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Coral heat tolerance under variable temperatures: Effects of different variability regimes and past environmental history vs. current exposure

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Abstract

Exposure to high-frequency temperature variability often but not always enhances coral heat tolerance, raising the question of whether this depends on the type of variability regime and past vs. current exposure. We collected corals from a macrotidal, highly fluctuating temperature environment and preconditioned them to either constant or variable daily temperatures for ~ 1.5 yr. Corals were then exposed to three new temperature variability regimes for ~ 1 month (constant control, symmetric variability, and tidal variability) to assess the effect of short-term environmental history, followed by a 12-d heat stress test. Measurements of visual coral health, photophysiology, photosynthesis, respiration, and calcification rates showed that preconditioning to constant vs. variable temperatures for 1.5 yr did not significantly impact coral physiology and heat tolerance. In contrast, environmental history experienced in the month prior to the heat stress test significantly influenced the physiological responses, with corals exposed to both types of variability having lower heat tolerance. Interestingly, corals in the tidal variability regime suffered greater health declines than in the symmetric variability regime although both treatments had the same cumulative heat exposure. Since heating rate and temperature amplitude were higher in the tidal variability regime (but time spent above the bleaching threshold was shorter), this suggests that short, extreme heat pulses may be more deleterious than longer but more moderate ones, though other factors likely also played a role. Overall, our findings demonstrate that daily temperature variability has significant potential to alter coral heat tolerance but only certain types of variability may enhance coral adaptive capacity.

Anthropogenic climate change is one of the biggest threats to coral reefs today. Ocean warming in combination with increasingly frequent and intense marine heatwaves (Frölicher et al. 2018; Oliver et al. 2018) has significantly contributed to the decline of coral reefs worldwide as the resulting mass bleaching events can lead to coral mortality on regional to global scales (Eakin et al. 2010; Hughes et al. 2018). In addition, rising atmospheric CO_2 concentrations also result in ocean acidification, defined as a reduction in seawater pH, which lowers the calcification rates of many marine calcifiers (Kroeker et al. 2013), including reef-building corals (Chan and Connolly 2013; Kornder et al. 2018). Thus, there is an urgent need to identify the mechanisms that may help corals persist in a rapidly changing ocean.

Many tropical coral reefs occur in waters where environmental conditions are relatively stable throughout the year. Thus, corals have evolved narrow environmental tolerance limits and live, for example, close to their upper thermal thresholds (Coles and Jokiel 1977; Fitt et al. 2001). When temperatures exceed their local maximum monthly mean (MMM) temperatures by only 1–2°C, the vital symbiosis with dinoflagellate algae (family Symbiodiniaceae) breaks down in a

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Additional Supporting Information may be found in the online version of this article.

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process referred to as coral bleaching (Berkelmans and Willis 1999), which is defined as a significant loss of symbionts and/or photosynthetic pigments from the coral tissue. Since corals meet up to 90% or more of their energetic requirements from autotrophic carbon translocated by their symbionts (Muscatine et al. 1981), this results in significant resource limitation, compromised physiology (e.g., reduced photosynthesis and calcification rates) and possibly death (Brown 1997; Baker et al. 2008), unless they can rely on alternative carbon sources such as zooplankton or their own tissue reserves (Grottoli et al. 2006; Anthony et al. 2009).

In recent years, evidence has accumulated that some corals persist in reef environments characterized by strong environmental variability and that exposure to such fluctuations has the potential to enhance stress tolerance (Palumbi et al. 2014; Schoepf et al. 2015; Rivest et al. 2017). In particular, high-frequency temperature variability—as for example encountered on a daily basis in back-reef pools and intertidal/shallow reefs—has been shown to promote heat tolerance and mitigate bleaching risk in a number of species and sites (Safaie et al. 2018). However, some studies have also demonstrated that temperature variability can have no or detrimental effects on coral heat tolerance (Putnam and Edmunds 2011; Schoepf et al. 2019; Klepac and Barshis 2020), yet we lack a mechanistic understanding of why that is. One possible explanation is that only certain types of temperature variability (i.e., certain combinations of magnitude, amplitude and frequency) enhance heat tolerance and that this also depends on the type of variability encountered in their native environment, that is, their environmental history. In addition, other environmental parameters such as light often covary with temperature and could therefore further modulate how temperature variability impacts coral heat tolerance. However, these mechanisms are currently poorly understood because only few studies to date have compared how different types of variability regimes differ in their potential to alter stress tolerance (Rivest et al. 2017).

To address these knowledge gaps, we used corals from a highly fluctuating, naturally extreme temperature environment to compare the effects of different temperature variability regimes on heat tolerance. The corals originated from the macrotidal Kimberley region in NW Australia where the world's largest tropical tides (up to 12 m) expose corals on shallow, intertidal reefs to short-term maximum temperatures of up to 38°C, daily temperature variability of up to 8°C, and frequent aerial exposure at low tide (Dandan et al. 2015; Schoepf et al. 2015). Long-term acclimatization and/or adaptation to these extreme conditions have resulted in enhanced heat tolerance, survival, and recovery capacity post bleaching (Schoepf et al. 2015; Le Nohaïc et al. 2017; Jung et al. 2021). However, these corals were nevertheless unable to increase their heat tolerance after 6 months of acclimation to 1°C warmer temperatures in the lab; furthermore, under these warming levels, daily temperature variability actually lowered their ability to cope with a heat stress event compared to corals exposed to constant daily temperatures (Schoepf et al. 2019). This raises the question of how environmental history interacts with different variability regimes as drivers of coral heat tolerance.

We preconditioned corals to either constant or variable daily temperatures for ~ 1.5 yr to create corals with different environmental history. Corals were then exposed to three different temperature variability regimes for ~ 1 month, followed by a heat stress test, to determine if (1) long- or short-term thermal history has a greater influence on coral heat tolerance and (2) different types of temperature variability differ in their ability to alter heat tolerance. In addition, we explored the influence of light variability on coral responses to different temperature variability regimes.

Materials and Methods

Overview

We used corals from an intertidal, highly variable reef environment in NW Australia as a model species and took advantage of these corals being grown long term (~ 1.5 yr) in the lab under two different temperature variability regimes (constant daily temperature and 4°C daily temperature variability; Fig. 1) to assess how environmental history influences coral heat tolerance. This preconditioning phase (*see* details below) was part of another experiment designed to investigate whether daily temperature variability enhances the capacity of corals to acclimate to future ocean warming (Schoepf et al. 2019). Unexpectedly, Schoepf et al. (2019) found that daily temperature variability did not promote long-term acclimation to ocean warming but instead often had negative effects on coral heat tolerance and physiology. The authors speculated that this result could be related to the fact that the somewhat artificial, symmetric temperature variability treatments did not simulate the tidally induced strong coupling of temperature and light variability experienced by intertidal corals in situ (Dandan et al. 2015; Schoepf et al. 2015, 2020). We therefore conducted another experiment (*see* the Temperature variability experiment section; Fig. 1) to expose the corals with different environmental history to three different types of temperature variability (constant daily temperature, 4°C daily temperature variability, and "tidal" temperature variability), combined with a more realistic "tidal" light regime (Fig. 2b). The "tidal" variability treatment mimicked the rapid changes observed in both temperature and light during spring tidal cycles at the collection site. Subsequently, we assessed how acclimation to these treatments influenced coral heat tolerance in a 12-d heat stress test.

Study species and collection site

Intertidal *Acropora aspera* (Dana, 1846) corals were collected from Shell Island (Shenton Bluff), Cygnet Bay, in the macrotidal Kimberley region of NW Australia. Collection permits were obtained from the Western Australia Department of Fisheries (exemption no. 2549, date of issue 03 March

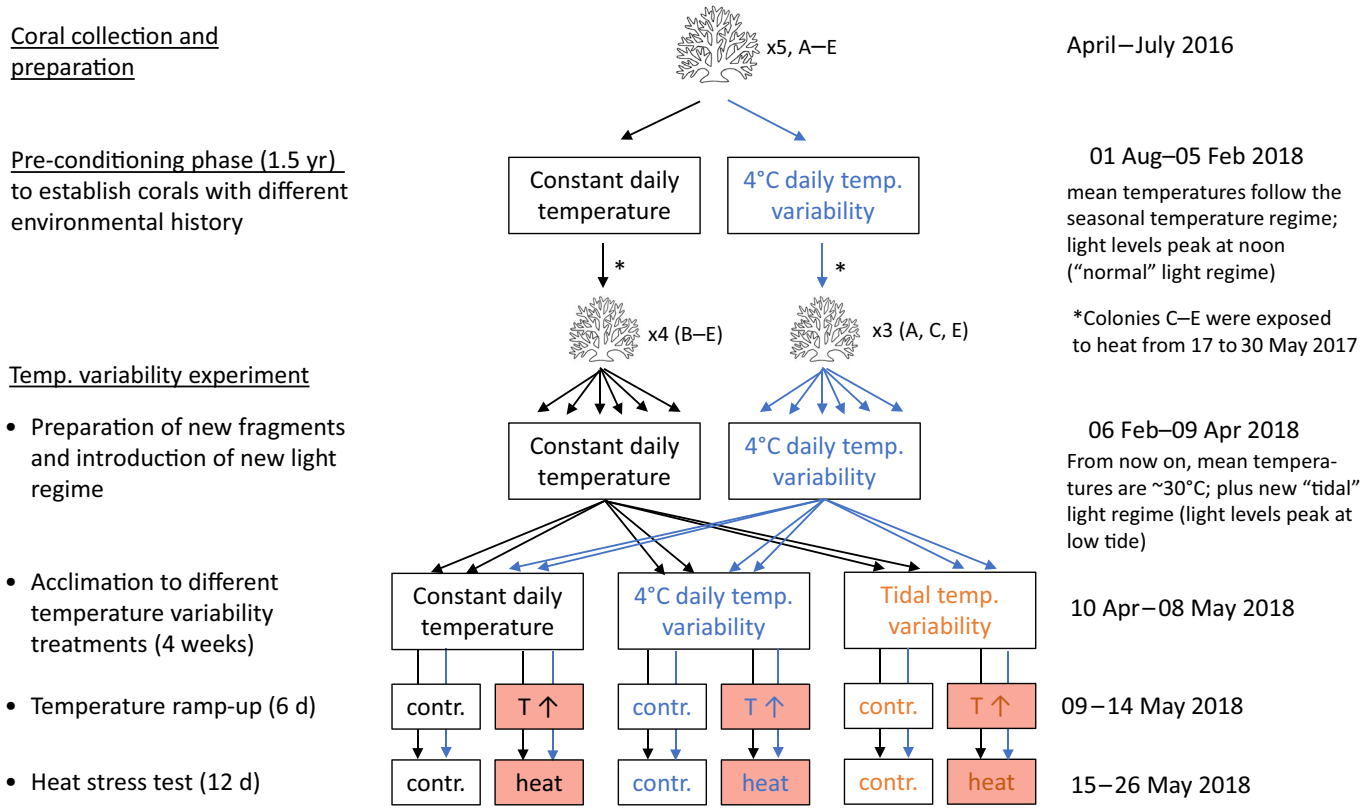

Fig. 1. Experimental design. Key events and experimental phases are shown on the left, while the timeline with details on temperature and light conditions is shown on the right. Black and blue colors represent the different environmental history established during the preconditioning phase. Arrows indicate replicate fragments per parent colony (A–E).

2015). The Kimberley region features the world's largest tropical tides (up to 12 m, ~8 m at Shell Island), thereby exposing shallow coral reefs to extreme environmental conditions as well as strong daily fluctuations in many environmental parameters (Schoepf et al. 2015; Cornwall et al. 2018). Five visibly healthy coral colonies (labeled A, B, C, D, E) were collected in April 2016 from the intertidal environment at Shell Island (16°28′45.8″S, 123°2′41.3″E), where they regularly experience prolonged aerial exposure during spring low tides (up to hours), high light levels (up to ~ 2000 μmol m^{-2} s^{-1}) and extreme daily temperature fluctuations of up to 7°C, with short-term maxima of up to 38°C (Dandan et al. 2015; Schoepf et al. 2015, 2020). In contrast to subtidal conspecifics, intertidal *A. aspera* have a naturally higher heat tolerance (Dandan et al. 2015; Schoepf et al. 2015) and survive/recover better from bleaching events (Le Nohaïc et al. 2017; Schoepf et al. 2020; Jung et al. 2021). Both intertidal and subtidal corals are dominated by symbionts from the genus *Cladocopium* (previously clade C; LaJeunesse et al. 2018) (Schoepf et al. 2015, 2020); however, symbiont community composition nevertheless differs between intertidal and subtidal corals and may be linked to their differential bleaching resilience (Jung et al. 2021). Monthly average temperatures at Shell Island range from ~ 25°C to 31°C, and the bleaching threshold was experimentally established to be ~ 32°C, approximately 1°C above local MMM sea surface temperatures (SST) (Schoepf et al. 2015). Corals were collected at least 10 m apart to avoid collecting clones.

Colonies were shipped live and submerged in water to the University of Western Australia and maintained in indoor, flow-through aquaria at the Watermans Bay seawater facility at ~ 29°C (± 1°C) to facilitate recovery and acclimation to tank conditions. From mid-June until the end of July 2016, corals were kept at their normal seasonal temperatures, with temperatures adjusted twice a month to track the seasonal profile at their collection site (Table S1) as detailed in Schoepf et al. (2019). In July 2016, each colony was fragmented into two pieces of 5–10 cm which were glued onto prelabeled plastic tiles. Light was provided on a 12 : 12 h light : dark cycle, following a natural diurnal light cycle with gradual increases up to 560 μmol m^{-2} s^{-1} at noon (Ledzeal S150 Plus). Corals were fed twice a week with live brine shrimp. Further details on the feeding regime and mesocosm tank setup are given below.

Preconditioning phase (01 August 2016–05 February 2018)

The preconditioning phase served to establish two sets of corals with different environmental history: either constant

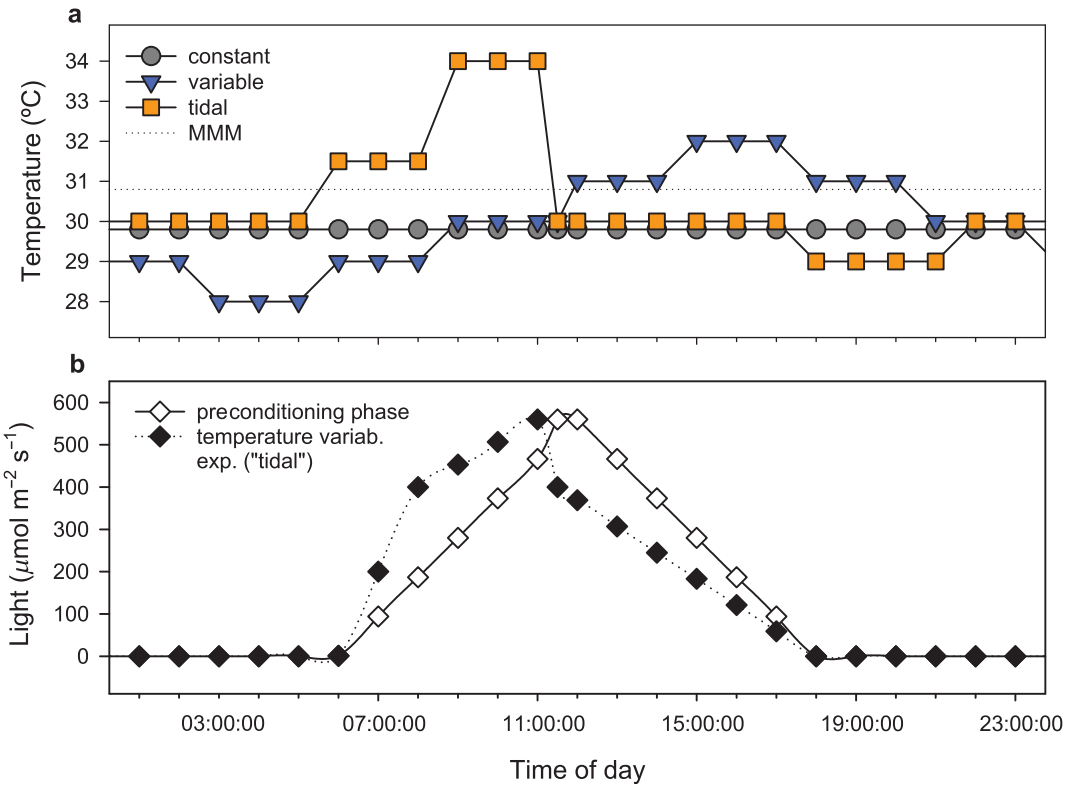

Fig. 2. Overview of experimental treatments. (**a**) The three temperature variability treatments during the experiment (10 Apr–26 May 2018). For reference, the maximum monthly mean (MMM) temperature at the collection site is also shown. (**b**) Comparison of the light treatments during the preconditioning phase (01 Aug 2016–05 Feb 2018) vs. the experimental phase (incl. fragment preparation; 06 Feb–26 May 2018).

daily temperatures or 4°C daily temperature variability (Figs. S1, 2a), while still following the seasonal temperature profile of their Kimberley collection site (Table S1). Each parent colony had one fragment exposed to constant daily temperature and another one exposed to 4°C daily temperature variability. Importantly, variability treatments were designed such that daily average temperature was the same in both constant and variable treatments. From 01 August 2016 until 30 May 2017, the corals were part of the seasonal control treatments (referred to as "native controls") in the experiment described in Schoepf et al. (2019). Three of the five colonies (C–E) were exposed to elevated temperatures (~ 32.4°C) from 17 to 30 May 2017 as part of the stress test in Schoepf et al. (2019); however, immediately after the stress test, temperature was returned to ambient seasonal temperatures, thus allowing these colonies to recover for more than 8 months (01 June 2017–05 February 2018; *see* Supplement for more details). From 01 June 2017 until 05 February 2018, all colonies continued to be kept in the same tank setup and under constant vs. variable daily temperatures while still following the seasonal temperature profile (Table S1).

The mesocosm setup is described in detail in previous papers (Schoepf et al. 2018, 2019). Briefly, both constant and variable temperature treatments had two replicate tanks per treatment. Coral fragments were maintained in 55-liter transparent plastic tanks where seawater was being replaced at a rate of ~ 0.5 L min^{-1}. Water motion was provided using a submersible pump (Macro Aqua; 3000 L h^{-1}). Temperature was maintained using titanium heaters (WeiPro; 500 or 1000 W) and controlled via ApexFusion software (Neptune Systems). The Apex temperature probes were calibrated 1–2 times a week using a high-precision thermometer (Fisher Scientific Traceable). Light was provided on a 12 : 12 h light : dark cycle (06:00–18:00 h) using 150 W LED lights (Ledzeal S150 Plus) with custom-designed LED arrangements and colors to ensure a light spectrum similar to shallow tropical reef environments. The lights were programed to follow a natural diurnal light cycle, with gradual increases up to 560 μmol m^{-2} s^{-1} at noon (measured using an Apogee MQ-200 cosine-corrected planar PAR-meter) (Fig. 2b). Relatively high maximum light levels were chosen because intertidal Kimberley corals regularly experience high light levels depending on tidal elevation, water clarity, and cloud cover (up to ~ 2000 μmol m^{-2} s^{-1}); however, these extreme light levels are only experienced short-term during spring low tide, and therefore intermediate levels were used for daily exposure in this study. The incoming seawater was pumped from 12 m depth and filtered through three sand filters (~ 20 μm nominal size). Corals were

fed twice a week with live brine shrimp. Approximately 2.5 g of brine shrimp eggs were hatched, and the stock solution with live nauplii was then equally divided among all tanks. HOBO v2 temperature loggers (Onset) were deployed in each tank and continuously recorded seawater temperature every 5 min.

Temperature variability experiment (February–May 2018)

Preparation of new coral fragments (06 February–09 April 2018)

After 1.5 yr in the mesocosms, the corals had grown significantly and could be fragmented to produce a greater number of new, small fragments. However, due to heater malfunctioning, not all initial parent colonies survived. At the beginning of February 2018, the remaining four large corals from the constant temperature treatment (colonies B, C, D, and E) and the remaining three large corals from the variable treatment (colonies A, C, and E) were split into six smaller fragments each of 3–4 cm in size. The new pieces were then glued to prelabeled plastic tiles and allowed to recover and grow out for 2 months until 09 April 2018. During this time, corals with a history of constant daily temperature continued to be kept under constant temperatures (six replicate tanks), whereas corals with a history of 4°C daily temperature variability continued to be kept under variable conditions (six replicate tanks). Temperatures from this point onward were kept at ~ 30°C since SST at the collection site stay at or above ~ 30°C from January through May (Table S1).

In addition, corals were now being acclimated to a new "tidal" light cycle that mimicked daily light regimes during spring tides at the collection site (Fig. 2b, *see* Supplement for details). Specifically, the "tidal" light cycle mimicked the strong increase in light level during the morning low tide, followed by a rapid drop in light levels when tide pools get flushed during the incoming tide and subsequent relatively low light levels throughout the afternoon due to high turbidity associated with strong tidal currents (Dandan et al. 2015; Schoepf et al. 2020). Corals continued to be fed twice a week with live brine shrimp.

Acclimation to different temperature variability regimes (10 April–08 May 2018)

Corals with different environmental history were then acclimated for 4 weeks (10 April–08 May 2018) to three different temperature variability regimes: (1) constant daily temperature (~ 30.0°C), (2) 4°C daily temperature variability (~ 30.0°C ± 2°C), and (3) "tidal" daily temperature variability (Figs. 1, 2a). The "tidal" temperature variability treatment mimicked strong increases in temperature across the morning spring low tide, followed by a rapid return to ambient temperatures with the incoming tide (06:00–08:59 31.5°C, 09:00–10:59 34.0°C, 11:00–17:59 30.0°C, 18:00–21:59 29.0°C, 22:00–05:59 30.0°C; Fig. 2a). Importantly, treatments were designed such that daily average temperatures were almost identical in all three treatments; in addition, they were designed such that daily cumulative heat stress exposure was almost identical in the variable and tidal treatment (Fig. 2a; Table S2). Each treatment had four replicate tanks. Two fragments per parent colony per environmental history were randomly distributed across the three temperature variability treatments, leading to all possible combinations of having experienced temperature variability in the past only (during the preconditioning phase), during the temperature variability experiment only, during both preconditioning and the experiment, or not at all (Fig. 1).

Temperature ramp-up and heat stress test (09–26 May 2018)

After 4 weeks of acclimation to the three temperature variability treatments, two replicate tanks per treatment were assigned to a heat stress treatment, whereas the other two replicate tanks were assigned as controls and remained at ~ 30°C (Fig. 1). Temperature was gradually increased by 0.5°C every 2 d in the heat stress tanks over 6 d to reach the known bleaching threshold of ~ 32°C for these corals (Schoepf et al. 2015, 2018, 2019). After 5 d at ~ 32°C, temperatures in heat stress tanks were increased by another 0.5°C on 20 May 2018, and by another 0.5°C on 22 May 2018 because F_v/F_m values remained relatively stable (*see* below). Thus, corals in heat stress tanks were kept at ~ 33°C for the last 5 d of the heat stress test (22–26 May 2018), which resulted in a significant stress response (*see* below).

Monitoring of treatment conditions

Water temperature was controlled using the Apex control system, as described above. HOBO Pro v2 temperature loggers (Onset) were deployed in each tank and continuously recorded seawater temperature every 15 min from the start of the acclimation phase until the end of the experiment (10 April–26 May 2018). To quantify heat stress, daily average temperatures were used to calculate degree heating days (DHDs) for the heat stress treatments (Maynard et al. 2008). Instead of long-term mean summer temperatures, a MMM value of 30.827°C was used to calculate DHD, as per previous work (Schoepf et al. 2020). Further details regarding monitoring of temperature, salinity, and seawater carbonate chemistry are provided in the Supplement.

Physiological analyses

Visual health status

Visual health (as well as partial mortality) was recorded using the CoralWatch® Coral Health Chart (Siebeck et al. 2006) at five time points during the experiment by the same observer: ~ 2 weeks prior to the start of the acclimation phase (27 March 2018), 2.5 weeks after the acclimation phase had started (26 April 2018), at the beginning of the temperature ramp-up phase (10 May 2018), after 9 d of heat stress (24 May 2018), and 3 d after the end of the heat stress test (29 May 2018). Corals were scored on the upper surface of the branches, with light intensity at the highest setting. Although

visual assessment of coral health is less sensitive than quantification of symbiont density and/or chlorophyll *a* (Chl *a*) content, we chose this method because it is nondestructive and thus allowed for repeated measurements. The brightness/saturation scale of the Coral Health Chart was developed and rigorously calibrated using analyses of symbiont density and Chl *a* content, such that a change of two units in brightness indicates a significant change in symbiont density and Chl *a* content and thus the bleaching state of corals (Siebeck et al. 2006).

Photophysiology

Photophysiological performance was assessed via both the effective (light-adapted) and maximum (dark-adapted) quantum yield of photosystem II ($\Delta F/F_m'$ and F_v/F_m, respectively), which is an indicator of photochemical efficiency and bleaching sensitivity (Warner et al. 1999). Measurements were taken before the acclimation phase started (09 April 2018), two times during the acclimation phase (16 and 30 April 2018) and on the last day of the temperature ramp-up (14 May 2018). During the heat stress test, photophysiology was measured almost daily (except on 15, 18, and 24 May 2018) but during the last 2 d (25 and 26 May), only F_v/F_m was measured since corals were used for respirometry during the day (*see* below). $\Delta F/F_m'$ was measured at 11:30 h when all temperature treatments were at the same temperature; during this time, light intensity was set to maximum levels (560 μmol m^{-2} s^{-1}). F_v/F_m was measured ~ 45 min after lights turned off to assess the photochemical efficiency in the dark-adapted state. These data were then used to calculate the maximum excitation pressure over photosystem II (Q_m) (Iglesias-Prieto et al. 2004), which is an indicator of symbiont performance at peak sunlight. Q_m was calculated as $Q_m = 1 - (\Delta F/F_m')/(F_v/F_m)$, with values close to 1 indicating photoinhibition and values close to 0 indicating light-limitation of photosynthesis under maximum irradiance. All photophysiological measurements were made using a Diving-PAM underwater fluorometer (Walz) with the following settings: measuring light intensity = 3, saturation pulse intensity = 12, saturation pulse width = 0.8 s, gain = 4, and damping = 2. Measurements were made at a constant distance of 2 mm from the coral tissue, approximately 2–3 cm below the tip. Variable and constant temperature treatments were assessed at the same temperature (i.e., temperatures in variable tanks were set to the same temperature as in the constant tanks during this time; during the heat stress test, all heated tanks were at the same temperature and all control tanks were at the same but lower temperature).

Metabolism

Net photosynthesis and respiration rates were measured using respirometry at the end of the heat stress test (25–29 May) following the methods of Schoepf et al. (2019). Briefly, corals were incubated in clear ~ 1 liter chambers under both light (560 μmol m^{-2} s^{-1}) and dark conditions for 1.3–2.4 h, with stir bars providing continuous water motion. Control chambers only contained a stir bar and no coral. Heat-stressed corals were incubated at 33°C, whereas control corals were incubated at 30°C. Heat-stressed corals were incubated prior to the control corals to minimize the risk of mortality due to cumulative heat stress exposure. Incubations were timed such that the variable temperature treatments were naturally at the same temperature as the constant treatments. At the beginning and end of each incubation, oxygen (Orion Star A323 RDO/DO meter, Thermo Fisher Scientific), salinity (YSI 85), pH, and temperature (Schott handylab pH 12, SI Analytics) were measured. The volume of the incubation seawater within the chambers was measured by pouring the seawater into a graduated cylinder after all measurements were completed. Hourly oxygen data were converted from percentage of O_2 saturation to μmol L^{-1} seawater using the equations of Garcia and Gordon (1992) and normalized to surface area (*see* below). Given the 12 : 12 h light : dark regime, P/R ratios were calculated as 12 h of gross P (= net $P + R$) divided by 24 h of R.

Calcification

Calcification rate was determined using the buoyant weighing technique (Jokiel et al. 1978) at the beginning and end of both the acclimation phase (including temperature ramp-up) and the heat stress test. The wet weight of the coral (minus the combined weight of the tile and epoxy) was converted to dry weight using the density of seawater based on measurements of salinity and temperature and the known density of aragonite (2.93 g cm^{-3}). Calcification rates were normalized to surface area and calculated as daily rates (mg d^{-1} cm^{-2}). Surface area was calculated as per Schoepf et al. (2019) using the relationship between coral skeletal mass (dry weight) and surface area determined via computed tomographic scans of skeletons of various sizes from the same coral species from the same location.

Statistical analyses

A three-way PERMANOVA was used to test whether preconditioning to either constant or variable temperatures for ~ 1.5 yr prior to the experiment impacted the physiological response to the three variability treatments and heat stress test. This was tested using the following five response variables measured during or at the end of the heat stress test: visual health score (after 9 d of heat stress), F_v/F_m (on the last day of the heat stress test), calcification, photosynthesis, and respiration rate. However, the effect of preconditioning was neither significant on its own, nor in any of the interactions with variability and heat stress (Table 2). Thus, data for the two preconditioning treatments were pooled for further analysis. Data were normalized prior to analysis due to different measurement scales. The PERMANOVA was performed using Euclidean distances, type III (partial) sums of squares, and 9999 permutations using the software Primer v7 with the PERMANOVA+ add-on package.

Table 1. Seawater temperature (°C) for all treatments during the experiment based on continuous logger measurements. Degree heating days (DHD) were calculated for the combined temperature ramp-up phase and heat stress test.

		Constant		Variable		Tidal	
		Control	Heated	Control	Heated	Control	Heated
Acclimation phase	Mean	30.04		30.36		30.56	
	SEM	0.01		0.02		0.02	
	n meas	6578		2720		2720	
	n tanks	4		4		4	
Temperature ramp-up	Mean	30.36	30.87	30.56	31.10	30.50	31.17
	SEM	0.01	0.04	0.05	0.06	0.05	0.05
	n meas	576	830	576	576	576	576
	n tanks	2	2	2	2	2	2
Heat stress test	Mean	30.23	32.38	30.29	32.53	30.64	32.66
	SEM	0.01	0.03	0.03	0.04	0.03	0.04
	n meas	1420	1429	1429	1429	1429	1429
	n tanks	2	2	2	2	2	2
DHD		0	26.5	0	28.6	0.6	29.7

Univariate statistical analyses were run separately for the acclimation phase and the phase involving heat stress and were performed in RStudio, R version 4.0.3 (R Core Team 2020). For the acclimation phase, linear mixed effect (LME) models were computed using the *lme4* package (Bates et al. 2015) for health score, F_v/F_m and Q_m. Variability regime (three levels: constant, variable, and tidal) and time (2–3 time points) were included as fixed factors. Time was included as a fixed factor because we were interested in whether the response variables changed over time; therefore, we included fragment ID (42 levels) to account for repeated measurements of individual coral fragments. Parent colony (five levels) was also included as a crossed random factor to account for colony-specific variability in physiological responses. Since assumptions associated with LME models were not met for health score and transformations were not successful, we instead ran a generalized linear mixed effects model (GLMM, Laplace approximation) using the *lme4* package and the Gamma distribution family (link = identity). The same model structure was used as for the LME models.

For the temperature ramp-up and heat stress phase, the above LME models were extended to include heat (two levels: control and heated) as a fixed effect in addition to variability regime and time, while fragment ID and parent colony remained random factors. However, with the exception of calcification rate, some modifications were required to account for response variables violating the assumptions of normality and homogeneity of variance (health score, F_v/F_m, Q_m) or the model failing to converge (health, F_v/F_m). For health score and F_v/F_m, GLMM models were computed (Gamma distribution family, link = identity) but time had to be converted to a random factor for the model to converge; thus, fragment ID was removed from the model and parent colony was the only other random factor for these variables. We additionally computed endpoint effects to test how variability regime and heat affected health score and F_v/F_m on the last two time points of the experiment. Q_m was cube root transformed to meet LME assumptions. Finally, photosynthesis and respiration rates were only measured once at the end of the experiment; thus a LME model was computed with variability regime and heat as fixed factors and parent colony as a random factor. Further details are provided in the Supplement. p-values < 0.05 were considered significant.

Results

Treatment conditions during the experiment

Seawater temperature, cumulative heat stress and carbonate chemistry for the acclimation phase, temperature ramp-up, and heat stress test are summarized in Tables 1 and 2, respectively. Seawater pH throughout the experiment was generally lower than ambient seawater (*see* Supplement for more details), with average values of ~ 7.8–7.9 that corresponded to pCO_2 levels of 520–780 μatm and an aragonite saturation state of 2.8–3.6 (Table S3).

Multivariate analysis and the effect of preconditioning

Preconditioning to either constant or variable temperatures for ~ 1.5 yr prior to the experiment did not significantly influence the overall physiological response as this effect was neither significant on its own, nor in any of the interactions with variability regime (during the experiment) and heat stress (Table 2). Thus, data for the two preconditioning treatments were pooled for univariate analyses (*see* below). However, the PERMANOVA also revealed that both variability regime and heat stress, as well as their interaction, significantly impacted physiological

Table 2. Results from three-way PERMANOVA analysis testing for the effect of preconditioning on the physiological response to temperature variability regimes and heat stress. Precond., preconditioning to either constant or variable temperatures; Var., variability treatments during the acclimation phase and heat stress test (three levels: constant, variable, and tidal); Heat, heat stress (two levels: control and heated); df, degrees of freedom; SS, sum of squares; MS, mean sum of squares; *P*(perm), permutational *p*-value; Unique perms, how many unique values of the test statistic were obtained under permutation. Significant *p*-values are highlighted in bold.

Effect	df	SS	MS	Pseudo-*F*	*P*(perm)	Unique perms
Precond.	1	6.65	6.65	1.70	0.2234	9963
Var.	2	36.17	18.09	4.63	**0.0033**	9960
Heat	1	57.03	57.03	14.60	**0.0001**	9959
Precond. × var.	2	4.22	2.11	0.54	0.6969	9974
Precond. × heat	1	2.73	2.73	0.70	0.5463	9967
Var. × heat	2	22.56	11.28	2.89	**0.0439**	9965
Precond. × var. × heat	2	4.73	2.36	0.60	0.6683	9962
Residuals	30	117.20	3.91			
Total	41	257.75				

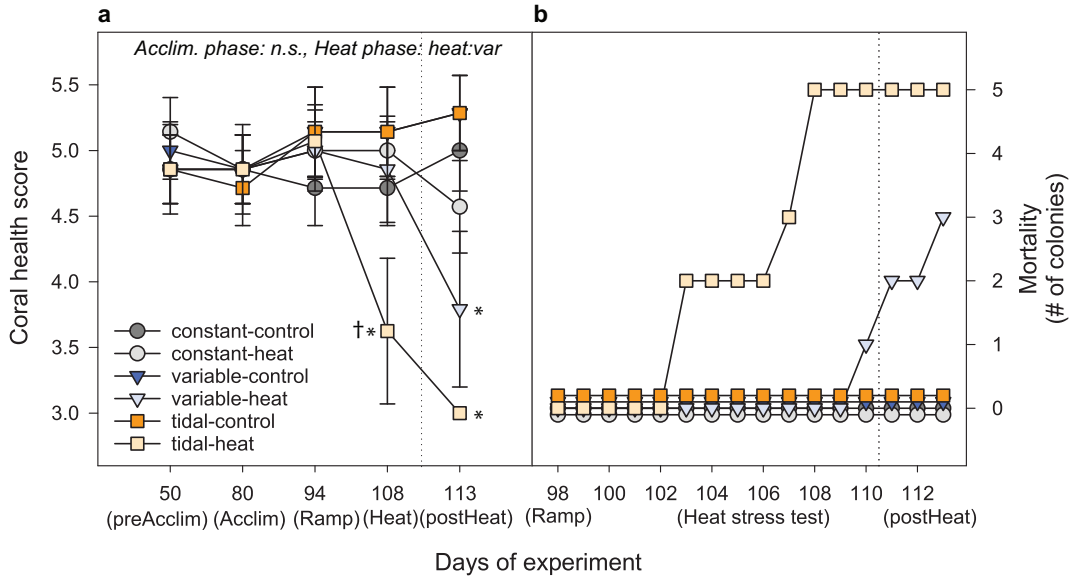

Fig. 3. Coral health. (**a**) Visual health of *A. aspera* (mean ± SEM) ~ 2 weeks prior to the start of the acclimation phase (preAcclim), 2.5 weeks after the acclimation phase had started (Acclim), at the start of the temperature ramp-up phase (Ramp), after 9 d of heat stress (Heat) and 3 d after the heat stress test (postHeat). (**b**) Number of colonies showing partial and/or full mortality during the last day of the temperature ramp-up (day 98), the heat stress test (days 99–110) and 3 d after the heat stress test (days 111–113). Numbers in the treatments without mortality are slightly offset from zero for visual purposes. Dotted vertical lines indicate the end of the heat stress test. Significant main effects are indicated in italics (*see* Tables S3, S4). *n.s.*, no significant main effects. Asterisks indicate significant differences between control and heated corals in each variability (= *var*) regime, whereas † indicates a significant difference between heated variable and heated tidal corals.

responses (Table 2). While heat stress did not significantly affect the physiology of corals maintained at constant temperatures during the experiment ($t = 1.26$, df = 10, $p = 0.20$), this was the case for corals in both the variable ($t = 2.07$, df = 10, $p = 0.02$) and tidal regime ($t = 3.68$, df = 10, $p = <0.01$).

Coral health and physiology during the acclimation phase

Coral health score was high (~ 5) and stable during the acclimation phase and was also not affected by variability regime (Fig. 3a; Table S4). The photochemical efficiency (F_v/F_m) significantly increased over time (+ 8%) but this effect also depended on variability regime (Fig. 4a; Table S4). Prior to the acclimation phase, there were no significant differences between treatments but during the second half of the acclimation phase, both constant and tidal corals had higher F_v/F_m than the variable corals (+4% and +6%, respectively). The excitation pressure over PSII (Q_m) was overall low (< 0.1) during the acclimation phase and, in contrast to F_v/F_m, stable over time,

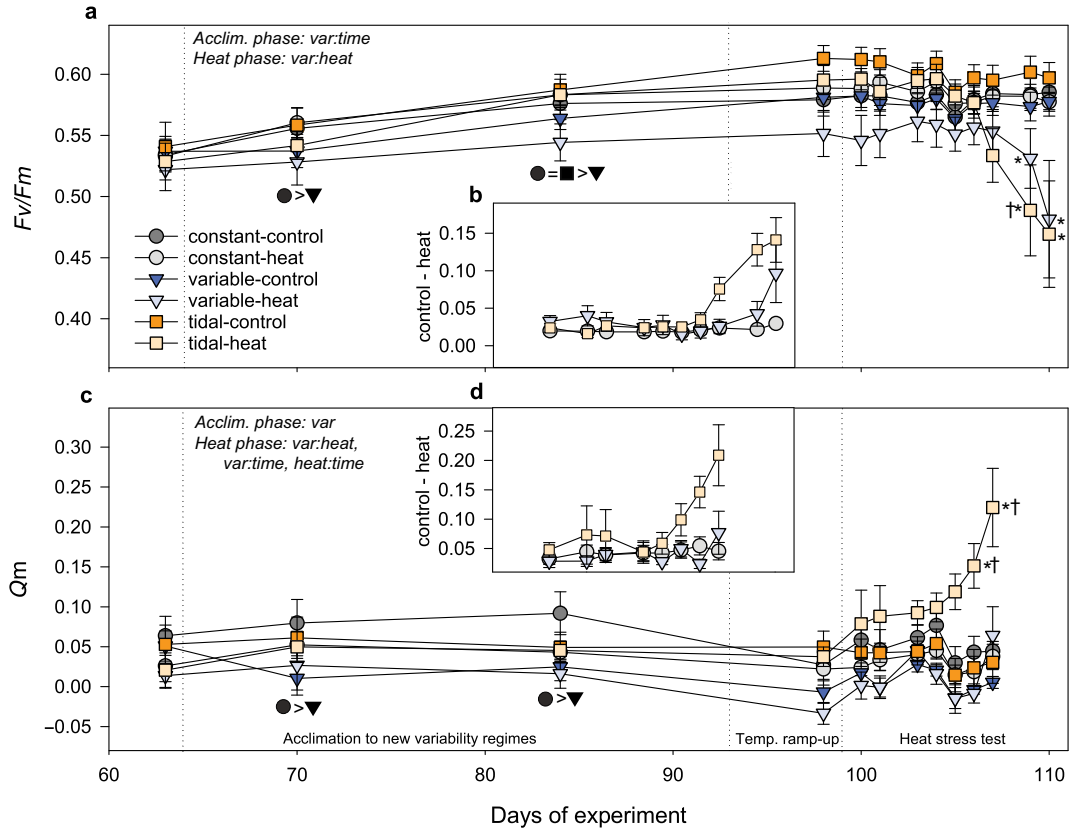

Fig. 4. Photophysiology (mean ± SEM). (**a**) Photochemical efficiency (F_v/F_m) and (**c**) maximum excitation pressure over photosystem II (Q_m) of *A. aspera* at various time points of the experiment. (**b**, **d**) Inserts show differences between control and heated corals during the temperature ramp-up phase and heat stress test. Significant main effects are indicated in italics (*see* Tables S3, S4). Asterisks indicate significant differences between control and heated corals in each variability (= *var*) regime, whereas † indicates a significant difference between heated variable and heated tidal corals. Symbols indicate which variability treatments differed significantly from each other (independent of heat). Post hoc tests for the heat phase were only conducted for the last two measurement time points.

but corals maintained at constant temperatures had significantly higher (+60%) Q_m than corals in the variable treatment (Fig. 4b; Table S4).

Coral health and physiology during the temperature ramp-up and heat stress phase

Coral health score was significantly affected by both variability regime and an interactive effect of variability and heat as heated corals in the variable and tidal regime increasingly lost their color (i.e., bleached) during the heat stress test (Fig. 3a; Table S5). After 9 d of heat stress (day 108), only heated tidal corals had significantly lower health scores (−30%) than their respective controls, whereas 3 d after the heat stress test had ended (day 113), this was also the case for heated variable corals (−28% and −43% for variable and tidal corals, respectively). In contrast, heated corals maintained under constant temperatures did not suffer from a significant loss of color at any time point. Coral mortality mirrored these patterns (Fig. 3b), with heated tidal corals dying earlier (from day 103) and at higher rates (n = 5 fragments) than heated variable corals (mortality from day 110, n = 3 fragments). No mortality occurred in any of the other treatments.

As for health score, significant effects of variability regime were observed for F_v/F_m but they depended on heat (Fig. 4a; Table S5). As heat stress progressed, heated corals in the variable and tidal regime increasingly experienced declines in F_v/F_m whereas this was not the case for constant heated corals. However, temporal trends differed slightly between these groups, with heated variable corals showing the earliest reductions in F_v/F_m. After the first week of the heat stress test, however, they were surpassed by heated tidal corals and after 10 d of heat stress (day 109), heated tidal corals not only had significantly lower F_v/F_m than their controls (−19%) but also significantly lower F_v/F_m than the heated variable corals (−8%). Nevertheless, 1 d later on the last day of heat stress (day 110), this difference was no longer significant, with heated variable and tidal corals now having 17% and 21% lower F_v/F_m than their respective control group.

Q_m showed a significant effect of variability regime and time; however, all two-way interaction terms including those

involving heat were also significant (Fig. 4b; Table S5). No significant differences between any treatments were observed during the first 5 d of the heat stress test but on day 6, heated corals in the tidal variability regime had significantly higher Q_m (+84%) than heated variable corals (though Q_m was not significantly higher than in the tidal controls). Q_m of heated tidal corals then continuously increased throughout the heat stress test (up to ~ 0.22), being 86% higher than in the tidal controls and 71% higher than in the heated variable corals after 9 d of heat stress (endpoint for Q_m). In contrast, neither heated variable nor heated constant corals ever showed significantly higher or lower Q_m than their respective controls at any point during the heat stress test.

Calcification rates were significantly influenced by variability regime, heat, and time; however, both the effect of variability regime and heat depended on the respective time point (Fig. 5; Table S5). During the combined acclimation and temperature ramp-up phase, neither heat nor variability regime significantly impacted calcification rates. However, during the heat stress phase, heated corals had significantly lower calcification rates (−83%) than the controls. Furthermore, corals maintained under the tidal variability regime had significantly lower calcification rates than corals maintained under either constant temperatures or in the variable treatment (−89% and −84%, respectively). This was largely due to heated tidal corals exhibiting negative calcification rates, that is, dissolution—the only treatment to do so.

The effects of variability regime and heat differed for photosynthesis and respiration rates as well as P/R ratios, and heat tended to have a greater effect than variability regime (Fig. 6; Table S6). Heated corals generally had significantly lower photosynthesis (−57%) but not respiration rates, resulting in 59% lower P/R ratios. Variability regime did not significantly affect either photosynthesis or respiration rates (although a weak interactive effect of variability and heat was detected for R, $p = 0.044$); however, corals in the tidal variability regime had significantly lower P/R ratios (−25%) than corals maintained under constant daily temperatures and this effect was independent of heat (Fig. 6b). Overall, heated tidal corals had the lowest P/R ratios of all treatments, barely exceeding the threshold where corals transition from net autotrophy ($P/R > 1$) to net heterotrophy ($P/R < 1$).

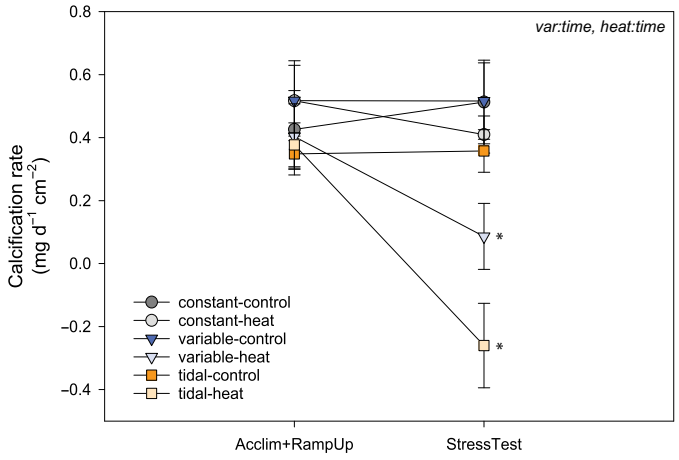

Fig. 5. Calcification (mean ± SEM). Calcification rates of *A. aspera* during the combined acclimation and temperature ramp-up phase as well as during the heat stress test. Significant main effects are indicated in italics (*see* Table S5). Asterisks indicate significant differences between control and heated corals in each variability (= *var*) regime.

Discussion

This study provides new insights into the effects of environmental history on coral stress tolerance and is one of the first to compare how different temperature variability regimes differ in their ability to alter heat resistance over two temporal scales in an intertidal coral population. Specifically, we found that daily temperature variability only altered heat tolerance when experienced in the recent past (~ 1 month vs. ~ 1.5 yr) and that it generally lowered heat tolerance compared to exposure to constant daily temperatures.

Effects of thermal history across two temporal scales

Although there is an increasing body of work demonstrating that a history of environmental variability has significant potential to alter coral resistance to climate change stressors (Rivest et al. 2017; Safaie et al. 2018; Kapsenberg and Cyronak 2019), few studies to date have specifically investigated the mechanisms and time scales over which environmental variability shapes stress tolerance. Many studies take advantage of natural gradients in environmental variability to compare the stress tolerance of coral populations along this gradient (Oliver and Palumbi 2011; Schoepf et al. 2015; Camp et al. 2016) but this approach, while powerful in detecting overall effects of environmental history, does not allow for distinguishing the underlying mechanisms. For example, environmental history may influence stress tolerance via long-term acclimatization and/or adaptation, environmental conditions experienced in the recent past (i.e., short-term acclimatization), carry-over effects across life stages or transgenerational acclimatization (Rivest et al. 2017), each mechanism acting over different temporal scales. In contrast, studies exposing corals to novel temperature conditions in the lab (Mayfield et al. 2012; Barshis et al. 2018; Schoepf et al. 2019) as well as reciprocal transplant experiments in combination with subsequent heat challenges (Palumbi et al. 2014; Klepac and Barshis 2020) enable us to better distinguish between short- and long-term acclimatization or adaptation or recent vs. native environment as dominant drivers of stress tolerance.

In the present study, preconditioning intertidal corals to either constant temperatures or 4°C daily temperature variability for ~ 1.5 yr had no effect on coral tolerance to a subsequent heat stress test. This finding is largely consistent with the lack of such an effect for this study species when

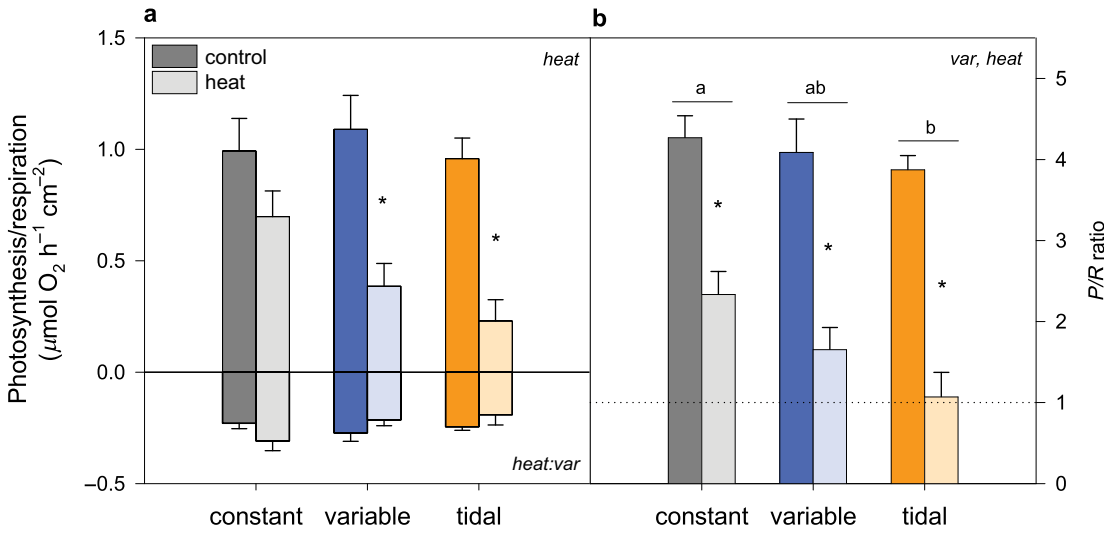

Fig. 6. Photosynthesis and respiration (mean ± SEM). (**a**) Net photosynthesis (*P*) and dark respiration (*R*) rates as well as (**b**) *P*/*R* ratios of *A. aspera* at the end of the heat stress test. Dotted line in (**b**) highlights the transition from net autotrophy (*P*/*R* > 1) to net heterotrophy (*P*/*R* < 1). Significant main effects are indicated in italics (*see* Table S6). Asterisks indicate significant differences between control and heated corals in each variability (= *var*) regime, whereas † indicates a significant difference between heated variable and heated tidal corals. Letters indicate which variability treatments differed significantly from each other (independent of heat).

preconditioning occurred over only ~ 9 months (Schoepf et al. 2019) (*see* Table S7 for how this study compares to previous work investigating the effects of temperature variability in corals from the macrotidal Kimberley region). Similarly, preconditioning *Porites lobata* corals from locations with differing levels of thermal variability to low and high thermal variation in common garden aquaria had minimal effects on their physiology and heat tolerance, although preconditioning only occurred for ~ 1 month (Barshis et al. 2018). Given that corals in the present study originated from an intertidal, highly variable temperature environment (up to 7°C daily temperature variability), it was expected that corals exposed to constant temperatures would have similar heat tolerance as the corals maintained under variable temperatures if long-term acclimatization and/or adaptation to high temperature variability at their native reef is the main mechanism shaping heat tolerance (Dixon et al. 2015; Kenkel et al. 2015; Barshis et al. 2018). In contrast, we expected them to have lower heat tolerance if it is primarily recent environmental conditions that shape future responses to heat stress (i.e., short-term acclimatization). For example, it has been shown that transplantation from highly variable to moderately variable temperature environments can lead to reduced heat tolerance in *Acropora hyacinthus* over 12–27 months (Palumbi et al. 2014). The lack of an observed effect of preconditioning suggests that intertidal *A. aspera* corals from the Kimberley region are long-term acclimatized or locally adapted to highly variable temperatures, which has led to enhanced bleaching resilience compared to conspecifics from the subtidal where daily temperature variability is much more moderate (Schoepf et al. 2020; Jung et al. 2021) (Table S7).

In contrast to the lack of an observed effect of long-term preconditioning, we found that thermal history experienced in the month prior to a heat stress event significantly altered bleaching sensitivity. This finding is in general agreement with several other laboratory studies investigating the effects of thermal history over similar time scales (i.e., days to ~ 1 month). For example, it has been shown that different heating rates (Middlebrook et al. 2010), thermal priming via short heat pulses (Bellantuono et al. 2012; Middlebrook et al. 2012; Ainsworth et al. 2016), or exposure to variable temperatures (Putnam and Edmunds 2011; Bay and Palumbi 2015) significantly influenced physiological responses and heat tolerance to subsequent heat stress. However, it is important to note that the majority of these studies observed that prior exposure to stressful temperatures or temperature variability improved heat tolerance (but see Putnam and Edmunds 2011; Schoepf et al. 2019; Klepac and Barshis 2020), whereas we observed the opposite (see below) and some studies also found no effect (Middlebrook et al. 2012; Barshis et al. 2018). Nevertheless, the results from this study highlight that recent thermal history can play an important role in shaping heat tolerance even when corals are long-term acclimatized or adapted to variable temperatures, such as in these intertidal corals from a highly fluctuating, macrotidal reef environment.

Daily temperature variability lowered coral heat tolerance and survival

Although a recent meta-analysis has shown that high-frequency temperature variability increases coral heat tolerance and lowers bleaching risk (Safaie et al. 2018), we found the opposite pattern as daily temperature variability of 4–5°C

significantly enhanced sensitivity to heat stress and mortality risk in both the variable and tidal regime. This is particularly highlighted by the fact that exposure to heat stress equivalent to ~ 27 DHDs in corals maintained at constant daily temperatures elicited only minor negative responses as they did not suffer significant color loss or mortality and maintained F_v/F_m and calcification rates (but they had 45% lower P/R ratios). While we observed a similar negative effect of temperature variability on heat tolerance of intertidal *A. aspera* in a previous lab experiment (Schoepf et al. 2019), it contradicts our findings of enhanced bleaching resilience for this coral population in the field (Schoepf et al. 2015; Le Nohaïc et al. 2017; Jung et al. 2021) (Table S7). So how can we reconcile these seemingly contradictory findings, and why does high-frequency temperature variability not always promote heat tolerance, as also observed in some other studies (Putnam and Edmunds 2011; Klepac and Barshis 2020)?

We propose that a specific exposure threshold exists that determines whether high-frequency temperature variability is beneficial and enhances heat tolerance or results in chronic stress that exacerbates cellular damage and reduces overall resilience. As a result, only certain variability exposure regimes would be beneficial, potentially explaining the range of responses observed to date. This proposed variability threshold likely depends on several factors that are cumulative in nature and, just like the existence of such a threshold itself, are currently poorly understood. Important factors likely include amplitude and duration, as it is well-established for coral bleaching thresholds and the degree heating week (DHW) measure of cumulative heat stress (Liu et al. 2014), frequency (Safaie et al. 2018), and heating rate (Middlebrook et al. 2010) as well as the relationship between local variability regime and the characteristics of a given stress trajectory (Rivest et al. 2017).

The existence of such a variability exposure threshold is supported by several lines of evidence. First, several studies that observed positive effects of daily temperature variability on coral heat tolerance only exposed corals to short periods of heat stress (8 h to 5 d), thus mimicking tidal heating and short heatwave events rather than the prolonged heat stress that typically causes bleaching events (Bay and Palumbi 2015; Barshis et al. 2018). If the heat stress test in this study had only lasted for 5 d, negative effects of daily temperature variability would not have been evident (based on measurements of F_v/F_m and Q_m, Fig. 4). Second, Klepac and Barshis (2020) also found reduced thermal tolerance in massive corals from a highly variable back-reef pool which contradicted previous work demonstrating enhanced heat tolerance in these corals (Barshis et al. 2010, 2018). This unexpected finding was attributed to a thermal anomaly (5–8 DHW) during the 12 months reciprocal transplant experiment that preceded the heat stress assay and may have exceeded the upper thermal limits of native *P. lobata* corals.

Third, this study showed that two different variability regimes with almost identical cumulative heat exposure on both a daily level (Tables 1, S2) and during the heat stress test (Table 1) differentially impacted coral heat tolerance. While both variability regimes increased sensitivity to heat stress, negative impacts were much more pronounced in the tidal variability regime for all responses measured. For example, tidal heated corals were the only treatment group to experience skeletal dissolution (Fig. 5) and P/R ratios indicating a transition from net autotrophy to net heterotrophy (P/R ~ 1; Fig. 6). It is possible that the more pronounced negative impacts on coral health were, at least in part, due to the fact that both daily average temperatures during the acclimation phase (30.56°C vs. 30.36°C) and cumulative heat exposure during the heat stress test (29.7 vs. 28.6 DHDs) were minimally higher in this treatment compared to the heated variable corals. However, given the small temperature differences, it seems more likely that other factors also played a role. For example, heated tidal corals spent less time daily at temperatures above the local bleaching threshold of ~ 31°C than the heated variable corals (5 vs. 9 h) but maximum daily temperatures were up to 2°C higher (34°C vs. 32°C), minimum daily temperatures were also higher (29°C vs. 28°C), they spent less time at the minimum daily temperatures (4 h at 29°C vs. 9 h at 28–29°C) and hourly heating rates were also higher (Fig. 2a; Table S2). In addition, maximum daily light levels were intentionally aligned with maximum daily temperatures in the tidal regime, whereas this was not the case in the variable regime, likely increasing overall stress in the heated tidal corals.

Finally, it is important to note that while the tidal regime mimicked the local variability regime at the collection site better than the variable regime (*see* Methods), the conditions simulated in the tidal regime are representative of spring rather than neap tides and thus the corals do not experience this kind of variability in their native environments for weeks on end. The acclimation phase demonstrated that intertidal corals can apparently cope with such extreme "spring-tide" temperature variability on a daily basis for prolonged periods of time, but suffer severe health declines and reduced heat tolerance when heat stress is super-imposed. The fact that we observed such contradictory findings of how strong daily temperature variability alters coral heat tolerance in this coral population (Table S7) further suggests the existence of a variability exposure threshold that is likely strongly dependent on the relationship between local variability regime and the characteristics of a given stress trajectory (Rivest et al. 2017).

Taken together, these lines of evidence suggest that (1) only certain variability exposures enhance coral stress tolerance depending on whether a time-integrated, cumulative exposure threshold is exceeded; (2) even when daily average temperatures and DHDs are very similar, stressor amplitude, time spent at both maximum and minimum daily temperatures (Mayfield et al. 2013), heating rate (Middlebrook et al. 2010), and covarying stressors play a key role in determining whether high-frequency temperature variability increases or lowers coral heat tolerance; and (3) when prolonged heat stress is

superimposed on an already highly variable temperature environment, protective mechanisms that enhance heat tolerance may quickly be overwhelmed—in some cases more easily or rapidly than in corals originating from or acclimated to more stable thermal environments (this study, Schoepf et al. 2019; Klepac and Barshis 2020).

Our findings provide new insights into how environmental history and different temperature variability regimes impact coral heat tolerance but it is important to note that seawater pH during the experiment was ~ 7.8–7.9 and thus lower than current ambient seawater pH (*see* Supplement for more details). We consider it unlikely that this significantly influenced coral heat tolerance because several independent studies have shown that bleaching sensitivity is not affected by seawater pH in six different coral species, including two *Acropora* species (e.g. Wall et al. 2013; Noonan and Fabricius 2015; Horvath et al. 2016). Importantly, one of these studies also mimicked daily temperature and pH variability in their treatments (van der Zande et al. 2020) and all tanks in our experiment received the same seawater, so that pH was similar across treatments (Table S3). Nonetheless, low seawater pH can impact several aspects of coral physiology, especially calcification (Chan and Connolly 2013; Kornder et al. 2018); therefore, when assessing absolute values of our response variables rather than comparing relative differences across treatments, this needs to be taken into account.

Conclusion

In summary, our study shows that a history of thermal variability had a greater effect on coral heat tolerance when experienced in the recent rather than distant past (~ 1 month vs. ~ 1.5 yr), at least in a population originating from a highly fluctuating, intertidal reef habitat. Further research is needed to determine whether corals from thermally less variable habitats, such as subtidal corals, show similar responses. In addition, our findings add to an increasing body of work demonstrating that strong daily temperature variability (4–5°C) can significantly lower coral heat tolerance when prolonged heat stress (12–18 d) is super-imposed on an already highly variable temperature regime (Putnam and Edmunds 2011; Schoepf et al. 2019; Klepac and Barshis 2020). While reef habitats with highly variable temperatures may select more effectively for heat-resistant genotypes than those with moderate variability (Palumbi et al. 2014; Kenkel et al. 2015; Schoepf et al. 2015), it is precisely the most variable habitats that may be at greatest risk during severe heat stress events because the combination of elevated background temperatures and natural variability may drive daily temperature maxima beyond sublethal thresholds (Klepac and Barshis 2020). Future research should therefore focus on identifying potential variability exposure thresholds as well as optimal variability characteristics such as amplitude, duration, and frequency to increase our understanding of when natural variability will mitigate or amplify bleaching and mortality risk.

Data availability statement

Data will be made available after publication in the online open access data repository Figshare.

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Conflict of Interest

None declared.

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