DR. RENE MANUEL VAN DER ZANDE (Orcid ID : 0000-0001-7321-0971)
DR. DOROTHEA BENDER-CHAMP (Orcid ID : 0000-0002-1279-7091)

Article type : Primary Research Articles

Paradise lost: End-of-century warming and acidification under business-as-usual emissions have severe consequences for symbiotic corals

Running Title: End-of-century coral reefs

Rene M van der Zande[1,2], Michelle Achlatis[1,2], Dorothea Bender-Champ[1,2], Andreas Kubicek[1,2], Sophie Dove[1,2], Ove Hoegh-Guldberg[1,2,3]

[1]Coral Reef Ecosystems Lab, School of Biological Sciences, The University of Queensland, St. Lucia, QLD 4072, Australia, [2]Australian Research Council Centre of Excellence for Coral Reef Studies, The University of Queensland, St. Lucia, QLD 4072, Australia, [3]Global Change Institute, The University of Queensland, St. Lucia, QLD 4072, Australia

Corresponding author: Rene M van der Zande, Coral Reef Ecosystems Lab, School of Biological Sciences, The University of Queensland, St. Lucia, QLD 4072, Australia. Email: rene.vanderzande@uq.net.au. ORCID iD: 0000-0001-7321-0971

Keywords: climate change, coral bleaching, warming, acidification, RCP8.5, calcification, photosynthesis, *Symbiodinium*

Abstract

Despite recent efforts to curtail greenhouse gas emissions, current global emission trajectories are still following the business-as-usual RCP8.5 emission pathway. The resulting ocean warming and acidification have transformative impacts on coral reef ecosystems, detrimentally affecting coral physiology and health, and these impacts are predicted to worsen in the near future. In this study, we kept fragments of the symbiotic corals *Acropora intermedia* (thermally sensitive) and *Porites lobata* (thermally tolerant) for 7 weeks under an orthogonal design of predicted end-of-century RCP8.5 conditions for temperature and pCO_2 (3.5 °C and 570 ppm above present-day respectively) to unravel how temperature and acidification, individually or interactively, influence metabolic and physiological performance. Our results pinpoint thermal stress as the dominant driver of deteriorating health in both species because of its propensity to destabilize coral-dinoflagellate symbiosis (bleaching). Acidification had no influence on metabolism but had a significant negative effect on skeleton growth, particularly when photosynthesis was absent such as in bleached corals or under dark conditions. Total loss of photosynthesis after bleaching caused an exhaustion of protein and lipid stores and collapse of calcification that ultimately led to *A. intermedia* mortality. Despite complete loss of symbionts from its tissue, *P. lobata* maintained small amounts of photosynthesis and experienced a weaker decline in lipid and protein reserves that presumably contributed to higher survival of this species. Our results indicate that ocean warming and acidification under business-as-usual CO_2 emission scenarios will likely extirpate thermally-sensitive coral species before the end of the century, while slowing the recovery of more thermally-tolerant species from increasingly severe mass coral bleaching and mortality. This could ultimately lead to the gradual disappearance of tropical coral reefs globally, and a shift on surviving reefs to only the most resilient coral species.

Introduction

Oceans are warming and acidifying rapidly due to anthropogenic CO_2 and other greenhouse gas (GHG) emissions. As a result, marine ecosystems are changing (Hoegh-Guldberg et al., 2014), and coral reefs are among the ecosystems most urgently threatened (Hughes et al., 2017). Despite recent success in stabilizing the global increase in GHG emissions between 2014 and 2016 (1.8% had dropped to 0.4% increase per year), GHG emission rates are currently back at 2007-2013 levels (Jackson et al., 2017; Le Quéré et al., 2018; Peters et al., 2017) and tracking the high emission, 'business-as-usual' representative concentration pathway (RCP) 8.5 scenario. Irrespective of our efforts to curtail GHG emissions, the lagging persistence of CO_2 in the atmosphere will cause increased frequency and intensity of heat stress over the coming decades (Hoegh-Guldberg et al., 2014), and reefs worldwide will likely start experiencing annual bleaching outside of El Niño years (van Hooidonk et al., 2016).

Heat stress from warming oceans disrupts the symbiosis between the photosynthetic dinoflagellate endosymbionts (Symbiodiniaceae) and the coral host, resulting in expulsion of the endosymbiont from the coral tissue. The sensitivity of corals to heat stress depends on several abiotic factors such as the magnitude, rate of change, and duration of the thermal anomalies (Hughes et al., 2017), the thermal history (Grottoli et al., 2014), and potential interaction with other environmental factors (Courtney et al., 2017; Wolff, Mumby, Devlin, & Anthony, 2018). Additionally, biotic factors such as *Symbiodiniaceae* type(s) hosted (Berkelmans & van Oppen, 2006; Fitt et al., 2009; Manzello et al., 2018), coral identity (Guest et al., 2016; Hoadley et al., 2019), coral microbiome composition (Ziegler et al., 2019; Ziegler, Seneca, Yum, Palumbi, & Voolstra, 2017), heterotrophic capacity (Ferrier-Pagès, Sauzéat, & Balter, 2018; Grottoli, Rodrigues, & Palardy, 2006) and skeleton morphology (Loya et al., 2001) lead to differences in thermal tolerance between coral species.

Healthy corals rely heavily on autotropic carbon from their dinoflagellate symbionts for their daily metabolic needs (Grottoli et al., 2006; Muscatine, McCloskey, & Marian, 1981). Bleaching greatly reduces photosynthetic rates and hence the amount of photosynthetic carbon translocated to the coral host (Grottoli et al., 2006). The decline in autotrophy can be partly compensated by heterotrophy (Grottoli et al., 2006; Hughes, Grottoli, Pease, & Matsui, 2010; Levas et al., 2016; Palardy, Rodrigues, & Grottoli, 2008) and the catabolism of lipid or protein stores (Anthony, Hoogenboom, Maynard, Grottoli, & Middlebrook, 2009; Grottoli, Rodrigues, & Juarez, 2004;

Schoepf et al., 2015). However, prolonged bleaching may deplete stored energy reserves, leading to reduced metabolic activity and growth, and ultimately increased mortality (Anthony et al., 2009; Grottoli et al., 2014; Rodrigues & Grottoli, 2007).

At the same time, the dissolution of atmospheric CO_2 in the ocean changes the carbonate chemistry and decreases the seawater pH and aragonite saturation state (Ω_{ARAG}). Ocean acidification (OA) and declining Ω_{ARAG} may affect corals by increasing bleaching susceptibility and holobiont productivity (Anthony, Kline, Diaz-Pulido, Dove, & Hoegh-Guldberg, 2008; but see Hoadley et al., 2016; Schoepf et al., 2013) and reducing nutrient uptake efficiency (Godinot, Houlbrèque, Grover, Ferrier-Pagès, & Larsen, 2011). More importantly, and although in some cases effects are minimal (e.g. Schoepf et al., 2013), a large body of literature has demonstrated that acidification reduces several key metrics of coral calcification such as skeleton microstructure (Cohen, McCorkle, de Putron, Gaetani, & Rose, 2009; Drenkard et al., 2013; Tambutté et al., 2015), linear extension rates (Crook, Cohen, Rebolledo-Vieyra, Hernandez, & Paytan, 2013) and overall $CaCO_3$ deposition (Edmunds, Brown, & Moriarty, 2012; Marubini, Ferrier-Pagès, Furla, & Allemand, 2008), while increasing skeleton porosity (Fantazzini et al., 2015; Tambutté et al., 2015). Ecologically, poorly developed coral skeletons lead to higher reef erosion and storm susceptibility (Manzello et al., 2008; Marshall, 2000), reduced capacity to compete for growing space (Darling, Alvarez-Filip, Oliver, McClanahan, & Côté, 2012) and the inability to keep up with sea level rise (van Woesik, Golbuu, & Roff, 2015).

Although it is known that elevated temperature and OA together impact coral health, metabolism and skeleton formation, the underlying interactive mechanisms of these factors is crucial in the assessment of the impact and magnitude of future changes (Bay, Rose, Logan, & Palumbi, 2017; Dove et al., 2013; Schoepf et al., 2019). The number of studies investigating the individual and combined effects of temperature and pCO_2 in an orthogonal design has steadily increased in recent years (Büscher, Form, & Riebesell, 2017; Edmunds et al., 2012; Reynaud et al., 2003; Schoepf et al., 2013). However, not many orthogonal studies address extreme warming and acidification conditions (Hoadley et al., 2016) such as under the RCP8.5 emission scenario, which predicts a rise of approximately +3.5 °C and +570 µatm CO_2 for non-El Niño years by 2100 compared to present-day levels (Meinshausen et al., 2011; van Vuuren et al., 2011). Importantly, most studies employed static elevations of temperature and CO_2, thereby losing the

diel and seasonal environmental cycles and variability of a natural system. Natural fluctuations in temperature and CO_2 significantly alter coral responses, and are often found to increase resilience to thermal and acidification stress (Chan & Eggins, 2017; Comeau, Edmunds, Spindel, & Carpenter, 2014; Jiang et al., 2019; Safaie et al., 2018). Using a novel system to manipulate warming and acidification, modelled on high-resolution present-day baselines, our study maintained this variability which is imperative to investigating organismal response to environmental changes (Rivest, Comeau, & Cornwall, 2017).

The present study therefore examines how warming and acidification under RCP8.5 may affect physiological parameters indicative of long and short-term coral health in two common reef-building coral species. *Acropora intermedia* and *Porites lobata* were selected as model species because of their contrasting life-history strategies and tolerance to environmental stress (Darling, McClanahan, & Côté, 2013; Levas, Grottoli, Hughes, Osburn, & Matsui, 2013). In an orthogonal design that respects diel and seasonal variability, present-day and end-of-century summer levels of temperature and pCO_2 were simulated over seven weeks. The chosen physiological parameters (long-term $CaCO_3$ deposition and skeleton extension, day and night calcification, photosynthetic and respiration rates, tissue lipid and protein reserves, bleaching and mortality) each give specific insights into organismal functioning, and collectively provide an ecophysiological framework for explaining future coral reef trajectories under climatic changes.

Materials and methods

Experimental design

Fragments of *Acropora intermedia* (Brook, 1891) and *Porites lobata* (Dana, 1846) were collected in November 2014 from Harry's Bommie on the leeward reef slope of Heron Island Reef (23°27′34″ S 151°55′45″ E) on the Southern Great Barrier Reef at 5 m water depth (Fig. 1a). Samples were transported back to the Heron Island Research Station, where *A. intermedia* branch tips were trimmed to 5 cm length and suspended upright in 35 L outdoor glass aquaria using fishing line. Cores (30 mm diameter) were drilled from *P. lobata* colonies using a pneumatic underwater drill and cut to 2 cm height. In this way, a total of 96 fragments per species were collected from 8 adult colonies at least 10 m apart, with 10-14 fragments collected

per colony. Aquaria were covered with blue filters (Lee Filter #131 Marine Blue Filter, Hampshire, England) to replicate light conditions on the reef slope at 5 m water depth (Dove et al., 2013), and were equipped with a small powerhead (Hydor Koralia nano 900, HYDOR srl, Bassano del Grappa, Italy) for gentle water circulation (900 L h^{-1}). Coral fragments fully recovered from sampling damage under untreated flow-through seawater for two weeks. Thereafter, treatment water from the sumps was gradually introduced and mixed with untreated seawater in 25% increments per week (to obtain 25, 50, 75 and 100% treatment water) until full treatment conditions were reached (December 3-27, 2014). Corals were then kept under 100% treatment conditions for 7 weeks over Austral summer, after which physiological measurements took place.

Temperature and pCO_2 treatments were established using a computer-controlled simulation system in which different levels of warming and acidification can be achieved (for a detailed description of the system see Dove et al., (2013) as well as Achlatis et al. (2017) Supplementary Material). Treatment conditions were created as offsets to a variable temperature and pCO_2 baseline, established by CSIRO and the NOAA Pacific Marine Environment Laboratory Ocean Program using two- or three-hourly measurements over the previous summer at a reference location (Harry's Bommie) on Heron Island (Fig. S1, Fig. S2 in Supporting Information). This approach carefully preserved natural diel and seasonal fluctuations in temperature and pCO_2. Such variability is crucial because corals respond differently to static or variable environments (Rivest et al., 2017; Wahl, Saderne, & Sawall, 2016). Temperature and pCO_2 were continuously maintained and monitored in individual 8000 L sumps (turnover rate 4-6 hours) using heater-chillers and gas injection (Achlatis et al., 2017; Dove et al., 2013). Four treatments were set up based on GHG emission trajectory RCP8.5 (IPCC 2013) for temperature and pCO_2 concentrations:

1. **Control.** Served as the baseline for all other modeled treatments; replicated present-day (PD) conditions for temperature and pCO_2 at the reference site.
2. **Elevated pCO_2.** Increased only pCO_2 concentrations while maintaining PD temperature levels. Conditions were increased to those typical of an average end-of-century non-El Niño year under RCP8.5 scenarios (570 ± 11 µatm above PD levels).

3. **Elevated T.** Increased only temperature as specified by the above scenario (3.5 °C above PD levels) while maintaining PD pCO_2 levels.
4. **Elevated T/pCO_2.** Increased both temperature and pCO_2 concentration according to the same RCP8.5 scenario.

Treatment water was pumped from the sumps through the downstream aquaria (n = 2 per treatment per species) containing the corals at 0.8 L min^{-1} (aquarium water turnover 30-40 minutes). Light intensity inside the downstream aquaria was monitored using submersible light loggers (Odyssey Dataflow Systems). Seawater pH was measured continuously (InPro4501 VP X, Mettler Toledo, Victoria, Australia) in the downstream aquaria (Fig. S3), and temperature (Table 1, Fig. S1) was logged every 10 minutes (HOBO Pendant temperature loggers, Onset, Bourne, USA). Average PD and RCP8.5 temperatures were 27.5 °C and 30.5 °C respectively (Table 1). The maximum monthly mean (MMM) temperature for Heron Island is 27.3 °C (Berkelmans, 2002), and degree heating weeks (DHW) started accumulating at MMM + 1 °C (28.3 °C). In the RCP8.5 and PD temperature treatments, this point was reached after December 25th 2014 and January 27th 2015 respectively. Water samples for total alkalinity (TA) were collected weekly at midday and midnight in the downstream aquaria. TA was determined by Gran titration after Dickson et al. (2003) (Mettler-Toledo T50 titrator, Mettler-Toledo, Greifensee, Switzerland). TA values from these measurements were used to calculate pCO_2 and aragonite saturation (Ω_{ARAG}) values in the downstream aquaria (Table 1).

Table 1. Treatment design and reference experimental conditions (mean ± sd) in the downstream aquaria during the 7-week experimental period. Seawater conditions were created in upstream sumps before being pumped through downstream aquaria containing the corals. Weekly aquarium temperature averages and measured TA and pH values were used to calculate downstream Ω_{ARAG} and pCO_2 using the program CO2SYS (version 2.1).

Experimental design			**Downstream aquarium conditions**				
Treatment	Temperature level	pCO_2 level	T (°C)	pCO_2 (µatm)	Total alkalinity (µmol kg^{-1})	pH_{NBS}	Ω_{ARAG}
Control (PD)	PD	PD	27.5 ± 1.6	490 ± 99	2210 ± 32	8.10 ± 0.07	3.24 ± 0.13

Elevated pCO_2	PD	RCP8.5	27.4 ± 1.9	925 ± 204	2218 ± 39	7.87 ± 0.08	2.18 ± 0.10
Elevated T	RCP8.5	PD	30.4 ± 1.8	524 ± 162	2258 ± 10	8.09 ± 0.08	3.39 ± 0.38
Elevated T/pCO_2	RCP8.5	RCP8.5	30.8 ± 2.0	890 ± 47	2261 ± 10	7.89 ± 0.02	2.32 ± 0.07

As the possibility of coral mortality was anticipated during the experimental period, each treatment was started with n = 24 corals to maximize the number of potentially surviving corals at the point of the physiological measurements. Twelve randomly selected fragments of either *A. intermedia* or *P. lobata* were kept in each aquarium, with two aquaria per species for each treatment. Coral fragments were randomly assigned to aquaria, and placement of the aquaria was randomized such as to receive one of four treatment conditions. Corals were rotated between aquaria of the same treatment every fourth day in order to eliminate potential tank or positional effects (e.g. light variations) (Hughes et al., 2010; Levas et al., 2013; Schoepf et al., 2014). Corals were always rotated in the same cohort to enable cohort effects to be calculated and compared. Aquaria were emptied and cleaned before rotation to prevent any carry-over effects (e.g. pathogens) between cohorts. All corals were supplementary fed thawed *Artemia* (~250 mg per aquarium) daily after sunset. Water flow was interrupted for one hour during the feeding, while powerheads were kept on to maintain a gentle mixing. Bleaching and mortality were recorded every second day starting at the initiation of the treatment increments. Onset of bleaching was determined when fragments dropped two colour codes on the Coral Watch coral health chart compared to their initial colour code (Siebeck, Marshall, Klüter, & Hoegh-Guldberg, 2006). Fragments were kept in the treatments as long as alive even when fully bleached. Mortality was determined as visual loss of all tissue, absence of tentacle extension at night and subsequent algae overgrowth. Dead corals were removed from the aquaria and not included in subsequent measurements.

Metabolic measurements

Metabolic oxygen flux was measured over light-dark cycle incubations to calculate photosynthetic and respiratory rates. Corals (n = 8 per treatment) were placed in 250 ml acrylic chambers containing 0.45 µm filtered seawater (FSW) from the respective treatments and equipped with magnetic stirrers for water circulation. Oxygen content of the FSW was reduced

to approximately 60% air saturation by nitrogen gas bubbling, which may have slightly affected the seawater carbonate chemistry. Chambers were sealed with acrylic lids equipped with oxygen sensors, and a water bath mimicked the temperature of the respective treatments (Julabo F33ME refrigerated/heating circulator, Seelbach, Germany). Seawater oxygen content was logged at 15 second intervals during 30/30-minute light/dark cycles (PreSens OXY-10 mini oxygen meter, PreSens, Regensburg, Germany). Net photosynthesis (P_{NET}) and dark respiration (R_{DARK}) rates were calculated from the oxygen measurements during the light period and after 20 minutes of dark acclimation respectively. P_{NET}:R_{DARK} ratios were calculated to gauge holobiont potential for remaining net photosynthetic over a 24-hour period, based on a 12.5/11.5-hour light/dark period. Incubations were done under 320 µmol quanta m^{-2} s^{-1} (mean summer maximum daily reef slope light intensity) using Aqua Medic Ocean Lights, Bissendorf, Germany; 1 x 250 W metal halide lamp and 2 x 24 W aqualine T5 fluorescent bulbs.

Measurements of skeletogenesis

Three separate measurements of skeletogenesis were performed. Two measurements integrated skeleton growth over the experimental period: long-term average $CaCO_3$ deposition (G_{DW}) and skeleton volume change (ΔVolume). One measurement recorded instantaneous, end-of-treatment day and night $CaCO_3$ accretion (G_{TA}) under the conditions of summer thermal maximum. G_{DW} was defined as the rate of $CaCO_3$ accretion calculated from the initial and endpoint dry weights of the treatment fragments averaged over the experimental period (Eq. 1).

$$G_{DW}\left(mg\ CaCO_3\ cm^{-2}\ d^{-1}\right) = \frac{(DW_{end} - DW_{initial})}{(mean\ SA_{initial} \cdot days)} \quad \text{Eq. 1}$$

In order not to sacrifice the treatment corals, their initial dry weights ($DW_{initial}$) were inferred from their initial buoyant weights ($BW_{initial}$). For this, a separate subset of coral fragments (n = 8 and n = 20 for *A. intermedia* and *P. lobata* respectively) were collected at the start of the experiment. Fragments in this subset were buoyant weighed, coral tissue was removed and skeletons were treated with 10% hypochlorite solution for 24 hours to remove remaining organic material (Gaffey & Bronnimann, 1993), and dried and reweighed for skeleton $DW_{initial}$. The relationship between skeleton buoyant and dry weights is determined the skeleton and seawater density (Spencer Davies, 1989). Skeletal density was assumed not to vary significantly within a

species, justified by the selection of nubbins of similar orientation and position within colonies exposed to similar light conditions. This rendered a linear relationship between the $BW_{initial}$ and $DW_{initial}$ of the subset fragments (Eq. 2, $r^2 = 0.9952$ and Eq. 3, $r^2 = 0.9941$ for *A. intermedia* and *P. lobata* respectively), which was used to infer $DW_{initial}$ of the treatment corals (Spencer Davies, 1989).

$$DW_{initial}(A.\,intermedia) = (1.5296 \cdot BW_{initial}) \quad \text{Eq. 2}$$

$$DW_{initial}(P.\,lobata) = (1.5779 \cdot BW_{initial}) \quad \text{Eq. 3}$$

Initial mean skeletal densities and volumes of the treatment fragments were 3.01 g cm^{-3} and 0.66 cm^3 for *A. intermedia* and 2.83 g cm^{-3} and 7.30 cm^3 for *P. lobata*. G_{DW} of the treatment fragments was calculated from their inferred initial ($DW_{initial}$) and measured end-point (DW_{end}) dry weights (Eq. 3). Initial and end-point skeleton volumes were calculated from skeleton buoyant and dry weights, and average daily rates of volume change between the start and end of the experiment were calculated according to Eq. 4 (adapted from Spencer Davies, (1989)).

$$\Delta Volume\left(mm^3\,cm^{-2}\,d^{-1}\right) = \frac{((DW_{end} - BW_{end}) - (DW_{initial} - BW_{initial}))}{(\Delta\,days \cdot \delta_{SW} \cdot mean\,SA_{initial})} \cdot 1000 \quad \text{Eq. 4}$$

End-of-treatment instantaneous calcification rates (G_{TA}, n = 8 per treatment) were determined under day and night conditions using the TA anomaly method (Chisholm & Gattuso, 1991). TA change was measured over separate 1-hour light and dark incubations at physiological day (11:00 - 12:00) and night (21:30 - 22:30) time to ensure natural light and dark rhythms. Incubations were done under the same settings as the metabolic oxygen flux measurements. Water samples for TA determination were collected before (triplicate sample from the filtered batch treatment water) and after each incubation from the individual chamber. TA was determined by Gran titration as above, and used to calculate day and night G_{TA} rates (Eq. 5).

$$G_{TA}\left(\mu mol\,CaCO_3\,cm^{-2}\,h^{-1}\right) = \left(\frac{\Delta TA\,(\mu mol)}{2 \cdot SA_{end}\,(cm^2) \cdot time\,(h)}\right) \cdot Vol\,(L) \quad \text{Eq. 5}$$

279

280 *Tissue parameters*

281 Tissue protein and lipid content (n = 8 per treatment) was measured at the end of the treatment
282 period. Tissue was collected from the skeletons using a simple airbrush and 30 ml FSW. Half of
283 the obtained mixture was stored at -20 °C for lipid analysis. The other half was centrifuged for
284 mass separation at 4500 RPM for 5 minutes, and a 2 ml sample of the supernatant was kept for
285 water-soluble host protein determination. The remaining pellet was washed with 5 ml FSW,
286 centrifuged at 4500 RPM for 5 minutes for a total of three washes to clean the pellet from coral
287 mucus, and then resuspended in 5 ml FSW for symbiont density determination by microscope
288 hemocytometer counts.

289 Water-soluble host protein content was determined by differential absorbance at 235 and 280 nm
290 using spectrometry (Spectra Max 2, Molecular Devices, Sunnyvale, California) (Whitaker &
291 Granum, 1980). Lipids were measured using a modified protocol of Dunn et al. (2012). The
292 frozen lipid sample was freeze-dried (ScanVac CoolSafe, LaboGene, Lillerød, Denmark), and
293 dry material was dissolved in 5 ml 2:1 chloroform/methanol solution, vortexed and left overnight
294 at 4°C to allow full lipid extraction. Next, the samples were centrifuged at 4000 RPM for 4
295 minutes and the organic solvent was transferred into a clean tube. The remaining pellet was
296 rinsed with 2 ml chloroform/methanol solution, and this solution was added to the original 5 ml
297 after one hour at 4 °C. Next, 1 ml of 0.1 mol l^{-1} KCl solution was added to the organic solvent,
298 and left overnight at 4°C to allow separation of organic and aqueous phases. After careful
299 removal of the aqueous phase, the remaining organic phase was washed with 5 ml 1:1
300 methanol/MQ solution three times. Each wash was left overnight at 4°C for phase separation and
301 subsequent removal of the aqueous phase. After the third wash the remaining organic solution
302 was poured into a pre-weighed aluminum tray, left to evaporate, and reweighed for lipid
303 quantification. The surface area covered by live coral tissue was calculated using the double
304 waxing method (Veal, Carmi, Fine, & Hoegh-Guldberg, 2010) applied to bleached and dried
305 skeletons.

306

307 *Statistical analyses*

The overall holobiont response for each species to the temperature and pCO_2 treatments was analyzed using multivariate two-way analysis of similarities (ANOSIM) with 9999 permutations. All data was square root transformed and ranked similarities were calculated using Bray-Curtis similarities. Treatment responses were graphically represented using non-metric multidimensional scaling (nMDS). Multivariate analyses were done in PRIMER V6 (PRIMER-e, Auckland, New Zealand), and included all measured physiological variables: symbiont density, P_{NET}, R_{DARK}, P_{NET}:R_{DARK}, averaged long-term $CaCO_3$ accretion rates (G_{DW}), skeleton volume increase, tissue lipid and protein content, and end-of-experiment light and dark calcification rates (G_{TA}).

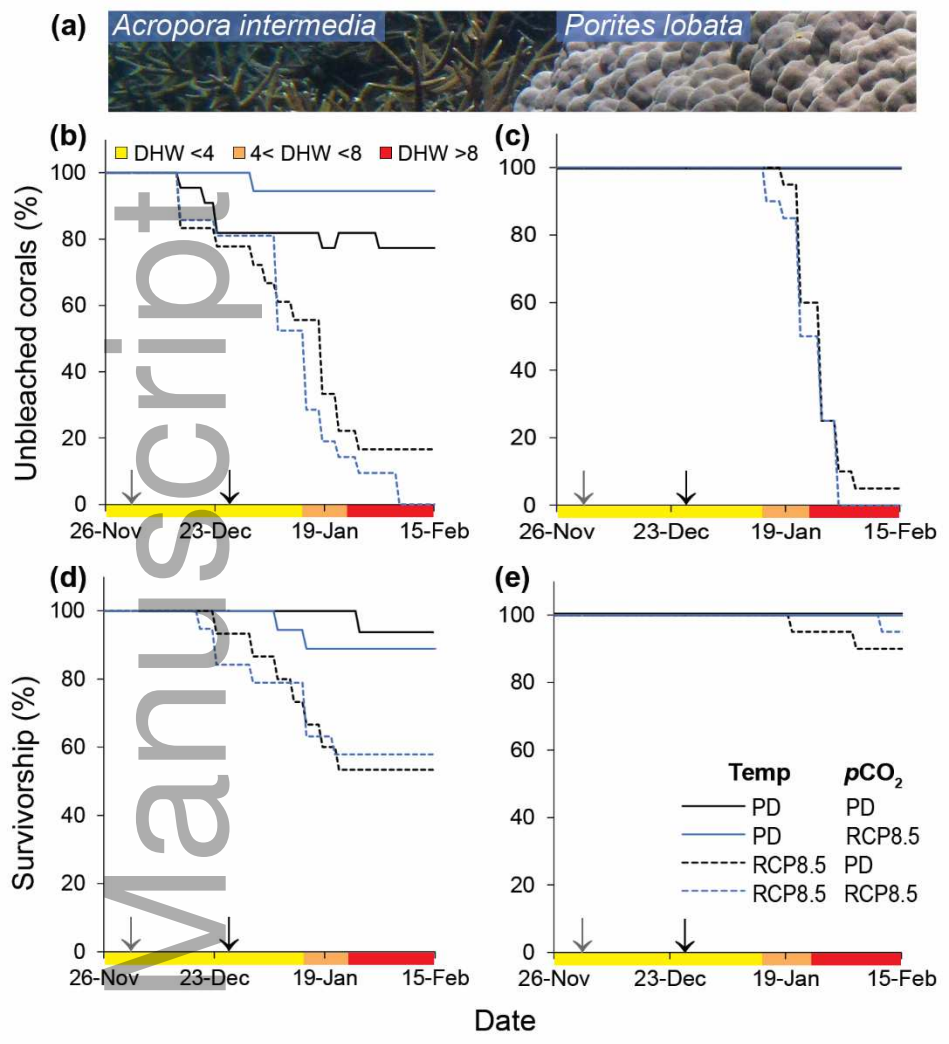
Further analysis of each individual physiological variable except the G_{TA} measurements was done using a nested two-factorial ANOVA design. The categorical factors temperature and pCO_2 had two levels each, PD and RCP8.5. Cohort was nested in the interaction of the factors to test for cohort-specific effects (Tolosa, Treignier, Grover, & Ferrier-Pagès, 2011), which were absent for all parameters tested. Measurements of G_{TA} were analyzed in a mixed three-factorial ANOVA, with temperature and pCO_2 as between subjects factors, and Time (Day/Night) as the within subjects factor. Cohort effect in light and dark G_{TA} rates was analyzed separately in a preliminary analysis, whereby cohort response was nested in the interaction of the factors (Table S1). No between-cohort effects were found and samples from the duplicate cohorts per treatment were therefore pooled (Tremblay et al., 2012; Tremblay, Gori, Maguer, Hoogenboom, & Ferrier-Pagès, 2016; Underwood, 1997) for the G_{TA} analysis. Coral bleaching and survival curves were analyzed using a two-proportion z-test. All analyses were tested for violations of normality (Shapiro-Wilk test) and homogeneity of variances (Levene's test), and transformed where necessary using square-root or log transformation. Results were tested against the $\alpha = 0.01$ level to reduce chances of a type-I error when assumptions were still violated after transformation (Underwood, 1997). In all other cases significance was tested against the $\alpha = 0.05$ level. All factorial analyses were done with Statistica 13.2 (Statsoft, Tulsa, OK, USA).

Results

Bleaching and mortality

Thermal stress regimes for the RCP8.5 temperature treatments were as follows: DHW < 4 between December 25th and January 13th; 4 < DHW < 8 between January 14th and 24th; DHW > 8 after January 24th, until a maximum of 15.6 °C weeks had been reached at the end of the experimental period on February 15th (Fig. 1). In the PD temperature treatments, thermal stress reached 0.5 °C weeks by the end of the experimental periods.

Bleaching of *A. intermedia* in the elevated temperature treatments started halfway through the treatment increment period. By the time full treatment was reached, 20% of specimens under elevated temperatures were visibly bleached, and the number of bleached corals continued to increase steadily (Fig. 1b). After seven weeks in the elevated T and elevated T/pCO_2 treatments, respectively 83% ($z = 3.43$, $p < 0.001$) and 100% ($z = 4.42$, $p < 0.001$) of *A. intermedia* had bleached. There was a low occurrence of *A. intermedia* bleaching in both PD temperature treatments irrespective of the pCO_2 concentration because of high baseline summer temperatures. Bleaching of *P. lobata* under both elevated temperature treatments started at approximately three weeks into full treatment (Fig. 1c). Respectively 95% ($z = 5.79$, $p < 0.001$) and 100% ($z = 6.04$, $p < 0.001$) of *P. lobata* specimens in the elevated T and T/pCO_2 bleached, while no significant *P. lobata* bleaching occurred under PD temperatures. Mortality in *A. intermedia* under elevated temperatures trailed the onset of bleaching by approximately 2 weeks (Fig. 1d). After seven weeks mortality reached 46.7% ($z = 2.51$, $p = 0.012$) and 42.1% ($z = 2.29$, $p = 0.022$) in the elevated T and T/pCO_2 treatments, respectively. No significant differences in *P. lobata* mortality were observed between treatments (Fig. 1e).



358

359 **Figure 1.** Bleaching and survival curves for *Acropora intermedia* (left panels) and *Porites lobata*
360 (right panels) during warming and acidification stress. Inset picture (a) shows co-occurring
361 colonies of the two species on Heron Island. Specimens were exposed to independent and
362 concurrent levels of temperature and pCO_2 according to end-of-century RCP8.5 emission
363 scenarios over seven weeks. The percentage of unbleached (b,c) and dead (d,e) corals were
364 recorded every second day. The seven-week experimental period was preceded by four weeks of
365 step-wise treatment exposure (25% increments weekly). Grey (December 3, 2014) and black
366 (December 27, 2014) arrows depict the start of the step-wise introduction and full treatment
367 phases respectively. The colored horizontal bar represents the degree heating weeks (DHW; °C
368 weeks) reached in the elevated temperature treatments, throughout the experiment; yellow for

DHW < 4 (November 26th 2014 - January 13th 2015), orange for 4 < DHW < 8 (January 14th - 24th 2015) and red for DHW > 8 (January 25th - February 15th 2015).

Multivariate analyses

Overall, the physiological response in *A. intermedia* (Fig. 2a) was strongly determined by the effect of elevated temperature (ANOSIM R = 0.878, p < 0.001), and less by elevated pCO_2 (ANOSIM R = 0.225, p = 0.011). The overall response of *P. lobata* was similar to *A. intermedia*, depending strongly on thermal stress (ANOSIM R = 1, p < 0.001) and less on acidification (ANOSIM R = 0.116, p = 0.043), consistent with the nMDS results (Fig. 2).

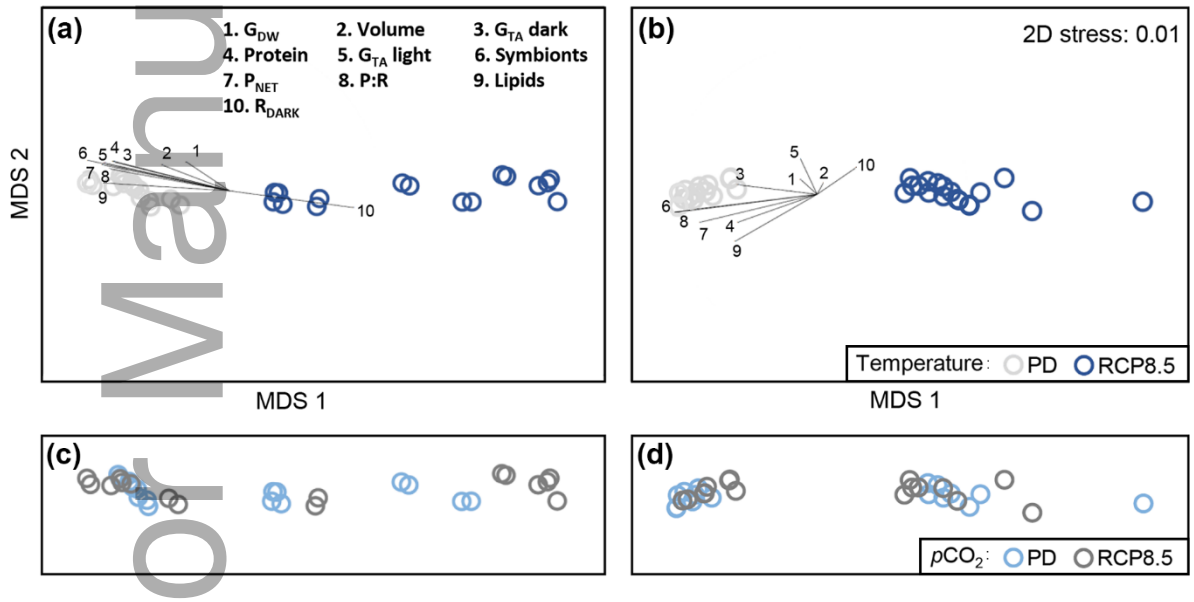
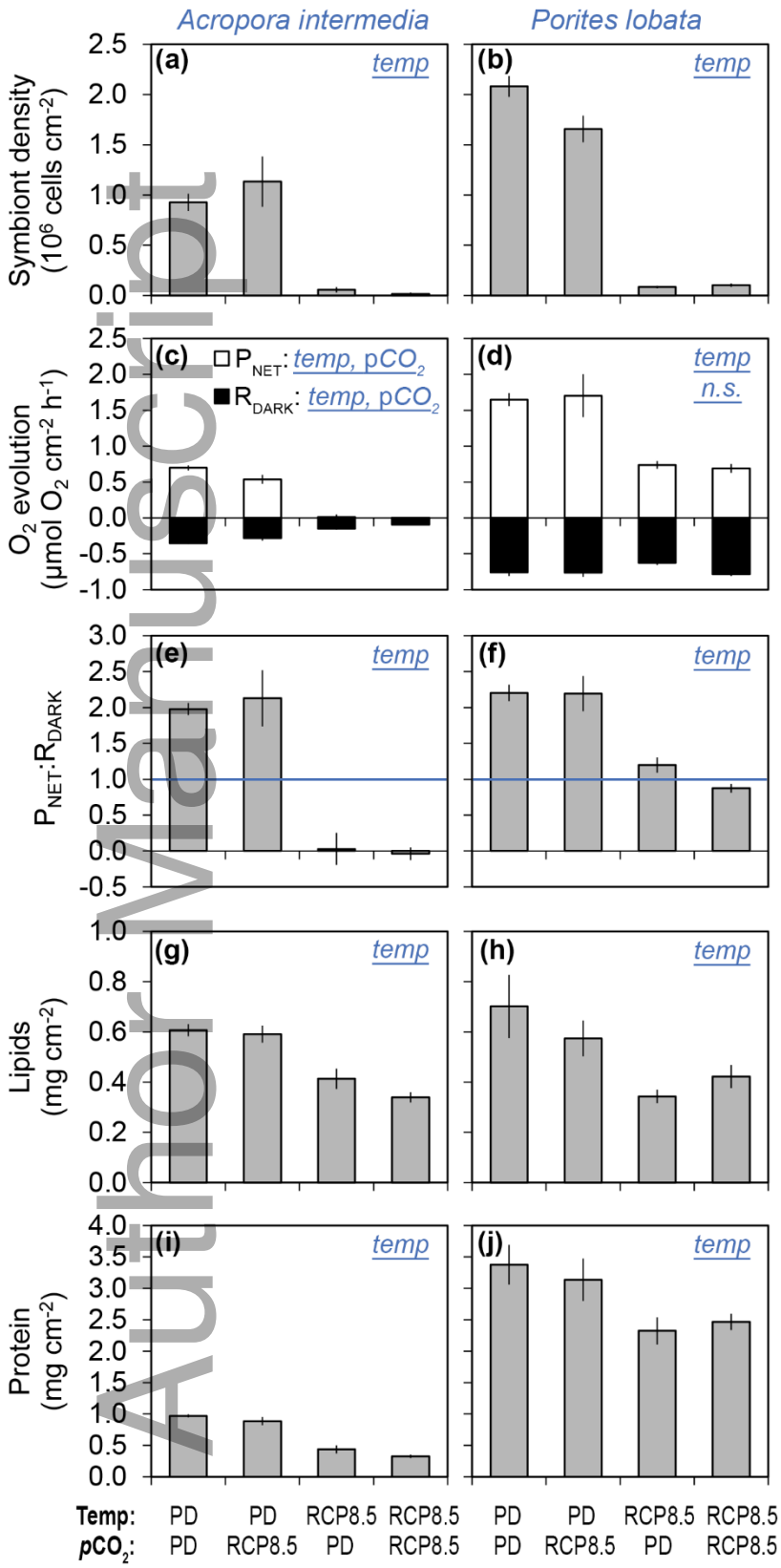


Figure 2. Non-metric multidimensional scaling (nMDS) plots showing similarities in overall holobiont response for *Acropora intermedia* (a) and *Porites lobata* (b) to differential temperature and pCO_2 treatments. Top panels show grouping based on response to warming, whereas bottom panels depict grouping based on acidification effects. Vector overlay depicts the proportional contribution of each biological variable (numbered) to the distribution.

Metabolic and tissue parameters

Specimens of *A. intermedia* and *P. lobata* under heat stress contained significantly lower amounts of dinoflagellate symbionts in their tissue (Fig. 3). Irrespective of the level of pCO_2, warming reduced symbiont concentrations by 28-fold in *A. intermedia* (main effect T; $F_{1,24} = 125.5$, $p < 0.001$; Fig. 3a) and 20-fold in *P. lobata* (main effect T; $F_{1,24} = 285.7$, $p < 0.001$; Fig. 3b). Rates of P_{NET} in *A. intermedia* (Fig. 3c) decreased when exposed to elevated temperature (main effect T; $F_{1,24} = 262.0$, $p < 0.001$) and pCO_2 levels (main effect pCO_2; $F_{1,24} = 5.2$, $p = 0.032$), but not their interaction, with highest P_{NET} values being measured in the control treatment. Similarly, R_{DARK} rates in *A. intermedia* were governed by elevated temperature (main effect T; $F_{1,24} = 106.5$, $p < 0.001$) and elevated pCO_2 levels individually (main effect pCO_2; $F_{1,24} = 12.0$, $p = 0.002$). In *P. lobata*, P_{NET} (Fig. 3d) was affected by warming alone, dropping more than 50% in elevated temperature treatments (main effect T; $F_{1,24} = 40.79$, $p < 0.001$). No significant differences were found in R_{DARK} rates for *P. lobata*. P_{NET}:R_{DARK} ratios for *A. intermedia* (Fig. 3e) declined from 1.98 ± 0.08 and 1.84 ± 0.14 in the control and elevated pCO_2 treatments respectively, to approximately zero values at elevated temperatures, irrespective of the level of pCO_2 (main effect T; $F_{1,24} = 193.9$, $p < 0.001$). Warming significantly reduced P_{NET}:R_{DARK} ratios in *P. lobata* (Fig. 3f) irrespective of the level of pCO_2. P_{NET}:R_{DARK} ratios were above 2 in both PD temperature treatments, and dropped to 1.20 ± 0.11 and 0.87 ± 0.06 for elevated T and elevated T/pCO_2 treatments respectively (main effect T; $F_{1,24} = 64.93$, $p < 0.001$).

Exposure to elevated temperatures decreased the tissue lipid concentration in both *A. intermedia* (main effect T; $F_{1,24} = 48.02$, $p < 0.001$) and *P. lobata* (main effect T; $F_{1,24} = 10.50$, $p = 0.003$) while tissue lipid concentration was unaffected by acidification (Fig. 3g, h). Similarly, host protein concentrations in both coral species declined as a result of heat stress (main effect T; $F_{1,24} = 111.7$, $p < 0.001$ and main effect T; $F_{1,24} = 9.410$, $p = 0.005$ for *A. intermedia* and *P. lobata* respectively). Host protein concentrations in both species were unaffected by different levels of pCO_2 (Fig. 3i, j).

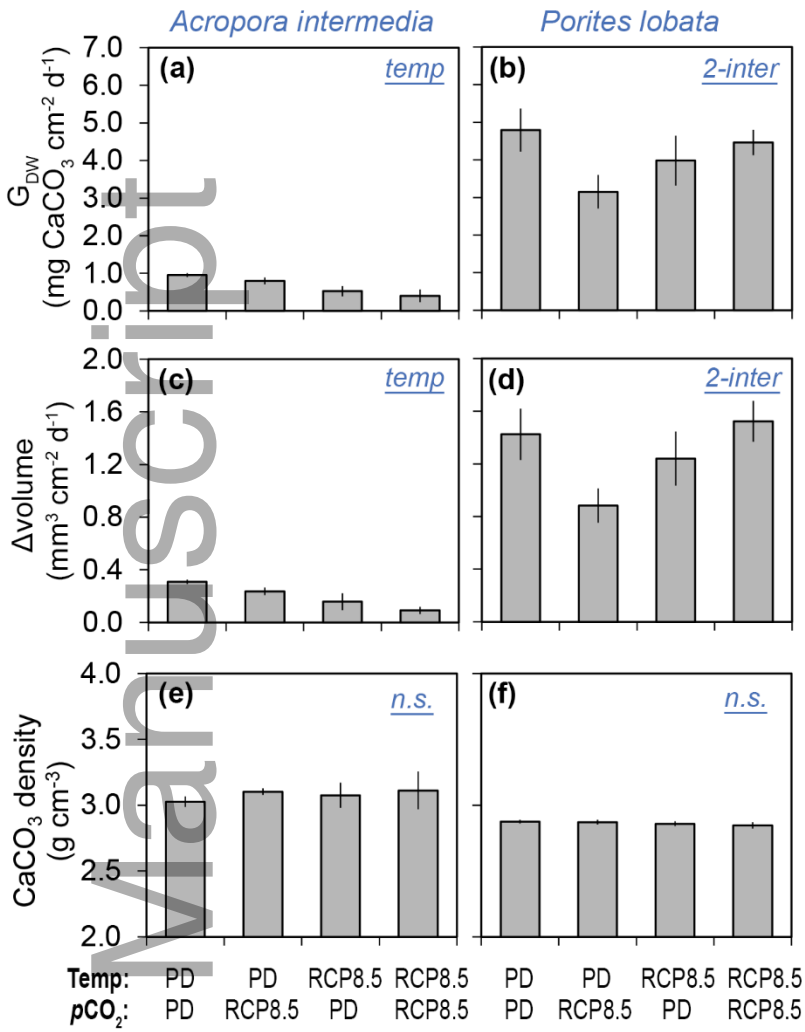


411

Figure 3. Parameters of photobiology and tissue composition (mean ± SE) of *Acropora intermedia* (left panels) and *Porites lobata* (right panels) after exposure to different treatments of warming and acidification. Dinoflagellate symbiont density (a,b), photobiology (c-f) and tissue lipid (g,h) and protein content (i,j) were measured on corals (n = 8 per treatment) exposed for seven weeks to independent and concurrent levels of temperature and pCO_2 according to end-of-century RCP8.5 projections. Horizontal blue lines in (e,f) at P_{NET}:R_{DARK} = 1 depict the autotrophic break-even ratio. The blue text inside the panels indicates the absence (n.s. = no significance) or presence of significant main effects of warming (temp) and/or acidification (pCO_2).

Skeletal accretion

Long-term average rates of $CaCO_3$ accretion (G_{DW}) were differentially affected by warming and acidification in each species. In *A. intermedia*, G_{DW} declined after exposure to elevated compared to PD temperatures (main effect T; $F_{1,24}$ = 14.30, p = 0.001), while it was unaffected by acidification (Fig. 4a). In *P. lobata*, exposure to elevated pCO_2 reduced G_{DW} rates only under PD (Fig. 4b), and not under elevated temperatures (interactive effect T × pCO_2; $F_{1,24}$ = 4.445, p = 0.046). Skeleton volume of *A. intermedia* (Fig. 4c) increased less over time under warming, while it was unaffected by pCO_2 levels (main effect T; $F_{1,24}$ = 16.65, p < 0.001). In *P. lobata*, skeleton volume change was governed by an interactive effect of temperature and pCO_2 (Fig. 4d). Volume expansion was reduced by acidification under PD temperatures, but it was unaffected under elevated temperature levels (interactive effect T × pCO_2; $F_{1,24}$ = 6.394, p = 0.018). Despite the observed differences in volume change between warming and acidification scenarios in both species, skeleton density did not differ between the treatments (Fig. 4e, f).



435

436 **Figure 4.** Parameters of long-term skeleton growth (mean ± SE) under different treatments of
437 warming and acidification for *Acropora intermedia* (left panels) and *Porites lobata* (right
438 panels). Seven-week averages of skeleton $CaCO_3$ accretion (G_{DW}; a,b) and skeleton volume
439 expansion rates (c,d) were determined for corals exposed to independent and concurrent levels of
440 temperature and pCO_2 according to end-of-century RCP8.5 projections. Averages span the entire
441 period, including before the onset of bleaching. Skeleton density (e,f) was determined at the end
442 of the experimental period. The blue text inside the panels indicates the presence of significant
443 main effects of warming (temp) or 2-way interactive effects of warming and acidification (2-
444 inter).

445

End-of-treatment rates of calcification (G_{TA}) in *A. intermedia* (Fig. 5a) were governed by a three-way interaction between temperature, pCO_2 and time of measurement (interactive effect Time × T × pCO_2; $F_{1,28}$ = 23.3, p < 0.001). When exposed to elevated pCO_2, daytime G_{TA} rates were threefold higher than nighttime G_{TA} rates (Tukey HSD p < 0.001). Warming decreased G_{TA} to below zero levels irrespective of light or dark conditions (Tukey HSD p < 0.001). When measured under dark conditions, exposure to elevated temperature reduced G_{TA} rates more under PD pCO_2 compared to elevated pCO_2 levels (Tukey HSD p < 0.001). Likewise, G_{TA} rates in *P. lobata* (Fig. 5b) depended on a three-way interactive effect of temperature, pCO_2 and time of measurement (interactive effect Time × T × pCO_2; $F_{1,28}$ = 4.64, p = 0.040). Daytime G_{TA} rates were positive across treatments but declined to negative values under dark conditions in all except the control treatments. During daytime G_{TA} rates were unaffected by levels of temperature and pCO_2, while elevated pCO_2 decreased G_{TA} rates at nighttime irrespective of temperature (Tukey HSD p = 0.018).

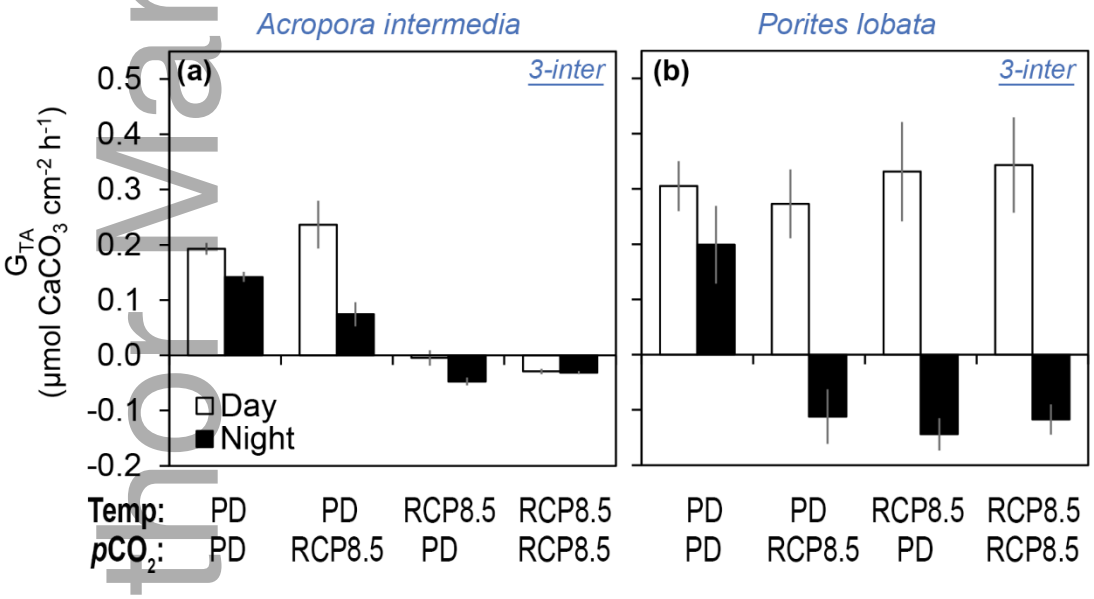


Figure 5. End-of-treatment day and night-time calcification rates (G_{TA}; mean ± SE) under different treatments of warming and acidification for *Acropora intermedia* (a) and *Porites lobata* (b). Rates (n = 8 per treatment) were measured after seven weeks of exposure to independent and concurrent levels of temperature and pCO_2 according to end-of-century RCP8.5 projections. The blue text inside the panels indicates the presence of significant 3-way interactive effects of time (day/night), warming and acidification (3-inter).

Discussion

The present study assessed the two global stressors most commonly associated with future emission scenarios, namely elevated temperature and pCO_2. We did so under an experimental design that preserved the natural diel and seasonal fluctuations in temperature and pCO_2 by superimposing future conditions on a present-day baseline. This allowed full interaction of environmental drivers under their naturally variable ranges, and produces accurate organismal responses to their environment. The present study reveals that tropical symbiotic corals experience physiological impairment, extensive bleaching and mortality when exposed to end-of-century, non-El Niño summer thermal and OA regimes under RCP8.5 scenarios (570 ppm pCO_2 and 3.5 °C above PD values). Thermal stress was identified as the main driver of physiological changes and mortality due to its correlation with coral bleaching. Collapse of primary productivity, stored energy reserves and skeleton accretion were the main drivers of observed mortality. These effects were evident in both species, though the decline was stronger in *A. intermedia* compared to *P. lobata*.

Thermal stress and bleaching

The RCP8.5 emissions scenario implies far more challenging thermal conditions than expected under the 2015 Paris Agreement, which aims to stabilize average global temperatures below 2 °C above preindustrial values (Hoegh-Guldberg et al., 2019). Emission rates currently follow the RCP8.5 pathway projections (Jackson et al., 2017; Le Quéré et al., 2018), and future reefs will likely experience annual heat waves exceeding present-day extremes (Frieler et al., 2013; van Hooidonk et al., 2016). Even before projected end-of-century conditions will be reached, summer bleaching and El Niño events will likely increase in frequency (Cai et al., 2014). The 2016 and 2017 bleaching events were the worst in GBR history, with >60% bleaching in the northern regions (Hughes et al., 2017), followed by significant subsequent mortality. During these bleaching events, northern GBR reefs experienced >4 (high likelihood for severe coral bleaching) and >8 (high likelihood for widespread coral mortality) °C weeks over approximately four and three months respectively, and peaking at approximately 15.5 °C weeks (NOAA CRF 5

km satellite data; Hughes et al., 2019). Thermal conditions in the high temperature treatment of the present study - which preceded the 2016-2017 bleaching events - exceeded 4 °C weeks for more than five weeks and 8 °C weeks for three weeks, before peaking at 15.6 °C weeks at the termination of the experiment in mid-February, approximately when annual thermal peaks are typically attained in this region of the GBR (NOAA virtual stations, 5km). By then, both *A. intermedia* and *P. lobata* had bleached severely and *A. intermedia* mortality had reached 50%, a proportion that would have likely increased further under extended periods of DHW >8, had the experiment been continued to the end of summer.

Treatment effects on growth, productivity and energy reserves

Long-term averages of skeleton accretion (G_{DW}) as well as increases in skeleton volume for both *A. intermedia* and *P. lobata* (Fig. 4) declined concurrently, although they remained positive. However, in *A. intermedia* these changes were primarily temperature driven compared to pCO_2 driven in *P. lobata*. The concurrent decrease in skeleton G_{DW} and volume suggests no shift between skeleton extension and bulk density, contrasting previous studies showing deteriorating skeleton density and structure under OA (Crook, Cohen, Rebolledo-Vieyra, Hernandez, & Paytan, 2013; Fantazzini et al., 2015; Tambutté et al., 2015). However, analysis of end-of-treatment rates of calcification (Fig. 5) revealed a negative effect of pCO_2 on skeletogenesis in both species, ultimately resulting in net skeleton dissolution in *A. intermedia*. However, this was only the case under dark conditions or otherwise absence of photosynthetic activity (i.e. bleaching), as demonstrated by the collapse of calcification in *A. intermedia* under thermal stress. Our results demonstrate the importance of photosynthetic activity to calcification, particularly in *A. intermedia*. The ability to maintain photosynthesis during daytime greatly mitigated the negative effects of acidification on G_{TA} through internal pH upregulation and energy supply (Dufault et al., 2013; McCulloch, Falter, Trotter, & Montagna, 2012; Wall et al., 2016), despite growing in a seawater Ω_{ARAG} of approximately 2.3. Effects of elevated pCO_2 were strong under night-time conditions, owing to a reduction in seawater pH which was exacerbated by additional respiration and deficiency of photosynthetic products at the calicoblastic layer (Colombo-Pallotta, Rodríguez-Román, & Iglesias-Prieto, 2010; Venn et al., 2013). In bleached *A. intermedia* G_{TA} was negative, despite average seawater Ω_{ARAG} values of 3.39 (Table 1) and

daytime G_{TA} was not reduced in either species as long as photosynthetic rates were maintained (Levas, Grottoli, Hughes, Osburn, & Matsui, 2013). The constraints of elevated temperature and acidification on long and short-term measures of skeleton growth will, provided that corals survive, limit reef capacity to outpace sea-level rise and decrease resilience to extreme weather (Manzello et al., 2008; Mollica et al., 2018; van Woesik, Golbuu, & Roff, 2015).

Elevated pCO_2 reduced R_{DARK} and P_{NET} in *A. intermedia* but not in *P. lobata*. The effect of seawater acidification on coral photosynthesis is uncertain, with previous studies observing either small or no changes of photosynthesis under lower pH (Anthony, Kline, Diaz-Pulido, Dove, & Hoegh-Guldberg, 2008; Comeau, Carpenter, & Edmunds, 2016; Hoadley et al., 2015; Marubini, Ferrier-Pagès, Furla, & Allemand, 2008). Reduction of the symbiont population density under heat stress in both species of this study was similar and unaffected by elevated pCO_2, consistent with the hypothesis that temperature is the dominant bleaching agent (Hughes et al., 2017; Schoepf et al., 2013, 2019). However, P_{NET} did not decline equally in the two species. In *A. intermedia* P_{NET} decreased proportionally to symbiont loss, whereas in *P. lobata* P_{NET} only dropped by 50% after a 95% symbiont decline. This could indicate a high degree of self-shading in endosymbionts present in unbleached *P. lobata* (Enríquez, Méndez, & Iglesias-Prieto, 2005; Hoogenboom, Connolly, & Anthony, 2008), or lower susceptibility of photosynthesis to heat stress in thermally tolerant *Cladocopium* C15 in massive *Porites* (Fisher, Malme, & Dove, 2012). Alternatively, P_{NET} could be compensated by a significant endolithic algae community typical of *Porites* sp. (Marcelino, Morrow, van Oppen, Bourne, & Verbruggen, 2017; Shashar, Banaszak, Lesser, & Amrami, 1997). Endolithic algae are known to increase in abundance in stressed corals, though it remains unclear why (Fine & Loya, 2002; Reyes-Nivia, Diaz-Pulido, Kline, Guldberg, & Dove, 2013). We observed a 3 mm thick green band underlying the coral tissue in *P. lobata*, approximately 5 mm into the skeleton, indicating that endolithic algae photosynthesis may have been responsible for the compensation in P_{NET} after symbiont loss. Retaining photosynthetic rates and a supply of photosynthates from endolithic algae partly mitigates the detrimental effects of heat stress and bleaching (Fine & Loya, 2002), and may help corals to sustain the theoretical autotrophic break-even point at P_{NET}:R_{DARK} = 1 (Muscatine, McCloskey, & Marian, 1981). In the present study, bleached *P. lobata* were able to maintain a P_{NET}:R_{DARK} ratio of approximately 1, while this ratio was nearly zero in bleached *A. intermedia*. This suggests that *P. lobata* may still be receiving some autotrophic carbon to maintain basic

556 metabolic functions even when bleached, while *A. intermedia* would have to switch to
557 heterotrophy or stored energy reserves for metabolism (Grottoli, Rodrigues, & Palardy, 2006;
558 Rodrigues & Grottoli, 2007). Additionally, high heterotrophic capacity and somatic energy
559 reserves in *P. lobata* compared to *A. intermedia* likely benefit this species during bleaching
560 (Levas, Grottoli, Hughes, Osburn, & Matsui, 2013; Palardy, Rodrigues, & Grottoli, 2008).

561 Heterotrophic compensation for photosynthetic losses could alleviate immediate energetic stress
562 after bleaching (Baumann, Grottoli, Hughes, & Matsui, 2014; Grottoli, Rodrigues, & Palardy,
563 2006; Hughes, Grottoli, Pease, & Matsui, 2010), and possibly aid recovery (Levas, Grottoli,
564 Hughes, Osburn, & Matsui, 2013). However, this is possibly insufficient for survival when corals
565 remain bleached over longer timescales (Anthony, Connolly, & Hoegh-Guldberg, 2007;
566 Anthony, Hoogenboom, Maynard, Grottoli, & Middlebrook, 2009; Grottoli et al., 2006).
567 Previous studies have demonstrated enhanced heterotrophic feeding capacity in selective coral
568 species under thermal stress (Ferrier-Pagès, Rottier, Beraud, & Levy, 2010; Grottoli et al., 2014;
569 Grottoli, Rodrigues, & Palardy, 2006; Hughes, Grottoli, Pease, & Matsui, 2010), and
570 improvement of coral thermal tolerance through heterotrophy-derived nutrients (Ferrier-Pagès,
571 Sauzéat, & Balter, 2018). In the present experiment, corals were fed thawed *Artemia* at
572 concentrations similar to those of ambient zooplankton *in situ*, since the 10 μm filter of our
573 water inlet had removed most larger prey normally contributing to the coral diet (Houlbrèque &
574 Ferrier-Pagès, 2009; Palardy, Grottoli, & Matthews, 2005). Visual inspection confirmed tentacle
575 extension and feeding behavior in both bleached and unbleached living corals, indicating that
576 feeding capacity was not affected by RCP8.5 scenario conditions. However, the decline in host
577 tissue protein and lipid concentrations under thermal stress indicates at least a partial failure of
578 heterotrophy to compensate for loss in photosynthates (Hughes et al., 2010).

579 Lipid and protein concentrations in unbleached specimens of both species were comparable to
580 concentrations found for healthy corals of similar genera in previous studies (Hoogenboom,
581 Rottier, Sikorski, & Ferrier-Pagès, 2015) but declined markedly under thermal stress, particularly
582 in *A. intermedia*. Lipid catabolism by bleached corals additionally fulfils immediate metabolic
583 demands in the absence of photosynthetic carbon (Fitt, Spero, Halas, White, & Porter, 1993;
584 Grottoli, Rodrigues, & Juarez, 2004; Grottoli & Rodrigues, 2011). However, the exhaustion of
585 stored energy reserves has been linked to rapid increases in mortality of coral larvae (Graham,

586 Baird, Connolly, Sewell, & Willis, 2017) and adult colonies (Anthony, Connolly, & Hoegh-
587 Guldberg, 2007; Bay, Guérécheau, Andreakis, Ulstrup, & Matz, 2013; Kenkel, Meyer, & Matz,
588 2013). We observed a significant increase in *A. intermedia* mortality when thermally stressed,
589 concomitant with diminished tissue protein and lipid concentrations. *P. lobata* mortality
590 remained low (10%), despite significant declines in tissue lipid and protein concentrations under
591 thermal stress. The present study ended in mid-February, before the end of the annual thermal
592 maximum period on Heron Island. Previous studies have described a lagging effect between
593 thermal stress and physiological decline in several coral species including *P. lobata* (Levas,
594 Grottoli, Hughes, Osburn, & Matsui, 2013; Rodrigues & Grottoli, 2007), thus energetic
595 exhaustion and mortality in our study could be worsened over the full duration of summer
596 (Hughes et al., 2017).

597

598 *Not all corals are equal*

599 *A. intermedia* and *P. lobata* clearly respond differently to elevated temperature and acidification.
600 Bleaching in *A. intermedia* started approximately 5 weeks earlier than in *P. lobata*, and *A.*
601 *intermedia* mortality was significant under elevated temperature. Furthermore, the collapse of
602 day and nighttime G_{TA} and productivity in *A. intermedia* was more severe than in *P. lobata*, but
603 acidification affected night-time G_{TA} more in *P. lobata*. Coral species are known to differ in their
604 sensitivity to environmental cues (Fabricius et al., 2011), determined by a combination of factors
605 such as host identity (Fitt et al., 2009; Hoadley et al., 2019), Symbiodiniaceae type(s) hosted (Fitt
606 et al., 2009; Sampayo, Ridgway, Bongaerts, & Hoegh-Guldberg, 2008) and nearby benthic
607 community composition (Dove et al., 2013). At Heron Island *A. intermedia* has been found to
608 harbor thermally sensitive *Cladocopium* C3, while *P. lobata* harbored predominantly thermally
609 tolerant *Cladocopium* C15 (Fisher, Malme, & Dove, 2012; LaJeunesse et al., 2004), likely
610 explaining the later onset of bleaching in *P. lobata*. The introduction of symbiont-specific traits
611 and other varying factors may lead to trade-offs in coral performance (Jones & Berkelmans,
612 2011), and invites further experiments studying different combinations of environments and
613 organisms to discern future climate impacts on reef health and survival (Bay, Rose, Logan, &
614 Palumbi, 2017; Hoadley et al., 2019; Wall, Mason, Ellis, Cunning, & Gates, 2017). Our results
615 show that *P. lobata* is more tolerant to thermal and OA stress than *A. intermedia*. Although

warming is the dominant driver of holobiont response in both species (Fig. 2), temperature impacts fundamental physiological and metabolic properties more strongly in *A. intermedia*. Aside from some exceptions (Kim et al., 2019), this is in accordance with findings from previous research that classify *Porites* sp. as temperature tolerant and *Acropora* sp. as temperature sensitive (Fabricius et al., 2011; Loya et al., 2001; Marshall & Baird, 2000), though this may shift as global warming intensifies (Grottoli et al., 2014; Rodolfo-Metalpa et al., 2014).

Concluding remarks

Changes in metabolism and physiology in both coral species under elevated temperature and acidification were invariably negative, and mostly driven by heat stress. Previous studies reported mixed, and often interactive effects (Bahr, Jokiel, & Rodgers, 2016; Büscher, Form, & Riebesell, 2017; Edmunds, Brown, & Moriarty, 2012; Reynaud et al., 2003; Schoepf et al., 2013), but these were under more moderate temperature and acidification conditions than the end-of-century conditions of the RCP8.5 scenario, and not during peak summer conditions. There was no evidence of synergistic behavior of thermal and acidification effects in this study. Our results demonstrate that under extreme, end-of-century summer conditions of the business-as-usual emissions scenario coral bleaching becomes inevitable even in heat-tolerant species, and furthermore suggest that the ensuing prolonged collapse of photosynthesis dominates all other processes (Anthony, Connolly, & Hoegh-Guldberg, 2007; Grottoli, Rodrigues, & Juarez, 2004). Additionally, the interaction of natural diel pCO_2 fluctuations with benthic community metabolism and decreased seawater buffer capacity under future conditions likely drives a severe widening of the CO_2 range that reefs will be exposed to in the future compared to that predicted by atmospheric models (Shaw, McNeil, Tilbrook, Matear, & Bates, 2013), exerting additional stress on these ecosystems.

Worldwide, coral health and growth have already significantly decreased over the last decades, often as a result of climate change (Baumann et al., 2019; Cantin, Cohen, Karnauskas, Tarrant, & McCorkle, 2010; Cooper, De'ath, Fabricius, & Lough, 2008; Mellin et al., 2019; Perry et al., 2015). Our study indicates that this pattern will become increasingly problematic in the future as conditions worsen (Lough, Anderson, & Hughes, 2018; van Hooidonk et al., 2016), unless corals are able to adapt rapidly. The acclimation or adaptation capacity of symbiotic corals to

environmental change is uncertain, (Berkelmans & van Oppen, 2006; Pandolfi, Connolly, Marshall, & Cohen, 2011; Sully, Burkepile, Donovan, Hodgson, & van Woesik, 2019; Wright et al., 2019), and differs between species (Grottoli et al., 2014). The finding that some present-day corals fare better under conditions of a century ago suggests that little adaptation has occurred so far (Dove et al., 2013). Meanwhile, some species are close to their upper limit in short-term thermal acclimation (Schoepf et al., 2019), and may not be able to keep pace under the rapidly increasing temperature conditions of the RCP8.5 scenario (Bay, Rose, Logan, & Palumbi, 2017; Hoegh-Guldberg, 2012). Thermally sensitive groups (e.g. Acroporids) have been severely impacted by warming in recent years (Kim et al., 2019; Le Nohaïc et al., 2017) and are already facing local extinction (Riegl et al., 2018). Recurring thermal anomalies predicted under RCP8.5 emission pathways will likely cause the disappearance of thermally-sensitive coral species from reefs globally before 2100 (Lough, Anderson, & Hughes, 2018), while annually recurring bleaching could prove devastating to even some of the most thermally-tolerant species (Grottoli et al., 2014). Overall, if warming continues unabated, future reefs will be severely reduced in diversity and populated by only the most resilient coral species.

Acknowledgements

This research was funded by the NOAA Coral Reef Watch and the Australian Research Council (ARC), the ARC Centre of Excellence for Coral Reef Studies grant CE0561435 and ARC Laureate grant FL120100066 (to OHG and SD), a University of Queensland International Scholarship UQI and a Holsworth Wildlife Research Endowment (Equity Trustees Charitable Foundation) grant (to RZ). We thank Aaron Chai, Giovanni Bernal-Carrillo, Annamieke van den Heuvel and Mark Snowball for support and assistance with the T/CO_2 system, as well as Stijn den Haan, Christopher Brunner and the HIRS staff for their help in the field. Sample collection and experimental work occurred under permit G14/37212.1 issued by the GBR Marine Park Authority.

Author contributions

RZ, SD and OHG conceived and designed the study. RZ and MA performed the experiment. Data were analyzed by RZ, SD and MA, and DB, AK and OHG contributed to data interpretation. RZ wrote the manuscript with all co-authors contributing to its final form.

Data sharing and accessibility

The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

Achlatis, M., van der Zande, R. M., Schönberg, C. H. L., Fang, J. K. H., Hoegh-Guldberg, O., & Dove, S. (2017). Sponge bioerosion on changing reefs: ocean warming poses physiological constraints to the success of a photosymbiotic excavating sponge. *Scientific Reports*, *7*(1), 10705. https://doi.org/10.1038/s41598-017-10947-1

Anthony, K. R. N., Connolly, S. R., & Hoegh-Guldberg, O. (2007). Bleaching, energetics, and coral mortality risk: Effects of temperature, light, and sediment regime. *Limnology and Oceanography*, *52*(2), 716–726. https://doi.org/10.4319/lo.2007.52.2.0716

Anthony, K. R. N., Hoogenboom, M. O., Maynard, J. A., Grottoli, A. G., & Middlebrook, R. (2009). Energetics approach to predicting mortality risk from environmental stress: a case study of coral bleaching. *Functional Ecology*, *23*(3), 539–550. https://doi.org/10.1111/j.1365-2435.2008.01531.x

Anthony, K. R. N., Kline, D. I., Diaz-Pulido, G., Dove, S., & Hoegh-Guldberg, O. (2008). Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(45), 17442–6. https://doi.org/10.1073/pnas.0804478105

Bahr, K. D., Jokiel, P. L., & Rodgers, K. S. (2016). Seasonal and annual calcification rates of the Hawaiian reef coral, *Montipora capitata* , under present and future climate change scenarios. *ICES Journal of Marine Science*, *74*(4), 1083–1091. https://doi.org/10.1093/icesjms/fsw078

Baumann, J., Grottoli, A. G., Hughes, A. D., & Matsui, Y. (2014). Photoautotrophic and heterotrophic carbon in bleached and non-bleached coral lipid acquisition and storage. *Journal of Experimental Marine Biology and Ecology*, *461*, 469–478. https://doi.org/10.1016/j.jembe.2014.09.017

Baumann, J. H., Ries, J. B., Rippe, J. P., Courtney, T. A., Aichelman, H. E., Westfield, I., & Castillo, K. D. (2019). Nearshore coral growth declining on the Mesoamerican Barrier Reef System. *Global Change Biology*, *25*(11), 3932–3945. https://doi.org/10.1111/gcb.14784

Bay, L. K., Guérécheau, A., Andreakis, N., Ulstrup, K. E., & Matz, M. V. (2013). Gene expression signatures of energetic acclimatisation in the reef building coral *Acropora millepora*. *PLoS ONE*, *8*(5), e61736. https://doi.org/10.1371/journal.pone.0061736

Bay, R. A., Rose, N. H., Logan, C. A., & Palumbi, S. R. (2017). Genomic models predict successful coral adaptation if future ocean warming rates are reduced. *Science Advances*, *3*(11), e1701413. https://doi.org/10.1126/sciadv.1701413

Berkelmans, R. (2002). Time-integrated thermal bleaching thresholds of reefs and their variation on the Great Barrier Reef. *Marine Ecology Progress Series, 229*, 73-82. https://doi.org/10.2307/24865053

Berkelmans, R., & van Oppen, M. J. . (2006). The role of zooxanthellae in the thermal tolerance of corals: a "nugget of hope" for coral reefs in an era of climate change. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1599), 2305–2312. https://doi.org/10.1098/rspb.2006.3567

Büscher, J. V., Form, A. U., & Riebesell, U. (2017). Interactive effects of ocean acidification and warming on growth, fitness and survival of the cold-water coral *Lophelia pertusa* under different food availabilities. *Frontiers in Marine Science*, *4*. https://doi.org/10.3389/fmars.2017.00101

Cai, W., Borlace, S., Lengaigne, M., van Rensch, P., Collins, M., Vecchi, G., … Jin, F.-F. (2014). Increasing frequency of extreme El Niño events due to greenhouse warming. *Nature Climate Change*, *4*(2), 111–116. https://doi.org/10.1038/nclimate2100

Cantin, N. E., Cohen, A. L., Karnauskas, K. B., Tarrant, A. M., & McCorkle, D. C. (2010).

729 Ocean warming slows coral growth in the central Red Sea. *Science*, *329*(5989).
730 https://doi.org/10.1126/science.1190182

731 Chan, W. Y., & Eggins, S. M. (2017). Calcification responses to diurnal variation in seawater
732 carbonate chemistry by the coral *Acropora formosa*. *Coral Reefs*, *36*(3), 763–772.
733 https://doi.org/10.1007/s00338-017-1567-8

734 Chisholm, J. R. M., & Gattuso, J.-P. (1991). Validation of the alkalinity anomaly technique for
735 investigating calcification of photosynthesis in coral reef communities. *Limnology and*
736 *Oceanography*, *36*(6), 1232–1239. https://doi.org/10.4319/lo.1991.36.6.1232

737 Cohen, A. L., McCorkle, D. C., de Putron, S., Gaetani, G. A., & Rose, K. A. (2009).
738 Morphological and compositional changes in the skeletons of new coral recruits reared in
739 acidified seawater: Insights into the biomineralization response to ocean acidification.
740 *Geochemistry, Geophysics, Geosystems*, *10*(7). https://doi.org/10.1029/2009GC002411

741 Colombo-Pallotta, M. F., Rodríguez-Román, A., & Iglesias-Prieto, R. (2010). Calcification in
742 bleached and unbleached *Montastraea faveolata*: evaluating the role of oxygen and glycerol.
743 *Coral Reefs*, *29*(4), 899–907. https://doi.org/10.1007/s00338-010-0638-x

744 Comeau, S., Carpenter, R. C., & Edmunds, P. J. (2016). Effects of pCO_2 on photosynthesis and
745 respiration of tropical scleractinian corals and calcified algae. *ICES Journal of Marine*
746 *Science*, *74*(4), 1092–1102. https://doi.org/10.1093/icesjms/fsv267

747 Comeau, S., Edmunds, P., Spindel, N., & Carpenter, R. (2014). Diel pCO_2 oscillations modulate
748 the response of the coral *Acropora hyacinthus* to ocean acidification. *Marine Ecology*
749 *Progress Series*, *501*, 99–111. https://doi.org/10.3354/meps10690

750 Cooper, T., De'ath, G., Fabricius, K. E., & Lough, J. M. (2008). Declining coral calcification in
751 massive *Porites* in two nearshore regions of the northern Great Barrier Reef. *Global Change*
752 *Biology*, *14*(3), 529–538. https://doi.org/10.1111/j.1365-2486.2007.01520.x

753 Courtney, T. A., Lebrato, M., Bates, N. R., Collins, A., de Putron, S. J., Garley, R., …
754 Andersson, A. J. (2017). Environmental controls on modern scleractinian coral and reef-scale
755 calcification. *Science Advances*, *3*(11), e1701356. https://doi.org/10.1126/sciadv.1701356

756 Crook, E. D., Cohen, A. L., Rebolledo-Vieyra, M., Hernandez, L., & Paytan, A. (2013). Reduced

calcification and lack of acclimatization by coral colonies growing in areas of persistent natural acidification. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(27), 11044–9. https://doi.org/10.1073/pnas.1301589110

Darling, E. S., Alvarez-Filip, L., Oliver, T. A., McClanahan, T. R., & Côté, I. M. (2012). Evaluating life-history strategies of reef corals from species traits. *Ecology Letters*, *15*(12), 1378–1386. https://doi.org/10.1111/j.1461-0248.2012.01861.x

Darling, E. S., McClanahan, T. R., & Côté, I. M. (2013). Life histories predict coral community disassembly under multiple stressors. *Global Change Biology*, *19*(6), 1930–1940. https://doi.org/10.1111/gcb.12191

Dickson, A. G., Afghan, J. D., & Anderson, G. C. (2003). Reference materials for oceanic CO_2 analysis: a method for the certification of total alkalinity. *Marine Chemistry*, *80*(2–3), 185–197. https://doi.org/10.1016/S0304-4203(02)00133-0

Dove, S. G., Kline, D. I., Pantos, O., Angly, F. E., Tyson, G. W., & Hoegh-Guldberg, O. (2013). Future reef decalcification under a business-as-usual CO_2 emission scenario. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(38), 15342–7. https://doi.org/10.1073/pnas.1302701110

Drenkard, E. J., Cohen, A. L., McCorkle, D. C., de Putron, S. J., Starczak, V. R., & Zicht, A. E. (2013). Calcification by juvenile corals under heterotrophy and elevated CO_2. *Coral Reefs*, *32*(3), 727–735. https://doi.org/10.1007/s00338-013-1021-5

Dufault, A. M., Ninokawa, A., Bramanti, L., Cumbo, V. R., Fan, T.-Y., & Edmunds, P. J. (2013). The role of light in mediating the effects of ocean acidification on coral calcification. *The Journal of Experimental Biology*, *216*, 1570–1577. https://doi.org/10.1242/jeb.080549

Dunn, S. R., Thomas, M. C., Nette, G. W., Dove, S. G., & Blackburn, S. (2012). A lipidomic approach to understanding free fatty acid lipogenesis derived from dissolved inorganic carbon within Cnidarian-Dinoflagellate symbiosis. *PLoS ONE*, *7*(10), e46801. https://doi.org/10.1371/journal.pone.0046801

Edmunds, P. J., Brown, D., & Moriarty, V. (2012). Interactive effects of ocean acidification and temperature on two scleractinian corals from Moorea, French Polynesia. *Global Change*

Biology, *18*(7), 2173–2183. https://doi.org/10.1111/j.1365-2486.2012.02695.x

Enríquez, S., Méndez, E. R., & Iglesias-Prieto, R. (2005). Multiple scattering on coral skeletons enhances light absorption by symbiotic algae. *Limnology and Oceanography*, *50*(4), 1025–1032. https://doi.org/10.4319/lo.2005.50.4.1025

Fabricius, K. E., Langdon, C., Uthicke, S., Humphrey, C., Noonan, S., De'ath, G., … Lough, J. M. (2011). Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. *Nature Climate Change*, *1*(3), 165–169. https://doi.org/10.1038/nclimate1122

Fantazzini, P., Mengoli, S., Pasquini, L., Bortolotti, V., Brizi, L., Mariani, M., … Goffredo, S. (2015). Gains and losses of coral skeletal porosity changes with ocean acidification acclimation. *Nature Communications*, *6*(1), 7785. https://doi.org/10.1038/ncomms8785

Ferrier-Pagès, C., Rottier, C., Beraud, E., & Levy, O. (2010). Experimental assessment of the feeding effort of three scleractinian coral species during a thermal stress: Effect on the rates of photosynthesis. *Journal of Experimental Marine Biology and Ecology*, *390*(2), 118–124. https://doi.org/10.1016/J.JEMBE.2010.05.007

Ferrier-Pagès, C., Sauzéat, L., & Balter, V. (2018). Coral bleaching is linked to the capacity of the animal host to supply essential metals to the symbionts. *Global Change Biology*, *24*(7), 3145–3157. https://doi.org/10.1111/gcb.14141

Fine, M., & Loya, Y. (2002). Endolithic algae: an alternative source of photoassimilates during coral bleaching. *Proceedings of the Royal Society of London B: Biological Sciences*, *269*(1497), 1205–1210. https://doi.org/10.1098/rspb.2002.1983

Fisher, P. L., Malme, M. K., & Dove, S. (2012). The effect of temperature stress on coral–*Symbiodinium* associations containing distinct symbiont types. *Coral Reefs*, *31*(2), 473–485. https://doi.org/10.1007/s00338-011-0853-0

Fitt, W. K., Gates, R. D., Hoegh-Guldberg, O., Bythell, J. C., Jatkar, A., Grottoli, A. G., … Lesser, M. P. (2009). Response of two species of Indo-Pacific corals, *Porites cylindrica* and *Stylophora pistillata*, to short-term thermal stress: The host does matter in determining the tolerance of corals to bleaching. *Journal of Experimental Marine Biology and Ecology*, *373*(2), 102–110. https://doi.org/10.1016/j.jembe.2009.03.011

Fitt, W. K., Spero, H. J., Halas, J., White, M. W., & Porter, J. W. (1993). Recovery of the coral *Montastrea annularis* in the Florida Keys after the 1987 Caribbean "bleaching event." *Coral Reefs*, *12*(2), 57–64. https://doi.org/10.1007/BF00302102

Frieler, K., Meinshausen, M., Golly, A., Mengel, M., Lebek, K., Donner, S. D., & Hoegh-Guldberg, O. (2013). Limiting global warming to 2 °C is unlikely to save most coral reefs. *Nature Climate Change*, *3*(2), 165–170. https://doi.org/10.1038/nclimate1674

Gaffey, S. J., & Bronnimann, C. E. (1993). Effects of bleaching on organic and mineral phases in biogenic carbonates. *Journal of Sedimentary Research*, *63*(4), 752–754. https://doi.org/10.1306/D4267BE0-2B26-11D7-8648000102C1865D

Godinot, C., Houlbrèque, F., Grover, R., Ferrier-Pagès, C., & Larsen, A. (2011). Coral uptake of inorganic phosphorus and nitrogen negatively affected by simultaneous changes in temperature and pH. *PLoS ONE*, *6*(9), e25024. https://doi.org/10.1371/journal.pone.0025024

Graham, E. M., Baird, A. H., Connolly, S. R., Sewell, M. A., & Willis, B. L. (2017). Uncoupling temperature-dependent mortality from lipid depletion for scleractinian coral larvae. *Coral Reefs*, *36*(1), 97–104. https://doi.org/10.1007/s00338-016-1501-5

Grottoli, A. G., & Rodrigues, L. J. (2011). Bleached *Porites compressa* and *Montipora capitata* corals catabolize δ13C-enriched lipids. *Coral Reefs*, *30*(3), 687. https://doi.org/10.1007/s00338-011-0756-0

Grottoli, A. G., Rodrigues, L. J., & Juarez, C. (2004). Lipids and stable carbon isotopes in two species of Hawaiian corals, *Porites compressa* and *Montipora verrucosa*, following a bleaching event. *Marine Biology*, *145*(3), 621–631. https://doi.org/10.1007/s00227-004-1337-3

Grottoli, A. G., Rodrigues, L. J., & Palardy, J. E. (2006). Heterotrophic plasticity and resilience in bleached corals. *Nature*, *440*(7088), 1186–1189. https://doi.org/10.1038/nature04565

Grottoli, A. G., Warner, M. E., Levas, S. J., Aschaffenburg, M. D., Schoepf, V., McGinley, M., … Matsui, Y. (2014). The cumulative impact of annual coral bleaching can turn some coral species winners into losers. *Global Change Biology*, *20*(12), 3823–3833. https://doi.org/10.1111/gcb.12658

Guest, J. R., Low, J., Tun, K., Wilson, B., Ng, C., Raingeard, D., … Steinberg, P. D. (2016). Coral community response to bleaching on a highly disturbed reef. *Scientific Reports*, *6*(1), 20717. https://doi.org/10.1038/srep20717

Hoadley, K. D., Lewis, A. M., Wham, D. C., Pettay, D. T., Grasso, C., Smith, R., … Warner, M. E. (2019). Host–symbiont combinations dictate the photo-physiological response of reef-building corals to thermal stress. *Scientific Reports*, *9*(1), 9985. https://doi.org/10.1038/s41598-019-46412-4

Hoadley, K. D., Pettay, D. T., Grottoli, A. G., Cai, W.-J., Melman, T. F., Schoepf, V., … Warner, M. E. (2015). Physiological response to elevated temperature and pCO_2 varies across four Pacific coral species: Understanding the unique host+symbiont response. *Scientific Reports*, *5*, 18371. https://doi.org/10.1038/srep18371

Hoadley, K. D., Pettay, D. T., Grottoli, A. G., Cai, W. J., Melman, T. F., Levas, S., … Warner, M. E. (2016). High-temperature acclimation strategies within the thermally tolerant endosymbiont *Symbiodinium trenchii* and its coral host, *Turbinaria reniformis*, differ with changing pCO_2 and nutrients. *Marine Biology*, *163*(6), 1–13. https://doi.org/10.1007/s00227-016-2909-8

Hoegh-Guldberg, O. (2012). The adaptation of coral reefs to climate change: Is the Red Queen being outpaced? *Scientia Marina*, *76*(2), 403–408. https://doi.org/10.3989/scimar.03660.29A

Hoegh-Guldberg, O., Cai, R., Poloczanska, E. S. S., Brewer, P. G. G., Sundby, S., Hilmi, K., … Jung, S. (2014). The Ocean. In C. U. Press (Ed.), R. C1001 (Trans.), *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 1655–1731). Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.

Hoegh-Guldberg, O., Jacob, D., Taylor, M., Guillén Bolaños, T., Bindi, M., Brown, S., … Zhou, G. (2019). The human imperative of stabilizing global climate change at 1.5°C. *Science*, *365*(6459), eaaw6974. https://doi.org/10.1126/science.aaw6974

Hoogenboom, M. O., Connolly, S. R., & Anthony, K. R. N. (2008). Interactions between

morphological and physiological plasticity optimize energy acquisition in corals. *Ecology*, *89*(4), 1144–1154. https://doi.org/10.1890/07-1272.1

Hoogenboom, M., Rottier, C., Sikorski, S., & Ferrier-Pagès, C. (2015). Among-species variation in the energy budgets of reef-building corals: scaling from coral polyps to communities. *Journal of Experimental Biology*, *218*(24), 3866–3877. https://doi.org/10.1242/jeb.124396

Houlbrèque, F., & Ferrier-Pagès, C. (2009). Heterotrophy in tropical scleractinian corals. *Biological Reviews*, *84*(1), 1–17. https://doi.org/10.1111/j.1469-185X.2008.00058.x

Hughes, A., Grottoli, A., Pease, T., & Matsui, Y. (2010). Acquisition and assimilation of carbon in non-bleached and bleached corals. *Marine Ecology Progress Series*, *420*, 91–101. https://doi.org/10.3354/meps08866

Hughes, T. P., Kerry, J. T., Álvarez-Noriega, M., Álvarez-Romero, J. G., Anderson, K. D., Baird, A. H., … Wilson, S. K. (2017). Global warming and recurrent mass bleaching of corals. *Nature*, *543*(7645), 373–377. https://doi.org/10.1038/nature21707

Hughes, T. P., Kerry, J. T., Baird, A. H., Connolly, S. R., Chase, T. J., Dietzel, A., … Woods, R. M. (2019, April 18). Global warming impairs stock–recruitment dynamics of corals. *Nature*. Nature Publishing Group. https://doi.org/10.1038/s41586-019-1081-y

Jackson, R. B., Le Quéré, C., Andrew, R. M., Canadell, J. G., Peters, G. P., Roy, J., & Wu, L. (2017). Warning signs for stabilizing global CO_2 emissions. *Environmental Research Letters*, *12*(11), 110202. https://doi.org/10.1088/1748-9326/aa9662

Jiang, L., Guo, Y.-J., Zhang, F., Zhang, Y.-Y., McCook, L. J., Yuan, X.-C., … Huang, H. (2019). Diurnally fluctuating pCO_2 modifies the physiological responses of coral recruits under ocean acidification. *Frontiers in Physiology*, *9*. https://doi.org/10.3389/fphys.2018.01952

Jones, A. M., & Berkelmans, R. (2011). Tradeoffs to thermal acclimation: energetics and reproduction of a reef coral with heat tolerant *Symbiodinium* Type-D. *Journal of Marine Biology*, *2011*, 1–12. https://doi.org/10.1155/2011/185890

Kenkel, C. D., Meyer, E., & Matz, M. V. (2013). Gene expression under chronic heat stress in populations of the mustard hill coral (*Porites astreoides*) from different thermal

environments. *Molecular Ecology*, *22*(16), 4322–4334. https://doi.org/10.1111/mec.12390

Kim, S. W., Sampayo, E. M., Sommer, B., Sims, C. A., Gómez-Cabrera, M. del C., Dalton, S. J., … Pandolfi, J. M. (2019). Refugia under threat: Mass bleaching of coral assemblages in high-latitude eastern Australia. *Global Change Biology*, *25*(11), 3918–3931. https://doi.org/10.1111/gcb.14772

LaJeunesse, T., Bhagooli, R., Hidaka, M., deVantier, L., Done, T., Schmidt, G., … Hoegh-Guldberg, O. (2004). Closely related *Symbiodinium* spp. differ in relative dominance in coral reef host communities across environmental, latitudinal and biogeographic gradients. *Marine Ecology Progress Series*, *284*, 147–161. https://doi.org/10.3354/meps284147

Le Nohaïc, M., Ross, C. L., Cornwall, C. E., Comeau, S., Lowe, R., McCulloch, M. T., & Schoepf, V. (2017). Marine heatwave causes unprecedented regional mass bleaching of thermally resistant corals in northwestern Australia. *Scientific Reports*, *7*(1), 14999. https://doi.org/10.1038/s41598-017-14794-y

Le Quéré, C., Andrew, R. M., Friedlingstein, P., Sitch, S., Hauck, J., Pongratz, J., … Zheng, B. (2018). Global carbon budget 2018. *Earth System Science Data*, *10*(4), 2141–2194. https://doi.org/10.5194/essd-10-2141-2018

Levas, S., Grottoli, A. G., Schoepf, V., Aschaffenburg, M., Baumann, J., Bauer, J. E., & Warner, M. E. (2016). Can heterotrophic uptake of dissolved organic carbon and zooplankton mitigate carbon budget deficits in annually bleached corals? *Coral Reefs*, *35*(2), 495–506. https://doi.org/10.1007/s00338-015-1390-z

Levas, S. J., Grottoli, A. G., Hughes, A., Osburn, C. L., & Matsui, Y. (2013). Physiological and biogeochemical traits of bleaching and recovery in the mounding species of coral *Porites lobata*: Implications for resilience in mounding corals. *PLoS ONE*, *8*(5). https://doi.org/10.1371/journal.pone.0063267

Lough, J. M., Anderson, K. D., & Hughes, T. P. (2018). Increasing thermal stress for tropical coral reefs: 1871–2017. *Scientific Reports*, *8*(1), 6079. https://doi.org/10.1038/s41598-018-24530-9

Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H., & van Woesik, R. (2001). Coral

bleaching: the winners and the losers. *Ecology Letters*, *4*(2), 122–131. https://doi.org/10.1046/j.1461-0248.2001.00203.x

Manzello, D. P., Kleypas, J. A., Budd, D. A., Eakin, C. M., Glynn, P. W., & Langdon, C. (2008). Poorly cemented coral reefs of the eastern tropical Pacific: possible insights into reef development in a high-CO_2 world. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(30), 10450–5. https://doi.org/10.1073/pnas.0712167105

Manzello, D. P., Matz, M. V., Enochs, I. C., Valentino, L., Carlton, R. D., Kolodziej, G., … Jankulak, M. (2018). Role of host genetics and heat tolerant algal symbionts in sustaining populations of the endangered coral *Orbicella faveolata* in the Florida Keys with ocean warming. *Global Change Biology*, *25*(3), 1016–1031. https://doi.org/10.1111/gcb.14545

Marcelino, V. R., Morrow, K. M., van Oppen, M. J. H., Bourne, D. G., & Verbruggen, H. (2017). Diversity and stability of coral endolithic microbial communities at a naturally high pCO_2 reef. *Molecular Ecology*, *26*(19), 5344–5357. https://doi.org/10.1111/mec.14268

Marshall, P. A. (2000). Skeletal damage in reef corals: relating resistance to colony morphology. *Marine Ecology Progress Series*, *200*, 177–189. https://doi.org/10.2307/24855870

Marshall, P. A., & Baird, A. H. (2000). Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs*, *19*(2), 155–163. https://doi.org/10.1007/s003380000086

Marubini, F., Ferrier-Pagès, C., Furla, P., & Allemand, D. (2008). Coral calcification responds to seawater acidification: a working hypothesis towards a physiological mechanism. *Coral Reefs*, *27*(3), 491–499. https://doi.org/10.1007/s00338-008-0375-6

McCulloch, M., Falter, J., Trotter, J., & Montagna, P. (2012). Coral resilience to ocean acidification and global warming through pH up-regulation. *Nature Climate Change*, *2*(8), 623–627. https://doi.org/10.1038/nclimate1473

Meinshausen, M., Smith, S. J., Calvin, K., Daniel, J. S., Kainuma, M. L. T., Lamarque, J.-F., … van Vuuren, D. P. P. (2011). The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. *Climatic Change*, *109*(1–2), 213–241. https://doi.org/10.1007/s10584-011-0156-z

953 Mellin, C., Matthews, S., Anthony, K. R. N., Brown, S. C., Caley, M. J., Johns, K. A., …
954 MacNeil, M. A. (2019). Spatial resilience of the Great Barrier Reef under cumulative
955 disturbance impacts. *Global Change Biology*, *25*(7), gcb.14625.
956 https://doi.org/10.1111/gcb.14625

957 Mollica, N. R., Guo, W., Cohen, A. L., Huang, K. F., Foster, G. L., Donald, H. K., & Solow, A.
958 R. (2018). Ocean acidification affects coral growth by reducing skeletal density. *Proceedings*
959 *of the National Academy of Sciences of the United States of America*, *115*(8), 1754–1759.
960 https://doi.org/10.1073/pnas.1712806115

961 Muscatine, L., R. McCloskey, L., & E. Marian, R. (1981). Estimating the daily contribution of
962 carbon from zooxanthellae to coral animal respiration. *Limnology and Oceanography*, *26*(4),
963 601–611. https://doi.org/10.4319/lo.1981.26.4.0601

964 National Oceanic and Atmospheric Administration Coral Reef Watch. 5-km pixel satellite data.
965 Available at: https://coralreefwatch.noaa.gov/satellite/index.php

966 Palardy, J. E., Rodrigues, L. J., & Grottoli, A. G. (2008). The importance of zooplankton to the
967 daily metabolic carbon requirements of healthy and bleached corals at two depths. *Journal of*
968 *Experimental Marine Biology and Ecology*, *367*(2), 180–188.
969 https://doi.org/10.1016/j.jembe.2008.09.015

970 Palardy, J., Grottoli, A., & Matthews, K. (2005). Effects of upwelling, depth, morphology and
971 polyp size on feeding in three species of Panamanian corals. *Marine Ecology Progress Series*,
972 *300*, 79–89. https://doi.org/10.3354/meps300079

973 Pandolfi, J. M., Connolly, S. R., Marshall, D. J., & Cohen, A. L. (2011). Projecting coral reef
974 futures under ghlobal warming andocean acidification. *Science*, *333*(6041), 418–422.
975 https://doi.org/10.1126/science.1204794

976 Perry, C. T., Steneck, R. S., Murphy, G. N., Kench, P. S., Edinger, E. N., Smithers, S. G., &
977 Mumby, P. J. (2015). Regional-scale dominance of non-framework building corals on
978 Caribbean reefs affects carbonate production and future reef growth. *Global Change Biology*,
979 *21*(3), 1153–1164. https://doi.org/10.1111/gcb.12792

980 Peters, G. P., Le Quéré, C., Andrew, R. M., Canadell, J. G., Friedlingstein, P., Ilyina, T., …

Tans, P. (2017). Towards real-time verification of CO_2 emissions. *Nature Climate Change*, *7*(12), 848–850. https://doi.org/10.1038/s41558-017-0013-9

Reyes-Nivia, C., Diaz-Pulido, G., Kline, D., Guldberg, O.-H., & Dove, S. (2013). Ocean acidification and warming scenarios increase microbioerosion of coral skeletons. *Global Change Biology*, *19*(6), 1919–1929. https://doi.org/10.1111/gcb.12158

Reynaud, S., Leclercq, N., Romaine-Lioud, S., Ferrier-Pages, C., Jaubert, J., & Gattuso, J.-P. (2003). Interacting effects of CO_2 partial pressure and temperature on photosynthesis and calcification in a scleractinian coral. *Global Change Biology*, *9*(11), 1660–1668. https://doi.org/10.1046/j.1365-2486.2003.00678.x

Riegl, B., Johnston, M., Purkis, S., Howells, E., Burt, J., Steiner, S. C. C., … Bauman, A. (2018). Population collapse dynamics in *Acropora downingi*, an Arabian/Persian Gulf ecosystem-engineering coral, linked to rising temperature. *Global Change Biology*, *24*(6), 2447–2462. https://doi.org/10.1111/gcb.14114

Rivest, E. B., Comeau, S., & Cornwall, C. E. (2017, December 1). The role of natural variability in shaping the response of coral reef organisms to climate change. *Current Climate Change Reports*. Springer. https://doi.org/10.1007/s40641-017-0082-x

Rodolfo-Metalpa, R., Hoogenboom, M. O., Rottier, C., Ramos-Esplá, A., Baker, A. C., Fine, M., & Ferrier-Pagès, C. (2014). Thermally tolerant corals have limited capacity to acclimatize to future warming. *Global Change Biology*, *20*(10), 3036–3049. https://doi.org/10.1111/gcb.12571

Rodrigues, L. J., & Grottoli, A. G. (2007). Energy reserves and metabolism as indicators of coral recovery from bleaching. *Limnology and Oceanography*, *52*(5), 1874–1882. https://doi.org/10.4319/lo.2007.52.5.1874

Safaie, A., Silbiger, N. J., McClanahan, T. R., Pawlak, G., Barshis, D. J., Hench, J. L., … Davis, K. A. (2018). High frequency temperature variability reduces the risk of coral bleaching. *Nature Communications*, *9*(1), 1671. https://doi.org/10.1038/s41467-018-04074-2

Sampayo, E. M., Ridgway, T., Bongaerts, P., & Hoegh-Guldberg, O. (2008). Bleaching susceptibility and mortality of corals are determined by fine-scale differences in symbiont

type. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(30), 10444–10449. https://doi.org/10.1073/pnas.0708049105

Schoepf, V., Carrion, S. A., Pfeifer, S. M., Naugle, M., Dugal, L., Bruyn, J., & McCulloch, M. T. (2019). Stress-resistant corals may not acclimatize to ocean warming but maintain heat tolerance under cooler temperatures. *Nature Communications*, *10*(1), 4031. https://doi.org/10.1038/s41467-019-12065-0

Schoepf, V., Grottoli, A. G., Levas, S. J., Aschaffenburg, M. D., Baumann, J. H., Matsui, Y., & Warner, M. E. (2015). Annual coral bleaching and the long-term recovery capacity of coral. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1819). https://doi.org/10.1098/rspb.2015.1887

Schoepf, V., Grottoli, A. G., Warner, M. E., Cai, W.-J., Melman, T. F., Hoadley, K. D., … Baumann, J. H. (2013). Coral energy reserves and calcification in a high-CO_2 world at two temperatures. *PLoS ONE*, *8*(10), e75049. https://doi.org/10.1371/journal.pone.0075049

Schoepf, V., Levas, S. J., Rodrigues, L. J., McBride, M. O., Aschaffenburg, M. D., Matsui, Y., … Grottoli, A. G. (2014). Kinetic and metabolic isotope effects in coral skeletal carbon isotopes: A re-evaluation using experimental coral bleaching as a case study. *Geochimica et Cosmochimica Acta*, *146*, 164–178. https://doi.org/10.1016/j.gca.2014.09.033

Shashar, N., Banaszak, A., Lesser, M., & Amrami, D. (1997). Coral endolithic algae: life in a protected environment. *Pacific Science*, *51*(2), 167–173. Retrieved from http://scholarspace.manoa.hawaii.edu/bitstream/10125/3107/1/v51n2-167-173.pdf

Shaw, E. C., McNeil, B. I., Tilbrook, B., Matear, R., & Bates, M. L. (2013). Anthropogenic changes to seawater buffer capacity combined with natural reef metabolism induce extreme future coral reef CO_2 conditions. *Global Change Biology*, *19*(5), 1632–1641. https://doi.org/10.1111/gcb.12154

Siebeck, U. E., Marshall, N. J., Klüter, A., & Hoegh-Guldberg, O. (2006). Monitoring coral bleaching using a colour reference card. *Coral Reefs*, *25*(3), 453–460. https://doi.org/10.1007/s00338-006-0123-8

Spencer Davies, P. (1989). Short-term growth measurements of corals using an accurate buoyant

1037 weighing technique. *Marine Biology*, *101*(3), 389–395. https://doi.org/10.1007/BF00428135

1038 Sully, S., Burkepile, D. E., Donovan, M. K., Hodgson, G., & van Woesik, R. (2019). A global
1039 analysis of coral bleaching over the past two decades. *Nature Communications*, *10*(1), 1264.
1040 https://doi.org/10.1038/s41467-019-09238-2

1041 Tambutté, E., Venn, A. A., Holcomb, M., Segonds, N., Techer, N., Zoccola, D., … Tambutté, S.
1042 (2015). Morphological plasticity of the coral skeleton under CO_2-driven seawater
1043 acidification. *Nature Communications*, *6*, 7368. https://doi.org/10.1038/ncomms8368

1044 Tolosa, I., Treignier, C., Grover, R., & Ferrier-Pagès, C. (2011). Impact of feeding and short-
1045 term temperature stress on the content and isotopic signature of fatty acids, sterols, and
1046 alcohols in the scleractinian coral *Turbinaria reniformis*. *Coral Reefs*, *30*(3), 763–774.
1047 https://doi.org/10.1007/s00338-011-0753-3

1048 Tremblay, P., Ferrier-Pagès, C., Maguer, J. F., Rottier, C., Legendre, L., & Grover, R. (2012).
1049 Controlling effects of irradiance and heterotrophy on carbon translocation in the temperate
1050 coral *Cladocora caespitosa*. *PLoS ONE*, *7*(9), e44672.
1051 https://doi.org/10.1371/journal.pone.0044672

1052 Tremblay, P., Gori, A., Maguer, J. F., Hoogenboom, M., & Ferrier-Pagès, C. (2016).
1053 Heterotrophy promotes the re-establishment of photosynthate translocation in a symbiotic
1054 coral after heat stress. *Scientific Reports*, *6*, 38112. https://doi.org/10.1038/srep38112

1055 Underwood, A. (1997). *Experiments in ecology: their logical design and interpretation using*
1056 *analysis of variance*. Cambridge University Press.
1057 https://doi.org/10.1017/S0025315400072064

1058 van Hooidonk, R., Maynard, J., Tamelander, J., Gove, J., Ahmadia, G., Raymundo, L., …
1059 Planes, S. (2016). Local-scale projections of coral reef futures and implications of the Paris
1060 Agreement. *Scientific Reports*, *6*(1), 39666. https://doi.org/10.1038/srep39666

1061 van Vuuren, D. P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., … Rose, S.
1062 K. (2011). The representative concentration pathways: an overview. *Climatic Change*, *109*(1–
1063 2), 5–31. https://doi.org/10.1007/s10584-011-0148-z

1064 van Woesik, R., Golbuu, Y., & Roff, G. (2015). Keep up or drown: Adjustment of western

Pacific coral reefs to sea-level rise in the 21st century. *Royal Society Open Science*, *2*(7). https://doi.org/10.1098/rsos.150181

Veal, C. J., Carmi, M., Fine, M., & Hoegh-Guldberg, O. (2010). Increasing the accuracy of surface area estimation using single wax dipping of coral fragments. *Coral Reefs*, *29*(4), 893–897. https://doi.org/10.1007/s00338-010-0647-9

Venn, A. A., Tambutté, E., Holcomb, M., Laurent, J., Allemand, D., & Tambutté, S. (2013). Impact of seawater acidification on pH at the tissue-skeleton interface and calcification in reef corals. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(5), 1634–1639. https://doi.org/10.1073/pnas.1216153110

Wahl, M., Saderne, V., & Sawall, Y. (2016). How good are we at assessing the impact of ocean acidification in coastal systems? Limitations, omissions and strengths of commonly used experimental approaches with special emphasis on the neglected role of fluctuations. *Marine and Freshwater Research*, *67*(1), 25. https://doi.org/10.1071/MF14154

Wall, C. B., Mason, R. A. B., Ellis, W. R., Cunning, R., & Gates, R. D. (2017). Elevated pCO_2 affects tissue biomass composition, but not calcification, in a reef coral under two light regimes. *Royal Society Open Science*, *4*(11), 170683. https://doi.org/10.1098/rsos.170683

Wall, M., Fietzke, J., Schmidt, G. M., Fink, A., Hofmann, L. C., de Beer, D., & Fabricius, K. E. (2016). Internal pH regulation facilitates in situ long-term acclimation of massive corals to end-of-century carbon dioxide conditions. *Scientific Reports*, *6*(1), 30688. https://doi.org/10.1038/srep30688

Whitaker, J. R., & Granum, P. E. (1980). An absolute method for protein determination based on difference in absorbance at 235 and 280 nm. *Analytical Biochemistry*, *109*(1), 156–159. https://doi.org/10.1016/0003-2697(80)90024-X

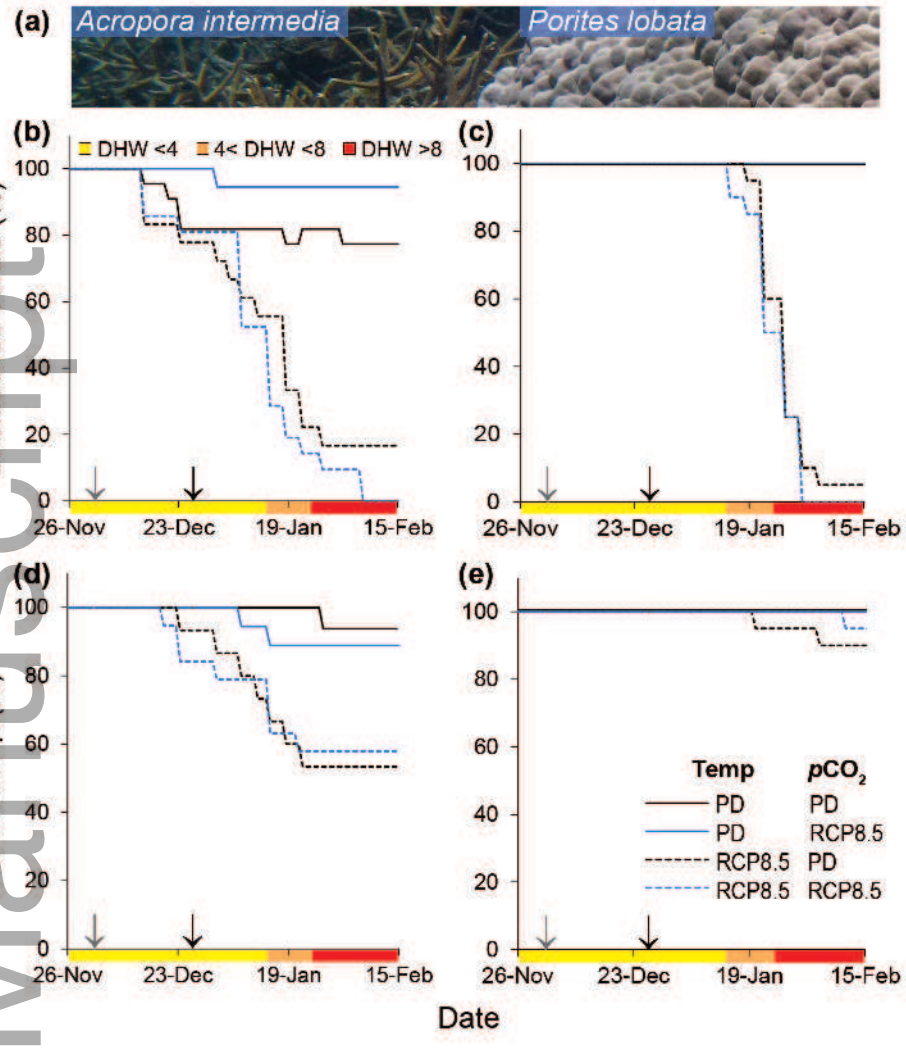
Wolff, N. H., Mumby, P. J., Devlin, M., & Anthony, K. R. N. (2018). Vulnerability of the Great Barrier Reef to climate change and local pressures. *Global Change Biology*, *24*(5), 1978–1991. https://doi.org/10.1111/gcb.14043

Wright, R. M., Mera, H., Kenkel, C. D., Nayfa, M., Bay, L. K., & Matz, M. V. (2019). Positive genetic associations among fitness traits support evolvability of a reef-building coral under

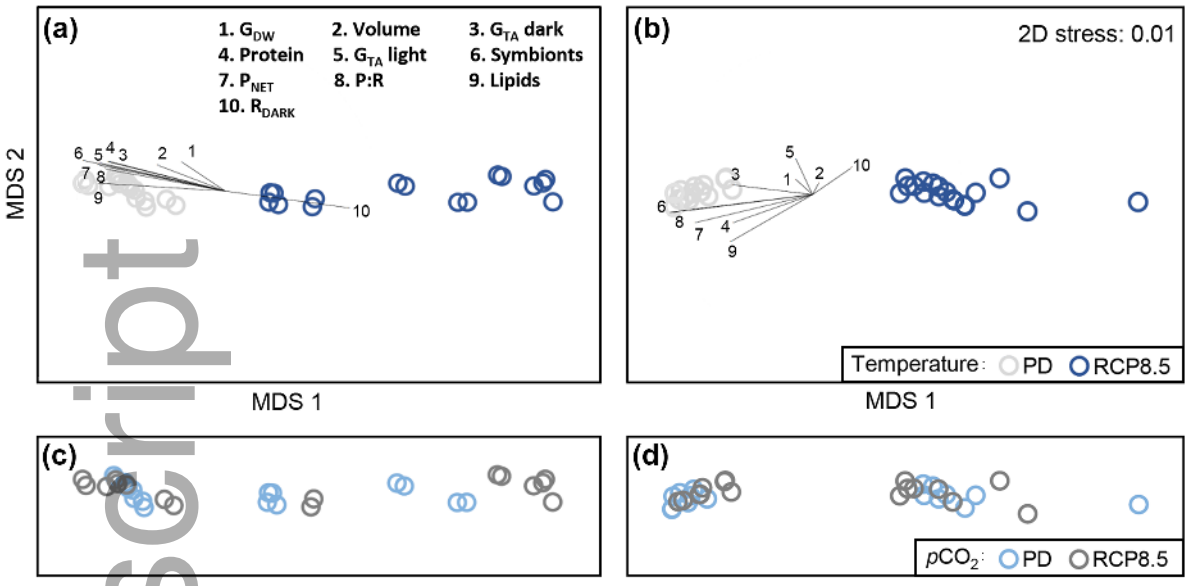
multiple stressors. *Global Change Biology*, *25*(10), 3294–3304. https://doi.org/10.1111/gcb.14764

Ziegler, M., Grupstra, C. G. B., Barreto, M. M., Eaton, M., BaOmar, J., Zubier, K., … Voolstra, C. R. (2019). Coral bacterial community structure responds to environmental change in a host-specific manner. *Nature Communications*, *10*(1). https://doi.org/10.1038/s41467-019-10969-5

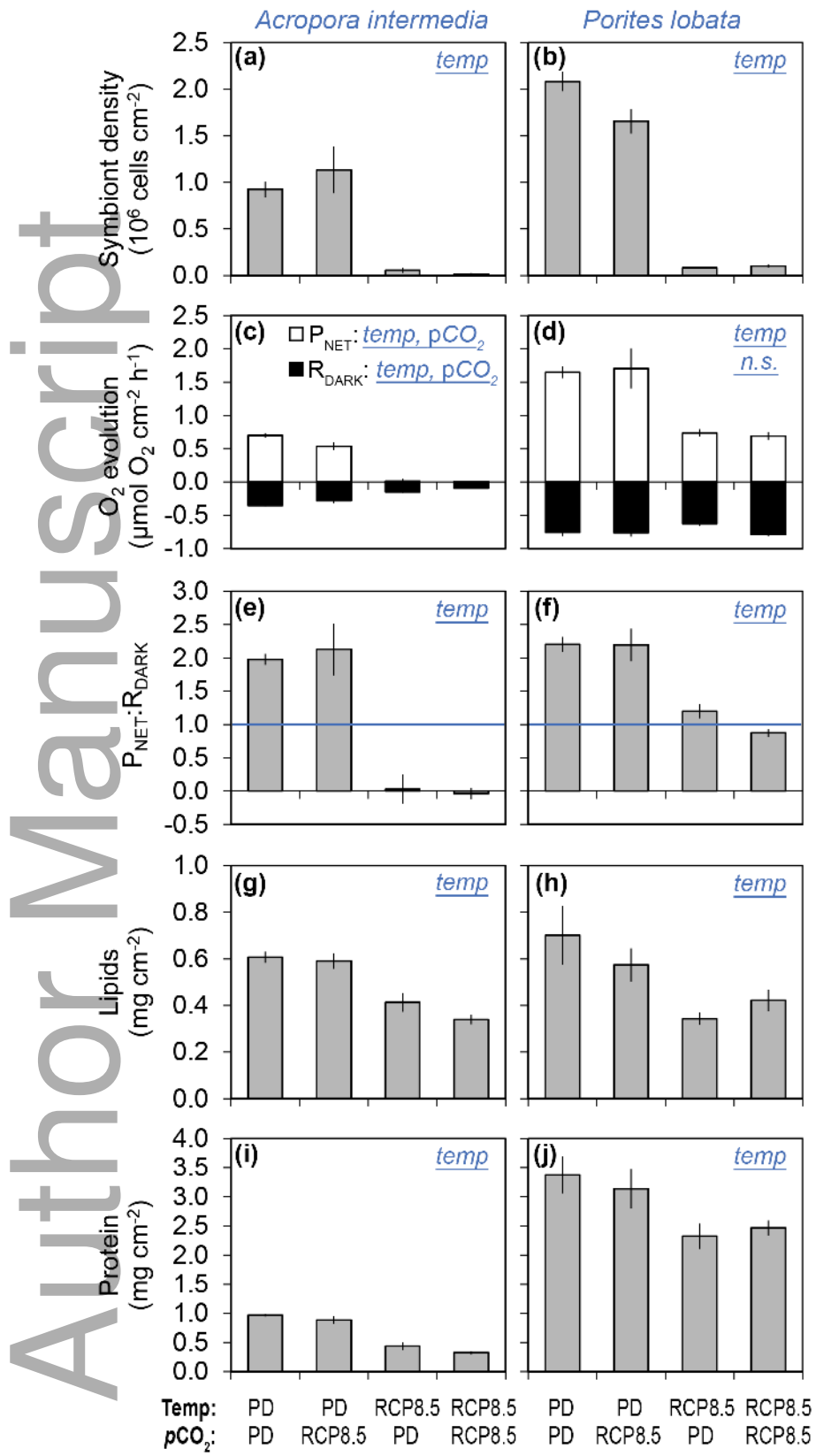
Ziegler, M., Seneca, F. O., Yum, L. K., Palumbi, S. R., & Voolstra, C. R. (2017). Bacterial community dynamics are linked to patterns of coral heat tolerance. *Nature Communications*, *8*. https://doi.org/10.1038/ncomms14213



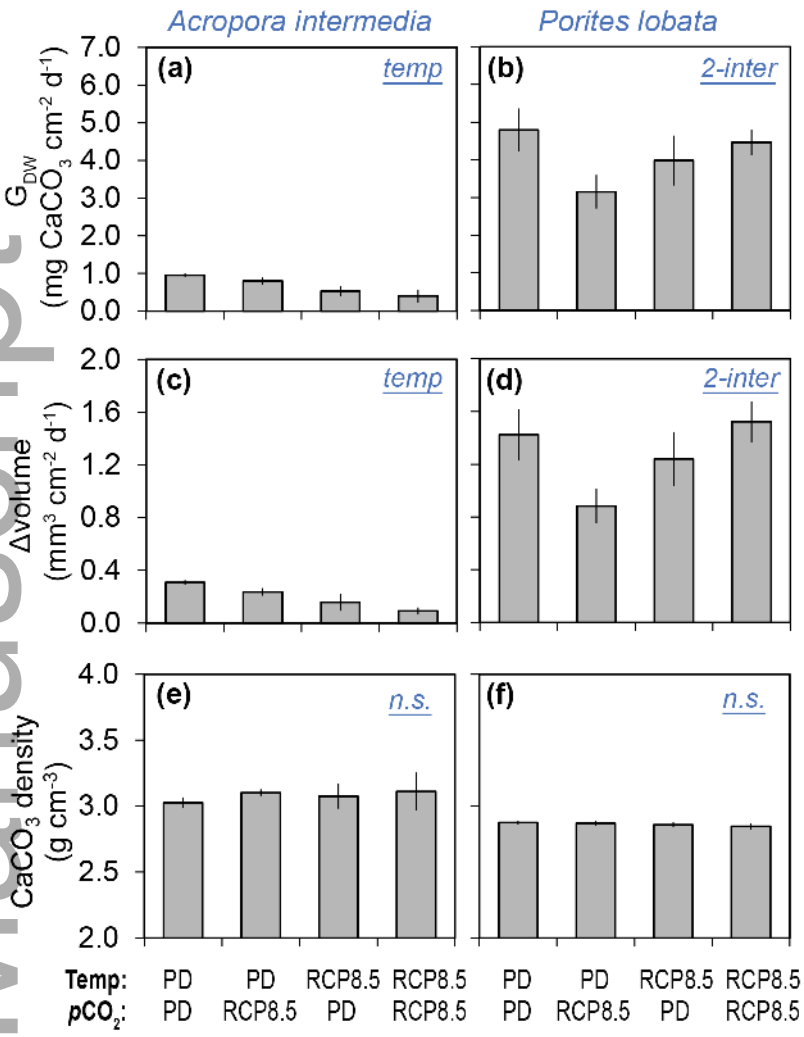
gcb_14998_f1.tif



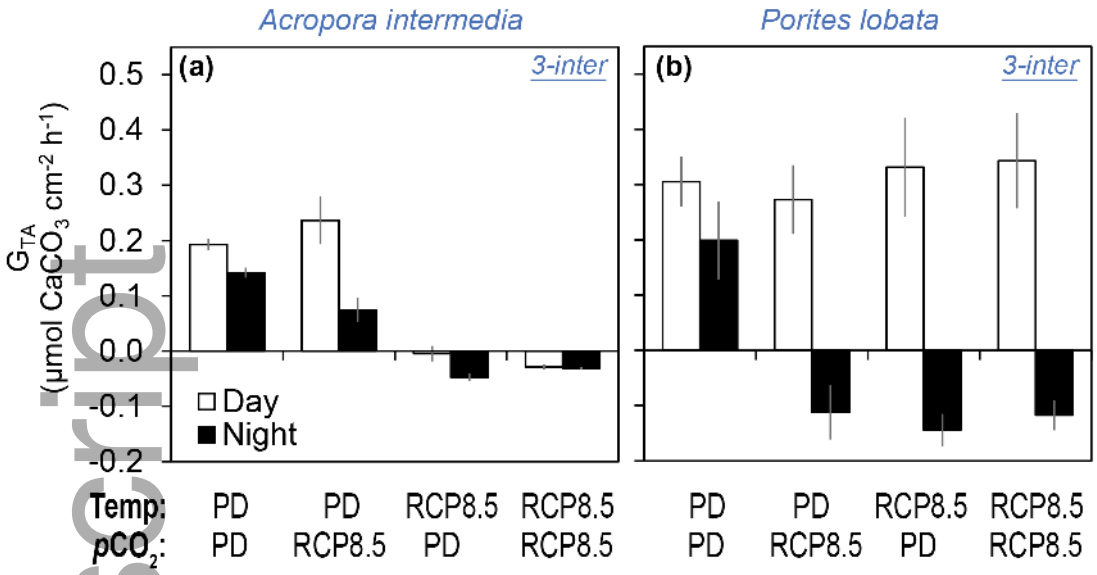
gcb_14998_f2.tif



gcb_14998_f3.tif



gcb_14998_f4.tif



gcb_14998_f5.tif