

## CORRECTION

# Correction: Size-dependent physiological responses of the branching coral *Pocillopora verrucosa* to elevated temperature and $P_{\text{CO}_2}$ (doi:10.1242/jeb.146381)

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There was an error published in *J. Exp. Biol.* (2016) **219**, 3896-3906 (doi:10.1242/jeb.146381).

In Table S1, some of the values were incorrectly assigned to tank treatments and were averaged over an incorrect period that did not correspond to the number of days from the beginning to the end of the experiment. This error does not affect the conclusions of the experimental work, and the values have been corrected in the current version of Table S1.

The authors apologise for any inconvenience this may have caused.

## RESEARCH ARTICLE

# Size-dependent physiological responses of the branching coral *Pocillopora verrucosa* to elevated temperature and $P_{\text{CO}_2}$

Peter J. Edmunds<sup>1,\*</sup> and Scott C. Burgess<sup>2</sup>**ABSTRACT**

Body size has large effects on organism physiology, but these effects remain poorly understood in modular animals with complex morphologies. Using two trials of a ~24 day experiment conducted in 2014 and 2015, we tested the hypothesis that colony size of the coral *Pocillopora verrucosa* affects the response of calcification, aerobic respiration and gross photosynthesis to temperature (~26.5 and ~29.7°C) and  $P_{\text{CO}_2}$  (~40 and ~1000  $\mu\text{atm}$ ). Large corals calcified more than small corals, but at a slower size-specific rate; area-normalized calcification declined with size. Whole-colony and area-normalized calcification were unaffected by temperature,  $P_{\text{CO}_2}$ , or the interaction between the two. Whole-colony respiration increased with colony size, but the slopes of these relationships differed between treatments. Area-normalized gross photosynthesis declined with colony size, but whole-colony photosynthesis was unaffected by  $P_{\text{CO}_2}$ , and showed a weak response to temperature. When scaled up to predict the response of large corals, area-normalized metrics of physiological performance measured using small corals provide inaccurate estimates of the physiological performance of large colonies. Together, these results demonstrate the importance of colony size in modulating the response of branching corals to elevated temperature and high  $P_{\text{CO}_2}$ .

**KEY WORDS:** Scleractinia, Climate change, Ocean acidification, Temperature

**INTRODUCTION**

Organism size and temperature have profound effects on biological processes (Schmidt-Nielsen, 1984), and these effects play fundamental roles in translating changes in environmental conditions into effects on population dynamics (Nisbet et al., 2000; Brown et al., 2004). The functional relationships between organism size and biological processes, and the extent to which they are modulated by temperature, therefore are of central importance in elucidating the causes of spatio-temporal variation in ecological processes (Nisbet et al., 2000; Brown et al., 2004). While these principles are gaining recognition for their potential to advance understanding of the response of populations to global climate change and ocean acidification (Gaylord et al., 2015; Bruno et al., 2015), the potential remains largely unrealized in colonial modular animals, and corals in particular (Edmunds et al., 2014).

For tropical coral reefs, there is much to be gained by considering organism size and temperature in evaluating their response to changing environmental conditions, because the scleractinian architects of these systems vary greatly in colony size (Barnes, 1973; Pratchett et al., 2015), and the ecosystem is sensitive to climate change and ocean acidification (Hoegh-Guldberg et al., 2007). In part, this sensitivity results from the susceptibility of scleractinians to temperature (Comeau et al., 2016), and their generally negative response to ocean acidification (Chan and Connelly, 2013). The functional relationships between metabolism and temperature are relatively well known for scleractinians (Coles and Jokiel, 1977; Edmunds, 2005; Comeau et al., 2016), particularly in the context of bleaching (Fitt et al., 2000), and similar details are emerging for the effects of ocean acidification (Comeau et al., 2013; Evenhuis et al., 2015). However, there has been little consideration of whether their responses to temperature and seawater pH will be modified by colony size (but see Chan et al., 2016). Perhaps colony size has been overlooked in these studies because the colonial modular design of most scleractinians is thought to confer freedom from allometric constraints (Sebens, 1987; Hughes, 2005). If colony growth occurs while conserving polyp dimensions, it is widely assumed that metabolism will scale isometrically (i.e. proportionally) with colony size (Jackson, 1979; Sebens, 1979, 1987), rather than being constrained through allometric principles (Nisbet et al., 2000; Brown et al., 2004). One consequence of the assumption of isometric scaling is that the field of coral biology has advanced on the premise that studies of small fragments from larger coral colonies ('nubbins', after Birkeland, 1976) are representative of a wide variety of corals in the population, regardless of colony size (e.g. Davies, 1984; Edmunds and Davies, 1986; Anthony and Fabricius, 2000; Anthony et al., 2007).

However, as early as 1986 there was evidence that large and small coral colonies were functionally dissimilar (Jokiel and Morrissey, 1986), and throughout the 1980s and early 1990s studies of the interactions of organisms with a fluid environment (Koehl, 1984; Denny et al., 1985; Patterson, 1992a) provided understanding of how colony size could affect physiological performance (Patterson, 1992a,b). Since this work, evidence has emerged that coral polyps can be unequal between colonies differing in size, and within colonies depending on the position of polyps. These effects arise, for example, because biomass varies within colonies (Lough and Barnes, 2000) and among colonies differing in size (Vollmer and Edmunds, 2000), and genotypes of endosymbiotic *Symbiodinium* can vary among conspecifics differing in age and across the surface of single colonies (Little et al., 2004; Kemp et al., 2008). Light microenvironments differ across the surface of colonies, and especially within branching species (Kaniewska et al., 2011), and the capacity for polyps to capture zooplankton varies among positions within the colony (Sebens et al., 1998). Moreover, for branching corals, corallum morphology interacts with flow to create

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emergent properties affecting mass transfer as a result of the passage of seawater among the branches (Patterson, 1992b; Reidenbach et al., 2006). Finally, colony size modifies the metabolic rate of non-scleractinian colonial taxa, including bryozoans (Hughes and Hughes, 1986; Peck and Barnes, 2004; White et al., 2011) and ascidians (Nakaya et al., 2003, 2005). Together, the aforementioned effects create a rich landscape in which it is reasonable to expect that coral colony size will affect their response to rising seawater temperature and ocean acidification.

The objective of this study was to test the hypothesis that the response of a branching coral to high  $P_{\text{CO}_2}$  (i.e. ocean acidification) and temperature is mediated by intraspecific variation in colony size. We focused on the coral *Pocillopora verrucosa*, which represents a morphological group (thick clustered branches, ‘branching-closed’ after www.coraltraits.org) that is important on many coral reefs, particularly in the Indo-Pacific (Veron, 2000; Pinzón et al., 2013; Schmidt-Roach et al., 2014), and is abundant in Moorea (where the study was conducted) (Edmunds et al., 2016). Colony size was evaluated by planar diameter, and three-dimensional tissue surface area, which typically is proportional to the total tissue biomass of each coral (Edmunds, 2011). A laboratory experiment was designed in which colonies differing in size were exposed during trials in 2014 and 2015 to combinations of temperature and  $P_{\text{CO}_2}$ , with the outcome evaluated through calcification, aerobic respiration and gross photosynthesis.

## MATERIALS AND METHODS

### Overview

*Pocillopora verrucosa* (Ellis and Solander 1786) was incubated under combinations of two temperature and two  $P_{\text{CO}_2}$  regimes, using colonies representing the size range of conspecifics found at 10 m depth on the outer reef of Moorea in April 2014 and April 2015. *Pocillopora verrucosa* was identified morphologically (Veron, 2000), although we cannot be certain that only one species was sampled (Edmunds et al., 2016). Colonies were incubated for 24 days (2014) or 25 days (2015) in flow-through tanks (150 l), creating four treatments in duplicate (8 tanks in 2014, Trial 1) or triplicate (12 tanks in 2015, Trial 2). To prevent the corals from affecting the total alkalinity ( $A_T$ ) of the seawater in the tanks through their metabolism, only one colony of each of four size ranges (described below) was placed in each tank, so that trials started with 32 corals in 2014 and 48 corals in 2015. Sample sizes were determined by results of previous experiments. Colony size was determined by planar diameter when collecting specimens in the field. For analyses, colony size was measured as tissue area and was treated as a continuously distributed variable to evaluate its relationships with physiology in the context of responding to the treatments (see ‘Statistical analyses’, below). All applicable international, national and/or institutional guidelines for the care and use of animals were followed throughout the study.

In our design, we reasoned that if physiological performance of coral modules (i.e. polyps) was independent of colony size, and polyp density was conserved, then area-normalized physiological rates (i.e. whole-colony rates divided by the tissue surface area) would be constant (a slope of zero) across a range of colony sizes, and whole-colony physiological rates would correspondingly increase in direct proportion to surface area. Similar slopes but differences in the intercepts of these relationships between temperature and  $P_{\text{CO}_2}$  treatments would indicate that treatment effects were independent of colony size. If the slope of the relationship between colony size and physiological performance differed between temperature and  $P_{\text{CO}_2}$  treatments (i.e. a two- or

three-way interaction with colony size), it would indicate that the mean physiological performance of polyps depended on colony size, in a way that varied among treatments. This outcome could arise from one or more of three possibilities, with effects modulated by temperature and/or  $P_{\text{CO}_2}$ : polyps varying in functionality with colony size, polyps differing in functionality within a colony, or polyps varying in density (polyps  $\text{cm}^{-2}$ ) over the colony surface.

### Trial 1, 2014

#### Coral collection

Thirty-two corals were collected on 9 April 2014 from 10 m depth at two sites ~3 km apart on the north shore of Moorea, and were pooled by site. Mean ( $\pm$ s.e.m. throughout) ambient seawater temperature at the time of collection was  $28.7 \pm <0.1^\circ\text{C}$ . Colonies were haphazardly selected in four size classes (1–3, 4–6, 7–8.5 and 8.5–14 cm diameter), removed from the substratum using a hammer and chisel, and returned to the shore submerged and shaded in buckets, where they were placed in a shallow tank supplied with flowing seawater. Colonies were trimmed of rock to allow them to rest upright, identified with a numbered tag, measured for size (as the mean of two planar diameters), and placed in a 1000 l tank for recovery and acclimation to laboratory conditions. The recovery tank was supplied with flowing seawater ( $\sim 10 \text{ l min}^{-1}$ ) at  $28.0^\circ\text{C}$ , and illuminated (with SOL White LED, 6500 K, Aqua-Illumination, Ames, IA, USA) at  $\sim 475 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  of photosynthetically active radiation (PAR, as measured with a LI-Cor 4- $\pi$  quantum sensor LI-193, Li-Cor Biosciences, Lincoln, NE, USA). Within the tank, corals were placed upright on a platform rotating at 2 revolutions per day to avoid position effects, and following 3–5 days, were buoyant weighed and allocated to treatment tanks for ~24 days.

#### Incubation

Eight 150 l tanks (Aqualogic, San Diego, CA, USA) were randomly assigned to one of four treatments crossing target temperatures of  $26.5^\circ\text{C}$  (low temperature; LT) and  $29.5^\circ\text{C}$  (high temperature; HT), and targeted  $P_{\text{CO}_2}$  values of  $400 \mu\text{atm}$  (ambient  $P_{\text{CO}_2}$ ; AC) and  $1000 \mu\text{atm}$  (elevated  $P_{\text{CO}_2}$ ; HC). The temperatures represented the seasonal range for seawater in Moorea (Edmunds et al., 2010) and the elevated  $P_{\text{CO}_2}$  represented a pessimistic projection for atmospheric  $P_{\text{CO}_2}$  by the end of the present century (Representative Concentration Pathway, RCP 8.5) (Riahi et al., 2007; van Vuuren et al., 2011). Seawater in each tank was independently chilled, heated, and circulated with a water pump, and tanks were illuminated (with SOL White LED, 6500 K, Aqua-Illumination) at a target PAR of  $\sim 650 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  (measured with a Li-Cor 4- $\pi$  quantum sensor LI-193). The light intensity simulated the maximum midday light intensity at the collection depth on the outer reef in April (P.J.E., unpublished data). Each tank received fresh seawater at  $\sim 200 \text{ ml min}^{-1}$ , which was pumped from ~8 m depth in Cook’s Bay and filtered through sand. One coral from each size class was placed in each tank on 14 April 2014, with corals selected for each tank at random. Thereafter, their position in each tank was randomly changed each day until the experiment ended on 9 May 2014.

$\text{CO}_2$  treatments were created by bubbling ambient air ( $\sim 400 \mu\text{atm } P_{\text{CO}_2}$ ), or a mixture of ambient air and pure  $\text{CO}_2$  (at  $\sim 1000 \mu\text{atm}$ ) into the tanks. The air and  $\text{CO}_2$  were mixed using a solenoid-controlled valve (Model A352, Qubit Systems, Kingston, ON, Canada) that was regulated dynamically by an infra-red gas analyzer (Model S151, Qubit) to blend the gases in a mixing chamber. Thereafter, the gas mixture was supplied at  $\sim 10\text{--}15 \text{ l min}^{-1}$  to the

elevated  $P_{\text{CO}_2}$  tanks. The conditions in the tanks were monitored throughout the experiment, with PAR (Li-Cor 4- $\pi$  quantum sensor LI-193), temperature ( $\pm 0.05^\circ\text{C}$  certified, model 15-077, Fisher Scientific, Pittsburgh, PA, USA), salinity (YSI 3100 Conductivity Meter, YSI Inc., Yellow Springs, OH, USA) and pH (Mettler DG115-SC probe fitted to an Orion 3 star meter, Mettler-Toledo, LLC, Columbus, OH, USA) recorded daily using hand-held instruments, and seawater samples ( $\sim 50$  ml) collected for the determination of seawater chemistry every 3–4 days. Seawater chemistry was evaluated according to standard operating procedures (SOP3b; Dickson et al., 2007), using potentiometric titrations in an open cell, automatic titrator (Model T50, Mettler-Toledo) fitted with a pH probe (Mettler DG115-SC) calibrated on the total scale using Tris/HCl buffers (Dickson et al., 2007). The accuracy of the titrations was evaluated using certified reference materials (CRMs) from A. Dickson (Scripps Institution of Oceanography; batch 122 and 130); measured values departed from certified values by a mean of  $0.13 \pm 0.47\%$  ( $N=9$ ). Seawater pH was measured spectrophotometrically using *m*-Cresol Purple dye (no. 211761, Sigma-Aldrich, St Louis, MO, USA; SOP7, Dickson et al., 2007) and, together with  $A_T$  determined from the titrations, was used to calculate dissolved inorganic carbon (DIC) parameters using the Seacarb package (<https://cran.r-project.org/web/packages/seacarb/index.html>) running in R (R Foundation for Statistical Computing). DIC parameters were calculated daily, using the pH recorded with the hand-held meter, salinity, temperature, and  $A_T$  from the most recent previous analysis of seawater ( $\leq 4$  days before); preliminary measurements demonstrated that  $A_T$  was stable among determinations. On days when  $A_T$  was determined and pH was measured spectrophotometrically, these values were used to calculate DIC parameters.

### Response variables

Calcification rate, aerobic dark respiration and gross photosynthesis were used as response variables. Calcification was determined by buoyant weighing corals in seawater (Spencer-Davies, 1989) prior to placing them in the treatments on 16 April 2014, and when the experiment concluded on 8 May 2014. The change in buoyant mass was converted to dry mass using the density of aragonite ( $2.93 \text{ g cm}^{-3}$ ) and the empirical density of seawater, and the change in mass was normalized to time and colony ( $\text{mg day}^{-1}$ ). The initial buoyant mass of the corals was converted to dry mass to characterize coral size based on the mass of the skeleton. The live coral tissue area was determined at the end of the experiment by wax dipping (Stimson and Kinzie, 1991), and was used as the measure of colony size, which was treated as a covariate in the statistical design.

Aerobic dark respiration (of the holobiont) and gross photosynthesis (of endosymbiotic *Symbiodinium*) were determined by measuring  $\text{O}_2$  flux in two confined chambers designed after Patterson et al. (1991). A limitation of this approach is that the contribution of the *Symbiodinium* to holobiont aerobic respiration cannot be determined, although classic work suggests this contribution is small (3–9%) (Muscatine et al., 1981), with recent work suggesting these numbers might be  $\sim 31\%$  high (Hawkins et al., 2016). The respiration chambers could not accommodate the largest corals, and measurements were limited to colonies  $\leq 8$  cm diameter. With two chambers, measuring respiration and gross photosynthesis of 32 corals took multiple days, and this task was completed in the third week of the experiment, with treatment tanks (at a single temperature and  $P_{\text{CO}_2}$ ) selected at random for processing of the corals they contained. The chambers had a volume of  $\sim 2130$  ml and included a pump (Rule 136  $\text{l h}^{-1}$ ) that could be

operated at varying voltages to control the flow speed within the chamber. Photographs of hydrated brine shrimp eggs were used to evaluate flow speed (Sebens and Johnson, 1991), which was adjusted to  $\sim 8 \text{ cm s}^{-1}$  to create ecologically relevant conditions for a 10 m depth on the outer reef. An acoustic Doppler current profiler (RDI Workhorse, Teledyne RD Instruments, Poway, CA, USA) at 15 m depth on the outer reef (Washburn, 2016) was used to determine *in situ* flow speeds in a representative year (2013), and for 10 m depth, mean daily flow speed was  $8.9 \pm 0.1 \text{ cm s}^{-1}$  ( $N=365$ ), and for April (the month in which the present study was conducted) it was  $9.5 \pm 0.3 \text{ cm s}^{-1}$  ( $N=30$ ). Chambers were fitted with a Ruthenium-based optode (Foxy-R, Ocean Optics, Dunedin, FL, USA) connected to a spectrophotometer (USB 2000, Ocean Optics) and light source (USB LS-450) and operated by a PC running the manufacturer's software (OOISensor). Optodes were calibrated in a zero solution of sodium sulfite and  $0.01 \text{ mol l}^{-1}$  sodium tetraborate, and 100%  $\text{O}_2$  using water-saturated air at the measurement temperature.

Aerobic respiration was measured in darkness, following 5–10 min in the chamber.  $\text{O}_2$  uptake was recorded continuously at 0.07 Hz for 10–30 min until a stable rate of decline in saturation was achieved. Trials were shortened to maintain  $\text{O}_2$  saturation  $\geq 80\%$  and, where necessary, aerated water was added for this purpose. Following measurements of respiration, net photosynthesis was recorded at  $\sim 670 \text{ } \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  PAR supplied with an LED lamp (SOL White, Aqua-Illumination, 6500 K), which was close to the maximum irradiance found *in situ*. Each daily set of measurements was accompanied by a control consisting of chambers filled with seawater alone.  $\text{O}_2$  fluxes in darkness (i.e. respiration) and light (i.e. photosynthesis) were determined by least squares linear regression, adjusted for control values, and converted to changes in  $\text{O}_2$  concentrations using the solubility of  $\text{O}_2$  in seawater (N. Ramsing and J. Gundersen, Unisense, Aarhus, Denmark). Aerobic dark respiration was added to net photosynthesis to obtain gross photosynthesis, and normalized to time and colony (in units of  $\mu\text{mol O}_2 \text{ h}^{-1}$ ). Surface area was determined by wax dipping as described above.

### Trial 2 (2015)

The second trial was as similar as possible to Trial 1 to facilitate pooling of the results; any changes were either unavoidable modifications associated with trials in different years or were implemented to improve the experiment. Only the features of the experiment that changed between trials are described.

### Coral collection

Forty-eight corals representing the four size classes were collected on 5 April 2015 from two sites at 10 m depth of the fore reef, and were pooled between sites. Mean ambient seawater temperature at the time of collection was  $29.0 \pm 0.1^\circ\text{C}$  (for April 2015), which did not differ from the temperature in April 2014 ( $t=1.006$ , d.f.=30,  $P=0.323$ ). Acclimation in the recovery tank took place over 9 days at  $\sim 398 \text{ } \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ; the corals were buoyant weighed on 14 April 2015, and placed into treatment tanks for 25 days, with the final buoyant mass recorded on 9 May 2015.

### Incubation

The experiment was expanded to 12, 150 l tanks that were randomly assigned to four treatments crossing the same target conditions as in Trial 1. High  $P_{\text{CO}_2}$  treatments were maintained by direct bubbling of pure  $\text{CO}_2$  through diffusers that were regulated by solenoids (DePaul Submersible) controlled by a  $\text{pH}_T$ -set point measured with



an electrode (calibrated with Tris buffers, model PRBPH, Neptune Systems, Morgan Hill, CA, USA) and attached to a microprocessor controller (Apex Aquacontroller, Neptune Systems). Preliminary trials confirmed that the pH in the tanks was stable throughout the day, and did not drift overnight (as determined by analyzing seawater samples collected at 05:30 h). Seawater pH was logged at a frequency of 0.002 Hz and typically varied 0.02–0.04 between consecutive measures. Direct bubbling with CO<sub>2</sub> provided more responsive pH regulation than was obtained in 2014, and therefore the flow-through of seawater was increased to 400 ml min<sup>-1</sup>. Seawater chemistry in the tanks was monitored as described in 2014, except that the pH used to calculate DIC parameters was measured spectrophotometrically using *m*-Cresol Purple dye. Throughout the experiment, certified reference material (batch 130 from A. Dickson, Scripps Institution of Oceanography) for *A<sub>T</sub>* was processed routinely, and measured values departed from certified values by 0.62±0.04% (mean±s.e., *N*=29).

### Response variables

Response variables were measured in a similar way to that in 2014, except that three sizes of chambers were used for the measurement of respiration and photosynthesis (after Patterson et al., 1991), with volumes optimized to the size range of corals. The three chambers had volumes of ~900 ml, ~2130 ml (the same chamber used in 2014) and ~6000 ml, and the pump circulating seawater in each chamber was operated at a unique voltage to obtain ~8 cm s<sup>-1</sup> flow speed in the working section.

### Statistical analyses

Physical and chemical conditions were compared between treatment levels and the replicate tanks within each treatment using nested ANOVA in which treatment was the main effect and tanks were nested in each treatment level. These analyses were conducted using Systat 13 software, and the assumptions of ANOVA were tested through graphical analyses of residuals.

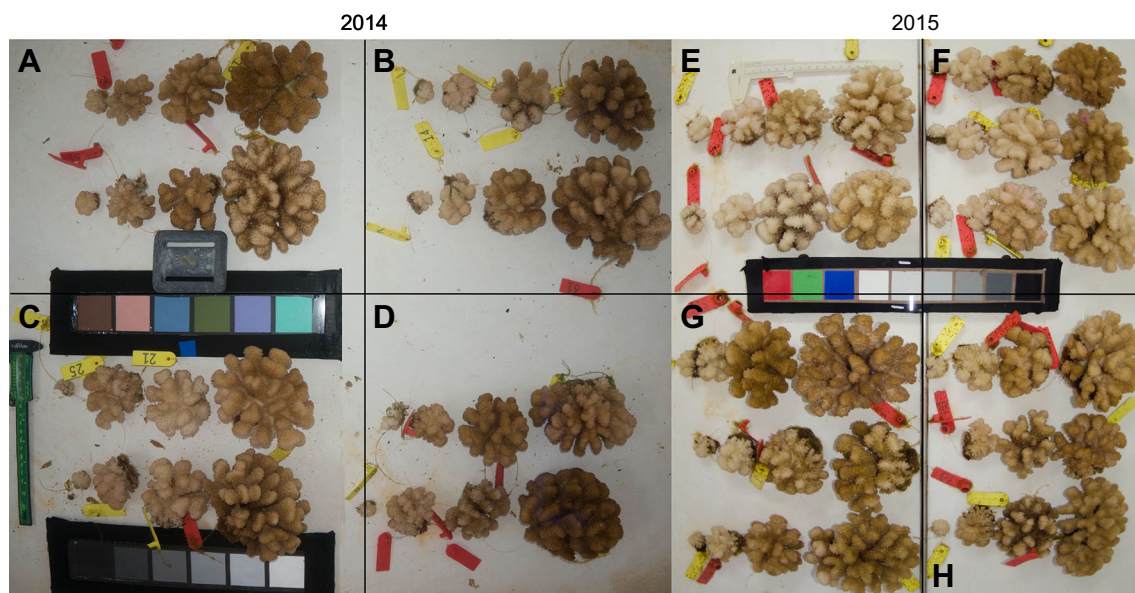
**Table 1. Summary of the characteristics of colonies of *Pocillopora verrucosa* used in experiments in 2014 (Trial 1) and 2015 (Trial 2)**

Trial	Size class	<i>N</i>	Diameter (cm)	Area (cm <sup>2</sup> )	Mass (g)
1	1	8	2.6±0.1	12.7±1.4	8.0±1.2
	2	8	5.6±0.3	72.8±7.7	55.9±6.4
	3	8	7.9±0.1	139.5±9.6	138.2±10.7
	4	8	12.0±0.3	422.2±42.5	356.5±28.7
2	1	10	2.7±0.1	15.9±1.6	12.4±1.6
	2	11	5.1±0.2	67.0±5.5	55.3±4.2
	3	11	8.1±0.1	207.9±18.2	175.8±10.4
	4	11	10.6±0.3 (11)	372.3±29.1	356.7±22.9

*N*, sample size.

Our goals were to estimate the effect of temperature and *P*<sub>CO<sub>2</sub></sub> on the corals, using colony size as a covariate, and either colony- or area-normalized physiological rates as dependent variables in separate univariate analyses. The statistical approach involved fitting parametric models and describing the extent to which the quantitative relationships (represented by parameters for the slopes and intercepts) between size and calcification, aerobic respiration and gross photosynthesis differed between the temperature and *P*<sub>CO<sub>2</sub></sub> treatments. We used Gaussian linear mixed-effects models where tissue surface area was a continuous predictor, while temperature and *P*<sub>CO<sub>2</sub></sub> were categorical predictors (each with two levels, an ANCOVA-like design). Trials (years) and tanks within years were treated as random effects to create 20 groups from eight tanks in 2014, and 12 tanks in 2015. For each response variable, using tissue surface area as the predictor, different slopes and intercepts were estimated in each of the four treatments, while accounting for two sources of variation around the fitted values: (1) variation due to different years and tanks, and (2) variation due to individual corals within each tank.

Models were fitted to data in a Bayesian framework using Markov Chain Monte Carlo (MCMC) methods in the R package MCMCglmm (Hadfield, 2010). Flat (uninformative) inverse-



**Fig. 1. Colonies of *Pocillopora verrucosa* following incubations in 2014 (left) and 2015 (right).** Corals were photographed in a single frame for each year; the scale bar for 2014 is shown in C, and that for 2015 is in E. Color cards are portions of Macbeth standards (McCamy et al., 2006), and corals in each quadrant correspond to the four treatments. Within each quadrant, corals are arranged by size class from left to right, with the rows showing the corals assigned to each tank (with two tanks per treatment in 2014, and three tanks per treatment in 2015 except LT-HC). (A) High temperature (HT)-high CO<sub>2</sub> (HC), (B) low temperature (LT)-ambient CO<sub>2</sub> (AC), (C) LT-HC, (D) HT-AC, (E) LT-HC, (F) LT-AC, (G) HT-HC and (H) HT-AC, where LT ~26.5°C, HT ~30.0°C, AC ~400 µatm *P*<sub>CO<sub>2</sub></sub> and HC ~1000 µatm *P*<sub>CO<sub>2</sub></sub> (Table S1).

Wishart priors were used. As the group-level variance (i.e. the estimate of variance due to years and tanks) was close to zero, a parameter expansion method was used to improve the mixing properties of the MCMC chain and provide a better description of the posterior distribution (following Hadfield, 2010). In all models, MCMC chains were run for  $10^6$  iterations with a burn-in of 3000 and a thinning interval of 10. The mixing properties of all parameters were checked to ensure no systematic trends, and the sensitivity of results to alternative prior specifications was also checked.

## RESULTS

### Treatment conditions and corals

#### Trial 1

Treatments were maintained with precision (Table S1), with mean salinities ranging from 33.8 to 34.0, and mean light intensities of 577–600  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ . Temperature differed between the temperature treatments ( $F_{1,6}=506.729$ ,  $P<0.001$ ) and among tanks ( $F_{6,480}=2.617$ ,  $P=0.017$ ), although mean tank temperatures differed  $\leq 0.6^\circ\text{C}$  within each treatment; overall, treatments contrasted  $26.5\pm 0.1$  with  $29.7\pm 0.1^\circ\text{C}$  (mean $\pm$ s.e.,  $N=244$ ). pH and  $P_{\text{CO}_2}$  differed between  $P_{\text{CO}_2}$  treatments ( $F_{1,60}=339.550$ ,  $P<0.991$ , and  $F_{1,6}=17,705.274$ ,  $P<0.001$ ) and tanks ( $F_{6,195}=4.709$ ,  $P<0.001$ , and  $F_{6,204}=57,144.154$ ,  $P=0.001$ ), although mean tank pH differed  $\leq 0.07$ , and mean  $P_{\text{CO}_2}$  differed  $\leq 101 \mu\text{atm}$ ; overall, treatment contrasted pH of  $7.71\pm 0.01$  with  $8.03\pm 0.01$  (mean $\pm$ s.e.,  $N=99$ –104) and  $403\pm 6$  versus  $982\pm 16 \mu\text{atm } P_{\text{CO}_2}$  (mean $\pm$ s.e.,  $N=100$ –112).  $A_T$  did not vary between main effects ( $F_{1,6}=0.359$ ,  $P=0.571$ ) and the grand mean ( $\pm$ s.e.) was  $2256\pm 5 \mu\text{mol kg}^{-1}$  ( $N=72$ ).

The corals used in Trial 1 ranged in diameter from 2.1 to 13.1 cm, with tissue areas of 7–646  $\text{cm}^2$ , and initial dry mass of 5–538 g (Table 1). All corals were similar in color at the start of the experiment, and throughout the experiment maintained a natural polyp expansion cycle. None of the colonies died during the incubation, but when the experiment ended there were slight differences in color among the corals. Qualitatively, the colonies formed a gradient from pale to dark for the smallest to largest colonies in all treatments (Fig. 1).

#### Trial 2

Treatments were maintained with precision (Table S1), with mean salinities ranging from 35.4 to 35.6, and mean light intensities of 671–713  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ . Temperature differed between the temperature treatments ( $F_{1,6}=1373.247$ ,  $P<0.001$ ) and tanks ( $F_{10,533}=2.726$ ,  $P=0.003$ ), with tanks differing  $<0.4^\circ\text{C}$  within each treatment; overall treatments contrasted  $26.5\pm 0.1^\circ\text{C}$  and  $29.7\pm 0.1^\circ\text{C}$  (mean $\pm$ s.e.,  $N=271$ –274). pH and  $P_{\text{CO}_2}$  differed between  $P_{\text{CO}_2}$  treatments ( $F_{1,10}=783.945$ ,  $P<0.001$ , and  $F_{1,10}=860.239$ ,  $P<0.001$ ) and among tanks within each treatment ( $F_{10,249}=6.694$ ,  $P<0.001$ , and  $F_{10,273}=38.339.539$ ,  $P<0.001$ ), with treatment means of  $7.662\pm 0.004$  versus  $8.010\pm 0.004$  pH units and  $436\pm 4$  versus  $1118\pm 11 \mu\text{atm } P_{\text{CO}_2}$  (all means $\pm$ s.e.).  $A_T$  did not vary between main effects ( $F_{1,108}=0.162$ ,  $P=0.688$ ) or tanks ( $F_{9,99}=0.850$ ,  $P=0.572$ ) and the grand mean ( $\pm$ s.e.) was  $2305\pm 2 \mu\text{mol kg}^{-1}$  ( $N=120$ ).

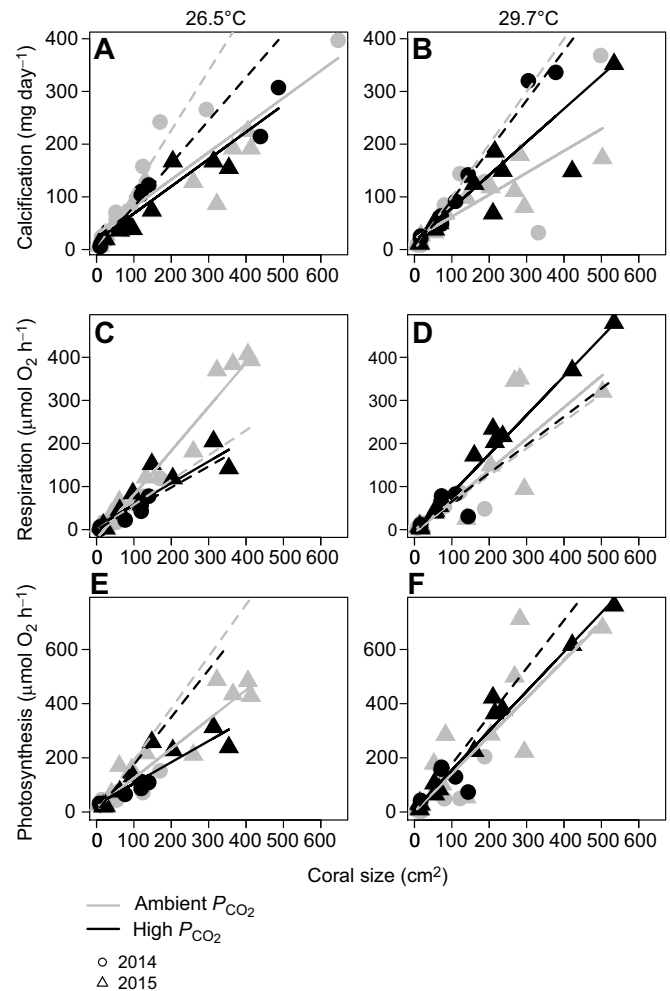
The corals used in Trial 2 ranged in diameter from 2.0 to 12.2 cm, with tissue areas of 8–534  $\text{cm}^2$ , and initial dry mass of 6–417 g (Table 1). All corals appeared similar in color at the start of the experiment, and throughout the experiment they maintained a natural expansion cycle of polyps. Of the 48 corals that started the experiment in 12 tanks, all corals in one tank in the LT-HC treatment died, and one of the smallest corals died in the HT-AC treatment. When the experiment ended, there were slight differences in color

among the corals, and qualitatively, the colonies formed a gradient from pale to dark for the smallest to largest colonies in all treatments (Fig. 1).

### Relationships between size and physiology as a function of temperature and $P_{\text{CO}_2}$

#### Calcification

All corals grew throughout the experiments, but the mass changes of two colonies (one LT-HC in 2014, and the other HT-HC in 2015) were not available because of logistical constraints. In 2014, the dry mass of colonies increased from  $5.7 \text{ mg day}^{-1}$  (a coral 2.3 cm diameter in LT-HC) to  $397.0 \text{ mg day}^{-1}$  (a coral 13.7 cm diameter in



**Fig. 2. Whole-colony responses of *P. verrucosa* to incubations under factorial combinations of temperature and  $P_{\text{CO}_2}$ , based on trials conducted in 2014 and 2015.** Trials were conducted at 26.5 versus 29.7°C and at ambient ( $\sim 400 \mu\text{atm}$ ) versus high ( $\sim 1000 \mu\text{atm}$ )  $P_{\text{CO}_2}$ , and values are plotted as a function of size (tissue surface area). (A,B) Calcification, (C,D) aerobic respiration and (E,F) gross photosynthesis. Each symbol represents the results from one coral colony, and the solid lines show the fitted partial regression coefficients from the linear mixed-effects model (Table 2). The dashed lines show the expected whole-colony responses calculated by scaling up the area-normalized responses for the average tissue surface area for corals in our small size class (14.49  $\text{cm}^2$ ) based on parameters in Table 3 [i.e. if the area-normalized regression in each treatment is  $y=\alpha+\beta x$ , where  $x$  is colony tissue surface area in  $\text{cm}^2$ , then the expected whole-colony response would be  $y_{\text{expected}}=\alpha+(\beta\times 14.49)x$ ]. Sample sizes in Trial 1:  $N=8$  for all treatment combinations; in Trial 2:  $N=12$  in LT-AC and HT-AC,  $N=8$  in LT-HC and  $N=11$  in HT-HC.

HT-AC), and in 2015, dry mass increased from 7.3 mg day<sup>-1</sup> (a coral 2 cm diameter in LT-AC) to 351.9 mg day<sup>-1</sup> (a coral 12.2 cm diameter in HT-HC). Whole-colony calcification increased with tissue surface area (Fig. 2A,B), though this relationship was not affected by temperature,  $P_{CO_2}$  or the interaction between the two (Table 2). When normalized to tissue area, calcification (mg cm<sup>-2</sup> day<sup>-1</sup>) was negatively related to colony size (Fig. 3A,B, Table 3), indicating that larger colonies calcified at slower area-normalized rates. Consequently, when scaled up to predict whole-coral calcification rate, area-normalized calcification rate for small corals tended to overestimate whole-colony calcification for larger corals (solid lines versus dashed lines in Fig. 2A,B).

### Aerobic respiration

Whole-colony respiration in 2014 ranged from 1.12  $\mu\text{mol O}_2 \text{ h}^{-1}$  (LT-HC) to 118.92  $\mu\text{mol O}_2 \text{ h}^{-1}$  (LT-AC), and in 2015 it ranged from 2.3  $\mu\text{mol O}_2 \text{ h}^{-1}$  (LT-HC) to 479.7  $\mu\text{mol O}_2 \text{ h}^{-1}$  (HT-HC). Whole-colony respiration increased with colony size (Fig. 2C,D), and the slopes of these relationships differed between some of the treatments ( $\beta_4$  and  $\beta_5$  in Table 2). Under ambient  $P_{CO_2}$  and low temperature, whole-colony respiration increased by 1.0  $\mu\text{mol O}_2 \text{ h}^{-1}$  (0.9–1.2  $\mu\text{mol O}_2 \text{ h}^{-1}$ , 96% credible interval, CI) for each 1 cm<sup>2</sup> increase in tissue area, but was reduced by 0.3  $\mu\text{mol O}_2 \text{ h}^{-1}$  (0.1–0.5  $\mu\text{mol O}_2 \text{ h}^{-1}$ , 95% CI) for each 1 cm<sup>2</sup> increase in tissue area at high temperature ( $P=0.005$ ) (Fig. 2C,D;  $\beta_4$  in Table 2). At low temperature, the slope of the relationship between whole-colony respiration and tissue surface area was reduced by 0.5  $\mu\text{mol O}_2 \text{ h}^{-1}$  (0.3–0.7  $\mu\text{mol O}_2 \text{ h}^{-1}$ , 95% CI) for each cm<sup>2</sup> increase in tissue area at high  $P_{CO_2}$  compared with ambient  $P_{CO_2}$  ( $P<0.001$ ) (Fig. 2C;  $\beta_5$  in Table 2). When standardized to tissue area (Fig. 3C,D), respiration was greater for larger corals, but no differences were detected between temperature and  $P_{CO_2}$  treatments (Table 3). When scaled up to predict whole-coral respiration, area-normalized respiration of small corals tended to underestimate whole-colony respiration of larger corals (solid lines versus dashed lines in Fig. 2C,D).

### Gross photosynthesis

In 2014, whole-colony gross photosynthesis ranged from 0.7 to 204.1  $\mu\text{mol O}_2 \text{ h}^{-1}$  (HT-AC), and in 2015 from 9.5 to

762.2  $\mu\text{mol O}_2 \text{ h}^{-1}$  (HT-HC) (Fig. 2E,F). At ambient  $P_{CO_2}$ , high temperature increased the slope of the relationship between whole-colony gross photosynthesis and tissue area by 0.3  $\mu\text{mol O}_2 \text{ h}^{-1}$  (0.0–0.7  $\mu\text{mol O}_2 \text{ h}^{-1}$ , 95% CI) for each cm<sup>2</sup> increase in tissue area ( $P=0.087$ ) compared with the slope at low temperature (Table 2). Area-normalized gross photosynthesis declined with increasing coral size (Fig. 3E,F, Table 3). At low temperature and ambient  $P_{CO_2}$ , photosynthesis declined by 0.0028  $\mu\text{mol O}_2 \text{ h}^{-1}$  (0.0001–0.0056  $\mu\text{mol O}_2 \text{ h}^{-1}$ , 95% CI) for each cm<sup>2</sup> increase in tissue area, with no detectable differences between treatments (Table 3). When scaled up to predict whole-coral photosynthetic rate, area-normalized estimates of photosynthetic rate for small corals tended to overestimate whole-colony photosynthesis for larger corals (solid lines versus dashed lines in Fig. 2E,F).

## DISCUSSION

### Overview

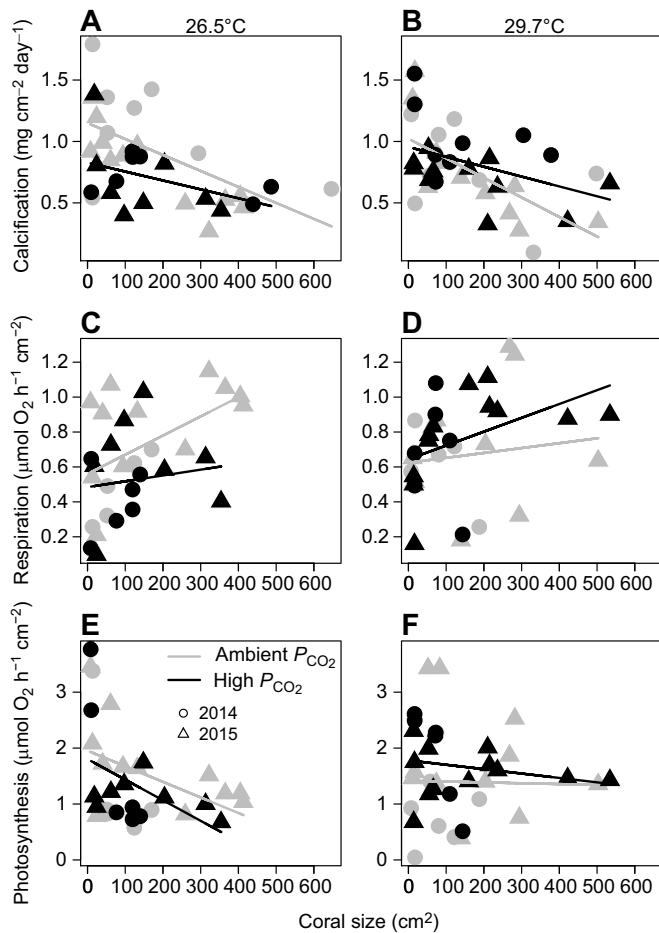
If physiological performance of coral polyps was independent of colony size, then physiological rates per unit surface area should be conserved in corals with a constant polyp density. Whole-colony physiological rates then would increase in proportion to surface area (i.e. dashed lines in Fig. 2), and scaling of physiological traits would be isometric. Our results for calcification, respiration and photosynthesis in *P. verrucosa* did not conform to this expectation, showing instead that area-normalized physiological rates are dependent on colony size as measured by tissue surface area, and therefore scale allometrically. For example, each unit area of coral surface, on average, grew less, consumed more oxygen and produced less oxygen through photosynthesis in larger versus smaller corals. Therefore, common measures of calcification, respiration and photosynthesis from small nubbins of branching corals are unlikely to accurately scale up to whole-coral physiological rates (compare dashed and solid lines in Fig. 2) that are needed for projections of future change in coral community structure (e.g. Pandolfi et al., 2011; Bramanti et al., 2015). Additionally, some size-dependent effects in *P. verrucosa* were mediated by temperature and  $P_{CO_2}$ , which has implications for evaluating the response of populations of this coral to climate change and ocean acidification. Compared with the scaling of whole-colony respiration with size at low temperature and ambient  $P_{CO_2}$ , whole-

**Table 2. Parameters from Bayesian linear mixed-effects models fit to three response variables measured in *P. verrucosa*: colony calcification, colony respiration and colony gross photosynthesis**

Parameter	Interpretation	Response variable		
		Calcification (mg day <sup>-1</sup> )	Respiration ( $\mu\text{mol O}_2 \text{ h}^{-1}$ )	Photosynthesis ( $\mu\text{mol O}_2 \text{ h}^{-1}$ )
$\alpha$	Response of corals in LT-AC at size 0 cm <sup>2</sup>	29.7 (–4.0 to 63.0)	21.0 (–60.2 to 17.9)	16.4 (–44.6 to 77.9)
$\beta_1$	Slope of coral surface area (cm <sup>2</sup> ) vs response in LT-AC	<b>0.5 (0.4 to 0.6)</b>	<b>1.0 (0.9 to 1.2)</b>	<b>1.1 (0.8 to 1.3)</b>
$\beta_2$	Difference in response of corals in HT-AC vs LT-AC at size 0 cm <sup>2</sup>	–8.4 (–57.5 to 40.9)	13.4 (–44.9 to 70.2)	–14.7 (–100 to 73.5)
$\beta_3$	Difference in response of corals in LT-HC vs LT-AC at size 0 cm <sup>2</sup>	–13.1 (–66.5 to 39.3)	27.9 (–31.0 to 87.1)	10.3 (–82.5 to 104.1)
$\beta_4$	Change in the slope of coral surface area (cm <sup>2</sup> ) vs response in HT-AC vs LT-AC	–0.1 (–0.3 to 0.1)	<b>–0.3 (–0.5 to –0.1)</b>	<b>0.3 (0 to 0.7)</b>
$\beta_5$	Change in the slope of coral surface area (cm <sup>2</sup> ) vs response in LT-HC vs LT-AC	0.001 (–0.2 to 0.2)	<b>–0.5 (–0.7 to –0.3)</b>	–0.3 (–0.7 to 0.1)
$\beta_6$	Difference in response of corals in HT-HC vs LT-AC at size 0 cm <sup>2</sup>	6.8 (–66.8 to 80.5)	–26.5 (–109.4 to 45.3)	–2.8 (–130.8 to 122.5)
$\beta_7$	Partial regression coefficient in HT-HC	0.2 (–0.1 to 0.5)	<b>0.7 (0.4 to 1)</b>	0.4 (–0.2 to 0.9)
$\sigma^2_\alpha$	Variance in response among tanks and years	318 (0 to 985)	1105 (0 to 2378)	1877 (0 to 4419)
$\sigma^2_\gamma$	Residual variance in response among corals within each tank	2256 (1441 to 3197)	1336 (768–2030)	4683 (2795 to 924)

Corals from a range of sizes (tissue surface area, cm<sup>2</sup>) were measured at either low (LT) or high (HT) temperature and ambient (AC) or high (HC)  $P_{CO_2}$ . The model was:  $y_{ij} \approx \alpha_{[ij]} + \beta_1 \text{area}_{i,LT-AC} + \beta_2 \text{area}_{i,LT-HC} + \beta_3 \text{area}_{i,HT-AC} + \beta_4 \text{area}_{i,HT-HC} + \beta_5 \text{area}_{i,LT-AC} + \beta_6 \text{area}_{i,LT-HC} + \beta_7 \text{area}_{i,HT-AC} + \epsilon_{ij}$ , where  $\alpha_{[ij]} \sim N(0, \sigma^2_\alpha)$  and  $\epsilon_{ij} \sim N(0, \sigma^2_\gamma)$ . The 95% credible intervals are given in parentheses; values in bold indicate 95% credible intervals that do not overlap with zero.





**Fig. 3. Area-normalized responses of *P. verrucosa* to incubations under factorial combinations of temperature and  $P_{\text{CO}_2}$ , based on trials conducted in 2014 and 2015.** Trials were conducted at 26.5 versus 29.7°C and at ambient ( $\sim 400 \mu\text{atm}$ ) versus high ( $\sim 1000 \mu\text{atm}$ )  $P_{\text{CO}_2}$ , and values are plotted as a function of size (tissue surface area). (A,B) Calcification, (C,D) respiration and (E,F) gross photosynthesis. Each symbol represents the results from one coral colony, and the lines show the fitted partial regression coefficients from the linear mixed-effects model (Table 3). A flat relationship was expected if colony size did not affect the physiological performance of individual modules (polyps). Sample sizes in Trial 1:  $N=8$  for all treatment combinations; in Trial 2:  $N=12$  in LT-AC and HT-AC,  $N=8$  in LT-HC and  $N=11$  in HT-HC.

colony respiration increased with colony size by a smaller amount when temperature and  $P_{\text{CO}_2}$  were increased independently, but increased with colony size by a greater amount under the combined effect of elevated temperature and  $P_{\text{CO}_2}$  (Table 2). Compared with the scaling of whole-colony photosynthesis with size at low temperature, whole-colony photosynthesis increased with size by a larger amount under elevated temperature under both  $P_{\text{CO}_2}$  conditions. Finally, and in contrast to previous research (Chan and Connolly, 2013; Kroeker et al., 2013; Comeau et al., 2014), our results from the full size range of *P. verrucosa* colonies found on the outer reefs of Moorea in 2014/2015 revealed no impact of temperature or  $P_{\text{CO}_2}$  on calcification over 24–25 days. Large corals did, however, deposit less  $\text{CaCO}_3$  per day than small corals. Together, these results underscore the role of emergent properties of multi-branch coral colonies (versus fragments) in responding to environmental conditions.

### Allometry in colonial corals

Our results are consistent with the hypothesis that polyps within a branching colony vary in performance with colony size, and

interactions of corallum morphology with seawater flow, temperature and  $P_{\text{CO}_2}$ . This interpretation contradicts the notion that the colonial modular design of scleractinians allows them to escape the allometric constraints of increasing size (Kleiber, 1932; Schmidt-Nielsen, 1984; Hughes and Hughes, 1986) through iterations of independent modules that are conserved in dimensions and function. Classically, coral colonies are thought to increase in size through multiplication of standardized polyps, thereby conferring the biologically rare property of isometry (Jackson, 1979; Sebens, 1979). This principle has had a profound effect on coral biology, by providing a rationale for research relying on the assumption that analyses of small fragments of corals (i.e. nubbins; Birkeland, 1976) are insightful for understanding the biology of a wide range of sizes of coral colonies. Despite the pervasive nature of this assumption, 30 years ago there was evidence that it might not be correct (Jokiel and Morrissey, 1986), and a few years later Patterson (1992b) described allometric scaling in corals as a result of the interactive effects of seawater flow, colony morphology and boundary layers.

A few studies have addressed scaling in corals, and often have revealed allometric scaling through theoretical approaches and mensurative experimentation (Patterson, 1992a,b; Kim and Lasker, 1998; Vollmer and Edmunds, 2000; Edmunds, 2006; Elahi and Edmunds, 2007). Little attention has been paid to the implications of these discoveries, one result of which is that studies investigating the response of corals to ocean acidification (e.g. Chan and Connolly, 2013; Comeau et al., 2014) have relied on experiments with coral nubbins to support inferences applying to large colonies (and higher functional levels), without addressing the assumptions inherent in such extrapolation (Reynaud et al., 2003; Anthony et al., 2008; Edmunds, 2012, and references therein). The mechanisms underpinning an expectation of allometry in colonial corals such as *P. verrucosa* fall into three non-exclusive groups: effects related to colony size and morphology, effects related to interactions with seawater flow, and effects related to the functional biology of scleractinians.

First, colony size has the potential to be associated with differential allocation of resources (e.g. energy) (Anthony et al., 2002). Further, together with morphology, size can create within-colony heterogeneity that can drive allometry, for example, through variation in tissue biomass (Barnes and Lough, 1992; Edmunds, 2012; P.J.E., unpublished data for *P. verrucosa*), and the creation of shaded microhabitats that facilitate shade acclimatization (Kaniewska et al., 2011; Wangpraseurt et al., 2014). These effects can be augmented by varying amounts of coenosarc separating polyps, the consequences of within-colony shade acclimatization (Kaniewska et al., 2011; Wangpraseurt et al., 2015) and differential zooplankton capture by peripheral versus inner branches (Sebens et al., 1998), which together are likely to modulate the reliance on autotrophic versus heterotrophic nutrition (Anthony and Fabricius, 2000; Houlbrèque and Ferrier-Pagès, 2009). For branching corals, colony growth creates a complex morphology that modulates the physical and chemical environment within its interstices (Mass et al., 2010; Kaniewska et al., 2011; Chan et al., 2016), making it unlikely that large colonies functionally are the sum of their component branches. Second, consideration of mass transfer between tissue and seawater for organisms varying in size and morphology supports an expectation of allometry (Patterson, 1992a). This expectation arises from the role of size and shape in determining fluid motion around organisms (i.e. the Reynold's number), and the extent to which metabolism is enhanced by water motion (i.e. the Sherwood number) (Patterson, 1992a,b). Finally, fundamental aspects of coral



**Table 3. Parameters from Bayesian linear mixed-effects models fitted to three response variables measured in *P. verrucosa* and calculated per unit surface area: calcification rate, respiration rate and photosynthesis rate**

Parameter	Interpretation	Response variable		
		Calcification (mg cm <sup>2</sup> day <sup>-1</sup> )	Respiration (μmol O <sub>2</sub> h <sup>-1</sup> cm <sup>2</sup> )	Photosynthesis (μmol O <sub>2</sub> h <sup>-1</sup> cm <sup>2</sup> )
$\alpha$	Response of corals in LT-AC at size 0 cm <sup>2</sup>	1.15 (0.94 to 1.37)	0.56 (0.34 to 0.78)	1.95 (1.33 to 2.59)
$\beta_1$	Slope of coral surface area (cm <sup>2</sup> ) vs response in LT-AC	<b>-0.0013 (-0.002 to -0.0007)</b>	<b>0.0011 (0.0002 to 0.002)</b>	<b>-0.0028 (-0.0056 to -0.0001)</b>
$\beta_2$	Difference in response of corals in HT-AC vs LT-AC at size 0 cm <sup>2</sup>	-0.12 (-0.44 to 0.18)	0.07 (-0.27 to 0.39)	-0.54 (-1.44 to 0.36)
$\beta_3$	Difference in response of corals in LT-HC vs LT-AC at size 0 cm <sup>2</sup>	-0.32 (-0.66 to 0.02)	-0.08 (-0.41 to 0.25)	-0.15 (-1.11 to 0.81)
$\beta_4$	Change in the slope of coral surface area (cm <sup>2</sup> ) vs response in HT-AC vs LT-AC	-0.0003 (-0.0013 to 0.0007)	-0.0008 (-0.0022 to 0.0006)	0.0026 (-0.0014 to 0.0067)
$\beta_5$	Change in the slope of coral surface area (cm <sup>2</sup> ) vs response in LT-HC vs LT-AC	0.0006 (-0.0005 to 0.0017)	-0.0008 (-0.0024 to 0.0009)	-0.0009 (-0.0058 to 0.0041)
$\beta_6$	Difference in response of corals in HT-HC vs LT-AC at size 0 cm <sup>2</sup>	0.26 (-0.21 to 0.72)	0.09 (-0.37 to 0.56)	0.52 (-0.79 to 1.81)
$\beta_7$	Partial regression coefficient in HT-HC	0.0002 (-0.0014 to 0.0018)	0.0013 (-0.0009 to 0.0034)	0.0003 (-0.0062 to 0.0064)
$\sigma_{\alpha}^2$	Variance in response among tanks and years	0.03 (0 to 0.06)	0.02 (0 to 0.05)	0.11 (0 to 0.35)
$\sigma_y^2$	Residual variance in response among corals within each tank	0.07 (0.04 to 0.1)	0.07 (0 to 0.1)	0.63 (0.4 to 0.9)

Corals from a range of sizes (tissue surface area; cm<sup>2</sup>) were measured at either low (LT) or high (HT) temperature and ambient (AC) or high (HC)  $P_{CO_2}$ . The model was:  $y_i \sim \alpha_{[i]} + \beta_1 \text{area}_{i,LT-AC} + \beta_2 \text{area}_{i,HT-AC} + \beta_3 \text{area}_{i,LT-HC} + \beta_4 \text{area}_{i,HT-HC} + \beta_5 \text{area}_{i,LT-HC} + \beta_6 \text{area}_{i,HT-HC} + \beta_7 \text{area}_{i,HT-HC} + \epsilon_i$ , where  $\alpha_{[i]} \sim N(0, \sigma_{\alpha}^2)$  and  $\epsilon_i \sim N(0, \sigma_y^2)$ . The 95% credible intervals are given in parentheses; values in bold indicate 95% credible intervals that do not overlap with zero.

biology favor allometry. For example, as the density and genotypes of the *Symbiodinium* symbionts of most reef corals can vary among locations within a colony (Rowan et al., 1997; Kemp et al., 2008), and *Symbiodinium* genotypes can have unique physiological properties (Sampayo et al., 2008; Parkinson and Baums, 2014), large colonies with numerous microhabitats among their branches may be capable of hosting a wider range of *Symbiodinium* genotypes, so that the physiology of large versus small colonies will not be proportional to their difference in size. Integration among polyps also can favor allometry, and while it contradicts the key assumption of module independence that underpins the expectation of isometry in colonial modular designs (Hughes, 2005), it is facilitated by the common gastrovascular cavity of colonial corals. Evidence of integration associated with chemical transfer among coral polyps is well known (Pearse and Muscatine, 1971; Oren et al., 2001), and has been evoked to explain temperature-associated switching in scaling of growth between isometry and allometry for small corals (Edmunds, 2006). A similar argument has been used to explain transitions between isometric and allometric scaling of metabolism in colonial ascidians (Nakaya et al., 2003).

### Colony size and the response to temperature and $P_{CO_2}$

None of the response variables measured for *P. verrucosa* changed in magnitude in response to the individual or synergistic effects of elevated temperature or high  $P_{CO_2}$ . A few variables did, however, show a change in slope of response against size, suggesting that treatment effects were size specific. These outcomes generally contrast with the expectation of the responses of tropical reef corals to the treatment levels applied. For temperature, previous studies suggest that coral metabolism should be stimulated by temperature (Coles and Jokiel, 1977; Jokiel and Coles, 1977), at least for the temperatures employed herein and assuming thermal optima of ca. 28–29°C (Pratchett et al., 2015; Comeau et al., 2016). Expectations for the response to high  $P_{CO_2}$  are less clear, but it is reasonable to hypothesize depressed calcification (Chan and Connolly, 2013; Comeau et al., 2014) and null effects for respiration and photosynthesis. For instance,  $P_{CO_2}$  at a magnitude similar to that employed here

(i.e. causing a reduction in aragonite saturation,  $\Omega_{\text{arag}}$ , of ~1.5) should depress calcification ~23% based on the results of a meta-analysis (Chan and Connolly, 2013), and previous studies of *Pocillopora* spp. show declines of ~55% at 913 μatm  $P_{CO_2}$  and 30.1°C (for *P. meandrina*; Brown and Edmunds, 2016), ~10% at 986 μatm  $P_{CO_2}$  and 27°C (*P. verrucosa*; Comeau et al., 2014) and 20% at 2072 μatm  $P_{CO_2}$  and 27°C (*P. damicornis*; Comeau et al., 2013). Calcification of *P. damicornis* was unaffected by  $P_{CO_2} \leq 1000$  μatm (at ~27°C) in one study that contrasted results from Moorea, Hawaii and Okinawa (Comeau et al., 2014). For respiration, despite the thermodynamic prediction that calcification will be energetically more costly at high  $P_{CO_2}$  (Erez et al., 2011; Pandolfi et al., 2011), and therefore will cause respiration to increase (McCulloch et al., 2012), most tests of this hypothesis have found no effect (Reynaud et al., 2003; Schneider and Erez, 2006; Comeau et al., 2016), or a decline (Edmunds, 2012; Kaniewska et al., 2012), including for *P. damicornis* (normalized by biomass, but not area; Comeau et al., 2016). For photosynthesis, the effects of high  $P_{CO_2}$  also are equivocal, with reports of increases (Reynaud et al., 2003), decreases (Anthony et al., 2008; Kaniewska et al., 2012) and no effect (Takahashi and Kurihara, 2013; Comeau et al., 2016), which together support a null outcome in a meta-analysis (Kroeker et al., 2013).

While the present experiment does not allow cause and effect to be established for the scaling of relationships, our analyses make a compelling case for allometry. In addition to the scaling principles and examples described above, two recent studies may have relevance in accounting for the present results. First, Jokiel (2011) has posited the ‘two compartment proton flux model’ to reconcile aspects of the morphological design of symbiotic reef corals with the physiological requirements of photosynthesis and calcification. In his model, coral morphology promotes spatial separation within a colony of an inner ‘zone of rapid photosynthesis’ and a peripheral ‘zone of rapid calcification’, that matches the restriction of rapid calcification in branching corals to branch apices (Pearse and Muscatine, 1971; Jokiel, 2011), and facilitates metabolic interchange between the two areas to promote functionality (Jokiel, 2011). Second, Chan et al. (2016) have shown that low

flow speeds favor the formation of thick boundary layers in *Favites* sp. and *P. damicornis*, in which the metabolic activity of the coral tissue creates pH levels adjacent to the tissue that are elevated relative to that of the ambient seawater. Therefore, under reduced seawater pH as a result of ocean acidification, the interaction of flow and coral morphology has the potential to ameliorate the negative effects of reduced pH on calcification. Together, the hypothesis of Jokiel (2011) and the results of Chan et al. (2016) suggest that morphology in branching corals can attenuate the effects of high seawater  $P_{CO_2}$  in a colony size-dependent way, potentially creating organismic results similar to those reported here (Fig. 2A,B).

Our results also reveal size-dependent responses of respiration and photosynthesis to temperature (at ambient  $P_{CO_2}$ ), and of respiration to high  $P_{CO_2}$  (at low temperature), and the interactive effects of temperature and  $P_{CO_2}$  (HT-HC versus LT-AC; Table 2). None of these effects correspond to a shift in magnitude of the response variable, and thus the response to temperature and  $P_{CO_2}$  will depend on the size of colonies considered. Further research will be required to identify the causes and implications of these trends, but given the influence of allometry for *P. verrucosa*, it is likely that these objectives will be well served by considering the emergent properties of branching morphologies.

### Summary and future directions

Our study is the first to address the effects of colony size on the response of a branching coral to elevated temperature and high  $P_{CO_2}$ , and is among only a handful that have addressed the role of colony size in responding to these conditions individually (Hoeksema, 1991; Shenkar et al., 2005; Brandt, 2009; van Woessik et al., 2012; Chan et al., 2016). There are two important contributions from this study. First, we build from foundational, but overlooked studies (cited above) to underscore the prevalence of allometry in colonial modular cnidarians and, therefore, to challenge the strong tendency to accept isometric scaling for this Bauplan. Our experiments show that area-normalized estimates of physiology from small corals provide misleading estimates of physiological performance of larger colonies. Second, we reveal a null result for the effects of elevated temperature and high  $P_{CO_2}$  on the calcification of a range of colony sizes, which we argue reflects properties emerging with the growth of single branches into larger colonies. As investigations of the effects of ocean acidification and climate change on coral reefs expand from coral fragments and small colonies to communities and ecosystems (Edmunds et al., 2016), greater attention will need to be given to emergent properties of coral colonies differing in size.

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### Competing interests

The authors declare no competing or financial interests.

### Author contributions

P.J.E. and S.C.B. designed the experiments, P.J.E. conducted all empirical research, S.C.B. analyzed primary results, P.J.E. and S.C.B. wrote the manuscript.

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### Data availability

Data in support of this manuscript are archived at the LTER Network Catalog <https://doi.org/10.6073/PASTA/840E360F30E8028EEECF800548E33A55> and are also available at the MCR LTER site <http://mcr.lternet.edu/cgi-bin/showDataset.cgi?docid=knbn-lter-mcr.5018>.

### Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.146381.supplemental>

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