact under future climate change scenarios (Langdon and Atkinson, 2005). The physiological response of *M. capitata* to elevated temperature and $p\text{CO}_2$ under various irradiance regimes over a seasonal cycle reveals insights into the importance of seasonal variability and interactions among these environmental factors. We conclude that models developed to predict the impact of future climate change on reef corals must consider that G_{net} shows a parabolic response to irradiance and temperature, which define growth thresholds at the end members. Increased temperature and the interaction between high irradiance and high temperature are the dominant factors controlling coral growth with OA playing a less important role. Therefore, in the future, corals growing in shallow, high light intensity environments will be more vulnerable to ocean warming.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

Authors' contributions

KDB designed and carried out the experiments as well as analysed and interpreted the data and wrote the manuscript. PLJ made substantial contributions to the conception and design as well as revised the article and provided facilities and support for the project. KSR helped collect data, maintain experiments, revised drafts of the manuscript, and provided important intellectual content. All authors had final approval of the version to be published.

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