Vol. 706: 33–46, 2023
https://doi.org/10.3354/meps14246

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published February 23

Heating rate explains species-specific coral bleaching severity during a simulated marine heatwave

Defne Sahin[1,2,3,*], Verena Schoepf[1,4], Karen Filbee-Dexter[1,2], Damian P. Thomson[1,5], Ben Radford[1,3], Thomas Wernberg[1,2,6]

[1]Oceans Institute, University of Western Australia, 6009 Crawley, Australia
[2]School of Biological Sciences, University of Western Australia, 6009 Crawley, Australia
[3]Australian Institute of Marine Science, 6009 Crawley, Australia
[4]Department of Freshwater and Marine Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, 1098 XH Amsterdam, The Netherlands
[5]CSIRO Oceans & Atmosphere, 6009 Perth, Australia
[6]Department of Science and Environment, Roskilde University, 4000 Roskilde, Denmark

ABSTRACT: Marine heatwaves (MHWs) are becoming more frequent as a consequence of climate change. These discrete events are causing widespread stress and mortality in marine ecosystems, including coral reefs. The heat tolerance of different coral species is often complex and depends on a combination of environmental and biological factors, making accurate predictions of the impact of MHWs on individual species challenging. Heating rate has been shown to influence coral bleaching in *Acropora* species, but it remains unknown how heating rate influences bleaching in other corals with contrasting morphology and bleaching sensitivities. In this study, we explored the sensitivity of *Pocillopora damicornis* and *Plesiastrea versipora*, representing branching and encrusting growth forms, respectively, to heating rate. We experimentally simulated MHWs with slow (0.5°C d^{-1}) and fast (1°C d^{-1}) heating rates and measured physiological responses to quantify changes in coral health, including photochemical efficiency, holobiont metabolism, tissue biomass, chl *a*, and symbiont density. Our results confirm that heating rate is a good predictor of coral bleaching sensitivity for these species, with faster heating rates causing more severe bleaching and declines in coral health. However, bleaching sensitivity differed between *P. damicornis* and *P. versipora*, with *P. damicornis* more affected by the faster heating rate. The use of heating rate, in addition to other metrics such as duration and intensity of heat, will enhance our capacity to predict the local impact of MHW events and their overarching ecological consequences for coral ecosystems.

KEY WORDS: Marine heatwave · Heating rate · Coral bleaching · Photo-physiology · Photosynthesis · Respiration · Western Australia

1. INTRODUCTION

Rising ocean temperatures are severely impacting marine ecosystems (Hoegh-Guldberg & Bruno 2010, Pecl et al. 2017, Pinsky et al. 2020), a trend expected to continue with increasing anthropogenic activity (Intergovernmental Panel on Climate Change [IPCC] 2021). In addition to gradual sustained temperature increases, marine ecosystems are further threatened by acute warming events, known as marine heatwaves (MHWs) (Smale et al. 2019). The frequency of MHWs has increased by over 50% during the last decade (Oliver et al. 2018, IPCC 2021), and more than 50% of the world's oceans are projected to be in a permanent MHW state (compared to today) by the end of the 21st century (Oliver et al. 2019). The predicted increases in MHWs pose a huge challenge to marine organisms, with upper thermal thresholds

*Corresponding author: aysedefne.sahin@research.uwa.edu.au

Publisher: Inter-Research · www.int-res.com

expected to be exceeded more regularly. Therefore, understanding organismal responses to extreme temperature events is imperative to understanding the impacts of MHWs on marine biodiversity.

Coral reefs are increasingly experiencing mass bleaching events and one-third of all scleractinian corals are at elevated risk of extinction (Frieler et al. 2013, Hughes et al. 2018). Most coral reefs worldwide have already suffered from widespread coral bleaching (Sully et al. 2019), a phenomenon which results in the loss of photosynthetic symbiotic dinoflagellates (Symbiodiniaceae) (Glynn 1996, LaJeunesse et al. 2018). As corals typically rely on their endosymbionts for the majority of their daily energy requirements (Muscatine et al. 1981, Dubinsky et al. 1990), the breakdown of this symbiotic relationship can lead to impairment of metabolic processes and, in severe cases, starvation and partial or whole colony mortality (Fitt et al. 2000, Grottoli et al. 2004, Rodrigues & Grottoli 2007, Rädecker et al. 2021).

Heat stress is one of the most common causes of coral bleaching and the severity of the bleaching event depends on both the intensity and duration of heat stress (Middlebrook et al. 2008); thus, the degree heating week (DHW) metric was developed (Liu et al. 2003) to better characterize the cumulative stress associated with warming events. DHW integrates sea surface temperature (SST) anomalies that are 1°C above the regional maximum climatological mean, with 1 DHW representing 1°C above the maximum monthly climatological mean for a period of 1 wk (Skirving et al. 2020). When DHW reaches 4°C, significant coral bleaching is likely, while >8°C DHW has been associated with widespread coral mortality (Liu et al. 2005). The DHW metric allows a general comparison of cumulative heat stress between events, but it can fail to accurately predict the impact of MHWs (i.e. events may be underestimated, or fine-scale events may be missed). A similar DHW may cause different bleaching responses between species and locations (Weeks et al. 2008, Bainbridge 2017, DeCarlo et al. 2017). This is, in part, because the capacity of corals to withstand heat stress is complex and influenced by a combination of environmental (e.g. Safaie et al. 2018) and biological factors including, but not limited to, coral taxa (Marshall & Baird 2000), colony morphology (Loya et al. 2001), symbiont genotype (Barshis et al. 2010), tissue thickness, and feeding behaviour (Rodrigues & Grottoli 2007, Grottoli et al. 2014). For instance, growth forms (i.e. colony morphology) are generally, but not always (Guest et al. 2012), informative in explaining bleaching tolerance: branching corals are generally more susceptible than massive and encrusting corals (reviewed by McCowan et al. 2012). Although the underlying mechanisms are not fully understood, this may be, in part, because massive and encrusting corals generally have thicker tissues (Marshall & Baird 2000, Loya et al. 2001). Additionally, corals that can increase their heterotrophic feeding whilst bleached appear to have an ecological advantage and higher chance of survival (Grottoli et al. 2004, Rodrigues & Grottoli 2007, Anthony et al. 2009, Conti-Jerpe et al. 2020). Bleaching response can be further influenced by regular exposure to anomalously high temperatures, particularly on tidal/daily time scales (Ainsworth et al. 2016, Camp et al. 2018, Safaie et al. 2018), with increased heat tolerance in corals located in thermally variable reef environments, such as back-reef pools (e.g. Palumbi et al. 2014) or intertidal reef environments (e.g. Schoepf et al. 2015).

Recently, the rate of heating from the onset of the MHW to the maximum intensity has been shown to be a better predictor of bleaching severity compared to DHWs for some species (Maynard et al. 2008, Hobday et al. 2016, Li & Donner 2022). *Acropora* spp. showed higher physiological stress when exposed to fast versus slow heating rates (Middlebrook et al. 2010, Martell & Zimmerman 2021). Therefore, understanding susceptibility to different heating rates may improve heat stress and bleaching predictions in combination with existing metrics (i.e. event intensity, duration, DHW) by enabling a unique description and comparison between different MHW events (Hobday et al. 2016). However, to date, the effects of heating rate have only been studied in *Acropora* spp. and it therefore remains unknown if other species and growth forms show similar responses, particularly massive and encrusting corals, which have often been shown to be less susceptible to heat stress.

To test the effect of heating rate on bleaching sensitivity, we experimentally simulated 2 different MHWs with the same cumulative intensity, but different rates of heating (0.5 vs. 1°C d^{-1} for slow and fast heating rates, respectively), replicating observed MHW temperature profiles described by Hobday et al. (2016). We investigated the effect of heating rate on photochemical efficiency, holobiont metabolism, tissue biomass, chl *a*, and symbiont density in 2 widespread coral species, *Pocillopora damicornis* and *Plesiastrea versipora*, representing branching and encrusting growth forms, respectively. We focused on subtropical Western Australia, as it is a global warming hotspot, warming faster than 90% of

the global ocean and therefore a sentinel for climate change (Hobday & Pecl 2014). This region also experienced an extreme MHW in 2011 with DHW > 16, SST anomalies reaching up to 5°C above the long-term averages, and a heating rate of 0.3°C d^{-1} (Wernberg et al. 2013, Schlegel & Smit 2018). Although this event resulted in widespread bleaching across the majority of the Western Australian coast (Moore et al. 2012), some corals in the subtropical region, including *P. versipora*, increased 4-fold in abundance after this event (Tuckett et al. 2017). We hypothesized that fast onset MHWs would have more damaging effects on the physiology of the 2 species compared to slow onset MHWs, and that these effects would be greater in the branching species (*P. damicornis*) compared to the encrusting species (*P. versipora*).

2. MATERIALS AND METHODS

2.1. Coral collection

The encrusting coral *Plesiastrea versipora* (Lamarck, 1816) and the branching coral *Pocillopora damicornis* (Linnaeus, 1758) are both widely distributed across the Indian and Pacific Oceans, and locally abundant along the mid-West Australian coast (Veron & Marsh 1988). We chose these 2 species as representatives of winners (*P. versipora*) and losers (*P. damicornis*) of the extreme MHW in 2011 (Tuckett et al. 2017). Eight visibly healthy parent colonies (approx. 15 cm in diameter) of each species were collected on 12 December 2019 (the austral summer) from Port Gregory (28° 20′ 04.6″ S, 114° 24′ 62.8″ E), Western Australia. Due to differences in habitat preferences (Veron & Marsh 1988, Veron 2000), *P. damicornis* colonies were collected from open reef areas at 8.5 m depth, where light intensity reached a maximum of approximately 290 µmol photons m^{-2} s^{-1}, whereas *P. versipora* colonies were collected from shaded crevices at 8 m depth, where the light intensity reached a maximum of approximately 200 µmol photons m^{-2} s^{-1} during the sampling period. Both light measurements were collected using a Li-Cor underwater quantum sensor (LI-192; sample rate 1 Hz) deployed around midday (11:00 to 13:00 h) over a few cloudless days in summer (10 to 12 December 2019) to determine maximum light intensities at our study sites. Colonies of both species were collected using hammer and chisel at least 10 m apart from each other to maximize the likelihood of obtaining different genotypes (Baums et al. 2006). Following collection, colonies were submerged in seawater in portable coolers and transported to laboratory facilities (5 h) where they were maintained in indoor, flow-through aquaria at 23.5 ± 0.2°C (ambient temperature at collection site) at approximately 290 µmol photons m^{-2} s^{-1} for 2 wk to allow recovery and acclimation to tank conditions.

2.2. Experimental design

Following a 14 d recovery and acclimation period, each colony was fragmented into 3 equal-sized pieces (i.e. *P. versipora*: 4 cm diameter; *P. damicornis*: 3 × 1 cm branches) and glued onto pre-labelled plastic tiles using super glue. Corals were kept for another 14 d at 23.5 ± 0.2°C prior to the start of the experiment under a reduced light intensity of approximately 120 µmol photons m^{-2} s^{-1} to aid recovery from fragmentation. Water motion was provided using submersible wave makers (JP-067, Sunsun, 2300 l h^{-1}). Seawater renewal rate was 1.5 l min^{-1}, resulting in a turnover time of approximately 30 min in 50 l tanks. Light was provided using custom-designed LED arrangements and colours (Ledzeal S150 Plus, 150 W). Lights were programmed to a 12 h light:12 h dark cycle, following a natural diurnal light cycle with gradual increase up to 160 µmol photons m^{-2} s^{-1} at noon. The experimental light levels were lower than those measured at the collection sites for *P. damicornis* to avoid light stress in *P. versipora*, which naturally grows in shaded areas and crevices. Corals were fed 3 times a week with freshly hatched *Artemia nauplii* at night. Approximately 2.5 g of brine shrimp eggs were hatched in seawater for 36 h, and the stock solution was equally distributed within all tanks. Pumps were turned off for 30 min to allow for feeding, and the remaining brine shrimp was presumed flushed out within the next 30 min after pumps were turned back on.

The MHW simulations started following the second 2 wk acclimation period on 6 January 2020 (i.e. 30 d after collection). One coral fragment from each parent colony was randomly assigned to each of 3 temperature treatments: (1) ambient control, (2) slow onset MHW, and (3) fast onset MHW (see details below), resulting in n = 8 coral parent colonies per species per treatment. The temperature profiles replicated observed MHW profiles described by Hobday et al. (2016). Each temperature treatment consisted of 3 replicate 50 l transparent, plastic flow-through tanks. Temperature increases were done using glass heaters (AquaManta 300W) corresponding to the simulated MHW onset; slow onset 0.5 ±

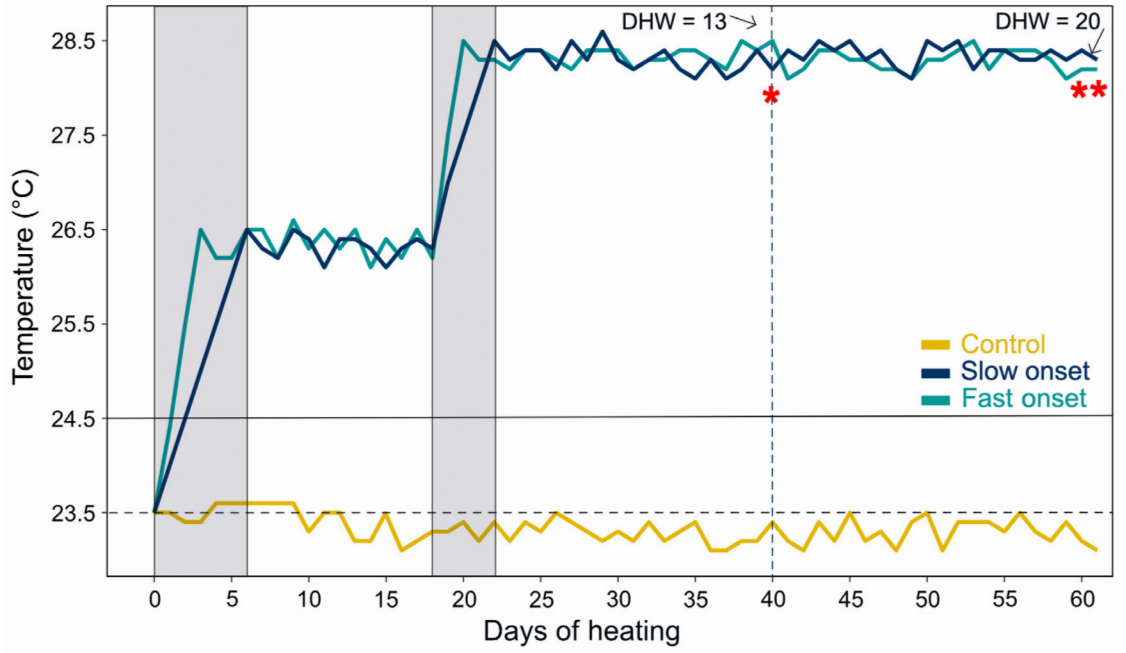

Fig. 1. Temperature regimes during the heat stress test. Shaded areas indicate the first and second ramping periods; horizontal dashed line: long-term maximum monthly mean (MMM) temperature at the collection site; horizontal solid line: presumed bleaching threshold (MMM + 1°C) and the short-term *in situ* collected MMM values; vertical dashed line: day the experiment was ended for *Pocillopora damicornis*. Degree heating weeks (DHW) are given at times when the experiment was ended for each species. Data collection times are indicated as end of the experiment for **P. damicornis*, and ***Plesiastrea versipora*

0.2°C d^{-1} and fast onset 1 ± 0.2°C d^{-1} (Fig. 1). Temperature in each tank (n = 9) was controlled with an Aquatronic temperature sensor and logged every 10 min. Temperature sensors were calibrated every week using a high-precision (0.01°C) thermometer (Fisher Scientific).

Slow onset treatments were kept an additional 1.5 d at the desired heat stress temperature to ensure that both treatments had the same DHWs at the end of the experiment (13 DHW for *P. damicornis* and 20 DHW for *P. versipora*). For the first phase of the simulated MHW, temperature was increased from 23.5 ± 0.2 to 26.5 ± 0.2°C in both heat stress treatments. To ensure comparability with DHWs calculated for real MHWs, experimental DHWs were calculated using 1°C increases from the maximum monthly mean (MMM) of 23.5°C (MMM provided for the nearby Houtman Abrolhos Islands, approximately 60 km to the west, by NOAA Coral Reef Watch, Skirving et al. 2020). However, 10 d at 26.5°C (4 DHW) proved insufficient to elicit changes in visual coral health (see Fig. 2), which may suggest that corals did not experience enough heat stress. Therefore, temperature was gradually increased to 28.5 ± 0.2°C (corresponding to the simulated MHW onset) and maintained for 6 d for *P. damicornis* and 26 d for *P. versipora*. The longer duration for *P. versipora* was necessary to induce bleaching (see Fig. 2). In total, *P. damicornis* fragments were subjected to heat treatment for 40 and 38 d and *P. versipora* fragments were subjected for 60 and 58 d for slow and fast onset treatments, respectively.

2.3. Visual coral health

Coral health was scored once a week to visually assess and quantify colour loss (i.e. paling or bleaching). Corals were scored on the upper surface of the fragments using the CoralWatch® Coral Health Chart, where a change of 2 units corresponds to significant changes in pigment concentration (i.e. bleaching, Siebeck et al. 2006).

2.4. Photochemical efficiency of Photosystem II

Maximum dark-adapted quantum yield (F_V/F_M) of chl *a* fluorescence (Schreiber et al. 1995) was measured 45 min after sunset (i.e. when the lights were turned off) to evaluate changes in photo-physiology throughout the experiment (Warner et al. 1996, Hill et al. 2004). All coral fragments were measured every 2 to 3 d. Measurements were done using a mini-PAM

fluorometer (Walz) using the following settings: measuring light intensity 3, saturation pulse intensity 12, saturation pulse width 0.8 s, gain 3, and damping 2. Measurements were made at a constant distance of 3 mm from the coral tissue using a piece of clear plastic tubing. The same part of each fragment was measured throughout the experiment, given the fixed position of each coral.

2.5. Holobiont metabolism (*P*:*R*)

Holobiont metabolism was measured as the ratio of oxygen production through photosynthesis (gross primary productivity, P_{gross}) (µmol O_2 h^{-1} cm^2) to oxygen consumption through respiration (R) (µmol O_2 h^{-1} cm^2). P_{gross}:R (hereafter P:R) was measured immediately following the end of heat stress (i.e. after 40 and 60 d for *P. damicornis* and *P. versipora*, respectively). Six fragments per treatment (representing control, slow onset, and fast onset) were randomly selected from 6 parent colonies. Fragments from the remaining 2 parent colonies were excluded due to time limitations. All incubations were done at control temperatures (~23°C) to avoid errors caused by the differences in oxygen solubility between different temperatures. This drop in temperature may have stressed the corals, although we consider this unlikely given that the cooler temperatures were well within the seasonal temperature range and may, in fact, have provided relief from heat stress. Corals were kept under constant light intensity of 160 photons m^{-2} s^{-1} during light incubations to match the maximum intensity in the experimental tanks. Incubations were performed between 10:00 and 14:00 h to avoid circadian effects of photosynthesis. All fragments were dark acclimated for at least 1 h before dark incubations and all incubations from the same fragments were performed on the same day. Oxygen, temperature, salinity, and pressure were measured continuously during incubation using a Presens SMA-OXY4 unit (Presens) calibrated once before the experiments started according to the manufacturer's instructions in an oxygen-free environment (i.e. using sodium sulphate). Corals were incubated for 60 to 75 min, depending on the size of the coral fragment, to achieve an approximately 15% change in O_2 saturation. Incubations were done in 1 l sealed, transparent plastic chambers placed in a water bath to keep the temperature constant during incubation. Each incubation round included 1 control chamber which was used to correct for the seawater microbial P_{gross} and R. The control chamber contained a plastic tile and a bleached, clean coral skeleton of similar size to displace a roughly equal amount of water. Mixing in the chamber was provided with a submersible magnetic stirrer. Slow onset treatments were incubated for 1.5 d after the fast onset treatments to ensure both treatments had reached the same DHW. Both rounds of incubations (i.e. light and dark) were completed over 3 d. Oxygen data were normalized to incubation volume, incubation duration, and surface area of the fragment (see Section 2.6.3). P:R ratios were calculated as 12 h of gross P (= net P + R) (µmol h^{-1} cm^{-2}) divided by 24 h of R (µmol h^{-1} cm^{-2}) given the 12 h light:12 h dark cycle.

2.6. Sample processing

Coral fragments were sacrificed immediately at the end of their respective heat stress period and preserved at −80°C for 4 mo. Coral tissue was removed from the skeletons with deionized (DI) water using an airbrush (*P. damicornis*) or Waterpik (*P. versipora*), as these were determined to be the most appropriate methods to suit each morphology (Schoepf et al. 2015).

2.6.1. Tissue biomass. A 3 to 4 ml aliquot per sample of the tissue slurry was dried at 60°C in pre-combusted aluminium pans to constant weight and ashed in a muffle furnace at 500°C for 4 h. Ash-free dry weight (tissue biomass) was determined as the difference between dry and ash weight (mg) and normalized to surface area (mg cm^{-2}, see Section 2.6.3).

2.6.2. Chl *a* and symbiont density. The remaining tissue slurry was centrifuged for 10 min (3220 × *g*) to separate the animal host and symbiont fraction. The symbiont fraction was resuspended in DI water and used for measuring chl *a* and symbiont density. Chl *a* was extracted in 100% acetone in the dark at 4°C for 24 h. Concentrations of chl *a* from each sample were determined spectrophotometrically using individual glass cuvettes following the equations of Jeffrey & Humphrey (1975) for dinoflagellates. Chl *a* concentrations were normalized to both surface area (µg cm^{-2}) and cell density (pg $cell^{-1}$). Symbiont cell density was calculated using 8 replicate counts on an improved Neubauer hemacytometer and standardized to surface area (10^6 cells cm^{-2}).

2.6.3. Surface area. Surface area was estimated using the most appropriate methods suiting each morphology (e.g. Schoepf et al. 2015). To this end, the wax-dipping technique (Veal et al. 2010) was used for *P. damicornis* and the aluminium foil technique was used for *P. versipora* (Marsh 1970).

2.7. Statistical analyses

All statistical analyses were done using R version 3.5.3 (R Development Core Team 2019). Generalized linear mixed models (GLMM) were computed using the 'glmer' function from the 'lme4' package (Bates et al. 2015) to analyse the effect of heating rate (fixed effect with 3 levels: control, slow onset, fast onset) on tissue biomass, endosymbiont density, chl *a*, *P*:*R*, respiration, gross photosynthesis, and F_V/F_M measurements for each species. Models were built separately because each species experienced different durations of heat stress and DHWs. Tukey's tests using Kenward-Roger degrees-of-freedom adjusted p-values were used to test for the effect of heating rate when main effects were significant, using the 'multcomp' package (Hothorn et al. 2008). Parent colonies were used as random group intercepts but had no influence on any of the response variables. We selected the model with the error distribution that best fit the data. Different models were compared using Akaike's Information Criterion (AIC), and a Gamma error distribution with a log link function was selected as it had the best balanced fit and parsimony. Residuals were visually inspected using the 'performance' package for violations of statistical assumptions (Lüdecke et al. 2021). Significance of fixed effects was determined using the ANOVA function of the 'rstatix' package (Kassambara 2021), which provided Analysis of Deviance tables (Type III Wald chi-square tests). Multiple pairwise comparisons were done for F_V/F_M for the days of the experiment that had the same cumulative heat stress exposure (13 DHW for *P. damicornis* and 20 DHW for *P. versipora*). This corresponded to the Day 40 value for slow onset with Day 38 value for fast onset for *P. damicornis*, and the Day 60 value for slow onset with Day 58 value for fast onset for *P. versipora*.

3. RESULTS

3.1. Visual coral health

All fragments appeared visibly healthy with full tissue cover, no discolouration, and no signs of disease at the start of the experiment, and control fragments remained visibly healthy throughout the experiment. Complete mortality of the tissue surface only occurred in heat-stressed fragments belonging to 1 *Pocillopora damicornis* parent colony. At the end of the experiment (i.e. on Days 40 and 60 for *P. damicornis* and *Plesiastrea versipora*, respectively), heat-stressed fragments of both species were visibly paler (health score 2 ± 1; mean ± SD, n = 8 per species and treatment) than the controls (health score 4 ± 1; n = 8).

3.2. Photochemical efficiency of photosystem II

F_V/F_M remained high and stable (*P. damicornis* 0.69 ± 0.05; *P. versipora* 0.67 ± 0.07; n = 8) within control fragments over the course of the experiment (Fig. 2). Heated *P. versipora* fragments maintained F_V/F_M values similar to their control treatments for 20 d longer than *P. damicornis* fragments, before experiencing a similar decrease (Fig. 2B).

Heating had a significant negative effect on F_V/F_M in both species. For *P. damicornis*, heat stress treatments had significantly lower (by 20%) F_V/F_M values at the end of the experiment compared to their controls (Tables 1 & 2) (Days 40 and 38 for slow and fast onset, respectively). However, there were no differences in reduction of F_V/F_M between slow and fast onset treatments (Fig. 2A). For *P. versipora*, declines in fast onset treatment corals were greater than in slow onset treatment corals, and only fast onset treatments were significantly different to the control treatments (12% lower) ($p = 0.007$) at the end of the experiment (Days 60 and 58 for slow and fast onset, respectively) (Fig. 2B, Table 2).

3.3. Holobiont metabolism (*P*:*R*)

Heating rate had a significant effect on *P*:*R* at the end of the experiment in *P. damicornis* ($p < 0.001$) (Table 1), but not *P. versipora* (Fig. 3C,F, Table 2). Fast heating rate resulted in greater declines in *P*:*R* than slow heating rate in *P. damicornis,* with fragments experiencing a 65% decrease compared to the controls and the loss of net autotrophy (*P*:*R* < 1) at the end of their heating treatment and slow onset fragments experiencing 26% decrease. No significant change was observed in the rate of gross photosynthesis (P_{gross}) for either species at the time of incubation (Tables 1 & 2). Similarly, heating rate had no significant impact on the respiration (*R*) of *P. versipora*; however, it had a significant effect on *P. damicornis*, with fast onset corals having significantly higher respiration rates (0.5 ± 0.2 µmol h^{-1} cm^{-2}, mean ± SE) than both control (0.2 µmol ± 0.1 h^{-1} cm^{-2}) and slow onset corals (0.2 µmol ± 0.1 h^{-1} cm^{-2}) (Fig. 3B, Table 1).

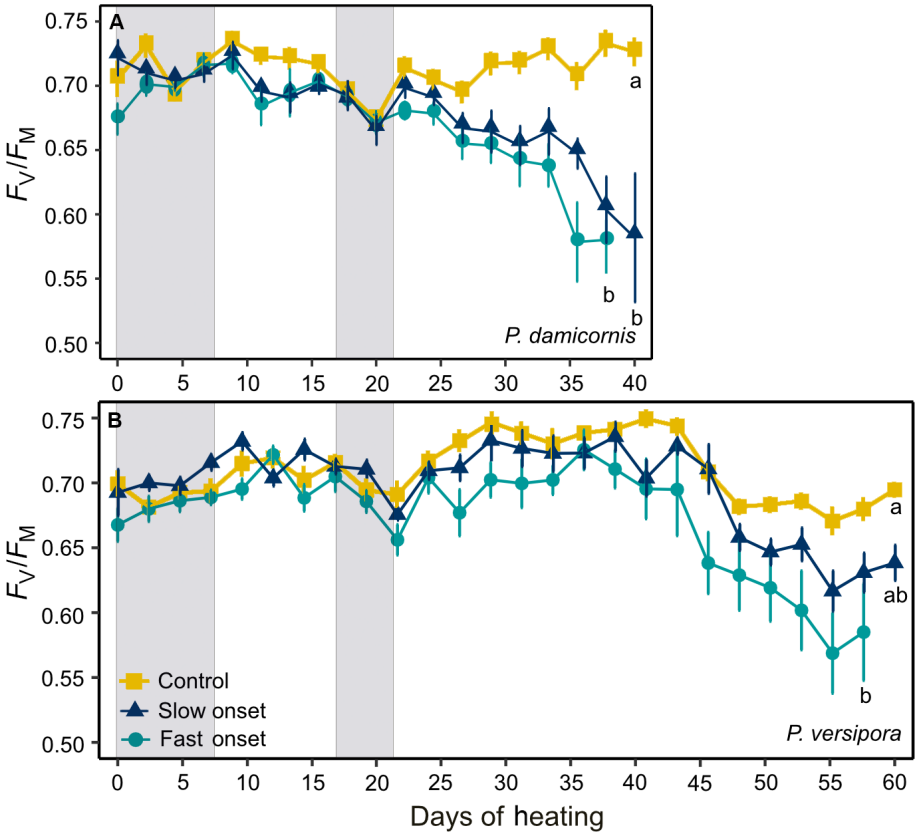

Fig. 2. Photochemical efficiency (F_V/F_M) of (A) *Pocillopora damicornis* and (B) *Plesiastrea versipora* (mean ± SE, n = 8). Lowercase letters indicate results from Tukey-adjusted multiple pairwise comparisons when the effect of heating rate was significant. Shading indicates the ramping periods

Table 1. Results from generalized linear mixed models for *Pocillopora damicornis* to test for the effect of heating (fixed effect) and heating rate (indicated by Tukey letter groupings) on F_V/F_M at the final time point (i.e. Days 40 and 38 for slow and fast onset treatments, respectively), photosynthesis (P_{gross}) to respiration ratios (P:R), P_{gross}, R, chl *a* per area, chl *a* per cell, symbiont density, and tissue biomass. p-values ≤ 0.05 are given in **bold**

Parameter	Fixed effect (Heating)	χ^2	df	p	Post-hoc (Heating rate)	Tukey group
F_V/F_M	Heating	13.442	2	**<0.001**	Control	a
					Slow onset	b
					Fast onset	b
P:R	Heating	14.682	2	**<0.001**	Control	a
					Slow onset	b
					Fast onset	ab
P_{gross} (µmol h^{-1} cm^{-2})	Heating	1.63	2	0.438	–	
R (µmol h^{-1} cm^{-2})	Heating	9.531	2	**0.008**	Control	b
					Slow onset	a
					Fast onset	b
Chl *a* area (µg cm^{-2})	Heating	56.057	2	**<0.001**	Control	a
					Slow onset	b
					Fast onset	b
Chl *a* cell (pg $cell^{-1}$)	Heating	27.91	2	**<0.001**	Control	b
					Slow onset	a
					Fast onset	ab
Symbiont density (10^6 cells cm^{-2})	Heating	99.085	2	**<0.001**	Control	a
					Slow onset	b
					Fast onset	b
Tissue biomass (mg cm^{-2})	Heating	32.656	2	**<0.001**	Control	a
					Slow onset	b
					Fast onset	b

Table 2. Results from generalized linear mixed models for *Plesiastrea versipora* to test for the effect of heating (fixed effect) and heating rate. Final time points are Days 60 and 58 for slow and fast onset treatments, respectively. See Table 1 for details

Parameter	Fixed effect (Heating)	χ^2	df	p	Post-hoc (Heating rate)	Tukey group
F_V/F_M	Heating	9.2417	2	**<0.001**	Control	a
					Slow onset	ab
					Fast onset	b
P:*R*	Heating	2.096	2	0.351	–	
P_{gross} (µmol h^{-1} cm^{-2})	Heating	3.176	2	0.205	–	
R (µmol h^{-1} cm^{-2})	Heating	3.148	2	0.207	–	
Chl *a* area (µg cm^{-2})	Heating	29.461	2	**<0.001**	Control	a
					Slow onset	b
					Fast onset	b
Chl *a* cell (pg $cell^{-1}$)	Heating	22.837	2	**<0.001**	Control	a
					Slow onset	b
					Fast onset	b
Symbiont density (10^6 cells cm^{-2})	Heating	11.5	2	**0.003**	Control	a
					Slow onset	b
					Fast onset	b
Tissue biomass (mg cm^{-2})	Heating	3.558	2	0.169	–	

3.4. Chl *a*, symbiont density, and tissue biomass

Chl *a* per area decreased significantly (85 to 87%) as a consequence of heat stress in *P. damicornis*, but there was no significant difference between the slow and fast onset treatments (Fig. 4A, Table 1). However, heating rate had a significant effect when chl *a* was normalized per cell (Fig. 4B) rather than per area. In fact, we found significantly higher chl *a* per cell in corals in fast onset treatments than corals in either slow onset ($p = 0.018$) or control treatments ($p < 0.001$). This was associated with significant declines in symbiont densities (87 to 90%) (Fig. 4C) in both slow and fast onset treatments compared to the control treatments, which were independent of heating rate.

Heating also had a significant negative effect on symbiont-related parameters in *P. versipora* corals, where chl *a* per area (Fig. 4E) and symbiont density (Fig. 4G) were both significantly lower than in the control (63 and 46%, respectively) (Table 2), but heating rate had no significant effect. However, unlike in *P. damicornis*, we found no difference between slow and fast onset treatments when chl *a* was normalized per cell rather than area, although heated corals in both treatments had significantly lower values (–30%) than the control. At the end of the heating period, heated *P. damicornis* had 36% less biomass (Fig. 4D) than the controls; however, heating rate had no significant effect. In contrast, heating rate had no significant impact on *P. versipora* tissue biomass (Fig. 4H, Table 2)

4. DISCUSSION

The present study compared the responses of 2 coral species, representing different growth forms, to 2 ecologically relevant MHW scenarios with the same cumulative heat exposure but different heating rates for each species, testing the hypothesis that heating rate can play an important role in bleaching responses. Consistent with other studies that have shown detrimental effects of rapid heating on branching *Acropora* corals (Middlebrook et al. 2010, Martell & Zimmerman 2021), our results showed sensitivity to heating rates but these responses were species-specific.

Species-specific responses to heating rate were most evident in *P*:*R* ratios, with encrusting *Plesiastrea versipora* not impacted by either MHW simulation, while rapidly progressing MHW conditions had detrimental effects on branching *Pocillopora damicornis*, which ultimately resulted in the loss of net autotrophy (i.e. $P:R < 1$). In contrast, under slowly progressing MHW conditions, *P. damicornis* fragments were able to maintain net autotrophy, although the lowered *P*:*R* ratios observed here may have led to partial depletion of energy reserves. Photosynthesis (P_{gross}) rates under rapidly evolving MHW conditions remained relatively comparable to control treatments at the end of the experiment, which might be explained by the fact that photosynthesis rates might be independent of total available chl *a* and inversely correlated with symbiont density (Dubin-

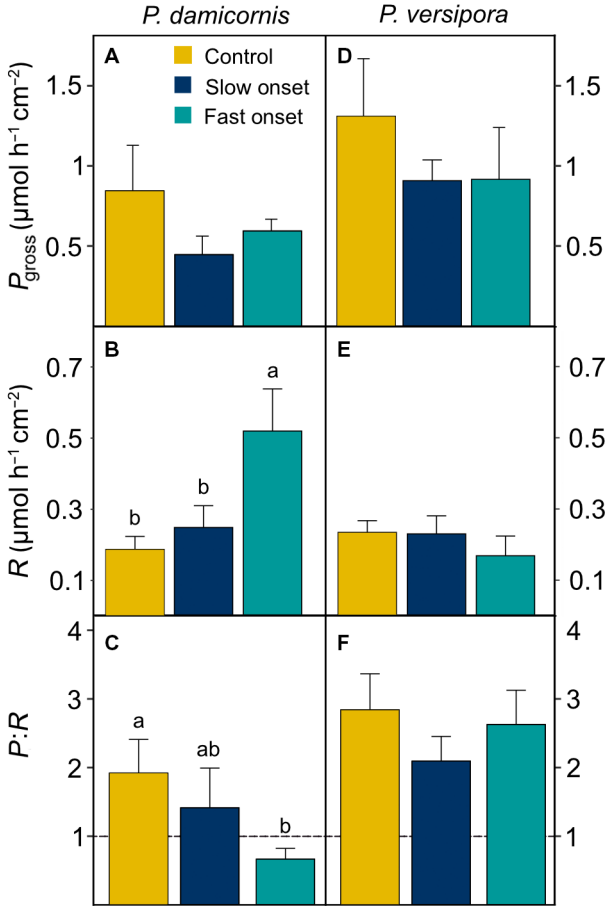

Fig. 3. (A,D) Gross photosynthesis (P_{gross}), (B,E) respiration (R), and (C,F) photosynthesis to respiration (P:R) ratios for (A,B,C) *Pocillopora damicornis* and (D,E,F) *Plesiastrea versipora* at the end of their respective heat treatments (mean ± SE). (C,F) Dashed line: loss of net heterotrophy (P:R < 1). Lowercase letters indicate results from Tukey-adjusted multiple pairwise comparisons when the effect of treatment was significant

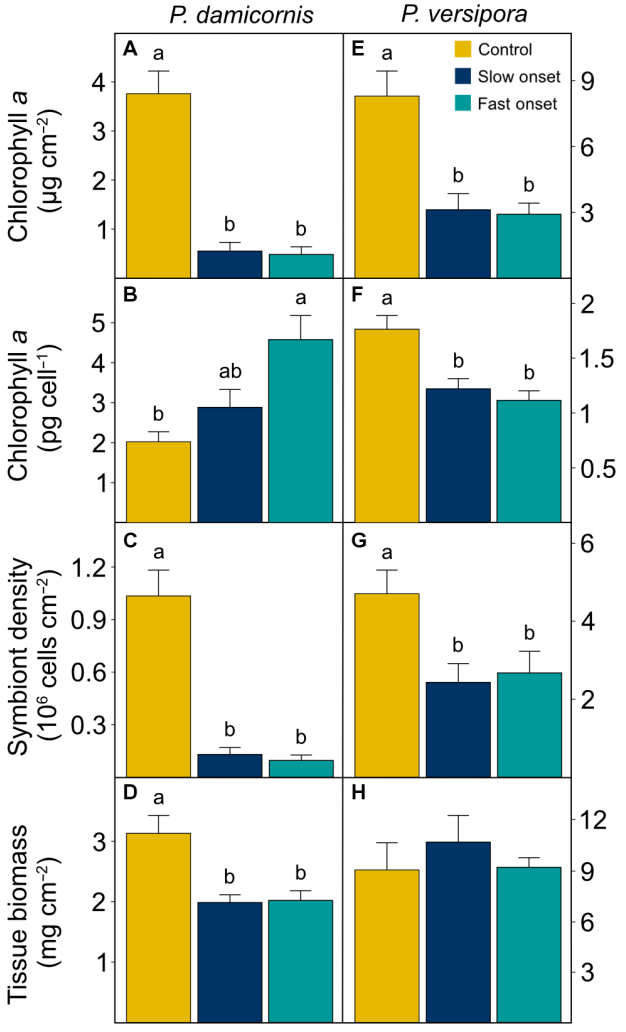

Fig. 4. Chl *a* normalized to (A,E) surface area and (B,F) symbiont cells, (C,G) symbiont density, and (D,H) tissue biomass of (A–D) *Pocillopora damicornis* and (E–H) *Plesiastrea versipora* at the end of their respective heat treatments (mean ± SE). Lowercase letters indicate results from Tukey-adjusted multiple pairwise comparisons when the effect of treatment was significant. Note the different scaling for the 2 species for all parameters

sky et al. 1990, Rodrigues & Grottoli 2007). Therefore, the significant change in P:R ratios of rapidly heated *P. damicornis* corals appears to be driven by the significant increase in respiration, which has also been observed in several other studies (Coles & Jokiel 1977, Hoogenboom et al. 2010, Baker et al. 2018) and might be one of the key mechanisms to explain susceptibility (e.g. Loya et al. 2001) of this species to rapid onset MHWs.

Additionally, our study showed that faster heating rate had a negative effect on photochemical efficiency, as highlighted by the greater declines in rapidly heated *P. versipora* compared to the slowly heated treatments. This finding is consistent with the previous studies on the negative effects of rapid heating rates on branching *Acropora* corals (Middlebrook et al. 2010, Martell & Zimmerman 2021). A similar response might have been expected from rapidly heated *P. damicornis* fragments, especially considering the significant reductions we observed in holobiont P:R ratios. However, as this species is generally sensitive to heating (i.e. Marshall & Baird 2000, Loya et al. 2001), it is likely that 0.5 and 1°C d^{-1} may have both been too rapid and/or similar to each other to allow a significant change for this species to be observed. In general, the fast onset treatment corals showed earlier declines in F_V/F_M than the slow onset treatments in both species, even though at the

end of the experiment they experienced the same overall declines in magnitude. Lack of a strong change in the F_V/F_M may also be due to the nature of the experimental design used in this study. We used more ecologically relevant heating rates (0.5 and 1°C d^{-1}) compared to the acute heat stress assays that are most often used (reviewed by McLachlan et al. 2020). As such, heating rate effects may have revealed some differences which could be difficult to detect in a short-term stress test. This further highlights the importance of employing more longer-term, ecologically relevant experiments.

It is further important to highlight that while the maximum light levels in the experiment were similar to natural levels at the collection site for *P. versipora*, they were somewhat lower than the maximum light levels that *P. damicornis* is naturally exposed to (i.e. 160 vs. maximum 290 photons m^{-2} s^{-1}, respectively). This could have contributed to the observed differences in bleaching sensitivity between species. However, the use of low light levels can be informative to understand how much heat stress is required to trigger thermally induced bleaching (Anthony et al. 2007, Middlebrook et al. 2010). *P. damicornis* was more sensitive to heat stress compared to *P. versipora*, indicated by the ability to maintain high and stable F_V/F_M 20 d longer during the experiment. The sustained photosynthetic response of *P. versipora* relative to *P. damicornis* suggests species-specific differences in tolerance of sustained heat stress, which is consistent with previous studies on heat tolerance within this region (Tuckett et al. 2017). It is important to note, however, that these different responses may also have been caused by the different types of Symbiodiniaceae hosted by these coral species in Western Australia (*Breviolum* and *Cladocopium* in *P. versipora* and *P. damicornis*, respectively) (Silverstein et al. 2011, LaJeunesse et al. 2018). For instance, while some symbiont genera and/or species are known to be susceptible to higher temperatures, others are exceptionally resilient (Hoadley et al. 2015, Hoogenboom et al. 2017). Nevertheless, higher heat tolerance could be a critical feature for *P. versipora* to adapt to the gradual increases in ocean temperature, which could promote resistance and recovery to future MHW events.

Our results did not show an effect of heating rate on colony biomass, which may be an important indicator for coral health and bleaching sensitivity (Thornhill et al. 2011, Grottoli et al. 2014, but see Wall et al. 2019). During bleaching where severe losses of symbionts take place, corals depend on alternative strategies to meet their daily metabolic energy requirements (Muscatine et al. 1981). Catabolism of energy reserves (i.e. lipid, protein, and carbohydrate levels) and heterotrophy are two such strategies (Fitt et al. 2000, Grottoli et al. 2006, Rodrigues & Grottoli 2007). Species that are able to increase their heterotrophic input of fixed carbon under heat stress are thought to have an ecological advantage in survival compared to species that deplete their restricted source of energy (i.e. Grottoli et al. 2006, Conti-Jerpe et al. 2020). *P. versipora* was able to maintain its tissue biomass under both heating rates. This could potentially indicate greater capacity for heterotrophic plasticity and may have provided bleaching resilience (Anthony et al. 2009). Alternatively, this could also be the result of this species' ability to maintain *P*:*R* ratios and net autotrophy under heat stress. Conversely, *P. damicornis* experienced a significant decline in tissue biomass which may be explained by the catabolism of stored energy reserves (Porter et al. 1989, Rodrigues & Grottoli 2007). A reduction in tissue biomass under ocean acidification, another climate change stressor, has also been shown for *Pocillopora acuta*, a species closely related to *P. damicornis* (Wall et al. 2017, but see Schoepf et al. 2013). Colonies with high tissue biomass are known to be less susceptible when exposed to thermal stress compared to those with low tissue biomass (Fitt et al. 2000, Loya et al. 2001, Thornhill et al. 2011). As an encrusting coral species, the tissue biomass in the control treatment for *P. versipora* was 3 times higher than in the control treatment for *P. damicornis*, which might have provided protection from light and more effective self-shading of the symbiont cells (Hoegh-Guldberg 1999, Cunning & Baker 2014). This finding is consistent with an ecological advantage provided by the differences in surface area to volume ratios and thicker tissues in massive and encrusting species compared to branching colonies (i.e. Loya et al. 2001).

The differences in heat tolerance and sensitivity to heating rate between 2 common coral species may have broader implications for the reef community. This might especially be the case in tropical–temperate transition zones where species are undergoing major redistributions (Vergés et al. 2014, Pecl et al. 2017). While many tropical coral reefs and temperate kelp forests continue to degrade and homogenize with warming oceans (Alvarez-Filip et al. 2009, Krumhansl et al. 2016, Wernberg et al. 2016, Perry & Alvarez-Filip 2019), the tropical–temperate transition zones are becoming 'tropicalized' with poleward-moving tropically affiliated corals (Precht & Aronson 2004: *Acropora* spp.; Thomson 2010: *Gonio-*

pora spp.; Yamano et al. 2011: *Acropora* spp., *Pavona* spp.; Baird et al. 2012: *Acropora* spp.). More opportunistic corals are increasing in abundance, enabled by competitive release from historic habitats. This has been observed in Western Australia as a result of the 2011 MHW, which resulted in major loss of canopy-forming kelps and the indirect increase in coral abundance (Wernberg et al. 2016, Tuckett et al. 2017). However, the structural complexity and biodiversity which might be supported by novel coral assemblages will ultimately depend on their resilience to future warming events (Vergés et al. 2019). For instance, in the tropical–temperate transition zone in Western Australia, *P. versipora* has shown high heat tolerance and survival under an extreme MHW (i.e. 16 DHW), particularly when compared to other locally abundant species (i.e. *P. damicornis*) (Tuckett et al. 2017). This is consistent with our findings of a sharp decline in F_V/F_M when DHW reached 18 for *P. damicornis*, yet *P. versipora* required an additional 20 d to show similar declines. While our study identifies some of the mechanisms behind this outcome, it also suggests that, under rapidly evolving MHWs, these novel coral communities might shift towards less complex morphologies (i.e. dominated by the encrusting *P. versipora*). Therefore, with the projected increases in frequency and intensity of MHWs (Oliver et al. 2019), the functional attributes that can be supported by these novel coral communities (i.e. tropicalized coral assemblages) (Vergés et al. 2019) might be lower than estimated.

Overall, our results confirm that in addition to *Acropora* species, corals from other genera are also susceptible to heating profiles of MHWs, such as the heating rate. Our experiment as a mid-term, gradual heat-stress onset design also allows comparison with many natural bleaching events (McLachlan et al. 2020, Grottoli et al. 2021). Although the responses were species-specific, the differences in heating rate appear to be consistent with the idea that massive and encrusting corals may be less sensitive to faster onset in heating than branching corals. Additionally, highlighted by the loss of net autotrophy, these corals may rely more upon heterotrophic feeding to overcome this disadvantage. Understanding species-specific sensitivities to heating rates in combination with existing metrics (i.e. DHW) is likely to enable us to make better predictions on impacts of MHW generally, but also particularly for species-specific responses. These subtle changes (i.e. heating rates) can influence responses of some coral species more than others, which can have consequences for future community assemblages and reef functions.

Data availability. The data and R code supporting the findings of this study are openly available in https://github.com/defneasahin/Heating_rates.

Acknowledgements. This study was funded by the Australian Research Council (DP170100023 and DP200100201 to T.W.), the Australian Government International Research Training Program (to D.S.), and the Holsworth Wildlife Research Endowment – Equity Trustees Charitable Foundation & the Ecological Society of Australia (to D.S.). We thank Albert Pessarrodona, Sofie Vranken, and Salvador Zarco-Perello for their assistance in the field. Coral collections were done under the relevant Department of Primary Industries and Regional Development permit (#3359).

LITERATURE CITED

Ainsworth TD, Heron SF, Ortiz JC, Mumby PJ and others (2016) Climate change disables coral bleaching protection on the Great Barrier Reef. Science 352:338–342

Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR (2009) Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. Proc R Soc B 276: 3019–3025

Anthony K, Connolly S, Hoegh-Guldberg O (2007) Bleaching, energetics, and coral mortality risk: effects of temperature, light, and sediment regime. Limnol Oceanogr 52:716–726

Anthony K, Hoogenboom M, Maynard J, Grottoli A, Middlebrook R (2009) Energetics approach to predicting mortality risk from environmental stress: a case study of coral bleaching. Funct Ecol 23:539–550

Bainbridge SJ (2017) Temperature and light patterns at four reefs along the Great Barrier Reef during the 2015–2016 austral summer: understanding patterns of observed coral bleaching. J Oper Oceanogr 10:16–29

Baird AH, Sommer B, Madin JS (2012) Pole-ward range expansion of *Acropora* spp. along the east coast of Australia. Coral Reefs 31:1063

Baker DM, Freeman CJ, Wong JCY, Fogel ML, Knowlton N (2018) Climate change promotes parasitism in a coral symbiosis. ISME J 12:921–930

Barshis DJ, Stillman JH, Gates RD, Toonen RJ, Smith LW, Birkeland C (2010) Protein expression and genetic structure of the coral *Porites lobata* in an environmentally extreme Samoan back reef: does host genotype limit phenotypic plasticity? Mol Ecol 19:1705–1720

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Soft 67:1–48

Baums I, Miller M, Hellberg M (2006) Geographic variation in clonal structure in a reef-building Caribbean coral, *Acropora palmata*. Ecol Monogr 76:503–519

Camp EF, Schoepf V, Mumby PJ, Hardtke LA, Rodolfo-Metalpa R, Smith DJ, Suggett D (2018) The future of coral reefs subject to rapid climate change: lessons from natural extreme environments. Front Mar Sci 5:4

Coles SL, Jokiel PL (1977) Effects of temperature on photosynthesis and respiration in hermatypic corals. Mar Biol 43:209–216

Conti-Jerpe IE, Thompson PD, Wong CWM, Oliveira NL, Duprey NN, Moynihan MA, Baker DM (2020) Trophic strategy and bleaching resistance in reef-building corals. Sci Adv 6:eaaz5443

Cunning R, Baker AC (2014) Not just who, but how many: the importance of partner abundance in reef coral symbioses. Front Microbiol 5:400

DeCarlo TM, Cohen AL, Wong GTF, Davis KA, Lohmann P, Soong K (2017) Mass coral mortality under local amplification of 2°C ocean warming. Sci Rep 7:44586

Dubinsky Z, Stambler N, Ben-Zion M, McCloskey LR, Muscatine L, Falkowski PG (1990) The effect of external nutrient resources on the optical properties and photosynthetic efficiency of *Stylophora pistillata.* Proc R Soc B 239:231–246

Fitt WK, Mcfarland FK, Warner ME, Chilcoat GC (2000) Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. Limnol Oceanogr 45:677–685

Frieler K, Meinshausen M, Golly A, Mengel M, Lebek K, Donner SD, Hoegh-Guldberg O (2013) Limiting global warming to 2 °C is unlikely to save most coral reefs. Nat Clim Chang 3:165–170

Glynn PW (1996) Coral reef bleaching: facts, hypotheses and implications. Glob Change Biol 2:495–509

Grottoli AG, Rodrigues LJ, Juarez C (2004) Lipids and stable carbon isotopes in two species of Hawaiian corals, *Porites compressa* and *Montipora verrucosa*, following a bleaching event. Mar Biol 145:621–631

Grottoli AG, Rodrigues LJ, Palardy JE (2006) Heterotrophic plasticity and resilience in bleached corals. Nature 440: 1186–1189

Grottoli AG, Warner M, Levas S, Aschaffenburg M and others (2014) The cumulative impact of annual coral bleaching can turn some coral species winners into losers. Glob Change Biol 20:3823–3833

Grottoli AG, Toonen RJ, van Woesik R, Vega Thurber R and others (2021) Increasing comparability among coral bleaching experiments. Ecol Appl 31:e02262

Guest JR, Baird AH, Maynard JA, Muttaqin EE and others (2012) Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. PLOS ONE 7:e33353

Hill R, Larkum AWD, Frankart C, Kühl M, Ralph PJ (2004) Loss of functional Photosystem II reaction centres in zooxanthellae of corals exposed to bleaching conditions: using fluorescence rise kinetics. Photosynth Res 82: 59–72

Hoadley KD, Pettay DT, Grottoli AG, Cai WJ and others (2015) Physiological response to elevated temperature and pCO_2 varies across four Pacific coral species: understanding the unique host+symbiont response. Sci Rep 5: 18371

Hobday AJ, Pecl GT (2014) Identification of global marine hotspots: sentinels for change and vanguards for adaptation action. Rev Fish Biol Fish 24:415–425

Hobday AJ, Alexander LV, Perkins SE, Smale DA and others (2016) A hierarchical approach to defining marine heatwaves. Prog Oceanogr 141:227–238

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. Mar Freshw Res 50:839–866

Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the world's marine ecosystems. Science 328: 1523–1528

Hoogenboom M, Beraud E, Ferrier-Pagès C (2010) Relationship between symbiont density and photosynthetic carbon acquisition in the temperate coral *Cladocora caespitosa.* Coral Reefs 29:21–29

Hoogenboom MO, Frank GE, Chase TJ, Jurriaans S and others (2017) Environmental drivers of variation in bleaching severity of *Acropora* species during an extreme thermal anomaly. Front Mar Sci 4:376

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biom J 50:346–363

Hughes TP, Kerry JT, Baird AH, Connolly SR and others (2018) Global warming transforms coral reef assemblages. Nature 556:492–496

IPCC (Intergovernmental Panel on Climate Change) (2021) Climate change 2021: the physical science basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Masson-Delmotte V, Zhai P, Pirani A, Connors SL and others (eds) Cambridge University Press, Cambridge and New York, NY

Jeffrey SW, Humphrey GF (1975) New spectrophotometric equations for determining chlorophylls *a*, *b*, c_1 and c_2 in higher plants, algae and natural phytoplankton. Biochem Physiol Pflanz 167:191–194

Kassambara A (2021) rstatix: pipe-friendly framework for basic statistical tests (R package version 0.7.0). https://CRAN.R-project.org/package=rstatix

Krumhansl KA, Okamoto DK, Rassweiler A, Novak M and others (2016) Global patterns of kelp forest change over the past half-century. Proc Natl Acad Sci USA 113: 13785–13790

LaJeunesse TC, Parkinson JE, Gabrielson PW, Jeong HJ, Reimer JD, Voolstra CR, Santos SR (2018) Systematic revision of Symbiodiniaceae highlights the antiquity and diversity of coral endosymbionts. Curr Biol 28:2570–2580

Lamarck JBM (1816) Histoire naturelle des animaux sans vertèbres. Tome 2. Verdière, Paris

Li X, Donner SD (2022) Lengthening of warm periods increased the intensity of warm-season marine heatwaves over the past 4 decades. Clim Dyn 59:2643–2654

Linnaeus C (1758) Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata (10th revised edn), Vol 1. Laurentius Salvius, Holmiae

Liu G, Strong AE, Skirving W (2003) Remote sensing of sea surface temperatures during 2002 Barrier Reef coral bleaching. Eos 84:137–141

Liu G, Strong AE, Skirving WJ, Arzayus LF (2005) Overview of NOAA Coral Reef Watch Program's near-real-time satellite global coral bleaching monitoring activities. Proc 10th Int Coral Reef Symp, Okinawa, p 1783–1793

Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, van Woesik R (2001) Coral bleaching: the winners and the losers. Ecol Lett 4:122–131

Lüdecke D, Ben-Shachar MS, Ptail I, Waggoner P, Makowski D (2021) performance: an R package for assessment, comparison and testing of statistical models. J Open Source Softw 6:3139

Marsh JA (1970) Primary productivity of reef-b calcareous red algae. Ecology 51:255–263

Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs 19:155–163

Martell HA, Zimmerman RC (2021) Heating rate modulates the metabolic response of the staghorn coral *Acropora cervicornis* (Lamarck, 1816). Mar Biol 168:83

Maynard JA, Anthony KRN, Marshall PA, Masiri I (2008) Major bleaching events can lead to increased thermal tolerance in corals. Mar Biol 155:173–182

McCowan DM, Pratchett MS, Baird AH (2012) Bleaching susceptibility and mortality among corals with differing growth forms. In: Yellowlees D, Hughes TP (eds) Proc 12th Int Coral Reef Symp, 9–13 July 2012. James Cook University, Cairns, p 1–6

McLachlan RH, Price JT, Solomon SL, Grottoli AG (2020) Thirty years of coral heat-stress experiments: a review of methods. Coral Reefs 39:885–902

Middlebrook R, Hoegh-Guldberg O, Leggat W (2008) The effect of thermal history on the susceptibility of reef-building corals to thermal stress. J Exp Biol 211: 1050–1056

Middlebrook R, Anthony KRN, Hoegh-Guldberg O, Dove S (2010) Heating rate and symbiont productivity are key factors determining thermal stress in the reef-building coral *Acropora formosa*. J Exp Biol 213:1026–1034

Moore JA, Bellchambers LM, Depczynski M, Evans RD and others (2012) Unprecedented mass bleaching and loss of coral across 12° of latitude in Western Australia in 2010–11. PLOS ONE 7:e51807

Muscatine LR, McCloskey L, Marian R (1981) Estimating the daily contribution of carbon from zooxanthellae to coral animal respiration. Limnol Oceanogr 26:601–611

Oliver ECJ, Donat MG, Burrows MT, Moore PJ and others (2018) Longer and more frequent marine heatwaves over the past century. Nat Commun 9:1324

Oliver ECJ, Burrows MT, Donat MG, Sen Gupta A and others (2019) Projected marine heatwaves in the 21st century and the potential for ecological impact. Front Mar Sci 6:734

Palumbi SR, Barshis DJ, Traylor-Knowles N, Bay RA (2014) Mechanisms of reef coral resistance to future climate change. Science 344:895–898

Pecl GT, Araújo MB, Bell JD, Blanchard J and others (2017) Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. Science 355:eaai9214

Perry CT, Alvarez-Filip L (2019) Changing geo-ecological functions of coral reefs in the Anthropocene. Funct Ecol 33:976–988

Pinsky ML, Selden RL, Kitchel ZJ (2020) Climate-driven shifts in marine species ranges: scaling from organisms to communities. Annu Rev Mar Sci 12:153–179

Porter JW, Fitt WK, Spero HJ, Rogers CS, White MW (1989) Bleaching in reef corals: physiological and stable isotopic responses. Proc Natl Acad Sci USA 86:9342–9346

Precht WF, Aronson RB (2004) Climate flickers and range shifts of reef corals. Front Ecol Environ 2:307–314

Rädecker N, Pogoreutz C, Gegner HM, Cárdenas A and others (2021) Heat stress destabilizes symbiotic nutrient cycling in corals. Proc Natl Acad Sci USA 118: e2022653118

R Development Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing. www.R- project.org

Rodrigues LJ, Grottoli AG (2007) Energy reserves and metabolism as indicators of coral recovery from bleaching. Limnol Oceanogr 52:1874–1882

Safaie A, Silbiger NJ, McClanahan TR, Pawlak G and others (2018) High frequency temperature variability reduces the risk of coral bleaching. Nat Commun 9:1671

Schlegel RW, Smit AJ (2018) heatwaveR: a central algorithm for the detection of heatwaves and cold-spells. J Open Res Softw 3:821

Schoepf V, Grottoli AG, Warner ME, Cai WJ and others (2013) Coral energy reserves and calcification in a high-CO_2 world at two temperatures. PLOS ONE 8:e75049

Schoepf V, Stat M, Falter JL, McCulloch MT (2015) Limits to the thermal tolerance of corals adapted to a highly fluctuating, naturally extreme temperature environment. Sci Rep 5:17639

Schreiber U, Bilger W, Neubauer C (1995) Chlorophyll fluorescence as a nonintrusive indicator for rapid assessment of in vivo photosynthesis. In: Schulze ED, Caldwell MM (eds) Ecophysiology of photosynthesis. Springer Study Edition, Vol 100. Springer, Berlin, p 49–70

Siebeck UE, Marshall NJ, Klüter A, Hoegh-Guldberg O (2006) Monitoring coral bleaching using a colour reference card. Coral Reefs 25:453–460

Silverstein RN, Correa AMS, LaJeunesse TC, Baker AC (2011) Novel algal symbiont (*Symbiodinium* spp.) diversity in reef corals of Western Australia. Mar Ecol Prog Ser 422:63–75

Skirving W, Marsh B, De La Cour J, Liu G and others (2020) CoralTemp and the Coral Reef Watch Coral Bleaching Heat Stress product suite version 3.1. Remote Sens 12: 3856

Smale DA, Wernberg T, Oliver ECJ, Thomsen M and others (2019) Marine heatwaves threaten global biodiversity and the provision of ecosystem services. Nat Clim Chang 9:306–312

Sully S, Burkepile DE, Donovan MK, Hodgson G, van Woesik R (2019) A global analysis of coral bleaching over the past two decades. Nat Commun 10:1264

Thomson DP (2010) Range extension of the hard coral *Goniopora norfolkensis* (Veron & Pichon 1982) to the south-east Indian Ocean. J R Soc West Aust 93:115–117

Thornhill DJ, Rotjan RD, Todd BD, Chilcoat GC and others (2011) A connection between colony biomass and death in Caribbean reef-building corals. PLOS ONE 6:e29535

Tuckett CA, de Bettignies T, Fromont J, Wernberg T (2017) Expansion of corals on temperate reefs: direct and indirect effects of marine heatwaves. Coral Reefs 36:947–956

Veal CJ, 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: 893–897

Vergés A, Steinberg, PD, Hay ME, Poore AGB and others (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proc R Soc B 281:20140846

Vergés A, McCosker E, Mayer-Pinto M, Coleman MA, Wernberg T, Ainsworth T, Steinberg PD (2019) Tropicalisation of temperate reefs: implications for ecosystem functions and management actions. Funct Ecol 33: 1000–1013

Veron JEN (2000) Corals of the World. Australian Institute of Marine Science, Townsville

Veron JEN, Marsh LM (1988) Hermatypic corals of Western Australia: records and annotated species list. Rec West Aust Mus Suppl No. 29. Western Australian Museum, Perth

Wall CB, Mason RAB, Ellis WR, Cunning R, Gates RD (2017) Elevated pCO_2 affects tissue biomass composition, but not calcification, in a reef coral under two light regimes. R Soc Open Sci 4:170683

Wall CB, Ritson-Williams R, Popp BN, Gates RD (2019) Spatial variation in the biochemical and isotopic composition of corals during bleaching and recovery. Limnol Oceanogr 64:2011–2028

Warner ME, Fitt WK, Schmidt GW (1996) The effects of elevated temperature on the photosynthetic efficiency of zooxanthellae *in hospite* from four different species of reef coral: a novel approach. Plant Cell Environ 19: 291–299

Weeks SJ, Anthony KRN, Bakun A, Feldman GC, Hoegh-Guldberg O (2008) Improved predictions of coral bleaching using seasonal baselines and higher spatial resolution. Limnol Oceanogr 53:1369–1375

Wernberg T, Smale DA, Tuya F, Thomsen MS and others (2013) An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. Nat Clim Chang 3:78–82

Wernberg T, Bennett S, Babcock RC, Bettignies T and others (2016) Climate-driven regime shift of a temperate marine ecosystem. Science 353:169–172

Yamano H, Sugihara K, Nomura K (2011) Rapid poleward range expansion of tropical reef corals in response to rising sea surface temperatures. Geophys Res Lett 38: L04601

Editorial responsibility: Chris Langdon, Coral Gables, Florida, USA
Reviewed by: C. B. Wall, H. Martell and 1 anonymous referee

Submitted: January 31, 2022
Accepted: January 10, 2023
Proofs received from author(s): February 17, 2023