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

Running head: Coral tolerance to variable heat stress

Verena Schoepf[1,2,3*], Hermione Sanderson[2,3,4], Ellis Larcombe[2,3,4, 5]

[1]Department of Freshwater and Marine Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Science Park 904, 1098 XH Amsterdam, The Netherlands

[2]Oceans Graduate School and UWA Oceans Institute, The University of Western Australia, 35 Stirling Highway, Perth WA 6009, Australia

[3]ARC Centre of Excellence for Coral Reef Studies, The University of Western Australia, 35 Stirling Highway, Perth WA 6009, Australia

[4]Department of Biosciences, Swansea University, Swansea, SA2 8PP, United Kingdom

[5]Present address: Institute of Biomedical and Environmental Health, School of Health and Life Sciences, University of the West of Scotland, Paisley, United Kingdom

*Corresponding author: Verena Schoepf (v.schoepf@uva.nl)

Orcid ID Verena Schoepf: 0000-0002-9467-1088

Orcid ID Ellis Larcombe: 0000-0002-1609-6954

Keywords: coral heat tolerance, environmental history, environmental variability, temperature, light, physiology

Supplemental Information

Additional Methods

Recovery of heat-stressed corals during the pre-conditioning phase

During the pre-conditioning phase, some colonies (C, D, E) were exposed to elevated temperatures (~32.4°C) from 17-30 May 2017 as part of the stress test in Schoepf et al. (2019), whereas others (A, B) served as ambient controls. Immediately after the stress test, temperature was returned to ambient seasonal temperatures, thus allowing the heat-stressed corals to recover for more than 8 months (1 June 2017 – 5 February 2018). Coral photochemical efficiency, calcification and visual health data show that they were fully recovered after 2, 4 and 8 weeks of recovery, respectively, when their values were no longer significantly different from the colonies that were not exposed to elevated temperatures (see below for details).

Coral photochemical efficiency (Fv/Fm), visual health and calcification rates were recorded every 2-4 weeks to monitor recovery following the methods described in the main text. t-tests were used to determine when values of recovering corals were no longer different from those of the ambient controls, i.e. by when they could be considered fully recovered with respect to these variables. Normality and homogeneity of variance was checked using the Shapiro-Wilk and F-test, respectively. When both assumptions were met, Student's t-test was used whereas the Welch's test was used when variances were not equal. When neither assumption was met, the non-parametric Wilcoxon test was used. All statistical analyses were run in R software.

Photochemical efficiency was already fully recovered 2 weeks after the heat stress test as Fv/Fm was no longer significantly different between control and recovering corals ($t = 1.6904$, df

= 5, p-value = 0.1517). Calcification rates measured 4 weeks after the heat stress test also showed no significant difference between control and recovering corals (Student's t = 0.37308, df = 5, p-value = 0.7244). Coral visual health was still significantly lower (-22%) in recovering compared to control corals 6 weeks after the heat stress test (Welch's t = 4.4907, df = 4, p-value = 0.0109) but that was no longer the case after 8 weeks (Wilcoxon's W = 7.5, p-value = 0.2059). Thus, with respect to these measurements, corals were fully recovered within 2-8 weeks after the heat stress test, while the pre-conditioning phase continued for another 6 months after this time period. Nevertheless, we acknowledge that other aspects of their physiology may not have been fully recovered, though we consider this unlikely given that (i) elevated temperatures during the stress test were only ~0.6°C above their bleaching threshold, (ii) heat stress only lasted for 2 weeks, (iii) recovery lasted for more than 8 months and (iv) corals were regularly fed throughout this period which has been shown to enhance recovery (e.g. Connolly et al. 2012).

Temperature variability experiment

Tidal light regime

From 2 Feb to 28 March 2018, light levels were 1 µmol m^{-2} s^{-1} at 06:00, 300 at 08:00, 560 at 11:00, 300 at 11:30 and 0 at 18:00, with gradual increases/decreases between set points. Light intensity in the morning and afternoon (but not maximum light levels at 11am) was then slightly increased from 29 March onwards for the rest of the temperature variability experiment and heat stress test (1 µmol m^{-2} s^{-1} at 06:00, 400 at 08:00, 560 at 11:00, 400 at 11:30 and 0 at 18:00; Fig. 2b).

Monitoring of experimental conditions

Due to logger malfunctioning, temperature was not recorded in one tank from 10 April – 10 May 2018 (constant heat-stress replicate tank #2). Therefore, during this time, we used data from the Apex temperature probe (10 min logging interval) for this tank to calculate treatment averages (Table 1).

From the acclimation phase onwards, pH_T, salinity and temperature were measured at ~weekly time intervals in each tank around noon using a Schott Handylab pH 12 electrode (SI Analytics, Xylem Analytics, Germany; calibrated using TRIS buffer) and YSI 85 salinity meter (YSI, Yellow Springs, OH, USA), respectively. Water samples were also collected for total alkalinity (A_T) analyses. These measurements revealed that pH (total scale) in the tanks was somewhat lower (~7.8 – 7.9) than ambient seawater pH but similar across treatments since all tanks received the same water (Table S3). Several independent studies have shown that bleaching sensitivity of 6 different coral species (including *Acropora* spp.) is not affected by seawater pH (Wall et al. 2013, 2018; Noonan and Fabricius 2015; Horvath et al. 2016; van der Zande et al. 2020); thus, the effect of the different temperature variability regimes on coral heat tolerance tested here should be independent of seawater pH. Water samples for alkalinity were refrigerated at ~2°C and analysed within 3 days or less. A_T of water samples and certified reference materials provided by A.G. Dickson was analysed using potentiometric titration on a Mettler Toledo T50 titrator (Greifensee, Switzerland) and calculated using a modified Gran function, as described in Dickson et al. (2007). A_T, pH_T, temperature and salinity were then used to calculate seawater carbonate chemistry using the seacarb package in R and the constants recommended by Dickson et al. (2007).

Statistical analyses

For LME models, significance of fixed effects were determined using Type-III sum of squares with Satterthwaite approximate of degrees of freedom from the *lmerTest* package (Kuznetsova et al. 2017). Significance of random effects was assessed using the ranova() function in *lmerTest* whereby each random-effect term is reduced or removed and likelihood ratio tests of model reductions are presented. For GLMM models, significance of fixed effects was determined using the Anova() function from the *car* package (Fox and Weisberg 2019), which provided Analysis of Deviance tables (Type III Wald chisquare tests). Since these are known to be anti-conservative, a stricter significance level of $p \leq 0.01$ was adopted for GLMM models. Pairwise contrasts were conducted using the *emmeans* package (Lenth 2021) when main effects and/or interaction terms were significant, with Tukey adjusted *p*-levels and the Kenward-Roger degrees-of-freedom method. Assumptions of normality and homoscedasticity for LME models were assessed using visual assessment of the residuals.

References

Connolly, S. R., M. A. Lopez-Yglesias, and K. R. N. Anthony. 2012. Food availability promotes rapid recovery from thermal stress in a scleractinian coral. Coral Reefs **31**: 951–960. doi:10.1007/s00338-012-0925-9

Dandan, S. S., J. L. Falter, R. J. Lowe, and M. T. McCulloch. 2015. Resilience of coral calcification to extreme temperature variations in the Kimberley region, northwest Australia. Coral Reefs **34**: 1151–1163. doi:10.1007/s00338-015-1335-6

Dickson, A. G., C. L. Sabine, and J. R. Christian. 2007. Guide to Best Practices for Ocean CO2 Measurements. PICES Spec. Publ. **3**: 191pp.

Fox, J., and S. Weisberg. 2019. An R Companion to Applied Regression, Third. Sage.

Horvath, K. M., K. D. Castillo, P. Armstrong, I. T. Westfield, T. Courtney, and J. B. Ries. 2016. Next-century ocean acidification and warming both reduce calcification rate, but only acidification alters skeletal morphology of reef-building coral Siderastrea siderea. Sci. Rep. **6**: 1–12. doi:10.1038/srep29613

Jung, E. M. U., M. Stat, L. Thomas, A. Koziol, and V. Schoepf. 2021. Coral host physiology and symbiont dynamics associated with differential recovery from mass bleaching in an extreme, macro-tidal reef environment in northwest Australia. Coral Reefs 1–13. doi:10.1007/s00338-021-02094-x

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. lmerTest Package: Tests in Linear Mixed Effects Models . J. Stat. Softw. **82**: 1–26. doi:10.18637/jss.v082.i13

Lenth, R. V. 2021. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.5.4.

Le Nohaïc, M., C. L. Ross, C. E. Cornwall, S. Comeau, R. Lowe, M. T. McCulloch, and V.

Schoepf. 2017. Marine heatwave causes unprecedented regional mass bleaching of thermally resistant corals in northwestern Australia. Sci. Rep. **7**: 14999. doi:10.1038/s41598-017-14794-y

Noonan, S. H. C., and K. E. Fabricius. 2015. Ocean acidification affects productivity but not the severity of thermal bleaching in some tropical corals. ICES J. Mar. Sci. J. du Cons. doi:10.1093/icesjms/fsv127

Schoepf, V., S. A. Carrion, S. M. Pfeifer, M. Naugle, L. Dugal, J. Bruyn, and M. McCulloch. 2019. Stress-resistant corals may not acclimatize to ocean warming but maintain heat tolerance under cooler temperatures. Nat. Commun. **10**: 4031. doi:10.1038/s41467-019-12065-0

Schoepf, V., J. P. D'Olivo, C. Rigal, E. M. U. Jung, and M. T. McCulloch. 2021. Heat stress differentially impacts key calcification mechanisms in reef-building corals. Coral Reefs. doi:10.1007/s00338-020-02038-x

Schoepf, V., E. M. U. Jung, M. McCulloch, N. E. White, M. Stat, and L. Thomas. 2020. Differential recovery from mass coral bleaching on naturally extreme reef environments in NW Australia. MarXiv. doi:10.31230/OSF.IO/S9XHA

Schoepf, V., M. Stat, J. L. Falter, and M. T. McCulloch. 2015. Limits to the thermal tolerance of corals adapted to a highly fluctuating, naturally extreme temperature environment. Sci. Rep. **5**: 17639. doi:10.1038/srep17639

Wall, C. B., T. Y. Fan, and P. J. Edmunds. 2013. Ocean acidification has no effect on thermal bleaching in the coral Seriatopora caliendrum. Coral Reefs 1–12. doi:10.1007/s00338-013-1085-2

Wall, C. B., C. A. Ricci, G. E. Foulds, L. D. Mydlarz, R. D. Gates, and H. M. Putnam. 2018. The effects of environmental history and thermal stress on coral physiology and immunity. Mar. Biol. **165**: 56. doi:10.1007/s00227-018-3317-z

van der Zande, R. M., M. Achlatis, D. Bender-Champ, A. Kubicek, S. Dove, and O. Hoegh-Guldberg. 2020. Paradise lost: End-of-century warming and acidification under business-as-usual emissions have severe consequences for symbiotic corals. Glob. Chang. Biol. gcb.14998. doi:10.1111/gcb.14998

Supplementary Tables

Table S1: Monthly seasonal sea surface temperature (SST) data for the Kimberley region in Western Australia. The SST data served as target temperatures during the pre-conditioning phase. Data sourced from the U.S. National Oceanic and Atmospheric Administration (NOAA), Coral Reef Watch (version 2), 5-km virtual station "North Western Australia".

Month	SST (°C)
January	30.1
February	30.2
March	30.6
April	30.8
May	29.7
June	27.9
July	26.1
August	25.6
September	26.5
October	28.0
November	29.3
December	29.6
Average	28.7

Table S2: Daily temperature variability regimes and hourly temperature offset (°C) of the variable treatments relative to the constant control. Following the principle of degree heating days (see Methods), cumulative hourly heat stress exposure was calculated as "degree heating hours" (DHH) where all positive hourly temperature anomalies (i.e. those exceeding the control temperature of ~30°C, highlighted in bold) were summed up. Treatments were designed so that they had almost identical average daily temperatures as well as cumulative hourly heat stress exposure (DHH) for the variable and tidal treatments.

Time	constant	variable	tidal	offset - variable	offset - tidal
05:00	30	28	30	-2	0
06:00	30	29	31.5	-1	**1.5**
07:00	30	29	31.5	-1	**1.5**
08:00	30	29	31.5	-1	**1.5**
09:00	30	30	34	0	**4**
10:00	30	30	34	0	**4**
11:00	30	30	30	0	0
12:00	30	31	30	**1**	0
13:00	30	31	30	**1**	0
14:00	30	31	30	**1**	0
15:00	30	32	30	**2**	0
16:00	30	32	30	**2**	0
17:00	30	32	30	**2**	0
18:00	30	31	30	**1**	-1
19:00	30	31	29	**1**	-1
20:00	30	31	29	**1**	-1
21:00	30	30	29	0	-1
22:00	30	30	29	0	0
23:00	30	30	30	0	0
00:00	30	29	30	-1	0
01:00	30	29	30	-1	0
02:00	30	29	30	-1	0
03:00	30	28	30	-2	0
04:00	30	28	30	-2	0
Average	30.00	30.00	30.35		
DHH				12.00	12.50

Table S3: Seawater carbonate chemistry based on discrete water samples. Mean ± s.e.m. The number of measurements (n) varied between experimental phases due to their different duration. Data from replicate tanks were averaged for each sampling day and experimental phase. A_T = total alkalinity, Ω_{arag} = aragonite saturation state.

		n	Temp. (°C)	Salinity (ppt)	pH_T	A_T (µmol kg^{-1})	pCO_2 (µatm)	Ω_{arag}
(a) acclimation phase								
constant		16	30.24 ±0.11	37.06 ±0.05	7.85 ±0.01	2363 ±2.6	689 ±12	2.97 ±0.04
variable		16	30.50 ±0.16	37.06 ±0.04	7.84 ±0.004	2363 ±2.9	712 ±9	2.93 ±0.03
tidal		16	30.33 ±0.08	37.04 ±0.05	7.84 ±0.01	2362 ±2.7	705 ±10	2.93 ±0.03
(b) temperature ramp-up phase								
constant	control	2	29.90 ±0.30	36.90 ±0.00	7.83 ±0.01	2356 ±0.2	726 ±29	2.81 ±0.05
	heated	2	31.20 ±0.20	36.90 ±0.00	7.82 ±0.02	2358 ±0.3	746 ±50	2.89 ±0.12
variable	control	2	30.20 ±0.20	36.95 ±0.05	7.84 ±0.01	2356 ±1.5	706 ±23	2.89 ±0.08
	heated	2	30.90 ±0.30	36.90 ±0.00	7.81 ±0.002	2354 ±0.7	753 ±4	2.83 ±0.04
tidal	control	2	30.45 ±0.05	36.90 ±0.10	7.81 ±0.01	2360 ±0.3	760 ±23	2.78 ±0.06
	heated	2	30.75 ±0.05	36.90 ±0.00	7.80 ±0.01	2357 ±1.0	777 ±17	2.76 ±0.05
(c) heat stress test								
constant	control	4*	30.58 ±0.28	36.63 ±0.11	7.92 ±0.04	2340 ±9.0	518 ±50	3.56 ±0.21
	heated	4*	32.33 ±0.35	36.60 ±0.08	7.89 ±0.03	2340 ±3.8	550 ±55	3.67 ±0.22
variable	control	4*	30.18 ±0.11	36.53 ±0.09	7.91 ±0.02	2339 ±6.8	563 ±42	3.33 ±0.12
	heated	4*	32.83 ±0.20	36.65 ±0.10	7.89 ±0.03	2350 ±8.7	586 ±57	3.58 ±0.24
tidal	control	4*	29.95 ±0.09	36.48 ±0.09	7.91 ±0.04	2341 ±6.5	554 ±63	3.37 ±0.23
	heated	4*	32.50 ±0.26	36.55 ±0.03	7.89 ±0.03	2335 n/a	535 n/a	3.56 n/a

* *temp, salinity, pH: n=4; all other parameters: CC n=3, CH n=2, VC n=3, VH n=3, TC n=3, TH n=1*

Table S4: Results from (generalized) linear mixed models testing for the effects of variability regime and time on health score, Fv/Fm and Qm of *Acropora aspera* during the acclimation phase. Parent colony and fragment ID were included as random factors. var (fixed effects) = variability regime. Df = degrees of freedom. *Var.* (random effects) = variance. SD = Standard deviation. SS = sum of squares. MS = mean squares. For LME random effects, the % of the residual variance explained by the random effect is indicated in the posthoc column. Npar = number of model parameters. LRT = likelihood ratio test statistic. Significant p-values are highlighted in bold.

GLMM MODELS				**Df**	**Chisq**	**p(>Chisq)**	**Posthoc**
Health (GLMM, Gamma, Link = identity)							
var				2	0.68	0.7128	
time				1	1.76	0.1849	
var:time				2	0.25	0.8846	
Random effects		*Var.*	*SD*				
colony	intercept	0.07	0.27				
fragment ID	intercept	0.06	0.24				
residual		<0.01	<0.01				

LME MODELS	**SS**	**MS**	**NumDF**	**DenDF**	**F**	**p(>F)**	**Posthoc**
Fv/Fm (LME)							
var	0.002	0.001	2	34.89	2.77	0.0764	
time	0.035	0.018	2	78.00	64.48	**<0.0001**	all sign. different
var:time	0.003	0.001	4	78.00	3.13	**0.0193**	see text
random effect	*npar*	*logLik*	*AIC*	*LRT*	*Df*	*p(>Chisq)*	
none	12	262.34	-500.69				
colony	11	254.47	-486.95	15.74	1	**0.0001**	48%
fragment ID	11	240.53	-459.05	43.63	1	**<0.0001**	33%
Qm (LME)							
var	0.009	0.004	2	34.98	3.52	**0.0406**	constant > variable

time	0.002	0.001	2	78.00	0.75	0.4776	
var:time	0.007	0.002	4	78.00	1.38	0.2475	
random effect	*npar*	*logLik*	*AIC*	*LRT*	*Df*	*p(>Chisq)*	
none	12	187.70	-351.40				
colony	11	180.60	-339.20	14.20	1	**0.0002**	37%
fragment ID	11	178.69	-335.38	18.02	1	**<0.0001**	27%

Table S5: Results from (generalized) linear mixed models testing for the effects of variability regime, heat and time on health score, Fv/Fm, Qm and calcification rate of *Acropora aspera* during the temperature ramp-up and heat stress phase. Model structure varied slightly for each response variable (see Methods). var (fixed effects) = variability regime. Df = degrees of freedom. *Var.* (random effects) = variance. SD = Standard deviation. SS = sum of squares. MS = mean squares. For LME random effects, the % of the residual variance explained by the random effect is indicated in the posthoc column. Npar = number of model parameters. LRT = likelihood ratio test statistic. Significant p-values are highlighted in bold.

GLMM MODELS				**Df**	**Chisq**	**p(>Chisq)**	**Posthoc**
Health - heat stress phase (GLMM, Gamma, link=identity)							
heat				1	0.11	0.7404	
var				2	11.06	**0.0040**	none sign.
heat:var				2	12.60	**0.0018**	see text
Random effects		*Var.*	*SD*				
colony	intercept	0.11	0.34				
time	intercept	0.03	0.17				
residual		0.02	0.15				
Health after 9 days of heat stress (day 108) (GLMM, Gamma, link=identity)							
heat				1	2.02	0.1550	
var				2	61.51	**<0.0001**	constant = variable > tidal
heat:var				2	42.81	**<0.0001**	see text
Random effects		*Var.*	*SD*				
colony	intercept	0.21	0.45				
residual		0.01	0.11				
Health 3 days after end of heat stress test (day 113) (GLMM, Gamma, link=identity)							
heat				1	0.60	0.4386	
var				2	15.28	**0.0005**	constant ≠ tidal
heat:var				2	10.77	**0.0046**	see text

Random effects		*Var.*	*SD*				
colony	intercept	0.21	0.46				
residual		0.03	0.18				
Fv/Fm - heat stress phase (GLMM, Gamma, link=identity)							
var				2	68.76	**<0.0001**	constant = tidal > variable
heat				1	0.87	0.3517	
var:heat				2	45.53	**<0.0001**	see text
Random effects		*Var.*	*SD*				
colony	intercept	<0.01	0.01				
time	intercept	<0.01	0.01				
residual		<0.01	0.05				
Fv/Fm after 10 days of heat stress (day 109) (GLMM, Gamma, link=identity)							
var				2	64.21	**<0.0001**	constant > variable = tidal
heat				1	0.001	0.9753	
var:heat				2	46.76	**<0.0001**	see text
Random effects		*Var.*	*SD*				
colony	intercept	<0.01	0.02				
residual		<0.01	0.05				
Fv/Fm after 11 days of heat stress (day 110) (GLMM, Gamma, link=identity)							
var				2	22.90	**<0.0001**	constant > variable = tidal
heat				1	0.026	0.8720	
var:heat				2	12.58	**0.0019**	see text
Random effects		*Var.*	*SD*				
colony	intercept	<0.01	0.03				
residual		0.01	0.11				

LME MODELS	**SS**	**MS**	**NumDF**	**DenDF**	**F**	**p(>F)**	**Posthoc**
Qm - heat stress phase (LME)							
var	0.08	0.04	2	29.41	8.19	**0.0015**	variable ≠ tidal
heat	0.01	0.01	1	29.73	1.36	0.2530	
time	0.15	0.02	7	157.89	4.27	**0.0002**	see text

var:heat	0.05	0.03	2	29.50	4.99	**0.0136**	see text
var:time	0.14	0.01	14	157.53	1.98	**0.0223**	see text
heat:time	0.21	0.03	7	157.90	5.91	**<0.0001**	see text
var:heat:time	0.10	0.01	14	157.60	1.46	0.1323	
random effects	*npar*	*logLik*	*AIC*	*LRT*	*Df*	*p(>Chisq)*	
none	51	160.69	-219.38				
colony	50	160.61	-221.22	0.16	1	0.6936	3%
fragment ID	50	127.08	-154.17	67.21	1	**<0.0001**	55%
Calcification - entire experiment (LME)							
var	0.45	0.23	2	31.87	7.27	**0.0025**	constant = variable > tidal
heat	0.35	0.35	1	31.87	11.24	**0.0021**	control > heated
time	0.55	0.55	1	36.00	17.50	**0.0002**	acclim > stress
var:heat	0.17	0.08	2	31.87	2.65	0.0865	
var:time	0.32	0.16	2	36.00	5.18	**0.0105**	see text
heat:time	0.78	0.78	1	36.00	25.04	**<0.0001**	see text
var:heat:time	0.19	0.10	2	36.00	3.08	0.0584	
random effects	*npar*	*logLik*	*AIC*	*LRT*	*Df*	*p(>Chisq)*	
none	15	-7.49	44.97				
colony	14	-13.89	55.77	12.80	1	**0.0003**	42%
fragment ID	14	-10.04	48.08	5.10	1	**0.0239**	22%

Table S6: Results from linear mixed effect models testing for the effects of variability regime and heat on photosynthesis (P) and respiration (R) rate as well as P/R ratios of *Acropora aspera*. Parent colony was included as random factor. Var. = variability regime. SS = sum of squares. MS = mean squares. Df = degrees of freedom. Significant p-values are highlighted in bold. For random effects, the % of the residual variance explained by the random effect is indicated in the posthoc column. Npar = number of model parameters. LRT = likelihood ratio test statistic.

	SS	MS	NumDF	DenDF	F	p(>F)	Posthoc
Photosynthesis							
var	0.33	0.16	2	29.15	2.28	0.1205	
heat	2.95	2.95	1	29.18	41.01	**<0.0001**	control > heated
var:heat	0.37	0.18	2	29.15	2.56	0.0946	
random effect	*npar*	*logLik*	*AIC*	*LRT*	*Df*	*p(>Chisq)*	
none	8	-11.92	39.847	0.00	0	0.0000	
colony	7	-14.56	43.129	5.28	1	**0.0216**	32%
Respiration							
var	0.01	0.01	2	29.02	1.19	0.3200	
heat	0.00	0.00	1	29.06	0.11	0.7379	
var:heat	0.04	0.02	2	29.02	3.49	**0.0438**	None sign.
random effect	*npar*	*logLik*	*AIC*	*LRT*	*Df*	*p(>Chisq)*	
none	8	30.93	-45.852	0.00	0	0.0000	
colony	7	29.45	-44.908	2.94	1	0.0862	25%
P/R ratio							
var	3.83	1.92	2	29.36	4.41	**0.0212**	constant > tidal
heat	51.82	51.82	1	29.40	119.23	**<0.0001**	control > heated
var:heat	1.03	0.51	2	29.36	1.18	0.3213	
random effect	*npar*	*logLik*	*AIC*	*LRT*	*Df*	*p(>Chisq)*	
none	8	-41.06	98.12	0.00	0	0.0000	
colony	7	-42.99	99.97	3.86	1	**0.0496**	25%

Table S7: Overview of research published to date to investigate the effects of temperature variability on coral physiology and heat tolerance in the macrotidal Kimberley region in NW Australia. The effects of temperature variability were investigated by comparing (1) corals from intertidal and subtidal habitats (high vs moderate daily temperature variability, respectively), or (2) different temperature variability regimes in the aquarium-based experiments. Studies highlighted in green indicate a positive effect of highly variable temperatures on coral heat tolerance, blue indicates no effect and red indicates a negative effect. Studies without highlighting demonstrated more complex effects.

Type of study	Main finding
(a) Field observations	
Dandan et al. 2015: Seasonal in situ calcification rates for three coral species from three habitats (intertidal[1], intermediate, subtidal)	Massive *Dipsastraea favus* and *Trachyphyllia geoffroyi* calcified faster in the intertidal/intermediate habitat, whereas branching *Acropora aspera* calcified faster in the subtidal
Le Nohaïc et al. 2017: Coral community composition and health status before and during the 2016 mass bleaching event (intertidal, subtidal)	Both intertidal and subtidal coral communities suffered from extensive bleaching, but the subtidal coral community had a greater percentage of severely bleached corals
Schoepf et al. 2020: Coral community composition and health status six months after the 2016	The intertidal coral community was fully recovered six months after the 2016 mass bleaching event, whereas the subtidal community suffered extensive mortality

mass bleaching event (intertidal, subtidal)	
Schoepf et al. 2021: Coral calcification mechanisms and skeletal trace element composition of *A. aspera* during a heatwave and "normal" year (intertidal, subtidal)	The biomineralization response was generally highly sensitive to heat stress but did not differ between thermally distinct reef habitats (intertidal vs subtidal)
Jung et al. 2021: Energy reserves, symbiont community composition, cell density and chlorophyll a concentration of *A. aspera* during and six months after the 2016 mass bleaching event (intertidal, subtidal)	Subtidal corals were more severely bleached than intertidal corals and suffered greater mortality. *Cladocopium* dominated all corals, but symbiont community composition differed significantly between environments and between bleached and healthy subtidal corals. Bleaching resilience was decoupled from energy reserve levels/catabolization.
(b) Experimental (aquarium-based) studies	
Schoepf et al. 2015: Aquarium-based heat stress test comparing the heat tolerance of two coral species from two habitats (intertidal, subtidal)	Intertidal corals of both species (*A. aspera*, *Dipsastraea* sp.) had higher heat tolerance and survival than subtidal conspecifics
Schoepf et al. 2019: Long-term exposure of intertidal *A. aspera* to warmer and cooler temperatures	Exposure to daily, symmetric temperature variability of 4°C over 9 months lowered coral heat tolerance compared to corals maintained at constant daily

under both constant and variable temperatures, followed by a heat stress test (intertidal only)	temperatures. Long-term exposure to 3-6°C cooler temperature did not affect heat tolerance. In contrast, corals were not able to acclimatize to +1°C warming over 6 months.
This study: Effects of short- and long-term environmental history and two different variability regimes on heat tolerance of intertidal *A. aspera* (intertidal only)	Pre-conditioning to constant vs variable temperatures for 1.5 years 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 physiological responses, with corals exposed to both types of variability having lower heat tolerance.

[1]referred to as 'isolated' in Dandan et al. 2015

Supplementary Figures

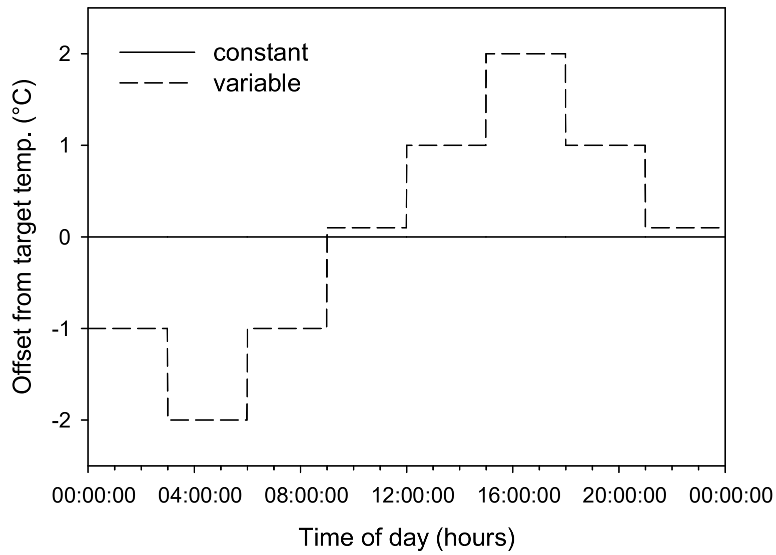

Figure S1: Daily temperature variability during the pre-conditioning phase, i.e. prior to the temperature variability experiment. Schematic of the temperature regimes in treatments with constant daily temperature versus 4°C daily variability from 1 August 2016 until 5 Feb 2018.