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The effects of marine heatwaves on acute heat tolerance in corals

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Abstract

Scleractinian coral populations are increasingly exposed to conditions above their upper thermal limits due to marine heatwaves, contributing to global declines of coral reef ecosystem health. However, historic mass bleaching events indicate there is considerable inter- and intra-specific variation in thermal tolerance whereby species, individual coral colonies and populations show differential susceptibility to exposure to elevated temperatures. Despite this, we lack a clear understanding of how heat tolerance varies across large contemporary and historical environmental gradients, or the selective pressures that underpin this variation. Here we conducted standardised acute heat stress experiments to identify variation in heat tolerance among species and isolated reefs spanning a large environmental gradient across the Coral Sea Marine Park. We quantified the photochemical yield (F_v/F_m) of coral samples in three coral species, *Acropora* cf *humilis*, *Pocillopora meandrina*, and *Pocillopora verrucosa*, following exposure to four temperature treatments (local ambient temperatures, and +3°C, +6°C and +9°C above local maximum monthly mean). We quantified the temperature at which F_v/F_m decreased by 50% (termed ED50) and used derived values to directly compare acute heat tolerance across reefs and species. The ED50 for *Acropora* was 0.4–0.7°C lower than either *Pocillopora* species, with a 0.3°C difference between the two *Pocillopora* species. We also recorded 0.9°C to 1.9°C phenotypic variation in heat tolerance among reefs within species, indicating spatial heterogeneity in heat tolerance across broad environmental gradients. Acute heat tolerance had a strong positive relationship to mild heatwave exposure over the past 35 years (since 1986) but was negatively related to recent severe heatwaves (2016–2020). Phenotypic variation associated with mild thermal history in local environments provides supportive evidence that marine heatwaves are selecting for tolerant individuals and populations; however, this adaptive potential may be compromised by the exposure to recent severe heatwaves.

KEYWORDS
coral bleaching, Coral Sea, heat stress, local adaptation, marine heatwaves, thermal history, thermal tolerance

1 | INTRODUCTION

Marine heatwaves have emerged as the principal threat to coral reef ecosystems (Oliver et al., 2018; Smale et al., 2019), driving mass coral bleaching events and resulting in extensive coral mortality throughout tropical oceans (Hughes, Kerry, et al., 2018; Lough et al., 2018). Recent bleaching events have demonstrated a clear link between heat accumulation and coral bleaching (Hughes et al., 2017), whereby photosynthetic symbionts (Symbiodiniaceae) disassociate from the coral host during heat stress (either prolonged or acute), threatening the health and survival of corals (Baker, 2003; Glynn, 1984). The increasing persistence of marine heatwaves exposes corals to temperatures near, or above, their upper thermal limits (Heron et al., 2016) and will continue to threaten coral reefs globally (van Hooidonk et al., 2016). Despite the growing concerns of coral bleaching, there remains limited understanding of how different species and individuals respond to heat stress or the ability for corals to adapt or acclimate to changing environmental conditions. Therefore, investigating the phenotypic and genotypic diversity that underpins heat tolerance in coral populations is critical to predict the capacity for corals to acclimate and/or adapt to marine heatwaves.

Variation in bleaching susceptibility among coral species indicates there is considerable phenotypic variation in heat tolerance. This variability is largely driven by physiological trade-offs associated with colony morphology and growth rates (Loya et al., 2001; van Woesik et al., 2011), heterotrophic feeding rates (Grottoli et al., 2006), or energy reserves (Grottoli et al., 2014). However, even within species, individual genotypes can exhibit variation in heat tolerance within the same environmental conditions (Barshis et al., 2013; Bay & Palumbi, 2014; Morikawa & Palumbi, 2019; Schoepf et al., 2015). Differences among genotypes are attributed to phenotypic plasticity (Oliver & Palumbi, 2011), underlying standing genetic variation of the coral host (Dixon et al., 2015; Drury, 2020; Fuller et al., 2020; Torda et al., 2017), and/or intraspecific variation in the symbiont community composition associated with individual colonies (Berkelmans & van Oppen, 2006; LaJeunesse et al., 2009). However, there is a paucity of data concerning the mechanisms or drivers of phenotypic variation in heat tolerance derived from standardised experimental approaches (Grottoli et al., 2020; McLachlan et al., 2020), in particular, those examining spatial variation in heat tolerance (Evensen et al., 2022).

Marine heatwaves on coral reefs are not evenly distributed in time and space and are key drivers of local- and regional-scale differences in coral community composition (Dietzel et al., 2021; Hughes, Anderson, et al., 2018; Oliver et al., 2018; Smale et al., 2019). Coral mortality associated with these events can result in strong selection for individuals with greater tolerance to heat stress (Palumbi et al., 2014; Sully et al., 2019). Therefore, heat tolerance in corals is expected to vary in relation to thermal exposure, influencing phenotypic diversity at the level of individual genotypes (Lundgren et al., 2013), fine-scale microhabitats (Cornwell et al., 2021; Hoogenboom et al., 2017; Schoepf et al., 2015), and populations (Berkelmans & Willis, 1999; Coles et al., 1976; Dixon et al., 2015; Guest et al., 2012; Howells et al., 2016). Meanwhile, temporal variability in thermal gradients, such as annual temperature ranges, the rate of summer warming, the frequency of warming events, and prior exposure to heat stress mediate the thermal optimum and thermal range of corals across days, seasons, and years (Ainsworth et al., 2016; Jurriaans & Hoogenboom, 2020; Middlebrook et al., 2008). Overall, a complex interplay of spatial and temporal variation in environmental conditions are important determinants of upper thermal limits in corals and may lead to spatial variation in heat tolerance.

Early studies of heat tolerance in corals used long-term experiments (weeks to months) to simulate the accumulation of heat stress during natural bleaching events, establishing the conditions that trigger bleaching and identifying their thermal maxima (Coles et al., 1976; Humanes et al., 2022; Jokiel & Coles, 1990). More recently, acute heat stress assays have demonstrated the capacity to effectively establish relative thermal tolerance of corals over much shorter periods (Barshis et al., 2013; Palumbi et al., 2014). While acute heat stress assays do not mimic natural bleaching events, proof-of-principle experiments have identified that short-term acute heat stress assays (7h) are comparable with longer-term (21-day) heat stress assays in bleaching responses using dark-adapted maximum quantum yield (F_v/F_m) as a physiological metric, but not chlorophyll *a* or Symbiodiniaceae densities (Evensen et al., 2021; Voolstra et al., 2020). Additional ground-truthing has shown that estimates of absolute heat tolerance vary according to season and should be considered when comparing across studies. However, relative estimates of heat tolerance rankings among coral genotypes remain consistent regardless of seasonality (Cunning et al., 2021). Hence, short-term acute heat stress assays provide a flexible and rapid approach to estimate heat tolerance for many individuals, populations and species, over much greater temporal and spatial scales than previously possible.

To understand the drivers of heat tolerance and improve forecasting for how coral assemblages will respond to future marine heatwaves, we quantified the spatial patterns of heat tolerance in three scleractinian coral species (*Acropora* cf *humilis*, *Pocillopora verrucosa*, and *Pocillopora meandrina*) across nine widely separated populations in the Coral Sea Marine Park (CSMP), Australia. Coral populations spanned 7.7 degrees in latitude (860km) along a 1.6°C gradient in maximum monthly mean (MMM) sea surface temperatures, providing a range of environmental conditions to investigate possible drivers of heat tolerance. The isolated nature of reefs in the CSMP makes it an ideal system to investigate the possibility of local adaptation in heat tolerance, where the distance between reefs is likely to limit gene-flow between populations and where reefs are removed from other anthropogenic stressors (e.g., poor water quality). To investigate possible drivers of phenotypic variation in heat tolerance, we compared spatial patterns of relative heat tolerance against trends in sea surface temperatures and the occurrence of marine heatwaves, consistent with local adaptation mediated by changing environmental conditions.

2 | METHODS

2.1 | Coral species and sampling locations

The Coral Sea Marine Park (CSMP) is a critically important and significant ecosystem owing to its unique marine biodiversity and habitats (Ceccarelli et al., 2013). This seascape is characterised by isolated reef atolls with fauna distinct from that of the Great Barrier Reef (GBR). The geographic isolation of this reef system contributes to the genetic separation from Australia's GBR and other western Pacific biogeographic provinces (Payet et al., 2022; van Oppen et al., 2008), as well as isolation from local anthropogenic stressors. We collected colony fragments from three species of scleractinian corals from nine reefs in the CSMP between February 16 and March 12, 2020 (Figure 1a). *A.* cf *humilis* (Dana, 1846; Figure 1b) is a digitate coral species, susceptible to heat stress and commonly found on exposed upper reef slopes (Hoogenboom et al., 2017). This species is denoted with "cf" as coral samples most closely resemble *Acropora humilis*, but we acknowledge that the complexities and rapidly changing taxonomy within the family Acroporidae may indicate multiple cryptic species are present in the collection (Cowman et al., 2020). *P. meandrina* (Dana 1846; Figure 1c) and *P. verrucosa* (Ellis & Solander, 1786; Figure 1d) are both branching corals, distinguished by restriction fragment length polymorphism (RFLP) assays (Johnston et al., 2018), both characterised with a moderate heat sensitivity and commonly found in shallow waters in exposed and sheltered environments (Al-Sofyani & Floos, 2013). All three species are abundant in shallow habitats on reefs in the CSMP.

We observed a high incidence of coral bleaching over the course of sampling, owing to a severe marine heatwave in the CSMP in 2020. Sampled corals had therefore experienced 5.7–10.0 degree heating weeks (°C-weeks) and exhibited different levels of bleaching prior to collection (Table 1). To account for the accumulated heat stress at each sampling location, we recorded the maximum DHW on the day each experiment took place (NOAA Coral Reef Watch 5 km product, Table 1) and accounted for the effects of the experiments coinciding with a marine heatwave in all statistical analyses.

2.2 | Sample collection and processing

All samples were collected on SCUBA at an average depth of 8.0±2.7 m, ranging between 1.9 and 16.4 m. Due to the ongoing bleaching event, we sampled colonies of all bleaching categories to avoid biasing collections toward bleached or unbleached coral colonies (SOM, Figure S1). During collection, each colony was assessed visually for bleaching from most bleached "1" to least bleached "6" using a Coral Watch Health Chart. Each coral colony was then photographed at three scales in the field, recording (1) the unique bag identification number, (2) the whole colony and surrounding habitat with coral health chart, and (3) a detailed close-up of the colony. Coral fragments were collected from coral colonies >5 m apart to minimise the likelihood of collecting identical genotypes. We collected five fragments from each colony; four were used in the heat stress experiment and the fifth was preserved in 100% ethanol for genetic analyses.

2.3 | Experimental aquaria design and setup

The portable experimental aquaria system (National Sea Simulator, Australian Institute of Marine Science) consists of independent heating, lighting, sump and flow control elements. The system has four independent treatments with three 14 L custom-made acrylic tanks per treatment, with space for 24 coral fragments in each tank (72 per treatment). Each treatment has independent custom lighting

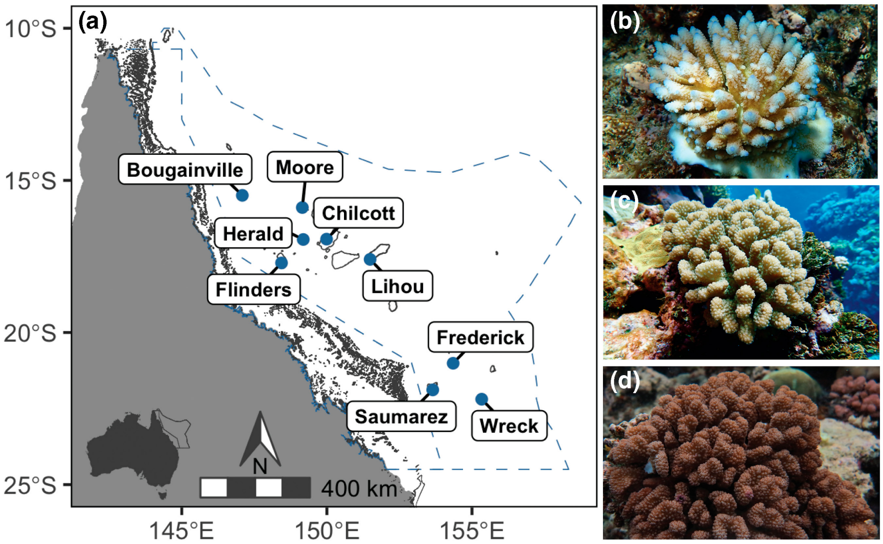

FIGURE 1 Map showing the location of the nine sampled reefs within the Coral Sea Marine Park (CSMP) (a). Coral fragments of each of the three coral species were collected from nine reefs between February and March 2020. The dashed line indicates the boundary of the CSMP. The three sampled coral species, *Acropora* cf *humilis* (b), *Pocillopora meandrina* (c), and *Pocillopora verrucosa* (d) are common on reefs throughout the CSMP. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

TABLE 1 Location and environmental conditions where corals were collected for acute heat stress experiments in the Coral Sea Marine Park (CSMP). Ambient sea surface temperature (SST,°C) and degree heating weeks (°C-weeks) were measured at the time of each experiment. Maximum monthly mean temperature (MMM, °C) is defined for each reef as the average SST of the hottest month in each year between 1986 and 2010. Number of DHW4 events is measured as the number of events above 4°C-weeks (1986–2020), averaged among sites within a reef. The number of corals of *Acropora* cf *humilis*, *Pocillopora verrucosa*, and *Pocillopora meandrina* collected from each reef that were included in the logistic regression model

Experiment location	Lat (DD. dddd)	Long (DD. dddd)	Ambient SST (°C)	MMM (°C)	DHW (°C-weeks)	*A.* cf *humilis* (*n* = 182)	*P. meandrina* (*n* = 101)	*P. verrucosa* (*n* = 93)
Bougainville	−15.4927	147.0863	29.99	28.96	10.00	23	10	17
Moore	−15.8921	149.1535	30.45	28.83	9.06	20	17	10
Chilcott	−16.9315	149.9898	29.93	28.59	6.65	18	10	3
Herald	−16.9434	149.1856	29.93	28.59	7.96	18	5	11
Lihou	−17.5970	151.4895	30.48	28.44	7.72	32	6	18
Flinders	−17.7135	148.4371	30.67	28.64	6.58	30	5	26
Frederick	−21.0113	154.3504	29.98	27.77	7.01	17	13	2
Saumarez	−21.8861	153.6476	29.63	27.90	5.50	–	22	–
Wreck	−22.1926	155.3340	29.55	27.41	5.71	24	13	6

panels (600 × 340 mm, 300 W white/blue LED) situated at a height of 650 mm above the tanks, heating elements (Omega 2 kW titanium) in the sump, and submersible pumps (Reefe RP2400LV 24v) to circulate water between the sump and insulating jackets (SOM, Figure S2a). Ambient seawater is directed through a titanium heating coil (Wateco 56″ titanium heat exchanger) to the corresponding tanks in each treatment. Water flow to each tank was kept constant throughout each experimental heat stress assay (0.2 L min^{-1}). Tanks were equipped with a powerhead to increase water circulation within each tank. Lights were adjusted to maintain 600 PAR (mmol photons.m^{-2} s^{-1}) per tank as per average, mid-day summer light levels at 10 m at Lizard Island Research Station between 2012 and 2018 (Australian Institute of Marine Science, 2020).

Each tank, sump and jacket are equipped with independent water temperature sensors and two PAR sensors situated randomly within tanks to monitor and control temperature and lighting throughout the experiment. The temperature control system consists of three main elements: (1) a Programmable Logic Controller (PLC) system (Siemens S7 1511–1 PN PLC, 6ES7 511-1AK02-0AB0), (2) a Weidmuller UR20 Remote IO Signal Inputs and Outputs, and (3) a Human Machine Interface (Siemens Simatic Human Machine Interface (HMI) KTP700 (6AV2123-2GB03-0AX0)). The PLC unit controls the lighting, pumps and heaters, interfacing with user parameters of the HMI to program parameter inputs, and to monitor and log temperatures in each tank.

2.4 | Experimental design of acute heat stress assays

We conducted individual experimental acute heat stress assays for each of the nine reefs where corals were collected. The planned experimental assay consisted of four temperature treatments: a control temperature treatment at the local MMM, and three temperature treatments at +3°C, +6°C and +9°C above the local MMM. The local MMMs were calculated using sea surface temperature data obtained from the NOAA Coral Reef Watch Operational Daily Near-Real-Time Global 5-km Satellite Coral Bleaching Monitoring Product Version 3.1 for each site within reef between 1986 and 2010. However, ambient temperatures were 1.0–2.2°C above local MMMs at the time of the experiments owing to a marine heatwave in the CSMP (Table 1), so the control treatments were done at ambient temperatures. Elevated temperature treatments (+3, 6 and + 9°C) were defined relative to the MMM. A fragment of each sampled coral colony was placed randomly into each of the four temperature treatments following each collection dive. All genotypes across all species were present in each of the four treatments, and randomly placed in one of the three replicate tanks per treatment to minimise the effect of tank. Each coral fragment was identified by a unique clip and rack number corresponding to the original coral colony. Coral samples were held at local ambient temperatures until the start of each experiment, which started between 8 am and 10 am.

Each treatment followed a standardised temperature profile previously established by Barshis et al. (2013), Palumbi et al. (2014), and Voolstra et al. (2020), to measure heat tolerance in corals. It consisted of a 3-h ramp up to the desired treatment temperature, a 3-h hold period at the treatment temperature and a 1-h ramp down to ambient temperature (SOM, Figure S2b). The treatment temperature of each sump was randomised between experiments to control for any variability in ambient light among tanks. At the end of the temperature profiles, corals were maintained at ambient temperature for 11 h prior to physiological measurements. This 11-h post-heat stress sampling time point differs from other recent studies that sample immediately after ramping down from heat stress, though it has no effect on measures of photochemical yield (Nielsen et al., 2022).

2.5 | Measuring photochemical yield

We used pulse amplitude-modulated (PAM) fluorometry to measure photochemical yield (hereafter F_v/F_m), a non-obtrusive metric of chlorophyll-*a* fluorescence of the symbiotic algae (Schreiber, 2004) widely used as a proxy to rapidly measure heat tolerance in corals (Evensen et al., 2021; Nitschke et al., 2018; Suggett & Smith, 2011). Following the completion of the temperature profiles, experimental tanks were covered with a tarp to block all light for a minimum of 5 h. All measurements took place under indirect red light between 2 am and 5 am using a Diving-PAM fluorometer (Heinz Walz GmbH, Effeltrich, Germany). A clear piece of tubing was used to maintain a constant distance (2 mm) between the fibre-optic probe (6 mm Ø) and the coral tissue. PAM settings were adjusted between experiments to account for the latitudinal gradient in light and temperature and maintain baseline F_0 values between 130 and 500 units following standard procedures (Ralph et al., 2015). Detailed PAM settings for each experiment are outlined in SOM Table S1.

The photochemical yield of all coral fragments in all temperature treatments was measured three times to obtain average and median measures of F_v/F_m. False readings, where no fluorescence was measured, were discarded prior to averaging.

2.6 | Species identification in Pocilloporidae

Species of *Pocillopora* can be difficult to distinguish in situ and from photographs, therefore all *Pocillopora* samples were identified to species level using an RFLP assay modified from (Johnston et al., 2018). Firstly, the mitochondrial open reading frame (mtORF) region was amplified with FatP6.1 primer (5′-TTTGGGSATTCGTTTAGCAG-3′) and RORF primer (5′-SCCAATATGTTAAACASCATGTCA-3′) (Flot et al., 2008). The PCR mix included 0.4 μl MyTaq Polymerase (5 units.μl^{-1}, Meridian Bioscience), 4 μl Buffer (5×), 0.3 μl Purified BSA (100×, New England Biolabs), 0.25 μl of each primer (10 mM), 13.8 μl of PCR-grade water and 1 μl of template DNA (5 ng μl^{-1}). PCR conditions were carried out with an initial denaturation step for 60 s at 94°C, followed by 30 cycles of 94°C for 30 s, 53°C for 30 s, and 72°C for 75 s, followed by a final elongation step at 72°C for 5 min. Secondly, PCR products were digested using one of two enzymes to confirm the species identity of each sample. The *Aci*I restriction enzyme was first used to distinguish *P. verrucosa* from all other species, and *Sac*I to distinguish *P. meandrina* from other Pocilloporidae. A volume of 8.9 μl of the PCR product was transferred to a new 96-well plate and 1.1 μl of *Aci*I restriction enzyme and buffer (New England Biolabs) was added to each sample. Samples were then incubated at 37°C for 60 min and transferred to 65°C for 20 min. The digest was run on a 2% agarose gel for 75 min at 70 V. Samples with three bands at 209, 338, and 431 base pairs were identified as *P. verrucosa*, with other species having only two bands at 430 and 548 base pairs. Any remaining samples that were not identified as *P. verrucosa* were then digested using *Sac*I to distinguish *P. meandrina* from other Pocilloporidae. A volume of 8.95 μl of PCR product was transferred to a new 96-well plate and 1.05 μl of *Sac*I restriction enzyme and buffer (New England Biolabs) was added to each sample. Digestions followed the same protocol as above. Samples with two bands at 298 and 680 base pairs were identified as *P. meandrina* and samples with only one band at 978 base pairs were identified as *Pocillopora* spp. From the 243 total collected *Pocillopora*, 49 samples were identified as neither *P. verrucosa* nor *P. meandrina* and thus excluded from downstream analyses.

2.7 | Modelling ED50 parameters for species and reefs

All analyses were performed in R v. 4.1.1 (R Core Team 2021) and are fully reproducible online (Appendix S1; https://github.com/HugoBH/CoralSea-ED50-GCB; publicly archived on https://doi.org/10.5281/zenodo.7145578). To determine how heat tolerance varied among species or sampled reefs, we fit a dose response curve to the median yield of F_v/F_m across temperature treatment and compared the effective temperature to induce a 50% loss in median yield of F_v/F_m (hereafter ED50). It is comparable to the ED50 metric presented in Evensen et al. (2021) and applied to other rapid heat stress experiments (Cunning et al., 2021; Evensen et al., 2022; Voolstra et al., 2021). We first removed any measurements where F_v/F_m values >0.75 or where F_0 was <110 to eliminate any false detections of the Diving PAM. For all ED50 estimate models, median yield was modelled against temperature relative to local MMM (°C) using a three-parameter dose response curve. Relative temperature was treated as a continuous variable and measured as the difference between the average temperature during the 3-h hold period, and the local MMM (SOM, Table S2). All ED50 models were first constructed using the *drm* package to obtain reasonable starting coefficients (Ritz et al., 2015), which were then used to fit models in the *nlme* package v3.1–152 to account for random effects (Pinheiro et al., 2021). Model selection was informed by comparing AICc scores in the *MuMIn* package version 1.43.17 (Barton, 2022) and post-hoc comparisons among fixed factors were performed using the *emmeans* package version 1.6.3 (Lenth, 2021).

To derive relative estimates of ED50 among the three coral species, we explored the importance of including parameter estimates for the slope, upper asymptote, and inflection point, as well as the influence of sampling depth, tank effects, and the severity of in situ bleaching of each coral colony. Lower asymptotes were fixed at zero. Model selection indicated all three parameters varied among species, with a small but non-negligible influence from the bleaching condition, but not depth or tank (SOM, Table S3). The best model included the interaction between “Bleaching Category” and “Species” for each parameter estimate of the dose response curve (SOM, Figure S3) and the random effect of “Reef” to capture variability in responses that could be attributed to spatial variation. Plots of model residuals were visually inspected to check for patterns with respect to fitted values and predictor variables. Post-hoc comparisons among fixed factors (“Species,” “Bleaching Category”) were conducted to compare whether ED50s were significantly different among species (SOM, Tables S4 and S5).

Separate models were constructed to derive estimates of ED50 among reefs since all species were not sampled at every reef. Model selection again included estimates for the slope, upper asymptote, and inflection point. Models were first run on the *A.* cf *humilis* data, which was the most comprehensive and informed which variables were used as predictors of each parameter in the dose response curve. The *A.* cf *humilis* model structure was then kept consistent for the other two species models (SOM, Table S6). The best fit model included the fixed factor of "Reef" for the ED50 term and random effect of "Bleaching Category" on the upper asymptote and "Coral ID" on the ED50 parameter. To check the effect of unbalanced sample design, we tested the "separate" reef models against a "combined" model that incorporated all species but only with reefs in common between all three species. Estimates of reef ED50 values were comparable between models (SOM, Figure S4). Post-hoc comparisons among fixed factors ("Reef") were conducted to compare whether ED50s were significantly different among reefs (SOM, Tables S7–S9). ED50 values were also calculated for "Absolute Temperatures" for each reef and species combination (SOM, Table S11) as an extension of the "Relative Temperature" ED50 model values presented in the results (SOM, Table S10). To obtain "Absolute Temperature" thresholds, we added the local MMM of each reef to the Relative ED50 of each reef.

2.8 | Environmental predictors of heat tolerance

To identify environmental drivers associated with coral heat tolerance, relative ED50 values derived from the Reef and Species models were related to a range of environmental predictors in the CSMP. These 24 environmental parameters represent recent (2016–2020) and historical (1986–2020) trends in the frequency and severity of marine heatwaves and sea surface temperatures in the CSMP (SOM, Table S12). The sea surface temperature and maximum degree heating weeks (DHW) values were generated from the NOAA Coral Reef Watch Operational Daily Near-Real-Time Global 5-km Satellite Coral Bleaching Monitoring Product Version 3.1 for each site within reefs from 1986–2020. These were used to calculate metrics that represent the temperature regimes and history of reefs in the CSMP. These included the historical (1986–2020) and recent (2016–2020) maximum and average DHW, the number of events where DHW was equal to or above 2, 3, 4, 6, 8 and 9°C-weeks (1986–2020), the average return time in years between these events, the DHW during the experiment, along with latitude and longitude (SOM, Figure S5). Each environmental predictor was individually fitted against relative ED50 values measured for each reef within species to assess the strength of their correlation. All predictors with a correlation coefficient below 0.40 were removed from further candidate model selection (SOM, Figure S6). This left 10 remaining variables of interest, which were each tested for collinearity. Any variables with a correlation >0.80 were excluded from further analysis, including "minSST," "meanSST," "DHW2020," "MMM," "Latitude," and "rangeSST" (SOM Table S12, SOM Figure S10). After removing highly collinear variables, this left four variables to represent the different climatic regimes between reefs: the number of events were DHW exceeded 4 ("DHW4"), the average maximum DHW between 2016 and 2020 ("recent.maxDHW"), the return time in years between events were DHW exceeded 6 DHW ("returnDHW6"), and the variance in SST ("varSST") (SOM, Figure S7). These response variables were tested in candidate model selection using the "dredge" function in the package *MuMIn* (Barton, 2022) and the model with the lowest AICc score was chosen. The final model included an interaction between Species and "DHW4," and additional fixed effects of "returnDHW6" and "recent.maxDHW" (SOM, Table S13). Results from the "dredge" model were cross validated with generalised boosted models (GBM) approach (Greenwell et al., 2022). While the GBM approach did not reach a parsimonious solution due to limited sample size, the results corroborated the importance of the number of mild bleaching events ("DHW4") as the strongest driver of increased ED50 values.

To consider the effects of MMM on ED50 and its interaction, the environmental predictor models were also tested against absolute ED50 values using the same above methods for relative ED50s. Candidate environmental variables were selected using the same criteria, with the exception that predictors with correlation coefficient below 0.30 were removed from further candidate model selection due to the lower overall correlation to absolute ED50 values (SOM Figures S11–S14). The final model included the fixed effects of "Species," "MMM," "recent.maxDHW," and "returnDHW6" (SOM, Table S14).

3 | RESULTS

3.1 | Photochemical performance under natural heat stress

Our experiments were conducted during a severe marine heatwave in the CSMP that led to widespread coral bleaching throughout the region. Accumulated heat stress ranged from 5.7°C-weeks (Wreck Reef) to 10.0°C-weeks (Bougainville Reef), with ambient water temperatures between 1 and 2.2°C above local MMM at the time of sampling (Table 1). The marine heatwave was ongoing and analysis of SST and DHW over the subsequent months suggests the experiments were conducted at the peak of this event. We collected 182 *A.* cf *humilis* and 194 *Pocillopora*, identified as 101 *P. verrucosa* and 93 *P. meandrina* across all categories of bleaching (SOM, Figure S8) from nine reefs in the CSMP. Fluorescence analysis using PAM fluorometry of coral fragments kept at ambient temperature indicate a minor loss in photochemical yield at higher levels of bleaching (Contrast Category 1–2 vs 3–6), consistent with natural levels of heat stress (SOM, Figure S9). We accounted for minor effects of natural bleaching by including the Bleaching Category as an interaction for estimates in ED50 values for both species and reef predictions (see Section 2.7).

3.2 | Photochemical performance under acute heat stress

We measured F_v/F_m of coral fragments across different temperature treatments to determine the tolerance of species and reefs to acute heat stress. Temperature treatments were maintained at ambient temperatures (29.55–30.67°C), and + 3°C, +6°C and + 9°C from local MMM (27.41–28.96°C). Temperatures exhibited some variability within and between experiments, though closely matched target temperatures (SOM, Table S2).

A greater inhibition of photochemical yield at the higher temperature treatments was observed as anticipated, reflecting the decline in F_v/F_m in response to increased temperature. We observed a median F_v/F_m yield of 0.61 (±0.06) for fragments maintained at ambient temperatures. Relative to controls, we observed a 1.3% increase in F_v/F_m in the +3°C treatment (median yield: 0.62 ± 0.05). At +6°C, F_v/F_m decreased by 11.8% relative to controls (median yield: 0.55 ± 0.11) with high levels of variation among coral colonies. At +9°C, F_v/F_m decreased by 86.0% relative to controls (median yield: 0.09 ± 0.09).

3.3 | Heat tolerances (ED50) among species and reefs

The effective temperature to induce a 50% loss in F_v/F_m (ED50) was used to compare heat tolerance among three species of corals and among reefs within species. Overall, we measured a 0.69°C range in ED50 between the most and least tolerant species (Figure 2a). For *A.* cf *humilis*, a 50% reduction in F_v/F_m was observed at 7.05°C above MMM (95%CI: 6.75–7.35) compared to 7.42°C above MMM in *P. meandrina* (95%CI: 7.11–7.74), and 7.74°C above MMM in *P. verrucosa* (95%CI: 7.43–8.06). *A.* cf *humilis* had significantly different heat tolerance than either *Pocillopora* species, with an ED50 0.69°C lower than *P. verrucosa* ($t = 9.067$, df = 1148, $p < .001$) and 0.37°C lower than *P. meandrina* ($t = 4.914$, df = 1148, $p < .001$) (SOM Table S5). Within *Pocillopora*, ED50 was 0.32°C greater in *P. verrucosa* than in *P. meandrina* with Tukey's pairwise comparison indicating the difference in heat tolerance between closely related species was significant ($t = 3.733$, df = 1148, $p = .006$) (SOM Table S5).

Heat tolerance also varied amongst reefs within species whereby the range of ED50 values was greater between the most and least tolerant reefs than it was between species (Figure 2b). In *A.* cf *humilis*, we measured a 1.89°C range in ED50 between the lowest value measured at Herald Reef (ED50 = 6.37, 95%CI: 6.14–6.59) and highest value at Wreck Reef (ED50 = 8.26, 95% CI: 8.08–8.43). In *P. meandrina*, there was a 1.15°C range in ED50 between the lowest value measured at Lihou Reef (ED50 = 6.96, 95%CI: 6.61–7.31) and highest value at Flinders Reef (ED50 = 8.11, 95% CI: 7.81–8.42). In *P. verrucosa*, we measured a 0.85°C range in ED50 between the lowest value measured at Herald Reef (ED50 = 7.26, 95%CI: 7.01–7.51) and Flinders Reef (ED50 = 8.11, 95% CI: 7.93–8.28). Though spatial patterns were not entirely consistent between species, some reefs showed significantly higher (e.g., Wreck Reef) or lower (e.g., Herald Reef) heat tolerance (Tukey's pairwise comparisons: Tables S7–S9).

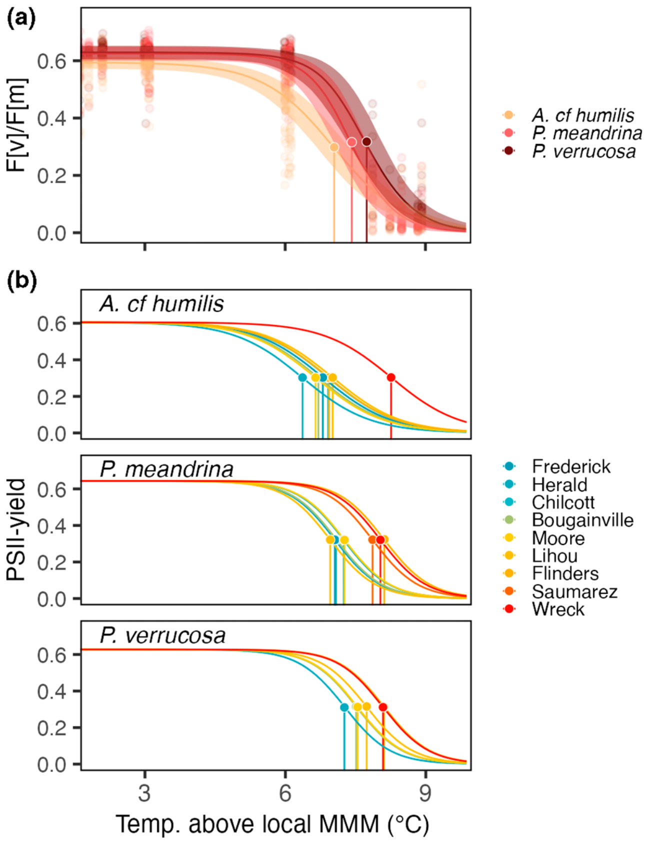

FIGURE 2 Temperature above local maximum monthly mean (MMM, °C) at which 50% loss in F_v/F_m occurs (ED50) for three coral species. (a) Phenotypic variation in heat tolerance among species measured throughout the Coral Sea Marine Park (CSMP). Points indicate measures of F_v/F_m for individual coral genets in each treatment. Confidence bands indicate 95% confidence intervals. (b) Phenotypic variation in heat tolerance among reefs for each species. Color represents samples collected from distinct reefs in the CSMP. Reefs are sorted by color from lowest ED50 values (blue) to highest (red) averaged across species. Vertical lines indicate the temperature above MMM to induce 50% loss in F_v/F_m (ED50).

3.4 | Predictors of heat tolerance

Spatial variation in ED50 values (Figure 3a) was explored against environmental variables that reflect the temperature regimes and exposure to temperature anomalies of reefs in the CSMP. A linear model that included three long-term and short-term thermal history metrics resulted in the best prediction of ED50 (SOM, Table S13). These environmental predictors included (1) the number of mild heatwaves above or equal to 4°C-weeks from 1986 to 2020 at each sampled reef (nDHW4), (2) the average maximum DHW experienced from 2016 to 2020 (recent maxDHW), and (3) the return time in years between heatwaves above or equal to 6°C-weeks (return DHW6). The model's total explanatory power was substantial ($R^2 = .81$). Species, the number of mild heatwaves (nDHW4) and their interaction explained 62.0% of model variance, while recent maximum DHW explained 21% of variation (recent maxDHW), and

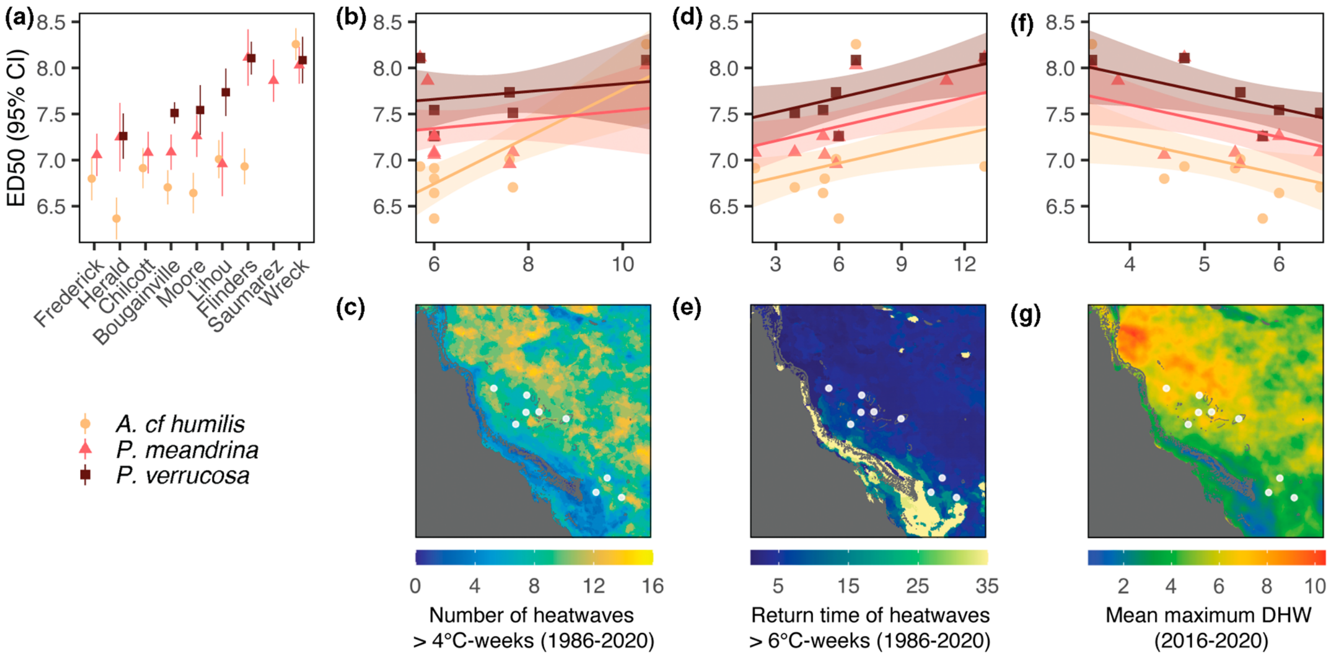

FIGURE 3 Spatial heterogeneity in relative heat tolerance (ED50) among reefs in the Coral Sea Marine Park (CSMP) is strongly associated with their exposure to the number of mild marine heatwaves. (a) Heat tolerance as measured by the temperature above local MMM to induce a 50% loss in F_v/F_m (ED50) varies between species and between isolated reefs in the CSMP. Reefs are sorted by lowest ED50 values (left) to highest (right) averaged across species. Estimated marginal means of three environmental predictors (b, d, f) while other parameters are held constant. (b, c) The number of marine heatwaves between 1986 and 2020 where DHW was above or equal to 4 was the best predictor of heat tolerance (ED50) of reefs in the CSMP. (d, e) The return time between heatwaves where DHW was above or equal to 6 between 1986 and 2020 also explained sufficient variation in heat tolerance of reefs in the CSMP. (f, g) The average maximum DHW between 2016 and 2020 was the third environmental predictor to explain variance in heat tolerance. Each of the three predictors vary spatially across the seascape (c, e, g), including at the nine reefs where heat tolerance was quantified experimentally and depicted as white points.

the return time between more severe heatwaves (return DHW6) accounted for 17% of variation. Other interactions among predictors were explored and none improved the model. Other variables, including reef complexity, longitude, reef area and a range of thermal history metrics (SOM, Figure S5) were either poorly correlated or insufficient to explain the spatial variation in heat tolerance.

The relative heat tolerance of all three species was most strongly driven by the number of mild heatwaves, the strength of which varied among species (Figure 3b) and for which spatial patterns were highly heterogeneous throughout the CSMP (Figure 3c). The strongest effect was observed for *A.* cf *humilis* whereby each mild heatwave increased ED50 by 0.25°C (Slope = 0.255, $t = 4.2$, $p < .001$). The effect was weaker and not significantly different from 0 for both *P. meandrina* (Slope = 0.048, $t = .83$, $p = .42$) and *P. verrucosa* (Slope = 0.042, $t = 0.61$, $p = .55$) (SOM, Table S13), although these were different to *A.* cf *humilis* ($t = 2.6$, $p = .05$). Overall, greater exposure to mild heatwaves resulted in higher estimates of heat tolerance as measured by ED50 only in *A.* cf *humilis*. Meanwhile, greater exposure to higher DHW values between 2016 and 2020 had an effect of decreasing ED50 values (Figure 3d-e; Slope = −0.176, $t = -2.3$, $p = .04$), and higher intervals between more severe heatwaves (≥6°C-weeks) had the effect of increasing ED50 values (Figure 3f,g; Slope = 0.053, $t = 2.4$, $p = .03$). One data point, corresponding to the ED50 value for *A.* cf *humilis* at Wreck Reef, was highly influential in the model (Cook's D > 0.8; Figure 3b) indicating a possible outlier. However, ED50 values were consistently high for all three species (SOM, Table S10), and may be more indicative of the extremely high exposure to mild heatwaves between 1986 and 2020 ($n = 11$). In addition, ED50 for both Pocilloporidae at Flinders Reef appeared high given the low exposure to mild heatwaves ($n = 5$; SOM, Table S10), which may be indicative of other factors not captured in our models.

4 | DISCUSSION

4.1 | Acute heat stress experiments identify phenotypic variation in heat tolerance

Identifying spatial mosaics of heat tolerance across climatic and disturbance gradients is key to understanding the adaptive potential of corals to the increasing frequency of marine heatwaves. To date, smaller reciprocal transplant experiments have identified genetic mechanisms of the coral host (Drury & Lirman, 2021; Kenkel et al., 2013) and symbiont community structure (Marhoefer et al., 2021) that influence thermotolerance and signify local adaptation to thermal regimes, but also indicate limits for corals to respond to temperatures outside of their local conditions (Howells et al., 2013). Building on these principles, standardised acute heat stress experiments have qualified as high-throughput scans for phenotypic variation, successfully demonstrating that heat tolerance variation exists across coral nursery gardens in the Florida Keys (Cunning et al., 2021), thermally variable patch reefs across the Palau archipelago (Cornwell et al., 2021), and among microhabitats (Voolstra et al., 2020) and contrasting reef populations in the Red Sea (Evensen et al., 2022; Voolstra et al., 2021). The portability and automation of the acute heat stress experimental aquaria system (National Sea Simulator, AIMS) allowed us to quantify heat tolerance across a large spatial scale comprised of variable thermal history. Our findings provide further evidence that inter-reef differences in thermal tolerance broadly correspond with localised differences in thermal exposure. Thus, providing evidence that coral populations may be locally adapted to climate history, as well as the frequency and severity of marine heatwaves they have been exposed to.

4.2 | Phenotypic variation in heat tolerance among species within reefs

While knowledge of the mechanisms that confer heat tolerance in reef-building corals remains limited, experimental studies demonstrate the capacity for short-term acclimation (DeCarlo et al., 2019; Howells et al., 2013) and long-term adaptation in response to heat stress (Bay & Palumbi, 2014; Dixon et al., 2015; Drury, 2020; Drury et al., 2017; Kenkel & Matz, 2017). Such variability between species, particularly within the same environment, are typically associated with gene-based adaptation (Fuller et al., 2020; Morikawa & Palumbi, 2019) and/or variation in symbiont community structure (Oliver & Palumbi, 2011). In our experiments, three coral species were exposed to the same local environmental and experimental conditions yet, exhibited variable ED50 thresholds ranging up to 0.7°C. In the case of two closely related *Pocillopora* species (Johnston et al., 2017), the differences in heat tolerance may be attributed to variation in heat tolerance among symbionts, as *P. verrucosa* and *P. meandrina* are highly specific in symbiont community selection (Turnham et al., 2021), attributed to vertical transmission of symbionts to offspring (Hirose et al., 2000). Heat tolerance differences in these symbiont species can influence the ability of the host to respond to heat stress changes (Manzello et al., 2019), depending on the heat tolerance potential of the symbiont itself. Phenotypic variation within *A.* cf *humilis* may also be attributed to variation in symbiont species, although we could not exclude cryptic host speciation in the CSMP, as these samples have not been genetically confirmed as one species. The question of species identification may also lend itself to the broad range of ED50 values for *A.* cf *humilis* compared to the relatively narrow range for both species of *Pocillopora*, for which species identification has been confirmed. These questions require additional genetic studies to fully disentangle species level patterns of heat tolerance for *Acropora*.

4.3 | Spatial variation in heat tolerance

Oceanic islands have served as model systems to evaluate the drivers of species richness, assembly rules of ecological communities and adaptive speciation, and provide insights into ecological and evolutionary processes (Borregaard et al., 2017; Santos et al., 2016). The geographic separation of reefs in the CSMP and distinct thermal histories may promote phenotypic variation within species and adaptation to local thermal regimes, where limited gene flow can reinforce processes of genetic drift and natural selection in spatially heterogeneous environments (Kawecki & Ebert, 2004; Savolainen et al., 2013). Of the 24 environmental variables measured, three thermal history metrics were identified as possible drivers of heat tolerance of reefs, driving responses more than latitude, sea surface temperature, depth and the 2020 marine heatwave. Notably, the frequency of mild heatwaves in a local environment was a key driver of increased relative heat tolerance in *A.* cf *humilis*. Populations harboring the most heat tolerant corals (e.g., Wreck Reef) experienced historically higher frequency of mild heatwaves over the past 35 years. Conversely, reefs which have evaded a high frequency of mild heatwaves (e.g., Herald Reef) tended to harbor assemblages of less tolerant individuals. For corals, a critical tipping point for bleaching-induced mortality occurs when accumulated heat exceeds 3–4°C-weeks, indicating that DHW values above this threshold can influence population dynamics and the relative frequency of traits associated with heat tolerance (Hughes, Kerry, et al., 2018). *A.* cf *humilis* displayed a strong relationship to exposure to mild heatwaves, which may be linked to this species' higher sensitivity to heat stress. However, it is worth noting that the relationship between ED50 and mild heatwaves was predominantly driven by *A.* cf *humilis* at Wreck Reef. In addition to mild heatwaves, a longer return time between severe heatwaves above or equal to 6°C-weeks increased acute heat tolerance, likely allowing sufficient time for populations to recover from lasting effects of severe heatwaves.

The beneficial selection of mild heatwaves, as well as a longer return time between heating events, may be hampered by recent severe heatwaves over the past 5 years, as indicated by the strong effect of recent maximum DHW on acute heat tolerance (i.e., average maximum DHW between 2016 and 2020). The effect of recent severe marine heatwaves over this period is an indication that corals may not be able to keep up with the pace of rapidly reoccurring marine heatwaves. Rapid environmental change, such as three mass bleaching events in 5 years, does not support rates of phenotypic plasticity for most individuals and species (Lindsey et al., 2013). Further, the lack of correlation between severe heatwaves (i.e., number of DHW events exceeding 6 or 9°C-weeks) and higher heat tolerance, suggests significant limits to adaptation potential in corals above a threshold where bleaching-induced mortality occurs (Ainsworth et al., 2016). The lack of improved prediction may be due to severe heatwaves causing increased coral mortality of all genotypes, rather than acting as a selective pressure. A similar phenomenon was observed during the back-to-back bleaching events of 2016 and 2017 on the GBR and Coral Sea, where a reduction in the incidence of bleaching in 2017 was attributed to extensive bleaching-induced mortality of corals in

2016, leaving few corals left to bleach in severely affected reefs (Harrison et al., 2019; Hughes, Kerry, et al., 2018). Thus, mild heatwaves and local conditioning to MMM provide environmental pressure that is strong enough to select for heat tolerance but not too strong to decimate entire populations.

A case can be made to use absolute ED50 values to consider the effects of MMM on ED50 and its interaction with other environmental drivers. To do so, we would suggest having consistent temperature treatments across all sampled populations rather than standardised to local MMM (but see SOM for details).

4.4 | Global comparisons of ED50 thresholds

The relative and absolute ED50 values allow for direct comparisons within and between studies, overcoming a major challenge in comparing heat stress experiments (Grottoli et al., 2020; McLachlan et al., 2020). There are several applications for coral acute heat stress data. A few examples include the ability to rank heat tolerance among individuals, populations, and species; to investigate genotype–phenotype associations to identify molecular signatures of heat tolerance; and to explore cross-study comparisons of heat tolerance thresholds of corals. Coral populations experiencing historically higher temperature regimes are generally less susceptible to bleaching than conspecifics in other regions (Howells et al., 2016). However, the absolute ED50 thresholds for *P. verrucosa* in the CSMP were very similar to conspecifics in the Red Sea (Absolute ED50/ED50: CSMP = 36.1°C; Red Sea = 36.0°C) (Evensen et al., 2022), despite the hotter conditions in the Red Sea, 1.3°C above those in the CSMP. Interestingly, *P. verrucosa* in the CSMP maintained overall higher relative ED50s (i.e.,°C above local MMM temperatures) than *P. verrucosa* in the Red Sea by 1.2°C (Relative ED50/ED50: CSMP = 7.7°C; Red Sea = 6.3°C) when comparing averages across each reef to characterise a region. The relative tolerance of corals in the CSMP compared with corals in other regions may indicate that corals in the CSMP are not living as close to their thermal limits as predicted. Potentially, the high disturbance history of the past three decades, layered with episodic heatwaves experienced in the last 5 years in the CSMP (Harrison et al., 2019) has selected for more heat tolerant individuals. Across a latitudinal gradient, *P. verrucosa* in both this study and Evensen et al. (2022) maintained higher relative thermal thresholds in high latitude reefs compared to low-latitude reefs, supporting previous evidence that high latitude reefs may harbor higher heat tolerance and therefore serve as spatial refugia from bleaching events (Osman et al., 2018). These comparisons provide valuable insight to identify reefs and regions of high or low tolerance, albeit the comparisons across variable aquaria systems (e.g., lights, flow, and sampling time-points) may confound these interpretations and should also be considered.

5 | CONCLUSIONS

Coral populations in this study demonstrate extensive phenotypic variation in heat tolerance between distinct populations and across environmental gradients. We identified that thermal regimes are a clear driving force in heat tolerance, explaining spatial variation in heat tolerance among coral reef populations. The strong link between acute heat tolerance and the occurrence of marine heatwaves is evidence that coral populations are likely adapting or acclimatizing to both recent and long-term thermal history in their local environment. However, decreased coral heat tolerance in response to recent severe heatwaves warrants concern for the potential limits to adaptation and acclimation of coral populations within ecologically relevant timeframes.

AUTHOR CONTRIBUTIONS

Hugo B. Harrison, Line K. Bay, Magena R. Marzonie, and Josephine J. V. Nielsen designed the experiment. Magena R. Marzonie and Hugo B. Harrison conducted the field experiment. Hugo B. Harrison, Andrew S. Hoey and Line K. Bay provided funding for the experiment. Magena R. Marzonie and Josephine J. V. Nielsen performed laboratory assays for species identification. Hugo B. Harrison, Samuel Matthews, and Magena R. Marzonie analysed the data. Magena R. Marzonie and Hugo B. Harrison wrote the original draft of the manuscript. All authors contributed to critical review of the manuscript.

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CONFLICT OF INTEREST

All authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and scripts for heat stress experiments are publicly available on GitHub. The authors would appreciate being notified if you intend to use these data or analyses in your own work https://github.com/HugoBH/CoralSea-ED50-GCB. The primary data and scripts are also publicly archived on https://doi.org/10.5281/zenodo.7145578.

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SUPPORTING INFORMATION

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