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REPORT

Local habitat heterogeneity rivals regional differences in coral thermal tolerance

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Abstract Variable temperature regimes that expose corals to sublethal heat stress have been recognized as a mechanism to increase coral thermal tolerance and lessen coral bleaching. However, there is a need to better understand which thermal regimes maximize coral stress hardening. Here, standardized thermal stress assays were used to determine the relative thermal tolerance of three divergent genera of corals (*Acropora*, *Pocillopora*, *Porites*) originating from six reef sites representing an increasing gradient of annual mean diel temperature fluctuations of 1–3 °C day^{-1}. Bleaching severity and dark-acclimated photochemical yield (i.e., F_v/F_m) were quantified following exposure to five temperature treatments ranging from 23.0 to 36.3 °C. The greatest thermal tolerance (i.e., F_v/F_m effective dose 50) was found at the site with intermediate mean diel temperature variability (2.2 °C day^{-1}), suggesting there is an optimal priming exposure that leads to maximal thermal tolerance. Interestingly, *Acropora* and *Pocillopora* originating from the least thermally variable regimes (<1.3 °C day^{-1}) had lower thermal tolerance than corals from the most variable sites (>2.8 °C day^{-1}), whereas the opposite was true for *Porites*, suggesting divergent responses across taxa. Remarkably, comparisons across global studies revealed that the range in coral thermal tolerance uncovered in this study across a single reef (<5 km) were as large as differences observed across vast latitudinal gradients (300–900 km). This finding indicates that local gene flow could improve thermal tolerance between habitats. However, as climate change continues, exposure to intensifying marine heatwaves is already compromising thermal priming as a mechanism to enhance coral thermal tolerance and bleaching resistance.

Keywords Acclimatization · Coral reefs · Environmental variability · Extreme environments · Priming · Thermal tolerance

Introduction

Ocean warming due to anthropogenic greenhouse gas emissions is the greatest threat to the persistence of coral reefs in the Anthropocene (Hoegh-Guldberg et al. 2019). Reef-building corals live at the upper edge of their thermal limits, and persistent temperatures just 1 °C above a coral's typical summer maximum can cause the breakdown of the symbiosis between the coral and its endosymbiotic algae (family Symbiodiniaceae)—a phenomenon known as coral bleaching (Hoegh-Guldberg 1999; van Woesik et al. 2022). Marine heatwaves resulting in mass coral bleaching are now occurring globally on multi-decadal time-scales, having gone from up to one mild event a decade last century to as many as five per decade in modern times (Hughes et al. 2018). It has thus become increasingly important to identify thermally tolerant coral populations capable of surviving intensifying marine heatwaves. Encouragingly, coral populations with elevated heat tolerance have been found within various thermally extreme environments, such as

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mangrove lagoons and tidally-dominated reef flats, which expose inhabitants to short-term temperature extremes not predicted to occur on ordinary reefs until 2100 (Schoepf et al. 2015; Camp et al. 2019; Brown et al. 2023a). Lifelong exposure to high diel temperature variability has thus emerged as an important factor in promoting elevated coral bleaching thresholds (Oliver and Palumbi 2011a; Barshis et al. 2013; Palumbi et al. 2014; Kenkel and Matz 2016; Voolstra et al. 2020). However, we still lack a clear understanding of the priming exposure (e.g., magnitude of diel thermal variability) most beneficial for coral stress hardening (Hackerott et al. 2021), as not all variable temperature regimes maximize coral thermal tolerance (Schoepf et al. 2019; Klepac and Barshis 2022).

A comprehensive understanding of how environmental drivers influence coral thermal tolerance requires a direct comparison of coral genera with different life-history strategies (e.g., competitive versus stress-tolerant) (Darling et al. 2012) and evolutionary histories (Kitahara et al. 2010). For example, the same highly variable habitats that promote elevated thermal tolerance in competitive *Acropora hyacinthus* do not lead to elevated thermal tolerance in stress-tolerant *Porites lobata* (Palumbi et al. 2014; Thomas et al. 2018; Klepac and Barshis 2020). Similarly, across larger spatial scales, relative thermal tolerance is not predictable across corals with distinct life-history strategies. For example, competitive corals (*Acropora hemprichii*) were identified as the most thermally tolerant when compared to weedy (*Pocillopora verrucosa*; *Stylophora pistillata*) or stress-tolerant (*Porites lobata*) taxa across the Red Sea (Evensen et al. 2022), whereas across the Coral Sea (eastern Australia), competitive acroporids were the least thermally tolerant when compared to weedy species (*P. verrucosa; P. meandrina*) (Marzonie et al. 2022). Discrepancies may be due to experimental design (Grottoli et al. 2021), fine-scale differences in Symbiodiniaceae genotypes (Oliver and Palumbi 2011b), seasonality (Berkelmans and Willis 1999), and/or increasing history of severe heat stress that may compromise thermal priming as a protective mechanism (Schoepf et al. 2015; Ainsworth et al. 2016; Klepac and Barshis 2020). To accurately evaluate thermal tolerance and predict the impact of climate change on coral reef ecosystems, standardized comparisons across diverse species and environmental mosaics are critically needed (Voolstra et al. 2020; Grottoli et al. 2021).

Here, we employed a standardized experimental heat stress assay (e.g., Evensen et al. 2023) to determine the relative thermal tolerance of three coral genera across Heron Island, southern Great Barrier Reef (GBR). Corals were collected from six sites encompassing five distinct geomorphological habitats (Phinn et al. 2012), which differ in their diel thermal variability, fluctuating by up to 7.7 °C day^{-1} (Brown et al. 2023a). These ranges are comparable to other study systems across the globe, including the highly variable pools of Ofu, American Sāmoa (up to 6 °C day^{-1}) (Thomas et al. 2018), exposed and protected sites of the central Red Sea (up to 6.5 °C day^{-1}) (Voolstra et al. 2020), intertidal and subtidal environments of the Kimberley in western Australia (up to 7 °C day^{-1}) (Schoepf et al. 2015), and mangrove lagoons of the GBR (7.7 °C day^{-1}) (Camp et al. 2019). Corals representing three distinct life-history strategies and the two clades of Scleractinia were investigated—*Acropora* cf. *aspera* (competitive; Complexa), *Pocillopora* cf. *damicornis* (weedy; Robusta) and *Porites* cf. *lobata* (stress-tolerant; Complexa)—to explore if thermal priming results in consistent benefits across species. Thermal tolerance was compared to coral community resilience in the aftermath of a recent marine heatwave in 2020 (Brown et al. 2023a) to see if increased thermal tolerance is protective during modern marine heatwaves. Finally, this standardized experimental approach allowed us to compare coral thermal tolerance across a single reef to thermal tolerance across different reef systems encompassing vast spatial gradients.

Materials and methods

Study location

This study was conducted across six sites spanning less than 5 km at Heron Island, southern Great Barrier Reef (23° 27′ S 151° 55′ E; Fig. 1), which included at least one representative from each geomorphological habitat of Heron Reef (site; depth ± standard deviation): reef slope [Fourth Point (FP; 4.2 ± 0.72 m); Harry's Bommie (HB; 6.1 ± 0.82 m)], reef crest (RC; 0.9 ± 0.59 m), reef flat (RF; 0.7 ± 0.59 m), shallow lagoon (SL; 1.3 ± 0.74 m), and deep lagoon (DL; 2.6 ± 0.59 m) (Phinn et al. 2012) (Fig. 1). Photosynthetically active radiation (PAR) levels (μmol m^{-2} s^{-1}), averaged across the year-long period from August 2015 to September 2016, were lower within reef slope habitats (HB: 75.9, FP: 179.4) than within the lagoon habitats (RC: 199.2, RF: 371.7, SL: 201.8, DL: 198.8) (Brown et al. 2023a). Historically, hard coral cover has been greatest within the reef slope (~ 60%), which is dominated by corals of the family Acroporidae, whereas within the lagoon, sites have peaked around 20% coral cover and are principally composed of *Pocillopora* and massive *Porites* (Connell et al. 1997; Roelfsema et al. 2021; Brown et al. 2023a). Experiments were performed in the austral spring to avoid any potentially confounding thermal stress that is becoming increasingly common during the summer (Marzonie et al. 2022). While absolute thermal tolerance can differ across seasons (Berkelmans and Willis 1999), relative thermal tolerance between individuals across seasons remains consistent (Cunning et al. 2021; Evensen et al. 2022).

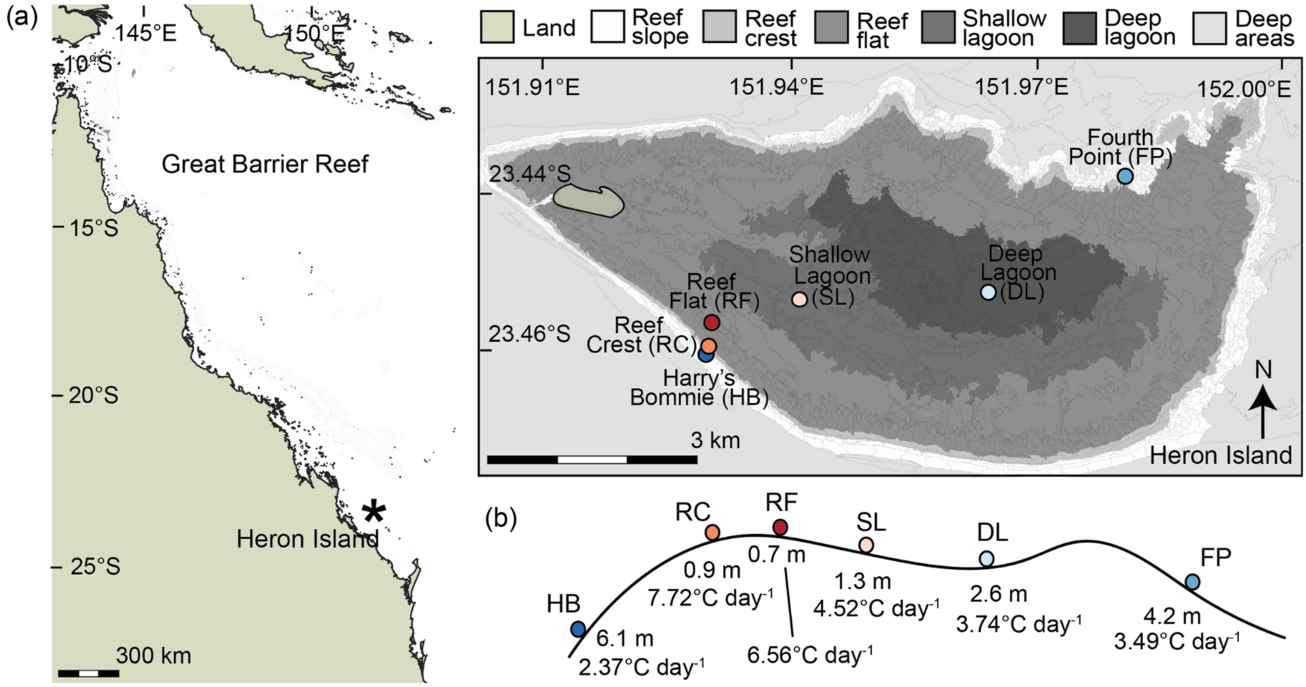

Fig. 1 Study location and reef profile of Heron Island, southern Great Barrier Reef. **a** Map of the Great Barrier Reef, with an asterisk showing the location of Heron Island. Map inset details the geomorphological habitats of Heron Reef, redrawn from the data of (Phinn et al. 2012), with sampling sites indicated. **b** Reef profile showing the depth and maximum diel temperature variability across the reef sites investigated in this study

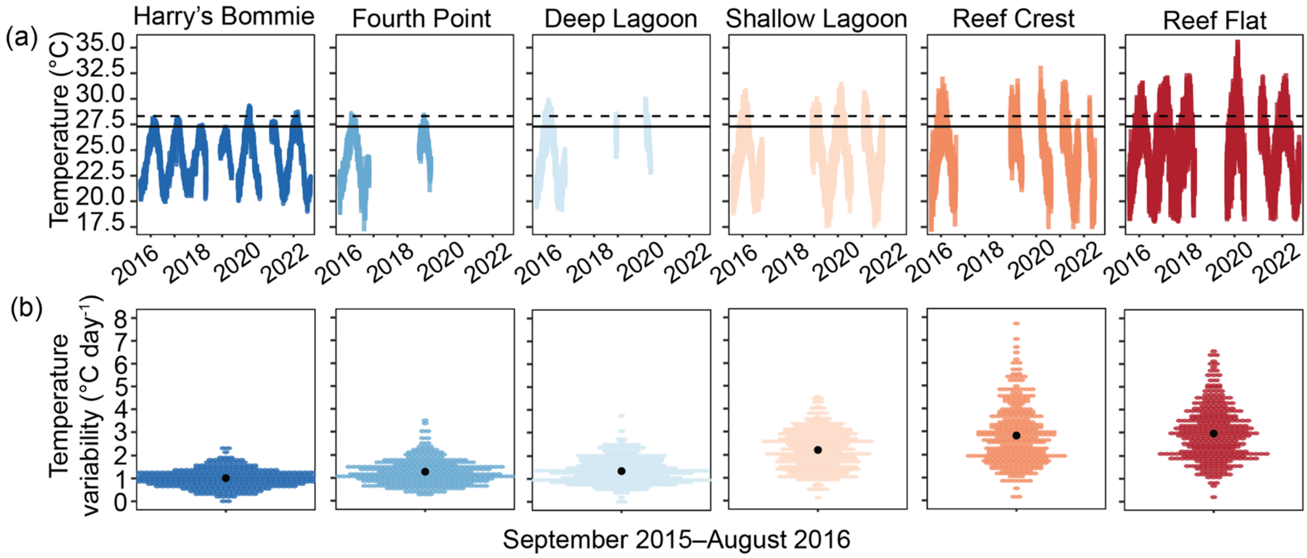

Fig. 2 Temperature profiles across Heron Reef from least to most thermally variable. **a** Hourly seawater temperatures were recorded from August 2015 to September 2022. Solid horizontal line indicates the region's climatological maximum monthly mean (MMM; 27.3 °C) and dashed horizontal line indicates the region's coral bleaching threshold (MMM + 1 °C; 28.3 °C). **b** Diel temperature variability across September 2015–August 2016, where individual points represent each day and the black point indicates the mean across the year

Evaluation of temperature variability

Seawater temperatures were recorded hourly from July 2015 to September 2022 (Fig. 2). From July 2015 to November 2016, seawater temperatures were recorded by use of conductivity temperature depth units (CTD; SBE 16plus V2 SEACAT) until their removal, at which time cross-calibrated HOBO Pendant loggers (HOBO UA-001-64, Onset Computer Corporation; accuracy: ± 0.552 °C at 25 °C) were deployed. Logger accuracy was assessed at the end of each deployment period using a water bath (Thermo Scientific Precision TSGP20). Temperature dynamics (e.g., mean, maximum, diel variability) were calculated at each site across the one-year period from September 2015 to August 2016, as this period included the most complete record across all sites and did not include a marine heatwave (Table 1).

Sample collection

Three morphologically distinct coral species with distinct life-history strategies were examined:

Acropora cf. *aspera* (competitive; branching open), *Pocillopora* cf. *damicornis* (weedy; branching closed), and *Porites* cf. *lobata* (stress-tolerant; massive) (Darling et al. 2012) (Fig. 3). Coral fragments were collected from 27 September to 6 October 2022 (Table S1). Ten colonies of each genus were sampled from each site except where noted ($n = 5$–10 colonies per species per site; Fig. 3). *Acropora* cf. *aspera* was not collected at the Shallow Lagoon and Deep Lagoon as it was absent or rare. Following collection, corals were transported to Heron Island Research Station (HIRS) and placed in outdoor, flow-through seawater troughs under ambient temperatures (22.86 ± 0.02 °C) until experimentation. Each colony was divided into five fragments (i.e., genetic clones) of ~ 5 cm using bone cutters (*Acropora* and *Pocillopora*) or a brick saw (*Porites*). *Acropora* and *Pocillopora* were then suspended within the experimental tanks using fishing line. *Porites* fragments were placed on plastic grating at the bottom of the experimental tanks. Coral thermal tolerance experiments were initiated within 3–48 h of collection (Table S1).

Acute heat stress experiment

A standardized temperature profile was used to measure heat tolerance in corals (e.g., Voolstra et al. 2020; Cunning et al. 2021; Marzonie et al. 2022; Evensen et al. 2023) with minor modification in temperature profiles. The climatological maximum monthly mean (MMM) of Heron Reef is 27.3 °C (Weeks et al. 2008). A pilot experiment with all three genera indicated no difference in F_v/F_m between MMM, MMM + 3 °C and MMM + 6 °C,

Table 1 Temperature metrics across Heron Island, southern Great Barrier Reef for the year-long period of September 2015–August 2016

Site	Geomorphological habitat	Yearly mean (°C)	Yearly minimum (°C)	Yearly maximum (°C)	Yearly amplitude (°C year^{-1})	Diel amplitude mean (°C day^{-1})	Diel amplitude minimum (°C day^{-1})	Diel amplitude maximum (°C day^{-1})	Degree heating weeks (2016)	Degree heating weeks (2020)
HB	Reef slope	24.40	19.76	28.31	8.55	1.01	0.00	2.37	0.00	5.60
FP	Reef slope	24.44	18.21	28.60	10.39	1.27	0.24	3.49	0.00	ND
DL	Deep lagoon	24.45	18.96	30.02	11.06	1.34	0.00	3.74	2.25	ND
SL	Shallow lagoon	24.91	18.74	30.90	12.16	2.22	0.13	4.52	2.26	7.51
RC	Reef crest	24.51	17.54	32.17	14.63	2.81	0.12	7.72	0.00	ND
RF	Reef flat	23.97	18.04	31.80	13.76	2.96	0.20	6.56	2.85	7.84

Sites are listed in order from least to most thermally variable and are indicated by abbreviation, where: HB = Harry's Bommie, FP = Fourth Point, DL = Deep Lagoon, SL = Shallow Lagoon, RC = Reef Crest, and RF = Reef Flat. ND indicates no data

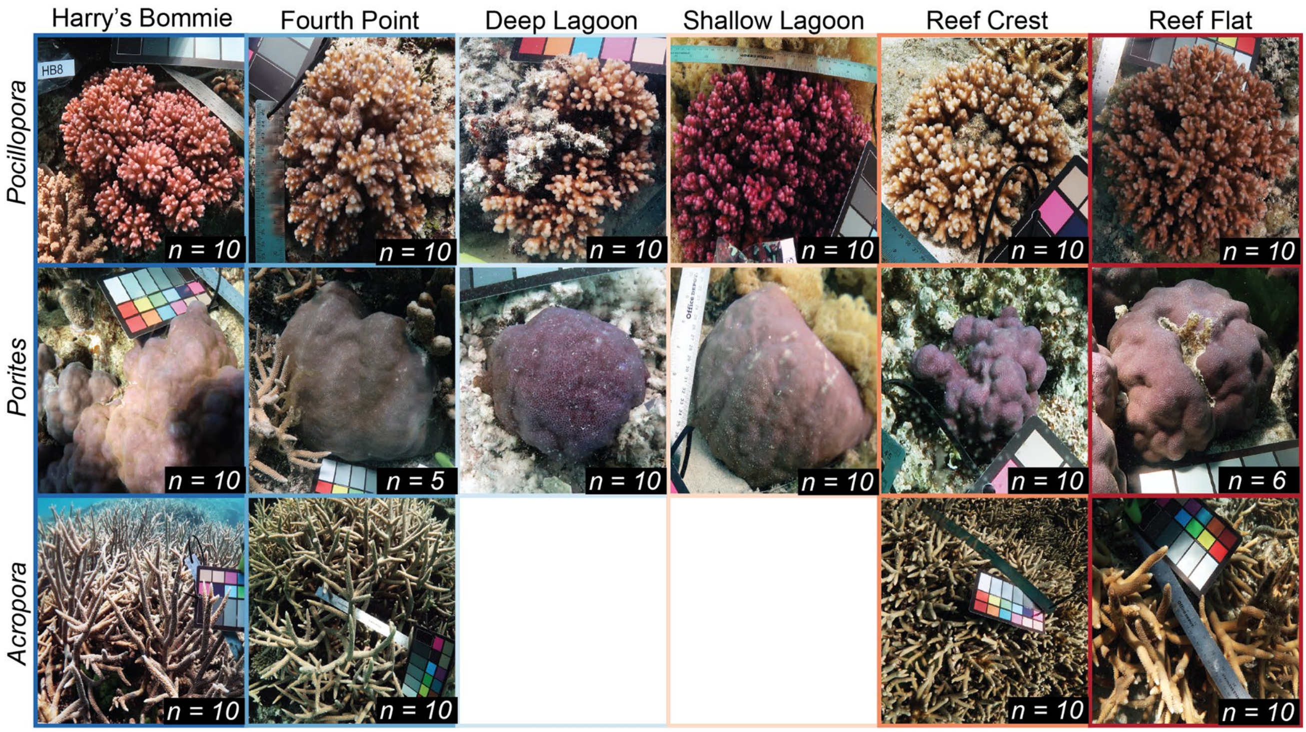

Fig. 3 Representative images of coral genera across sites at Heron Island, southern Great Barrier Reef. Inset indicates the number of colonies collected at each site. At the Deep Lagoon and Shallow Lagoon, *Acropora* was absent or rare so was not evaluated

so the latter two treatments were increased to more accurately assess the decline in performance, such that the five treatments used here included ambient, MMM, MMM + 4 °C, MMM + 6.5 °C, and MMM + 9 °C. Generally, experiments began at ~ 12:00 with a 3-h ramp to respective treatment temperatures (23 °C, 27.3 °C, 31.3 °C, 33.8 °C, 36.3 °C), a 3-h hold, and a 1-h ramp down to MMM (Evensen et al. 2023) (Figure S1). Lights were turned off at the onset of the 1-h ramp down to correspond with sunset. Due to experimental constraints (space, equipment, and time), only two treatments ($n = 1$ tank) were performed per day and each site was done in isolation. Accordingly, a complete assay took two days per site, with treatments tested each day selected randomly (Table S1, Fig. S1). A fragment from each coral colony was randomly placed into each treatment, so that all colonies were present in each treatment. Temperatures were controlled using an Apex controller (Neptune Systems). Apex temperature probes were calibrated against a high-precision temperature probe (HANNA HI-98190; accuracy: ± 0.4 °C at 25 °C; resolution: ± 0.10 °C) at the onset of the experiment. Temperatures were also recorded using cross-calibrated temperature loggers (HOBO UA-001-64, accuracy: ± 0.29 °C at 25 °C). Photosynthetically active radiation (PAR) was static and controlled using aquarium lights (NICREW HyperReef LED, Shenzhen NiCai Technology Co.), averaging 250 µmol m^{-2} s^{-1}.

Physiological responses to acute heat stress

At the end of the ramp and after 1 h of darkness (~ 19:00), corals were assessed for dark-adapted photochemical yield (F_v/F_m) using a Diving-PAM (Walz GmbH) 5-mm diameter fiber-optic probe at a standardized distance (5 mm) above the coral tissue after F_o stabilized. Two random spots on either side of a single fragment were measured to obtain average measures of F_v/F_m. All readings with F_o values that were less than 110 were removed to avoid any false detections (Marzonie et al. 2022). The following morning at 07:00 corals were photographed with a color standard (WDKK Waterproof Color Chart, DGK Color Tools) to assess the effect of temperature on coral color, a proxy for relative chlorophyll density and bleaching severity (Winters et al. 2009; Voolstra et al. 2020).

Image analysis of coral color, a proxy for bleaching severity

Coral color was determined from each photograph in a semi-automated manner. Each photograph was first cropped to a standard size to remove excess background via a custom automated batch script in Adobe Photoshop (Version 21.1.2). Photographs were then loaded into ImageJ (v1.53c (Schneider et al. 2012)), and the performance of 16 built-in segmentation models were tested on a subsample of coral images to remove the background of the cropped image, which was turned to black, thus leaving only the coral fragment. The segmentation model that best segmented all coral fragments from the background effectively with limited coral fragment cut off (Model Li) was then implemented on all images, which were batch processed using a custom image segmentation macro script modified from Strock 2021. Once segmented, the script then extracted red pixel intensity of the fragment in RGB, HSB, and LAB color spaces. Finally, the mean red pixel intensity of the red color standard from the original (unsegmented) images was extracted from a region of interest drawn by hand in ImageJ. Pixel intensities of the coral and corresponding red standard were then converted to a 'darkness' score by subtracting the red channel 'brightness' from the maximum value (255). The mean red channel darkness of each coral was then normalized by dividing by the mean red pixel darkness of the red color standard from the same photograph. These red-normalized color values were then used to calculate the changes in bleaching severity between species, sites, and treatments. For visualization, the red-normalized color values were divided by the mean color under ambient (MMM) conditions for that species.

Statistical analyses

All statistical analyses were conducted using R software version 4.0.3 (R Core Team 2021), and graphical representations were produced using *ggplot2* (Wickham 2016). Differences in seawater temperature metrics were explored between sites (six levels: HB, FP, DL, SL, RC, RF) using linear models. Similarly, differences in temperature profiles (five levels: ambient, MMM, MMM + 4 °C, MMM + 6.5 °C, MMM + 9 °C) and experimental assays ($n = 6$ per temperature; see Table S1) were explored using a linear model. To assess for differences in coral color and photochemical yield between sites, treatments, and genera (three levels: *Acropora*, *Pocillopora*, *Porites*), linear mixed effects (lme) models were used, with colony as a random effect. For all models, the ANOVA function in the package *car* was used to determine the significance of fixed effects and their interactions, with type II error structures applied for models that were not suggestive of interactions, and type III for models that were (Fox et al. 2012). Significant interactive effects were followed by pairwise comparison of estimate marginal means using the *emmeans* package with Tukey HSD adjusted p values (Lenth et al. 2018). Data were tested for, and met the assumptions of, homogeneity of variance and normality of distribution through graphical analyses of residual plots for all models.

To determine how heat tolerance differed amongst genera and sites, three-parameter log-logistic dose–response curves were fit to the median photochemical yield (F_v/F_m) across all five temperature treatments (i.e., starting at ambient temperature) using the function drm in the package *drc* (Ritz et al. 2015). From these curves, the effective temperature to induce a 50% loss in F_v/F_m (effective dose 50; ED50) was obtained using the ED function in the package *drc* following the methodology of Evensen et al. 2022. No random effects were included in dose–response curves. Further, generalized additive models (GAMs) were fit to the median color score across temperatures by genera and sites using the gam function from the package *mgcv* (Wood 2006), as three-parameter log-logistic dose–response curves fit to the median color score did not produce the best model, as determined by comparison using the Akaike information criterion for small sample sizes (AICc). Colony genotype was included as a random effect. Smooth terms were fit using thin plate regression splines (tp), and the number of knots were restricted ($k = 3$) to avoid overfitting. The color score at the midpoint of the experimental heat assay was calculated by site and species, and compared to the F_v/F_m ED50 using a linear model to determine the relationship between the two metrics. Finally, to explore the relative influence of seawater temperature metrics (i.e., yearly mean, yearly maximum, yearly minimum, mean daily amplitude, and DHW in 2016; Table 1) on coral thermal tolerance (i.e., F_v/F_m ED50), GAMs were fit to allow for any possible nonlinear effects. We fit all possible model combinations using the gam function from the package *mgcv* (Wood 2006) (Table S2). The model structure was developed using a stepwise procedure, where models were compared and selected using AICc and the model with the lowest AICc was selected as the best model (Dove et al. 2020) (Table S2). Again, smooth terms were fit using tp regression splines, and the number of knots were restricted ($k = 3$) to avoid overfitting.

Three published studies using the standardized experimental approach (i.e., (Evensen et al. 2023)) were identified to compare coral thermal thresholds across reef systems and spatial scales: 1. Florida Reef Tract in the Caribbean (~ 300 km) (Cunning et al. 2021), 2. Coral Sea in eastern Australia (~ 860 km) (Marzonie et al. 2022), and 3. Red Sea (~ 900 km) (Evensen et al. 2022). Reported values of coral thermal tolerance (i.e., F_v/F_m ED50) were compiled by nursery/reef/site. To compare regional (Florida Reef Tract, Coral Sea, Red Sea) coral thermal tolerance with local (Heron Island), the range of coral thermal tolerance was calculated for each species by computing the difference between the site with greatest thermal tolerance and the site with the lowest thermal tolerance.

Results

Temperature variability differed across reef sites

Multiple years (2015–2022) of in situ temperature data demonstrated that daily (24-h) mean ($F = 4.1$, $p = 0.001$), diel temperature amplitude ($F = 1446.7$, $p < 0.0001$), maximum temperatures ($F = 91.9$, $p < 0.0001$), and minimum temperatures ($F = 40.1$, $p < 0.0001$) significantly differed amongst sites (Fig. 2). However, because an identical record (i.e., timeframe) was not obtained across all sites during the seven-year period, these significant differences were potentially driven by the patchiness of the time series. Therefore, the one-year period for which the most complete temperature record was obtained (September 2015–August 2016) was used for a more rigorous comparison of temperature dynamics across the six sites. During this period, daily mean temperatures were not significantly different across sites ($F = 0.35$, $p = 0.88$) (Table 1). In contrast, sites significantly differed in diel thermal variability (i.e., amplitude) ($F = 338.1$, $p < 0.0001$) (Fig. 2), in order from the least to most variable (annual mean °C day^{-1} ± SE): Harry's Bommie (1.01 ± 0.05), Fourth Point (1.27 ± 0.05), Deep Lagoon (1.34 ± 0.05), Shallow Lagoon (2.22 ± 0.05), Reef Crest (2.81 ± 0.05), and Reef Flat (2.96 ± 0.05) (Fig. 2, Table 1). Pairwise comparisons revealed significant differences in mean daily temperature amplitude between all sites ($p < 0.0006$), except the Reef Crest and Reef Flat ($p = 0.22$) and Deep Lagoon and Fourth Point (p = 0.89) (Fig. 2). Maximum diel temperature fluctuations followed similar patterns, in order from the smallest to largest daily fluctuations (°C day^{-1}): Harry's Bommie (2.37), Fourth Point (3.49), Deep Lagoon (3.74), Shallow Lagoon (4.52), Reef Flat (6.56), and Reef Crest (7.72) (Fig. 1, Table 1). Extreme temperature incursions leading to variability above 5 °C day^{-1} were only observed at Reef Crest and Reef Flat, with the most extreme ranges observed at the Reef Crest (up to 7.7 °C day^{-1}), yet the highest frequency of extreme values occurred at the Reef Flat (Table 1, Fig. 2).

Relative thermal tolerance under acute heat stress

Target temperature profiles were successfully attained across the experimental heat stress assays (Figure S1). Importantly, there were no significant differences in temperature profiles of corresponding treatments between assays ($F = 0.41$, $p = 0.84$) (Fig. 4a).

Photochemical yield (F_v/F_m) was significantly influenced by the three-way interaction of treatment, genus, and site ($X^2 = 87.7$, $p < 0.0001$). Pairwise comparisons generally revealed significant declines in F_v/F_m in the hottest treatment (MMM + 9 °C) across all genera (Fig. 4b, S2). Across all sites, we measured a 1.45 °C range in ED50 between the least and most heat tolerant genera (*Acropora* < *Pocillopora* < *Porites*) (Figure S2). *Acropora* was the least heat tolerant, with an ED50 of 35.65 °C (95% CI 35.2–36.1), followed by *Pocillopora* at 35.81 °C (95% CI 35.5–36.1) (Fig. S2). The most heat tolerant genus was *Porites,* with an ED50 of 37.1 °C (95% CI 36.4–37.8) (Fig. S2).

Significant differences in F_v/F_m ED50 were uncovered across sites (Fig. 4b, Table 2). For *Acropora*, ED50 (mean; 95% CI) differed by 1.10 °C between the least and most heat tolerant sites (HB < FP < RF < RC), ranging from 35.1 °C (95% CI 34.4–35.8) and 35.4 °C (95% CI 34.9–35.8) at the less variable (i.e., < 1.34 °C day^{-1}) reef slope sites of Harry's Bommie and Fourth Point, respectively. ED50's increased up to 36.1 °C (95% CI 35.6–36.7) at the Reef Flat and peaked at 36.2 °C (95% CI 35.7–36.6) at the Reef Crest (Figs. 4–5). *Pocillopora* exhibited the greatest range in ED50 (1.71 °C) across the sites (FP < HB < RC < RF < DL < SL) (Figs. 4–5). Again*,* *Pocillopora* from Fourth Point (ED50: 35.1 °C; 95% CI 34.6–35.6) and Harry's Bommie (ED50: 35.4 °C; 95% CI 34.8–35.9) had the lowest thermal tolerance (Figs. 4–5). Interestingly, *Pocillopora* from the sites with the greatest diel thermal variability (Reef Flat and Reef Crest) were not the most thermally tolerant (ED50: 35.9–36.1 °C) (Figs. 4–5). Instead, *Pocillopora* from the site with intermediate diel temperature variability (Shallow Lagoon) had the greatest thermal tolerance (ED50: 36.81 °C; 95% CI 34.9–38.6) (Figs. 4–5). For *Porites*, the ED50 ranged 1.43 °C between the least and most heat tolerant sites (RF < RC < HB < DL < FP < SL). Surprisingly, the less variable sites Fourth Point (ED50: 37.45 °C; 95% CI 33.6–41.3) and Deep Lagoon (ED50: 37.40 °C; 95% CI 34.8–40.0) were associated with greater thermal tolerance for *Porites* than the two most variable sites, Reef Flat (ED50: 36.3 °C; 95% CI 35.7–36.9) and Reef Crest (ED50: 36.5 °C; 95% CI 35.8–37.2) (Figs. 4–5). Yet, heat tolerance in *Porites* (ED50: 37.75 °C; 95% CI 30.8–44.7) was again greatest at the site with intermediate diel temperature variability (Shallow Lagoon) (Figs. 4–5).

Bleaching severity varied by genus and site under acute heat stress

Significant differences in coral color between genera and sites were found at MMM ($X^2 = 20.1$, $p = 0.009$) (Fig. S3). Pairwise comparisons revealed no differences in *Acropora* pigmentation across sites ($p > 0.79$) (Fig. S3). Yet,

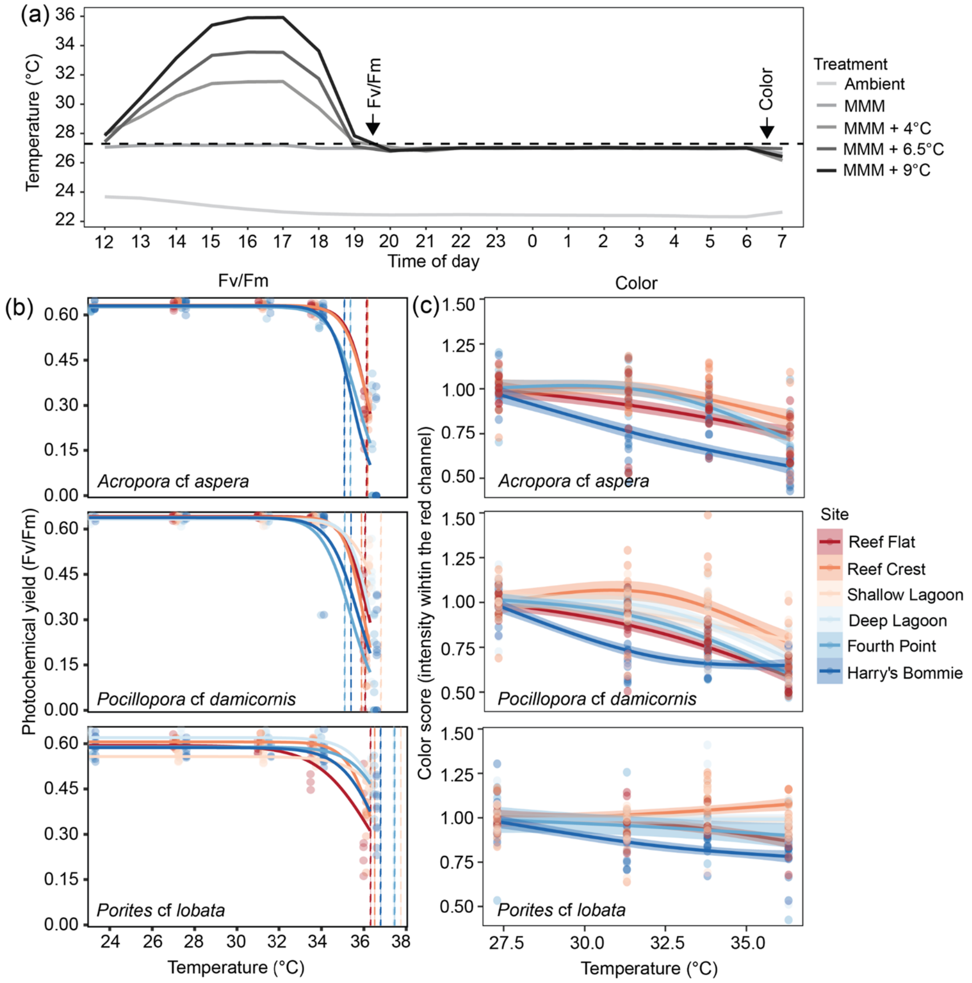

Fig. 4 Physiological performance and coral heat tolerance across sites and species. **a** Hourly temperature measurements of the standardized experimental heat stress assays, with arrows indicating when physiological measurements were determined. MMM (dashed horizontal line) is the region's climatological maximum monthly mean (27.3 °C). **b** Three-parameter log-logistic dose response curves were fitted for F_v/F_m measurements in response to temperature, where points indicate individual measures for coral genets ($n = 5$–10) in each treatment. Dashed vertical lines indicate the effective dose 50 (ED50). **c** Generalized additive mixed models were fitted for color score in response to temperature, where points indicate individual measures for coral genets in each treatment and confidence bands indicate 95% confidence intervals. A higher color score indicates greater pigmentation (i.e., less bleaching)

Pocillopora originating from the Reef Crest and Deep Lagoon were less pigmented than corals from all other sites ($p < 0.04$), and *Porites* originating from the most (Reef Flat) and least thermally variable habitats (Harry's Bommie) were significantly more pigmented than *Porites* originating from intermediate sites (Shallow Lagoon and Deep Lagoon) ($p < 0.02$) (ig. S3).

Normalized coral color was significantly influenced by the three-way interaction of treatment, genus and site ($X^2 = 37.8$, $p = 0.036$) (Fig. 4c). The severity of the bleaching response differed between genera. For *Acropora*, corals from the least (Harry's Bommie) and most (Reef Flat) thermally variable sites showed the sharpest declines in pigmentation (Fig. 4c). Pairwise comparisons revealed significant declines in color between MMM and all other temperatures in corals from Harry's Bommie ($p < 0.0001$), whereas for the Reef Flat corals, there was no difference between MMM and MMM + 4 °C ($p = 0.22$), yet significant declines at MMM + 6.5 °C and MMM + 9 °C ($p < 0.04$) (Fig. 4c). *Acropora* from the Reef Crest and Fourth Point did not show a decline in color between MMM, MMM + 4 °C, or MMM + 6.5 °C ($p > 0.42$), however, there was a significant decline in color at MMM + 9 °C in *Acropora* from both sites ($p < 0.0001$) (Fig. 4c).

For *Pocillopora*, corals from Harry's Bommie showed the sharpest decline in pigmentation, with pairwise comparisons revealing significant initial losses in color between MMM and MMM + 4 °C ($p < 0.0001$), yet no further declines between MMM + 4 °C, MMM + 6.5 °C, and MMM + 9 °C ($p > 0.42$). *Pocillopora* from the Reef Flat and Fourth Point showed similar trends (Fig. 4c). Corals from the Reef Flat showed significant initial losses in pigmentation between MMM and MMM + 4 °C ($p = 0.02$) as well as further declines between MMM + 6.5 °C and MMM + 9 °C ($p < 0.0001$), whereas for corals from Fourth Point, there were no initial losses in color between MMM and MMM + 4 °C ($p = 0.99$), yet stepwise declines with each increasing temperature treatment ($p < 0.0001$) (Fig. 4c). For *Pocillopora* from the Deep Lagoon, Reef Crest, and Shallow Lagoon, there were no differences in color between MMM and MMM + 4 °C or MMM + 6.5 °C ($p > 0.13$), yet significant declines at MMM + 9 °C ($p < 0.0001$) (Fig. 4c).

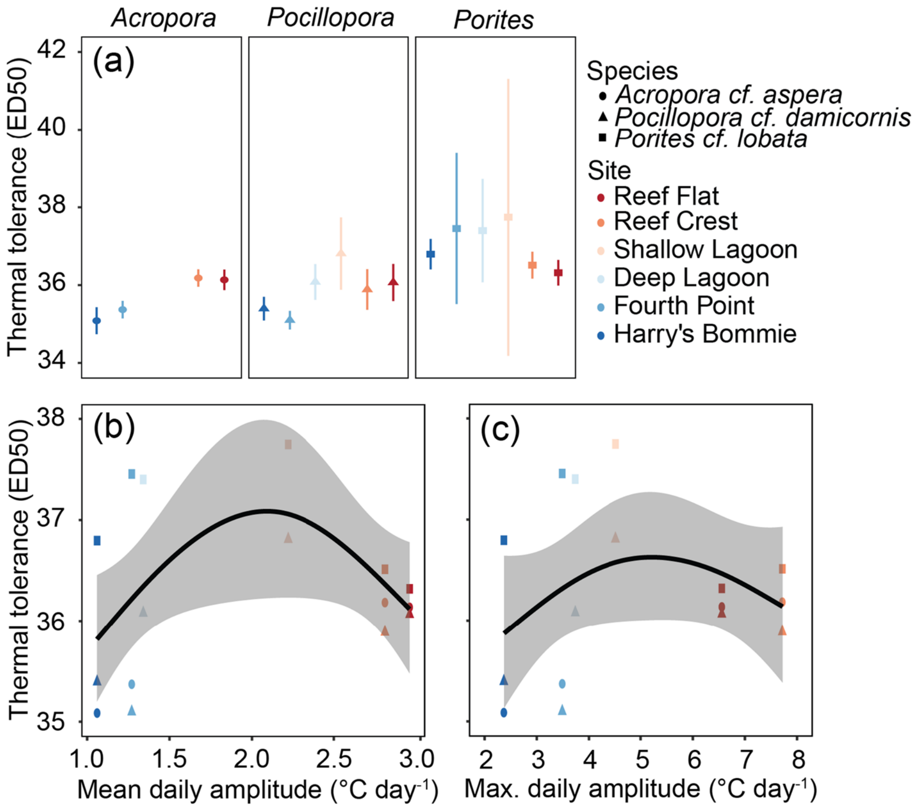

Fig. 5 Relationship between coral thermal tolerance and thermal variability. **a** Relative thermal tolerance (F_v/F_m ED50) by genus and site. Points ($\pm$SE) indicate the mean of 5–10 coral genets per species and site. **b** Relationship between coral thermal tolerance and mean diel temperature variability for the best generalized additive model (GAM). **c** Relationship between coral thermal tolerance and maximum diel temperature variability. Points indicate ED50 for each species and each site and confidence bands indicate 95% confidence intervals

Table 2 The relative thermal tolerance by species and site.

Species	Site	Thermal tolerance (Effective dose 50; ED50)	Standard error (SE)	Lower confidence interval (95%)	Upper confidence interval (95%)
Acropora cf. *aspera*	Fourth Point	35.396	0.302	34.804	35.988
	Harry's Bommie	35.086	0.344	34.410	35.762
	Reef Crest	36.183	0.224	35.743	36.622
	Reef Flat	36.136	0.264	35.618	36.654
Pocillopora cf. *damicornis*	Deep Lagoon	36.067	0.474	35.136	36.999
	Fourth Point	35.099	0.238	34.632	35.566
	Harry's Bommie	35.371	0.224	34.930	35.811
	Reef Crest	35.888	0.520	34.867	36.909
	Reef Flat	36.080	0.459	35.178	36.982
	Shallow Lagoon	36.810	0.928	34.988	38.632
Porites cf. *lobata*	Deep Lagoon	37.400	1.327	34.795	40.006
	Fourth Point	37.455	1.940	33.646	41.263
	Harry's Bommie	36.796	0.389	36.032	37.559
	Reef Crest	36.513	0.345	35.835	37.190
	Reef Flat	36.319	0.328	35.675	36.964
	Shallow Lagoon	37.747	3.560	30.757	44.736

Thermal tolerance was determined by photochemical yield (F_v/F_m) effective dose 50 (ED50), with standard error (SE), lower and upper 95% confidence intervals

Remarkably, *Porites* exhibited no significant losses in pigmentation across temperatures at any site ($p > 0.05$) except Harry's Bommie, where bleaching severity significantly increased between MMM and all other temperatures ($p < 0.02$) (Fig. 4c). Interestingly, for *Porites* from the Reef Crest, pigmentation was lowest in the coolest treatment (MMM), significantly increasing at MMM + 6.5 °C ($p < 0.0001$) (Fig. 4c).

Interestingly, coral color scores declined at lower temperatures (e.g., MMM + 4 °C) than F_v/F_m (e.g., MMM + 9 °C). To determine whether color scores (i.e., pigmentation) were predictive of photochemical yield, the relationship between F_v/F_m ED50 and the color score at the midpoint of the experimental heat assay was assessed and found to be significantly correlated ($R^2 = 0.486$, $p = 0.003$) (Figure S4).

Diel temperature variability was the best predictor of coral heat tolerance

Variation in ED50 was explored against in situ temperature conditions recorded September 2015–August 2016. A nonlinear model that included the individual effect of mean diel temperature amplitude resulted in the best prediction, as determined by the lowest AICc. Thermal tolerance increased in corals from habitats with a mean diel temperature amplitude of 1.06 °C day^{-1}, reaching the vertex or optimum at 2.2 °C day^{-1}, and decreasing when amplitude exceeded 2.81 °C day^{-1} (Fig. 5a). While the inclusion of coral species did improve explanatory power by ~ 10%, it did not result in the best model (i.e., lowest AICc). Further, other environmental predictors and interactions including mean, minimum, and/or maximum temperature as well as maximum DHW experienced in 2016 or 2020 were explored and none improved the model.

To increase comparability with other studies investigating diel temperature variability on coral thermal tolerance, we also plotted variation in ED50 against maximum diel temperature amplitude. A nonlinear model that included the individual effect of maximum diel temperature amplitude resulted in the second best prediction after mean diel amplitude (Fig. 5b). The trend mirrored that for mean diel temperature variability, with a maxima observed at intermediate variability. The inclusion of coral species did not improve explanatory power.

Comparison of coral thermal tolerance across studies

A comparable range of thermal tolerance (1.1–1.71 °C) was observed across the six reef habitats investigated when compared to the Florida Reef Tract (0.8 °C), Coral Sea (0.85–1.89 °C), and Red Sea (1.1–1.6 °C) (Fig. 6). By genera, a greater range in thermal tolerance was observed in *P.* cf. *damicornis* (1.71 °C) across Heron Reef than congeners *P. meandrina* (1.15 °C) or *P. verrucosa* (0.85 °C) across the Coral Sea and *P.* cf. *verrucosa* (1.55 °C) across the Red Sea (Fig. 6). For acroporids, there was a nearly equivalent range in thermal tolerance to the Florida Reef Tract (0.8 °C) compared to Heron Reef (0.9 °C), which was slightly lower than the Red Sea (1.1 °C) but half the range in the Coral Sea (1.89 °C) (Fig. 6). For coral of the genus *Porites*, the range in thermal tolerance was slightly lower at Heron Reef (1.2 °C) than the Red Sea (1.6 °C) (Fig. 6). While our results are comparable to studies across vast environmental gradients, some experimental parameters did differ among studies (i.e., temperature profiles, PAR levels, treatments over two consecutive days) and may account for some variability between studies.

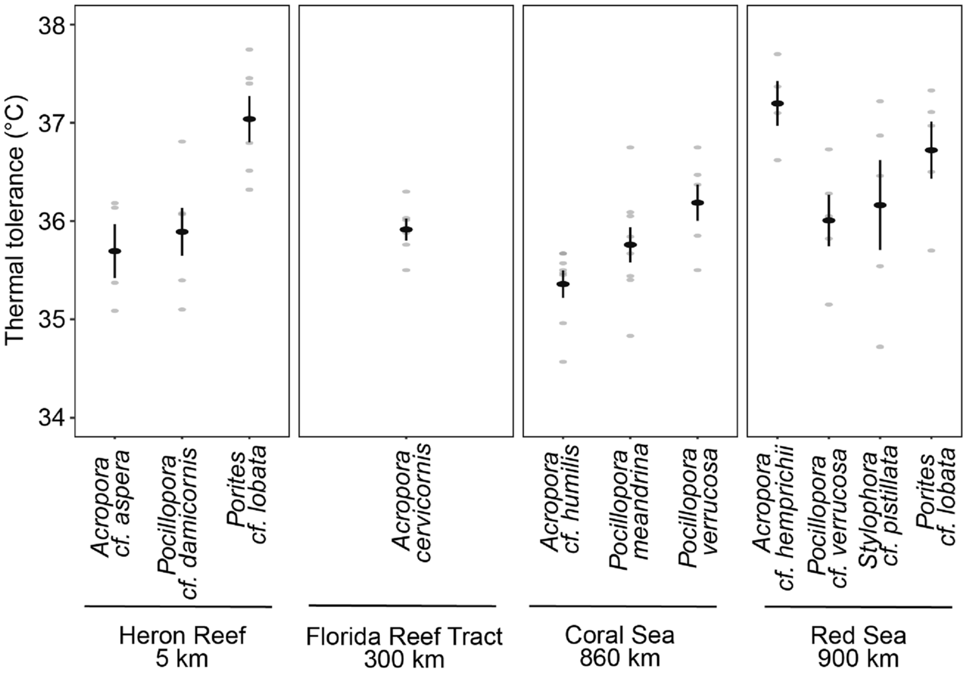

Fig. 6 Global comparison of coral thermal tolerance by region and species. Coral thermal tolerance (i.e., F_v/F_m ED50) is displayed as the mean ± SE (black symbols), with individual points indicating the ED50 of each site (gray symbols)

Discussion

Relative heat tolerance is strongly associated with the amplitude of daily temperature fluctuations

By investigating the thermal tolerance of three species of corals originating from six reef habitats representing a wide range of diel temperature fluctuations, we revealed a consistent parabolic response to increasing diel thermal variability across species, whereby coral thermal tolerance was highest at sites with intermediate temperature variability. Critically, the consistent response across corals of diverse life-history strategies (competitive, weedy, and stress-tolerant) and phylogenies (Complexa and Robusta) is powerful, as it expands upon previous studies investigating one (Palumbi et al. 2014; Kenkel and Matz 2016; Voolstra et al. 2020) or two species (Schoepf et al. 2015; Klepac and Barshis 2020) in isolation. Further, the investigation of thermal tolerance across a rigorously quantified thermal spectrum demonstrates that a larger range in variability (i.e., beyond two habitats) may be needed to reveal the full influence of temperature variability on coral thermal tolerance. For example, focusing on only the least and most variable habitats at Heron Reef would have led to an erroneous conclusion that increasing temperature variability decreases heat tolerance for *P.* cf. *lobata*, as this species was 0.5 °C less thermotolerant at the most variable habitat. Yet at intermediate variability, *P.* cf. *lobata* were 1 °C more thermotolerant than the least variable habitat, indicating that there is an optimal intermediate priming exposure for this species, beyond which becomes too physiologically stressful for corals within the most extreme environments. Importantly, this parabolic relationship rests heavily on the response of two species (*P.* cf. *lobata, P.* cf. *damicornis*) from the one intermediate variable site (Shallow Lagoon), and expanding this study to include other sites and/or species is needed to determine the generalizability of this response pattern. Additionally, other factors such as seawater pCO_2 or dissolved oxygen dynamics at the Shallow Lagoon may have contributed to the relative thermal tolerance and deserve additional investigations in the future work. Elevated thermal tolerance in corals exposed to intermediate diel temperature variability also occurs in *Porites lobata* from the pools of Ofu, American Sāmoa, where corals native to the moderately variable pool have higher thermal tolerance than corals from the low or highly variable pools (Klepac and Barshis 2022). However, these findings are in contrast to a number of earlier studies on *Acropora hyacinthus* from these same American Sāmoan pools, which consistently exhibit greater heat tolerance in the most highly variable pools (Palumbi et al. 2014; Thomas et al. 2018). These discrepancies highlight the need to evaluate thermal tolerance using standardized comparisons across diverse species (Grottoli et al. 2021). A strong positive relationship was uncovered between thermal tolerance and bleaching severity, suggesting that color score is predictive of thermal tolerance (as measured by photochemical yield), even at intermediate temperatures that did not instigate a photochemical response in the experimental assay. The fact that a loss in pigmentation is observed at lower temperatures than the decline in photochemical yield is interesting, as signs of stress precipitate prior to any measurable impact on photosystem II of the endosymbiotic dinoflagellates. Our results agree with a previous study which saw a decline in symbiont density at intermediate temperatures prior to significant declines in photochemical yield (Evensen et al. 2021) and suggests that declines in coral color here were attributable in part to a loss in symbionts. Ultimately, we build support for observations that not all temperature regimes result in greater thermal tolerance (Schoepf et al. 2019; Klepac and Barshis 2022) and provide new evidence that this mechanism is congruent across diverse coral species.

Elevated thermal tolerance does not protect against bleaching and mortality during marine heatwaves

Temperature regimes that expose corals to sublethal heat stress have been recognized as a mechanism to increase the physiological preparation for marine heatwaves (Ainsworth et al. 2016; Safaie et al. 2018; Thomas et al. 2018; Sully et al. 2019), and coral populations acclimated and/or adapted to variable thermal conditions are posited to be a source of climate resilience (e.g., Palumbi et al. 2014). However, during the 2020 marine heatwave that hit Heron Reef, coral bleaching and mortality were highest in the most thermally variable sites relative to the least thermally variable sites (Ainsworth et al. 2021; Brown et al. 2023a). For example, branching *Acropora* exhibited 50-fold lower symbiont densities at the most thermally variable site relative to those from the least variable habitat (Ainsworth et al. 2021), resulting in a loss of nearly all branching *Acropora* (Brown et al. 2023a). This was despite our observation that *Acropora* native to these same sites exhibited 1.1 °C higher bleaching thresholds than conspecifics from the least variable habitats, suggesting that even a 1 °C advantage in thermal tolerance gained from lifelong exposure to thermally variable conditions does not protect against current marine heatwaves. On the other hand, as our study was conducted 2 years after the marine heatwave, significant coral mortality stemming from this event may have resulted in selection for the most thermally-tolerant individuals (Sampayo et al. 2008; Burgess et al. 2021; Marzonie et al. 2022). Additional studies are needed to determine the mechanisms driving elevated heat tolerance in variable and moderately variable environments, such as genetic variability in the host and/or associated Symbiodiniaceae (e.g., Oliver and Palumbi 2011b), and whether individuals capable of surviving extreme temperature variability can also withstand prolonged and repeated marine heatwaves. Nonetheless, our results add to a body of evidence that corals exposed to extreme thermal regimes are unable to cope with the additional heat stress of marine heatwaves superimposed on top of thermally variable conditions (Schoepf et al. 2015, 2020; Ainsworth et al. 2021; Brown et al. 2023a).

As climate change intensifies, the response of corals and trajectories of ecosystems are becoming more contingent on previous marine heatwaves (e.g., Hughes et al. 2019). There is growing evidence that surviving corals can acclimatize (i.e., acquire stress tolerance through hardening) or sensitize (i.e., accumulate stress leading to weakening) via the environmental memory of thermal stress (Hackerott et al. 2021; Brown and Barott 2022). Whether the corals investigated in this study are acclimatizing or suffering from long-term damage from the 2020 marine heatwave, and if this environmental memory influenced thermal tolerance, cannot be determined and is likely species-specific (Evensen et al. 2022; Marzonie et al. 2022; Brown et al. 2023b). However, it is plausible that the lower thermal tolerance of *P.* cf. *lobata* from the most thermally variable habitat, which experienced disproportionately higher heat stress during the 2020 marine heatwave (Brown et al. 2023a), is a result of stress accumulation across repetitive marine heatwaves—similar to the recent findings of reduced thermal tolerance of *Porites* from the Red Sea and American Sāmoa following heatwaves (Klepac and Barshis 2020, 2022; Evensen et al. 2022). Conversely, greater thermal tolerance of *P.* cf. *lobata* from the least thermally variable habitats could have stemmed from a magnitude and duration of heat stress during the 2020 heatwave that promoted stress hardening of this species (Hackerott et al. 2021; Marzonie et al. 2022; Brown et al. 2023b). Ultimately, it remains inconclusive whether the patterns observed here are related to acclimatization or sensitization, but a better understanding of these processes is key to predicting the future of coral reefs in warming oceans and are an important avenue of future studies (Hackerott et al. 2021; Brown and Barott 2022).

Local temperature heterogeneity promotes similar range of coral thermal tolerance as regional temperature gradients

The range in coral thermal tolerance across geomorphological zones within the single reef system of Heron Reef (< 5 km) were as high as differences observed across vast latitudinal gradients in the Caribbean (~ 300 km, Florida Reef Tract) (Cunning et al. 2021), eastern Australia (~ 860 km, Coral Sea) (Marzonie et al. 2022), and the Red Sea (~ 900 km) (Evensen et al. 2022). For example, *A.* cf. *humilis, P. verrucosa*, and *P. meandrina* on reefs across the Coral Sea—spanning 7.7 degrees of latitude and corresponding with a 1.6 °C gradient in MMM—led to 0.85 °C to 1.89 °C range in heat tolerance across sites (Marzonie et al. 2022). Similarly, *A.* cf. *hemprichii, P.* cf. *verrucosa*, and *P.* cf. *lobata* from reefs across the Red Sea spanning 17 degrees of latitude and a 3.7 °C gradient in MMM displayed a 1.1 °C to 1.6 °C range in thermal tolerance (Evensen et al. 2022). In this study, we observed a comparable range of thermal tolerance (1.1–1.71 °C) across the six reef habitats investigated, suggesting fine-scale temperature heterogeneity can increase thermal thresholds similar to large-scale differences in temperature across latitudinal gradients. While microhabitats are known to shape patterns in coral thermal tolerance across small spatial scales (Schoepf et al. 2015; Thomas et al. 2018; Voolstra et al. 2020), our standardized comparison across three coral species with distinct life-history strategies allows for the comparison of these traits for the first time across regions and spatial scales. These differential patterns in thermal tolerance could be a result of: (i) variation in host or symbiont communities (Sampayo et al. 2008; Oliver and Palumbi 2011b; Burgess et al. 2021), (ii) adaptation to latitudinal thermal regimes over evolutionary time (Dixon et al. 2015; Osman et al. 2018), and/or (iii) recent exposure to marine heatwaves (Hughes et al. 2019; Evensen et al. 2022; Marzonie et al. 2022). While genetic confirmation was not conducted on the corals in this study, recent studies of *P. damicornis* have identified that coral and Symbiodiniaceae species associations can be shared across distinct Heron Reef habitats (e.g., *P. damicornis* can host the same symbiont species across the reef flat and reef slope) (Brown et al. 2022). This is encouraging, particularly as gene flow from the thermally variable habitats could increase thermal tolerance within the least thermally variable habitats within the same reef system. Yet, investigations into *P. damicornis* across the thermally variable reef flat and thermally stable reef slope of Heron Island have indicated that there is limited gene flow between these populations, which is surprising, given that the small spatial distances between reef habitats (< 100 m) would not be expected to restrict dispersal (van Oppen et al. 2018). However, in this study, we investigated species with different modes of reproduction (i.e., broadcast spawning, brooding), and it may be more likely to see gene flow across these habitats with broadcast spawners (e.g., *Acropora* or *Porites*) as opposed to brooders (i.e., *P. damicornis*). Given limited gene flow previously observed, human interventions like assisted gene flow and/or selective breeding may be a viable strategy to increase heat tolerance of certain coral populations across thermally-distinct reef habitats (Van Oppen et al. 2017), offering an easier and safer alternative to moving thermally tolerant corals across latitudes (e.g., Dixon et al. 2015). Indeed, *P. damicornis* can survive transplantation from the most to least thermally variable habitats at Heron Reef, and even retains greater heat tolerance than native conspecifics for at least 18 months following transplantation (Marhoefer et al. 2021). While it may be impossible to perform these tasks across the entirety of the Great Barrier Reef, reefs such as Heron Reef, which is a high-value tourism and world-class research destination, are ideal candidates for such stewardship to increase coral resilience in a changing climate.

Conclusions

The results of this study highlight that fine-scale temperature heterogeneity can increase coral heat tolerance thresholds in diverse coral lineages and reveal that there is an optimal priming exposure at intermediate temperature variability that leads to maximal thermal tolerance. Greater thermal tolerance, however, does not necessarily translate into greater community resilience during marine heatwaves, as the coral communities that had higher bleaching thresholds experienced more prevalent and severe bleaching and greater declines in hard coral cover following the 2020 heatwave due to disproportionately greater heating in these habitats (Ainsworth et al. 2021; Brown et al. 2023a). This suggests that elevated heat tolerance gained from life-long exposure to sublethal thermal variability already appears ineffective against current levels of ocean warming. Encouragingly, the range in coral thermal tolerance across geomorphological zones within a single reef system (<5 km) were as large as differences observed across vast latitudinal gradients (300–900 km), and future studies could investigate the mechanisms (e.g., physiological plasticity, constitutive upregulation of stress-response genes, and/or epigenetic modifications) enabling these corals to develop resistance to acute heat stress. Further, while co-occurring environmental conditions (e.g., pCO_2, oxygen, and irradiance) were not quantified in this study, pCO_2 fluctuations and irradiance are known to differ across these same habitats (Brown et al. 2022), and the combined effect of ocean warming and deoxygenation can lower the thermal threshold of some corals (Alderdice et al. 2022). As such, more research is needed to understand the interactions between physicochemical conditions that co-occur within thermally variable habitats and their influence on coral thermal tolerance. To encourage the best future for coral reefs, the potential for assisted gene flow to increase heat tolerance of coral populations should continue to be explored, while concurrently adopting strict global policies to limit climate-induced temperature increases to 1.5 °C (Hoegh-Guldberg et al. 2019).

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Declarations

Conflict of interest No conflict of interest declared.

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