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

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Abstract

Despite recent efforts to curtail greenhouse gas emissions, current global emission trajectories are still following the business-as-usual representative concentration pathway (RCP) 8.5 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.

KEYWORDS

acidification, calcification, climate change, coral bleaching, photosynthesis, RCP8.5, Symbiodiniaceae, warming

1 | 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 autotrophic 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 are 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 (PD) 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, modeled on high-resolution PD 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, PD and end-of-century

summer levels of temperature and pCO_2 were simulated over 7 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.

2 | MATERIALS AND METHODS

2.1 | Experimental design

Fragments of *A. intermedia* (Brook, 1891) and *P. 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 (Figure 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 eight 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, UK) 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) for gentle water circulation (900 L/hr). Coral fragments fully recovered from sampling damage under untreated flow-through seawater for 2 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; Supporting Information). 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 (Figures S1 and S2 in Supporting Information). This approach carefully

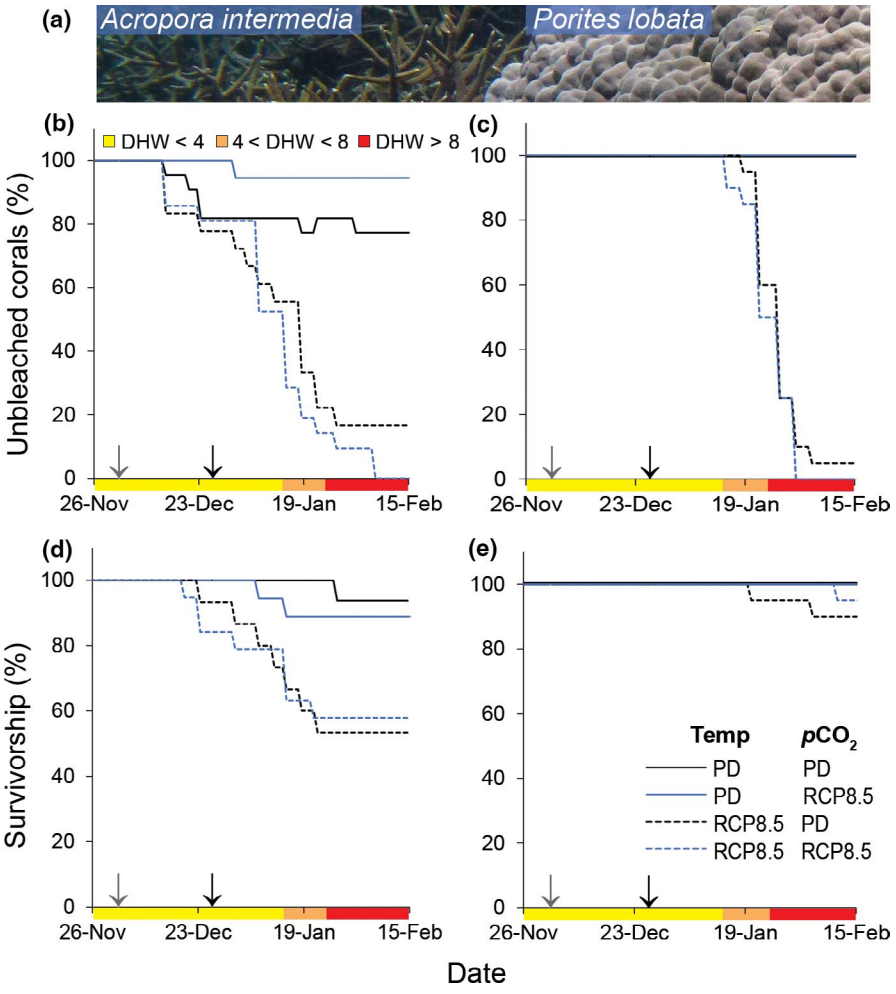

FIGURE 1 Bleaching and survival curves for *Acropora intermedia* (left panels) and *Porites lobata* (right panels) during warming and acidification stress. Inset picture (a) shows co-occurring colonies of the two species on Heron Island. Specimens were exposed to independent and concurrent levels of temperature and pCO_2 according to end-of-century RCP8.5 emission scenarios over 7 weeks. The percentage of unbleached (b, c) and dead (d, e) corals were recorded every second day. The 7 week experimental period was preceded by 4 weeks of stepwise treatment exposure (25% increments weekly). Gray (December 3, 2014) and black (December 27, 2014) arrows depict the start of the stepwise introduction and full treatment phases, respectively. The colored horizontal bar represents the degree heating weeks (DHW; °C weeks) reached in the elevated temperature treatments, throughout the experiment; yellow for DHW < 4 (November 26, 2014–January 13, 2015), orange for 4 < DHW < 8 (January 14–24, 2015), and red for DHW > 8 (January 25–February 15, 2015) [Colour figure can be viewed at wileyonlinelibrary.com]

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 8,000 L sumps (turnover rate 4–6 hr) 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 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 (aquarium water turnover 30–40 min). 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) in the downstream aquaria (Figure S3), and temperature (Table 1; Figure S1) was logged every 10 min (HOBO Pendant temperature loggers; Onset). Average PD and RCP8.5 temperatures were 27.5 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 25, 2014 and January 27, 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, Afghan, and Anderson (2003; Mettler-Toledo T50 titrator; Mettler-Toledo). TA values from these measurements were used to calculate pCO_2 and aragonite saturation (Ω_{ARAG}) values in the downstream aquaria (Table 1).

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 1 hr 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 color codes on the Coral Watch coral health chart compared to their initial color 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.

2.2 | 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

TABLE 1 Treatment design and reference experimental conditions (mean ± *SD*) in the downstream aquaria during the 7 week experimental period

Experimental design			Downstream aquarium conditions				
Treatment	Temperature level	pCO_2 level	T (°C)	pCO_2 (µatm)	Total alkalinity (µmol/kg)	pH_{NBS}	Ω_{ARAG}
Control (PD)	PD	PD	27.5 ± 1.6	490 ± 99	2,210 ± 32	8.10 ± 0.07	3.24 ± 0.13
Elevated pCO_2	PD	RCP8.5	27.4 ± 1.9	925 ± 204	2,218 ± 39	7.87 ± 0.08	2.18 ± 0.10
Elevated T	RCP8.5	PD	30.4 ± 1.8	524 ± 162	2,258 ± 10	8.09 ± 0.08	3.39 ± 0.38
Elevated T/pCO_2	RCP8.5	RCP8.5	30.8 ± 2.0	890 ± 47	2,261 ± 10	7.89 ± 0.02	2.32 ± 0.07

Note: 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).

Abbreviation: PD, present-day.

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 s intervals during 30/30 min light/dark cycles (PreSens OXY-10 mini oxygen meter; PreSens). Net photosynthesis (P_{NET}) and dark respiration (R_{DARK}) rates were calculated from the oxygen measurements during the light period and after 20 min of dark acclimation, respectively. P_{NET}:R_{DARK} ratios were calculated to gauge holobiont potential for remaining net photosynthetic over a 24 hr period, based on a 12.5/11.5 hr 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 × 250 W metal halide lamp and 2 × 24 W aqualine T5 fluorescent bulbs.

2.3 | 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 (Equation 1).

$$G_{DW}\left(\text{mg CaCO}_3\,\text{cm}^{-2}\,\text{day}^{-1}\right)=\frac{\left(DW_{end}-DW_{initial}\right)}{\left(\text{mean SA}_{initial}\cdot\text{days}\right)}. \quad (1)$$

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 hr 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 (Equation 2; r^2 = .9952 and Equation 3; r^2 = .9941 for *A. intermedia* and *P. lobata*, respectively), which was used to infer $DW_{initial}$ of the treatment corals (Spencer Davies, 1989).

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

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

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 endpoint (DW_{end}) dry weights (Equation 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 Equation (4; adapted from Spencer Davies, 1989).

$$\Delta\text{Volume}\left(\text{mm}^3\,\text{cm}^{-2}\,\text{day}^{-1}\right)=\frac{\left(\left(DW_{end}-BW_{end}\right)-\left(DW_{initial}-BW_{initial}\right)\right)}{\left(\Delta\text{days}\cdot\rho_{SW}\cdot\text{mean SA}_{initial}\right)}\cdot 1{,}000. \quad (4)$$

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-hr 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 eh incubation from the individual chamber. TA was determined by Gran titration as above, and used to calculate day and night G_{TA} rates (Equation 5).

$$G_{TA}\left(\text{µmol CaCO}_3\,\text{cm}^{-2}\,\text{hr}^{-1}\right)=\left(\frac{\Delta\text{TA(µmol)}}{2\cdot\text{SA}_{end}\left(\text{cm}^2\right)\cdot\text{time(hr)}}\right)\cdot\text{Vol (L)}. \quad (5)$$

2.4 | Tissue parameters

Tissue protein and lipid content (n = 8 per treatment) was measured at the end of the treatment period. Tissue was collected from the skeletons using a simple airbrush and 30 ml FSW. Half of the obtained mixture was stored at −20°C for lipid analysis. The other half was centrifuged for mass separation at 3,493 *g* for 5 min, and a 2 ml sample of the supernatant was kept for water-soluble host protein determination. The remaining pellet was washed with 5 ml FSW, centrifuged at 3,493 *g* for 5 min for a total of three washes to clean the pellet from coral mucus, and then resuspended in 5 ml FSW for symbiont density determination by microscope hemocytometer counts.

Water-soluble host protein content was determined by differential absorbance at 235 and 280 nm using spectrometry (Spectra Max 2; Molecular Devices); Whitaker & Granum,

1980). Lipids were measured using a modified protocol of Dunn, Thomas, Nette, Dove, and Blackburn (2012). The frozen lipid sample was freeze-dried (ScanVac CoolSafe; LaboGene), and dry material was dissolved in 5 ml 2:1 chloroform/methanol solution, vortexed, and left overnight at 4°C to allow full lipid extraction. Next, the samples were centrifuged at 2,760 *g* for 4 min and the organic solvent was transferred into a clean tube. The remaining pellet was rinsed with 2 ml chloroform/methanol solution, and this solution was added to the original 5 ml after 1 hr at 4°C. Next, 1 ml of 0.1 mol/L KCl solution was added to the organic solvent, and left overnight at 4°C to allow separation of organic and aqueous phases. After careful removal of the aqueous phase, the remaining organic phase was washed with 5 ml 1:1 methanol/Milli-Q water solution three times. Each wash was left overnight at 4°C for phase separation and subsequent removal of the aqueous phase. After the third wash, the remaining organic solution was poured into a pre-weighed aluminum tray, left to evaporate, and reweighed for lipid quantification. The surface area covered by live coral tissue was calculated using the double waxing method (Veal, Carmi, Fine, & Hoegh-Guldberg, 2010) applied to bleached and dried skeletons.

2.5 | 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 9,999 permutations. All data were 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), 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 α = .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 α = .05 level. All factorial analyses were done with Statistica 13.2 (Statsoft).

3 | RESULTS

3.1 | Bleaching and mortality

Thermal stress regimes for the RCP8.5 temperature treatments were as follows: DHW < 4 between December 25 and January 13; 4 < DHW < 8 between January 14 and 24; DHW > 8 after January 24, until a maximum of 15.6°C weeks had been reached at the end of the experimental period on February 15 (Figure 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 (Figure 1b). After 7 weeks in the elevated T and elevated T/pCO_2 treatments, respectively, 83% (z = 3.43; p < .001) and 100% (z = 4.42; p < .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 3 weeks into full treatment (Figure 1c). 95% (z = 5.79; p < .001) and 100% (z = 6.04; p < .001) of *P. lobata* specimens in the elevated T and T/pCO_2 bleached, respectively, 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 (Figure 1d). After 7 weeks, mortality reached 46.7% (z = 2.51; p = .012) and 42.1% (z = 2.29; p = .022) in the elevated T and T/pCO_2 treatments, respectively. No significant differences in *P. lobata* mortality were observed between treatments (Figure 1e).

3.2 | Multivariate analyses

Overall, the physiological response in *A. intermedia* (Figure 2a) was strongly determined by the effect of elevated temperature (ANOSIM R = .878; p < .001), and less by elevated pCO_2 (ANOSIM R = .225; p = .011). The overall response of *P. lobata* was similar to *A. intermedia*, depending strongly on thermal stress (ANOSIM R = 1; p < .001) and less on acidification (ANOSIM R = .116; p = .043), consistent with the nMDS results (Figure 2).

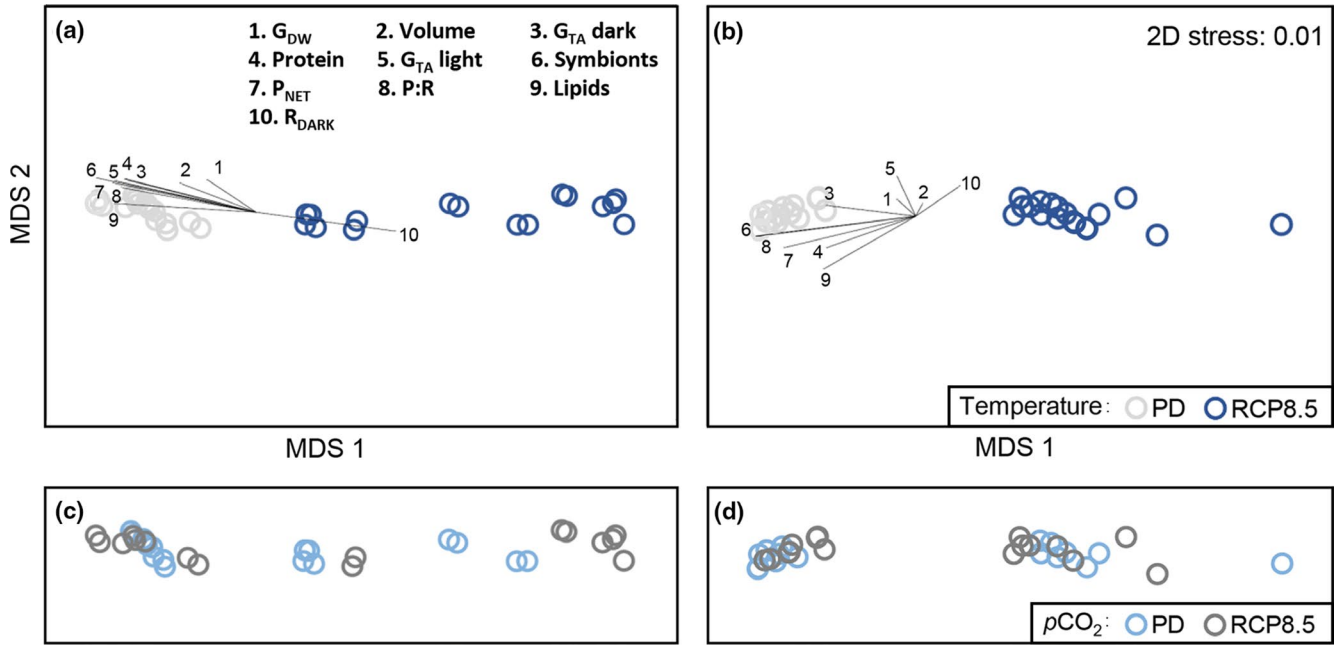

FIGURE 2 Non-metric multidimensional scaling (nMDS) plots showing similarities in overall holobiont response for *Acropora intermedia* (a, c) and *Porites lobata* (b, d) to differential temperature and pCO_2 treatments. Top panels show grouping based on response to warming, whereas bottom panels depict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

3.3 | Metabolic and tissue parameters

Specimens of *A. intermedia* and *P. lobata* under heat stress contained significantly lower amounts of dinoflagellate symbionts in their tissue (Figure 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 < .001; Figure 3a) and 20-fold in *P. lobata* (main effect *T*; $F_{1,24}$ = 285.7; p < .001; Figure 3b). Rates of P_{NET} in *A. intermedia* (Figure 3c) decreased when exposed to elevated temperature (main effect *T*; $F_{1,24}$ = 262.0; p < .001) and pCO_2 levels (main effect pCO_2; $F_{1,24}$ = 5.2; p = .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 < .001) and elevated pCO_2 levels individually (main effect pCO_2; $F_{1,24}$ = 12.0; p = .002). In *P. lobata*, P_{NET} (Figure 3d) was affected by warming alone, dropping more than 50% in elevated temperature treatments (main effect *T*; $F_{1,24}$ = 40.79; p < .001). No significant differences were found in R_{DARK} rates for *P. lobata*. P_{NET}:R_{DARK} ratios for *A. intermedia* (Figure 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 < .001). Warming significantly reduced P_{NET}:R_{DARK} ratios in *P. lobata* (Figure 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 < .001).

Exposure to elevated temperatures decreased the tissue lipid concentration in both *A. intermedia* (main effect *T*; $F_{1,24}$ = 48.02; p < .001) and *P. lobata* (main effect *T*; $F_{1,24}$ = 10.50; p = .003) while tissue lipid concentration was unaffected by acidification (Figure 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 < .001 and main effect *T*; $F_{1,24}$ = 9.410; p = .005 for *A. intermedia* and *P. lobata*, respectively). Host protein concentrations in both species were unaffected by different levels of pCO_2 (Figure 3i,j).

3.4 | 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 = .001), while it was unaffected by acidification (Figure 4a). In *P. lobata*, exposure to elevated pCO_2 reduced G_{DW} rates only under PD (Figure 4b), and not under elevated temperatures (interactive effect T × pCO_2; $F_{1,24}$ = 4.445; p = .046). Skeleton volume of *A. intermedia* (Figure 4c) increased less over time under warming, while it was unaffected by pCO_2 levels (main effect *T*; $F_{1,24}$ = 16.65; p < .001). In *P. lobata*, skeleton volume change was governed by an interactive effect of temperature and pCO_2 (Figure 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 = .018). Despite the observed differences in volume

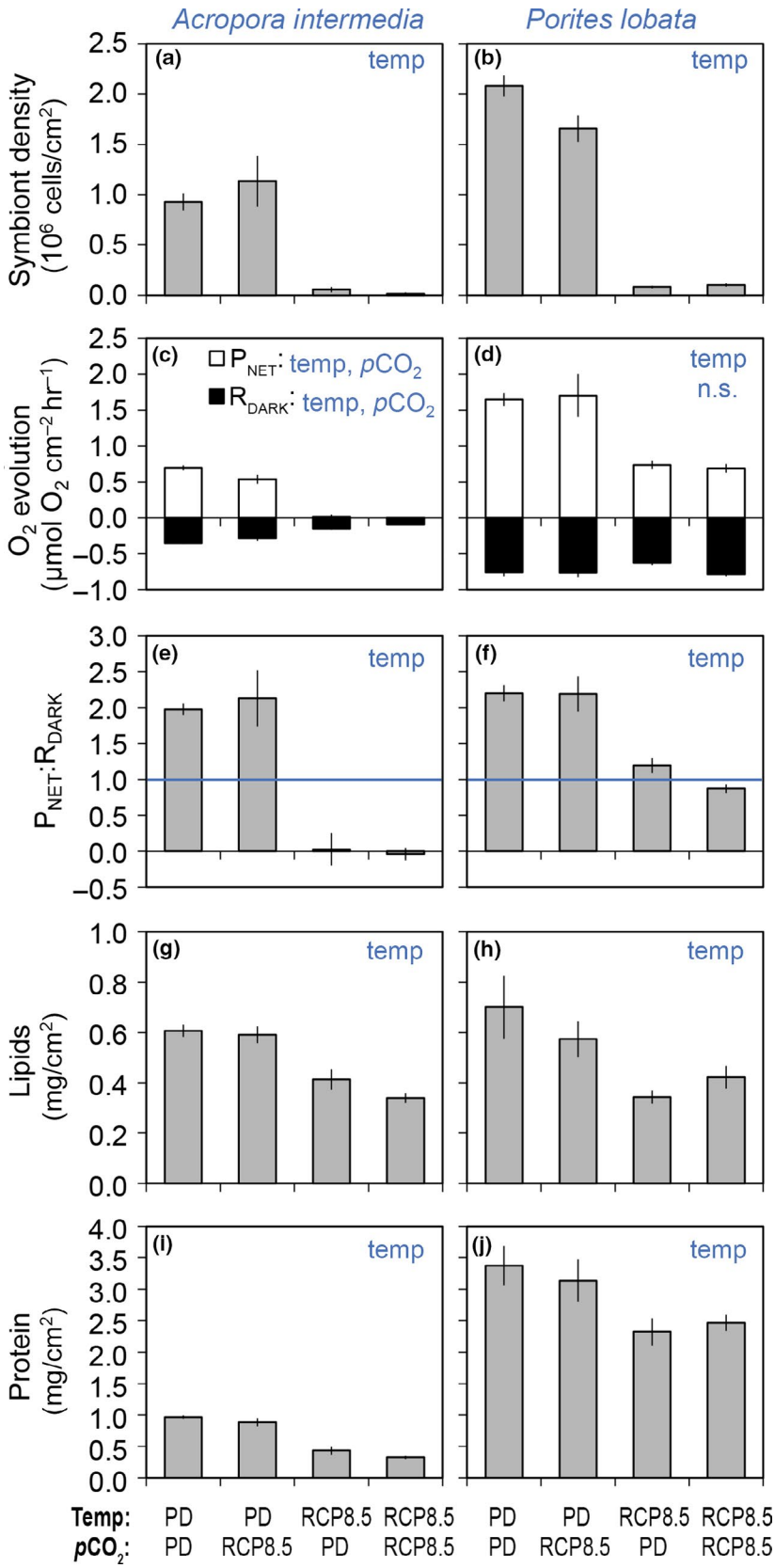

FIGURE 3 Parameters of photobiology and tissue composition (mean ± *SE*) of *Acropora intermedia* (left panels) and *Porites lobata* (right panels) after exposure to different treatments of warming and acidification. Dinoflagellate symbiont density (a, b), photobiology (c–f), and tissue lipid (g, h) and protein content (i, j) were measured on corals (n = 8 per treatment) exposed for 7 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) [Colour figure can be viewed at wileyonlinelibrary.com]

change between warming and acidification scenarios in both species, skeleton density did not differ between the treatments (Figure 4e,f).

End-of-treatment rates of calcification (G_{TA}) in *A. intermedia* (Figure 5a) were governed by a three-way interaction between temperature, pCO_2, and time of measurement (interactive effect

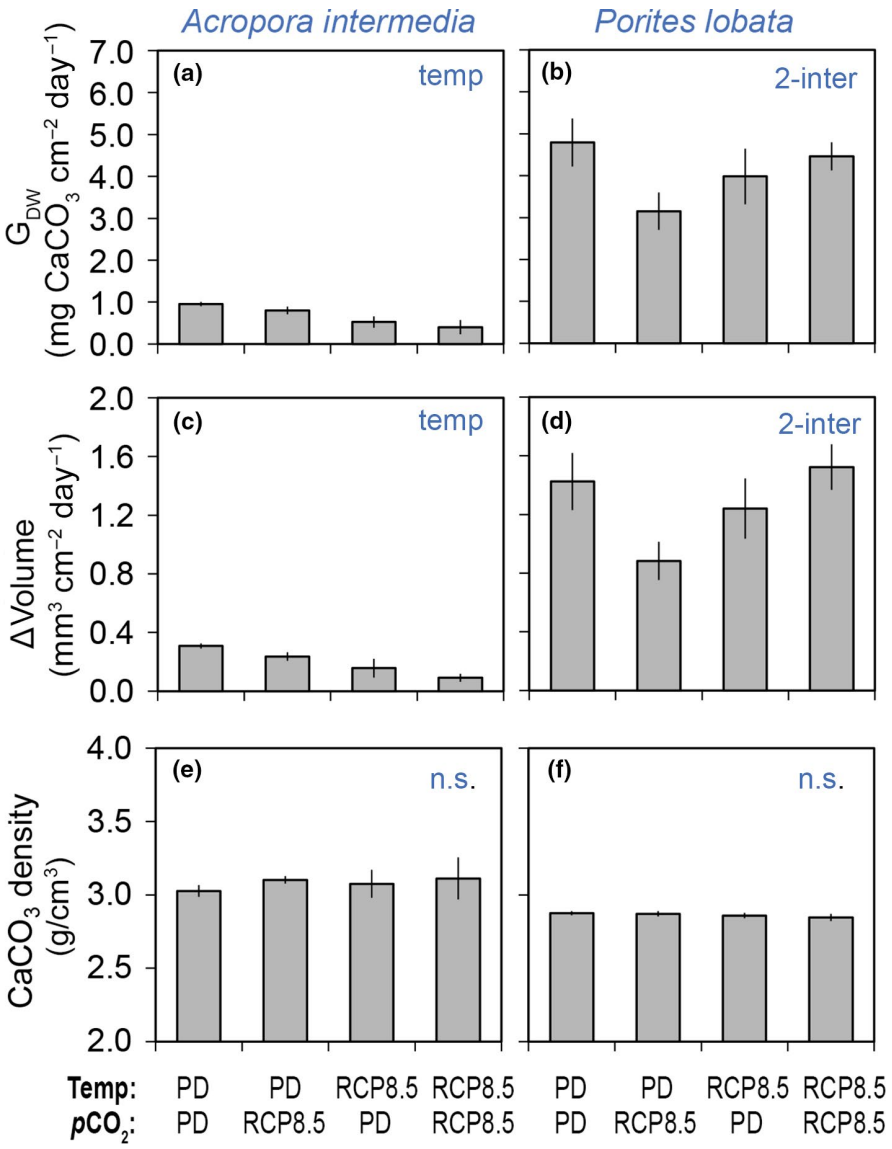

FIGURE 4 Parameters of long-term skeleton growth (mean ± *SE*) under different treatments of warming and acidification for *Acropora intermedia* (left panels) and *Porites lobata* (right panels). Seven week averages of skeleton $CaCO_3$ accretion (GDW; a, b) and skeleton volume expansion rates (c, d) were determined for corals exposed to independent and concurrent levels of temperature and pCO_2 according to end-of-century RCP8.5 projections. Averages span the entire period, including before the onset of bleaching. Skeleton density (e, f) was determined at the end of the experimental period. The blue text inside the panels indicates the presence of significant main effects of warming (temp) or two-way interactive effects of warming and acidification (2-inter) [Colour figure can be viewed at wileyonlinelibrary.com]

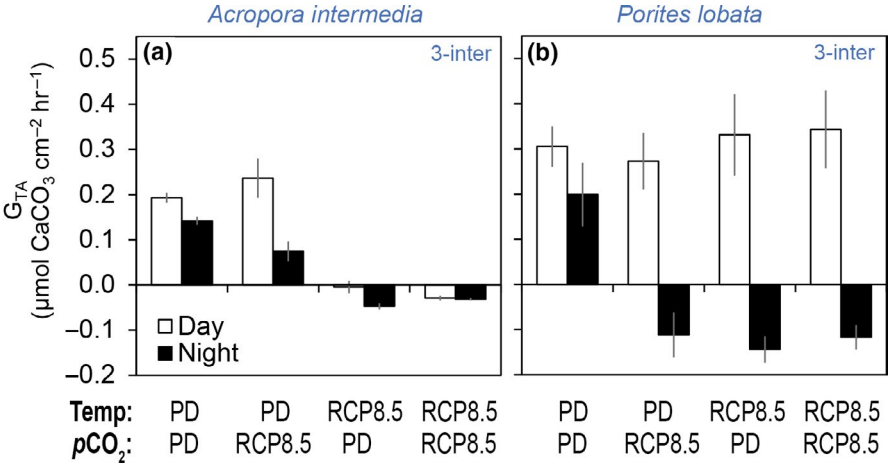

FIGURE 5 End-of-treatment day- and nighttime calcification rates (G_{TA}; mean ± *SE*) under different treatments of warming and acidification for *Acropora intermedia* (a) and *Porites lobata* (b). Rates (n = 8 per treatment) were measured after 7 weeks of exposure to independent and concurrent levels of temperature and pCO_2 according to end-of-century RCP8.5 projections. The blue text inside the panels indicates the presence of significant three-way interactive effects of time (day/night), warming, and acidification (3-inter) [Colour figure can be viewed at wileyonlinelibrary.com]

Time × T × pCO_2; $F_{1,28}$ = 23.3; p < .001). When exposed to elevated pCO_2, daytime G_{TA} rates were threefold higher than nighttime G_{TA} rates (Tukey HSD p < .001). Warming decreased G_{TA} to below zero levels irrespective of light or dark conditions (Tukey HSD p < .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 < .001). Likewise, G_{TA} rates in *P. lobata* (Figure 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 = .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 = .018).

4 | 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 PD 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*.

4.1 | 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 PD 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 4 and 3 months, respectively, and peaking at approximately 15.5°C weeks (NOAA CRF 5 km satellite data, https://coralreefwatch.noaa.gov/satellite/index.php; 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 5 weeks and 8°C weeks for 3 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, 5 km). 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.

4.2 | 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* (Figure 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 et al., 2013; Fantazzini et al., 2015; Tambutté et al., 2015). However, analysis of end-of-treatment rates of calcification (Figure 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 et al., 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 et al., 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 et al., 2008; Comeau, Carpenter, & Edmunds, 2016; Hoadley et al., 2015; Marubini et al., 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 et al., 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 metabolic functions even when bleached, while *A. intermedia* would have to switch to heterotrophy or stored energy reserves for metabolism (Grottoli et al., 2006; Rodrigues & Grottoli, 2007). Additionally, high heterotrophic capacity and somatic energy reserves in *P. lobata* compared to *A. intermedia* likely benefit this species during bleaching (Levas et al., 2013; Palardy et al., 2008).

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

Lipid and protein concentrations in unbleached specimens of both species were comparable to concentrations found for healthy corals of similar genera in previous studies (Hoogenboom, Rottier, Sikorski, & Ferrier-Pagès, 2015) but declined markedly under thermal stress, particularly in *A. intermedia*. Lipid catabolism by bleached corals additionally fulfils immediate metabolic demands in the absence of photosynthetic carbon (Fitt, Spero, Halas, White, & Porter, 1993; Grottoli & Rodrigues, 2011; Grottoli et al., 2004). However, the exhaustion of stored energy reserves has been linked to rapid increases in mortality of coral larvae (Graham, Baird, Connolly, Sewell, & Willis, 2017) and adult colonies (Anthony et al., 2007; Bay, Guérécheau, Andreakis, Ulstrup, & Matz, 2013; Kenkel, Meyer, & Matz, 2013). We observed a significant increase in *A. intermedia* mortality when thermally stressed, concomitant with diminished tissue protein and lipid concentrations. *P. lobata* mortality remained low (10%), despite significant declines in tissue lipid and protein concentrations under thermal stress. The present study ended in mid-February, before the end of the annual thermal maximum period on Heron Island. Previous studies have described a lagging effect between thermal stress and physiological decline in several coral species including *P. lobata* (Levas et al., 2013; Rodrigues & Grottoli, 2007); thus, energetic exhaustion and mortality in our study could be worsened over the full duration of summer (Hughes et al., 2017).

4.3 | Not all corals are equal

Acropora intermedia and *P. lobata* clearly respond differently to elevated temperature and acidification. Bleaching in *A. intermedia* started approximately 5 weeks earlier than in *P. lobata*, and *A. intermedia* mortality was significant under elevated temperature. Furthermore, the collapse of day- and nighttime G_{TA} and productivity in *A. intermedia* was more severe than in *P. lobata*, but acidification affected nighttime G_{TA} more in *P. lobata*. Coral species are known to differ in their sensitivity to environmental cues (Fabricius et al., 2011), determined by a combination of factors such as host identity (Fitt et al., 2009; Hoadley et al., 2019), Symbiodiniaceae type(s) hosted (Fitt et al., 2009; Sampayo, Ridgway, Bongaerts, & Hoegh-Guldberg, 2008), and nearby benthic community composition (Dove et al., 2013). At Heron Island, *A. intermedia* has been found to harbor thermally sensitive *Cladocopium* C3, while *P. lobata* harbored predominantly thermally tolerant *Cladocopium* C15 (Fisher et al., 2012; LaJeunesse et al., 2004), likely explaining the later onset of bleaching in *P. lobata*. The introduction of symbiont-specific traits and other varying factors may lead to trade-offs in coral performance (Jones & Berkelmans, 2011), and invites further experiments

studying different combinations of environments and organisms to discern future climate impacts on reef health and survival (Bay et al., 2017; Hoadley et al., 2019; Wall, Mason, Ellis, Cunning, & Gates, 2017). Our results 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 (Figure 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).

5 | 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 et al., 2017; Edmunds et al., 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 et al., 2007; Grottoli et al., 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 (van Hooidonk et al., 2016; Lough, Anderson, & Hughes, 2018), 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 PD 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 et al., 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 et al., 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.

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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 AVAILABILITY STATEMENT

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

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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