

1 Natural thermal stress-hardening of corals through 2 cold temperature pulses in the Thai Andaman Sea

3
4 Marlene Wall^{1,2}, Talisa Doering^{1,3}, Nina Pohl¹, Lalita Putchim⁴, Tipwimon Ratanawongwan⁵, Anna Roik^{2,6}

5
6 ¹GEOMAR, Helmholtz Centre for Ocean Research, Kiel, Germany

7 ²Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research, Bremerhaven, Germany

8 ³School of BioSciences, University of Melbourne, Parkville, VIC, Australia

9 ⁴Marine and Coastal Resources Research Center, Upper Eastern Gulf of Thailand, Songklong, Bangpakong,
10 Chachoengsao 24130

11 ⁵Marine and Coastal Resources Research Center Lower Andaman Sea, Sikao District, Trang 92150, Thailand

12 ⁶Helmholtz Institute for Functional Marine Biodiversity at the University of Oldenburg (HIFMB), Oldenburg,
13 Germany

14
15 Keywords

16 thermal variability, coral, bleaching, short-term acute heat stress, thermal resistance, thermal tolerance, plasticity,
17 environmental history, large amplitude internal waves, solitons, Thailand, Andaman Sea

18 Abstract

19
20 Thermal variability can render corals stress resistant through a phenomenon coined as “stress-hardening
21 induced by environmental priming”. Fluctuations that involve high temperature peaks have been
22 commonly investigated, however, the effects of a stress-hardening stimulus generated by cold-water
23 pulses has rarely been studied. Offshore island reefs in the Andaman Sea offer an ideal natural setting
24 to study these effects, as cooling water of internal waves induce strong variability with peak intensity
25 in January to June and absence in August to November. While western island shores are exposed to
26 this stimulus, eastern shores remain sheltered. This study examined (1) whether corals from exposed
27 reefs were more heat stress resistant compared to stimulus-sheltered conspecifics and (2) whether this
28 trait can last in the absence of the stimulus. We quantified the thermal stress resistance in two
29 ecologically important coral species, *Pocillopora* sp. and *Porites* sp., from the two island shores, during
30 the two seasons. Coral bleaching intensity and photosynthetic efficiency of algal symbionts were
31 measured as response variables after a short-term heat stress assay (24-48 h, 34 °C) to assess thermal
32 stress resistance. Stress responses of all stimulus-exposed corals were either undetectable (during the
33 season of stimulus presence) or very weak (during stimulus absence), while corals from the stimulus-
34 sheltered shore responded strongly to heat stress irrespective of the season. Hence, thermal resistance
35 was overall greater in corals originating from the stimulus-exposed shore, but it was slightly diminished
36 during the season of stimulus absence, emphasizing the relevance of stimulus recurrence in maintaining
37 the resistance trait. We exemplify that the stimulus of fluctuating low temperature pulses successfully
38 induced stress-hardening in corals. This suggests that priming stimuli do not necessarily need to
39 transgress certain upper thermal thresholds, but can also touch on lower thresholds to be effective. Even
40 more, we argue that cooling pulses might represent a safer stress-hardening regime, since warming-
41 stress accumulation can be avoided. More research is required to obtain a better understanding of

42 environmental priming, but current findings should encourage the development of artificial stress-
43 hardening approaches to enhance coral resistance in reef restoration efforts.

44 Introduction

45
46 Reef-building corals live near their thermal limits, so that the growing thermal stress caused by ocean
47 warming poses the most pressing threat to the existence of many coral species and the tropical reef
48 ecosystems (Hoegh-Guldberg 1999). Thermal anomalies that culminate during long-lasting heat-waves
49 (Sully et al. 2019) impose intense stress on corals, which triggers “coral bleaching”, i.e., the loss of
50 symbiotic algae from the coral holobionts that is apparent through the paling of the coral tissues (Glynn
51 1991). Bleached corals are exposed to starvation, as the nutrient exchange between the host and
52 dinoflagellate symbionts is disrupted (Brown 1997; Rådecker et al. 2021). As a result, coral bleaching
53 events have already been fatal to vast portions of coral populations worldwide, resulting in significant
54 losses of the coral reef ecosystem (Hughes et al. 2018).

55 Tropical corals have adapted to mostly stable thermal conditions of the tropical waters which feature
56 only little seasonal change (Kleypas et al. 1999). Consequently, they do not cope well with even slight
57 increases in temperature. However, observations of coral reef habitats that feature comparably high
58 thermal (and other) fluctuations provide a glimpse into the remarkable plasticity of certain individuals
59 or populations. Such studies have demonstrated that corals, pre-exposed to challenging conditions, can
60 feature a higher thermal resistance, especially in terms of their thermal threshold and/or show a higher
61 ability to recover after (thermal) stress compared to their counterparts living in more stable
62 environments nearby. Subsequently, this phenomenon has been coined “environmental priming” or
63 “environmental memory” (Brown et al. 2002; Rivest et al. 2017; Hackerott et al. 2021; Martell 2023).
64 Most of these observations originate from reefs that experience strong environmental variability, e.g.,
65 inshore reef habitats (Kenkel and Matz 2016), reef flats and tidal pools that are temporarily exposed to
66 extreme conditions (Oliver and Palumbi 2011a; Schoepf et al. 2015), sites exposed to internal waves or
67 other upwelling events (Doering et al. 2021; Buerger et al. 2015), or reef-adjacent habitats, such as
68 lagoons and mangroves (Camp et al. 2016, 2017). Also, temporal stress events, such as moderate heat
69 waves (Bellantuono et al. 2012b; Ainsworth et al. 2016; Fox et al. 2021) or consecutive bleaching events
70 (Maynard et al. 2008; Guest et al. 2012; Penin et al. 2013), have been observed to be associated with
71 greater stress resistance and/or a faster recovery of corals following such events, where mechanisms
72 underlying adaptation and/or acclimation can be suspected.

73 The phenomenon of stress resistance gain is not unique to corals. Stress-hardening through
74 environmental priming relies on the phenotypic and physiological plasticity of an organism (Hilker et
75 al. 2016) and has long been observed and studied across many taxa of the tree of life, most prominently
76 in plants (Nicotra et al. 2010; Tanou et al. 2012; Li et al. 2014). Past environmental challenges can
77 “prime” organisms to respond to future stressors more efficiently and/or rapidly. In contrast to the
78 mechanisms of adaptation, which arise from genetic variation and selection dynamics over several
79 generations, the effect of environmental priming can occur within one generation and in the same
80 individual (Whitman and Agrawal 2009; Foo and Byrne 2016). For long-lived coral species with
81 relatively long generation times and, hence, naturally slower adaptive processes, rapid acclimation
82 through plasticity can become life-saving (Palumbi et al. 2014). As such, environmental priming could
83 fundamentally increase the odds for corals to successfully resist rapid ocean warming.

84 Today, reefs that exhibit high thermal variability have become attractive sites to obtain stress tolerant
85 corals to study the mechanisms underpinning plasticity and thermal resistance (Oliver and Palumbi
86 2011b; Ziegler et al. 2017; Hackerott et al. 2021; Majerova et al. 2021). Furthermore, study of these

87 stress resistant phenotypes can assist the development of interventions to enhance coral stress tolerance
88 (Doering et al. 2021; Epstein et al. 2019; Howells et al. 2021). Most recently, *ex situ* experiments aiming
89 to develop stress-hardening procedures for the laboratory have gained traction. Such studies have shown
90 that artificial preconditioning treatments applying fluctuating temperatures in artificial aquarium
91 environments, can improve thermal stress resistance of corals (Hawkins and Warner 2017; Majerova et
92 al. 2021; Alexander et al. 2022; DeMerlis et al. 2022). However, findings are still equivocal, as several
93 other studies did not report any stress-hardening effects (Putnam and Edmunds 2011; Klepac and
94 Barshis 2020; Alexander et al. 2022; Schoepf et al. 2022). Obtaining an understanding of the greater
95 detail of these phenomena is of urgent relevance. Hence, important questions concerning the “dosage”
96 of a priming stimulus, including the exposure duration and the regime of the priming conditions which
97 is required to achieve the desired effect, remain to be answered (Brown et al. 2023; Martell 2023).
98 To shed light on some of the questions, this study took advantage of the environmentally and seasonally
99 dynamic reef sites located in the Andaman Sea in Thailand, where island shores are seasonally exposed
100 to a stimulus of thermal variability induced by large amplitude internal waves (Osborne and Burch
101 1980). Internal waves are oceanographic features that are ubiquitous in the world's oceans and, contrary
102 to surface waves, travel deep along strong density gradients (Jackson et al. 2012). Particularly in the
103 Thai Andaman Sea, western reef sites are exposed to the internal waves and experience the strongest
104 impacts. Internal waves induce variations of temperature (i.e., negative anomalies with minima at 26 to
105 24 °C), pH, salinity and other environmental variables during their peak season of wave intensity that
106 is from January to June. They can impose tremendous stress on corals, but can provide protective
107 cooling during natural marine heat waves (Wall et al. 2015; Wyatt et al. 2019). In contrast, reefs on the
108 east shores of the islands are sheltered from these impacts, fostering stable environmental conditions
109 (Schmidt et al. 2012; Wall et al. 2012). During the second half of the year, impacts of internal waves
110 are typically minor or absent on the western shores, which allows the study of coral thermal stress
111 resistance in presence and absence of the priming stimulus. While a majority of studies have focused
112 on coral stress-hardening by exposing them to high temperature regimes under constant or variable
113 conditions (Middlebrook et al. 2008; Bellantuono et al. 2012b; Putnam and Gates 2015; Hackerott et
114 al. 2021; Martell 2023), internal wave sites provide the opportunity to study the effect of high variability
115 conditions that do not involve high but rather low thermal pulses.
116 A previous study has established that internal wave impact, in the Andaman Sea region, was linked to
117 higher coral thermal stress resistance, specifically in *Porites* sp. corals studied during the season of high
118 internal wave intensity (Buerger et al. 2015). We followed up on these previous findings and
119 investigated whether this stress-hardening effect reported for *Porites* sp. is a species-specific
120 phenomenon or can be also found in other coral species. Second, we investigated whether a greater
121 thermal resistance of corals originating from the stimulus-exposed reefs is a persistent or a transient
122 trait, which occurs only during the season when environmental variability is at its peak. To address
123 these questions, we employed high-throughput short-term heat stress assays (duration: 24 - 48h, peak
124 of 34 °C) (Doering et al. 2021; Evensen et al. 2021) to assess the thermal stress responses in two coral
125 species, *Pocillopora* sp. and *Porites* sp., from a stimulus-exposed and a sheltered site during the two
126 seasons.

127 Materials and Methods

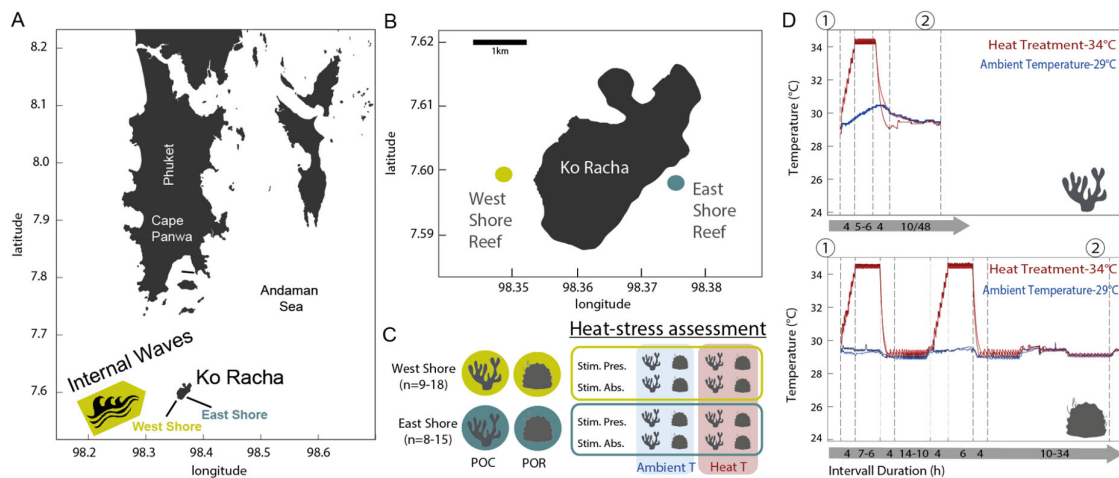
128 Study sites and coral collection

129 Study sites were located at Racha Island in the Andaman Sea off the coast of Thailand, both at 15 m
130 water depth (Figure 1 A-B). A reef on the western shore was chosen (7.595530°N, 98.354320°E, Figure

131 1 B) where internal wave forcing induced environmental variability through frequent upwelling of deep,
132 cool, and nutrient rich water onto the shelf (Wall et al. 2012; Schmidt et al. 2016). A reef on the eastern
133 shore, sheltered from the internal wave stimulus, was chosen to represent a low variability reef
134 (7.598910°N, 98.373100°E, Figure 1 B). Temperature fluctuations were monitored *in situ* as a proxy
135 for internal wave impact and environmental variability. Temperature loggers (HOBO Pendant
136 Temperature/Light 8K Data Logger, Onset, USA) were deployed at the study sites one month before
137 heat stress assays were performed. In each study site, visually healthy coral colonies of *Pocillopora* sp.
138 and *Porites* sp. were permanently tagged to assess their thermal resistance levels during the two seasons
139 (n=8 to n=18, Figure 1 C, Table S1). These two coral species are cosmopolitan reef-builders in Thailand
140 and within the entire Indo-Pacific region (Brown and Phongsuwan 2012; Schmidt et al. 2012; Jain et
141 al. 2023). Coral fragments were collected at the end of April 2018, an episode of strongest internal wave
142 impact, and at the end of October (*Porites* sp.) and November (*Pocillopora* sp.), during the absence of
143 internal wave stimulus. Two fragments (*Porites* sp.: $\varnothing \sim 6$ cm; *Pocillopora* sp.: length ~ 5 cm) per
144 colony were collected using a chisel and a hammer (Table S1).

145 Short-term heat stress assays

146 Collected fragments were instantly transported to the Phuket Marine Biological Center (Phuket,
147 Thailand) where they were maintained in two 500 L flow-through tanks with a flow rate of 2.8 ± 1.31
148 L/min until the start of each heat stress assay. Another 500 L source tank constantly supplied both flow-
149 through tanks with 5 μ m-filtered seawater from the reef adjacent to the research center. Its temperature
150 was held at constant 29.43 ± 0.32 °C using a temperature-controlling device including a chiller and a
151 heater (Titanium Heater 100 W, Schego, Germany; Temperature Switch TS 125, HTRONIC, Germany;
152 Aqua Medic Titan 1500 Chiller, Germany). LED lights (135 W, Hydra Fiftytwo HD LED, Aqua
153 Illumination, USA) mimicked the average light conditions of the sampling sites (Text S1).
154 For each heat stress assay (Figure 1 D), two 40 L experimental tanks were set up inside each of the 500
155 L flow-through tanks that were used as temperature-controlling water baths (Table S2). The seawater
156 of all four experimental tanks was supplied by daily, manual 50% water changes from the source-tank.
157 Each experimental tank was equipped with a temperature-controlling device, one heater, air supply, a
158 small current pump and a temperature logger (Temperature Switch TS 125, HTRONIC, Germany;
159 Titanium Heater 100 W, Schego, Germany; Koralia nano 900 L/h, Hydor, Italy; HOBO Pendant
160 Temperature/Light 8K Data Logger, Onset, USA). Two coral fragments per coral colony were randomly
161 distributed among the four tanks “34°C” ($N = 2$) and “29°C” ($N = 2$), resulting in one fragment per
162 colony per treatment. The 34°C-treatment was established over the course of one day by ramping
163 temperatures from 29°C to 34°C for 4 h, holding at 34°C for 5 h or 6 h (*Pocillopora* sp.) or for 6 h or 7
164 h (*Porites* sp.), and decreasing temperatures to 29 °C within 4 h. After the heat exposure, corals were
165 maintained at ambient temperatures for 10 h until the next day. While *Pocillopora* sp. fragments were
166 subjected to the short-term heat exposure once, resulting in a 24 h experiment, *Porites* sp. corals were
167 exposed to the treatment over two consecutive days resulting in a duration of 72 h (Figure 1 D).



168

169 **Figure 1 Study sites, experimental design, and temperature profiles of short-term heat stress**
 170 **assays.** (A) The study area was located at Ko Racha in the Andaman Sea off the coast of Thailand, a
 171 region that is exposed to large amplitude internal waves (light green arrow). These deep waves cause
 172 high thermal (and environmental) variability at western reef sites (light green), while the eastern
 173 shores (dark green) remain sheltered. (B) Two reef sites were chosen, on each shore side. (C)
 174 Fragments of colonies ($n =$ replicate numbers) of *Pocillopora* sp. (POC) and *Porites* spp. (POR)
 175 were collected for heat tolerance assessment during two seasons - the season of stimulus presence and peak
 176 of internal wave frequency and intensity (Stim. Pres.) and peak of internal wave frequency and
 177 intensity in April and the season of stimulus and internal wave absence (Stim. Abs.) in
 178 October/November. Fragments were subjected to a short-term heat stress assay exposing them to a
 179 heat pulse treatment of 34 °C (Heat T). A control group was maintained at ambient temperature of 29
 180 °C (Ambient T). (D) Temperature profiles were customized for each coral species, accounting for
 181 their taxon-specific temperature sensitivity. Pocilloporid fragments were challenged with a single heat
 182 stress pulse over one day (upper panel, branching coral icon), while *Porites* sp. fragments required
 183 two heat stress pulses over two days to show a heat stress response (lower panel massive coral icon).
 184 Measurement timepoints at the start (1) and the end (2) of each experiment are indicated.

185 Coral stress response variables

186 We measured two variables that assessed the stress response of each fragment before and after each
 187 heat stress assay (timepoints (1) and (2) in Figure 1 D). Tissue coloration, a proxy for microalgal
 188 symbiont cell density in coral tissues and therefore an indicator of holobiont health and coral bleaching
 189 severity, was assessed using a “bleaching score”. The coloration of each individual fragment was
 190 visually categorized on the scale from 1 (bleached, pale tissues) to 6 (healthy, dark tissues) using a coral
 191 bleaching chart (Siebeck et al. 2006). A minimum and maximum score was recorded per fragment and
 192 averaged. Photosynthetic efficiency of microalgal symbionts was determined by measuring effective
 193 quantum efficiency ($\text{yield } \Phi \text{ PSII} = (F_m' - F) / F_m' = \Delta F / F_m'$, Genty et al. 1989) of electron transport
 194 using a pulse amplitude-modulated fluorometer (Diving-PAM, Walz, Germany).

195 Statistical analyses

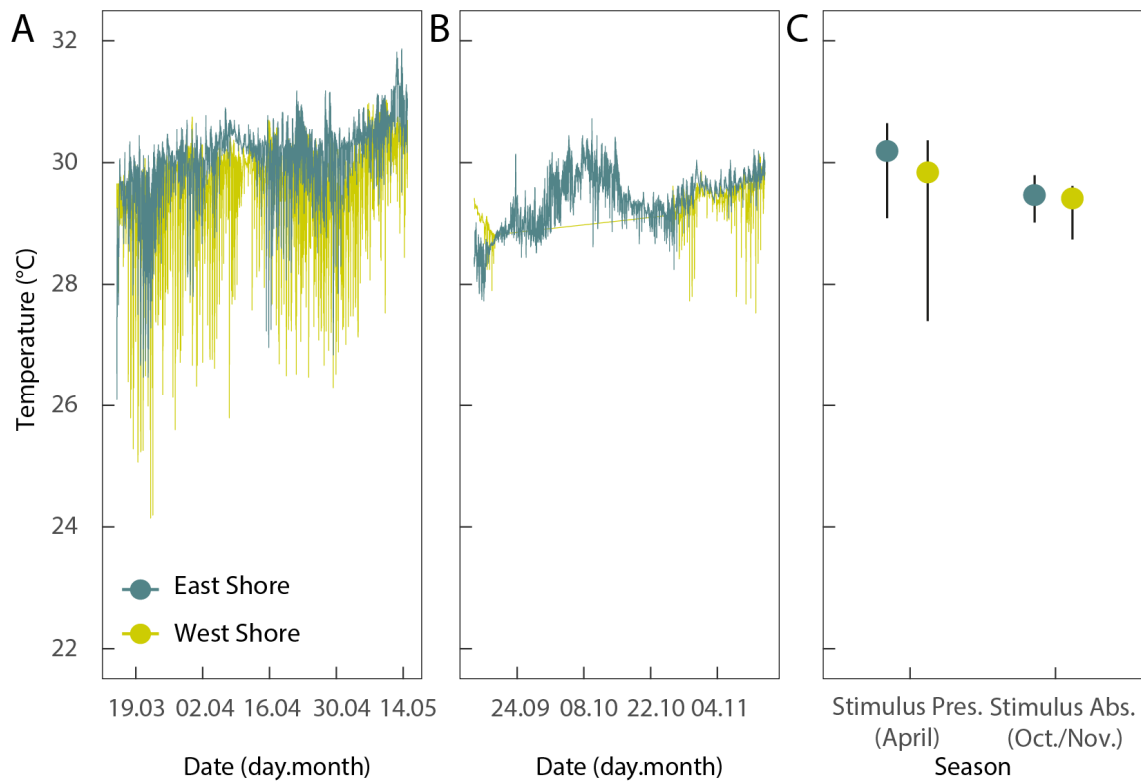
196 Δ -values of each stress response variable (end – start of each experimental part) were calculated to
 197 represent the change or the variable over time. Based on these Δ -values, effect sizes were estimated

198 using *dabestR* v0.2.3 6 (Ho et al. 2019). Effects of the high temperature treatment (“34 °C” vs. “29 °C”)
199 were compared between the sites of origin (“West | High variability site” and “East | Low variability
200 site”) and between the seasons (“Season of stimulus presence” and “Season of stimulus absence”).
201 Statistical significance was tested in *R* (R Core Team 2013) using linear mixed effect models (*nlme* v4
202 3.1-148 and *lme4* v1.1-23 package). Where applicable, coral colony genotype was used as a random
203 factor.

204 Results

205 Environmental variability of the study sites

206 Temperature was recorded as a proxy for internal wave forcing and provided a measure of
207 environmental variability on the study sites. The temperature profiles revealed that the intensities of
208 internal waves were seasonal (Figure 2). Strong and mainly negative temperature anomalies occurred
209 during March to April, which provided the strongest stimulus for environmental priming with a diurnal
210 amplitude ranging between 0.7 - 5.4 °C (average amplitude of 3.0 °C ± 1.0 SD) and minimal temperature
211 values as low as 24 °C (Figure 2 A, C). The impact of internal waves dwindled in September to
212 November, when the anomalies decreased (Figure 2 B, C). Importantly, temperature anomalies driving
213 the environmental variability were more frequent and intense on the exposed west shore of Ko Racha
214 compared to the sheltered east shore (Figure 2 C). During the season when the stimulus of internal
215 waves was present, the differences were largest between both island sides, east and west (Figure 2 A).
216 Once the stimulus faded during the second half of the year, conditions on both island sides became more
217 similar (Figure 2 B).
218



219

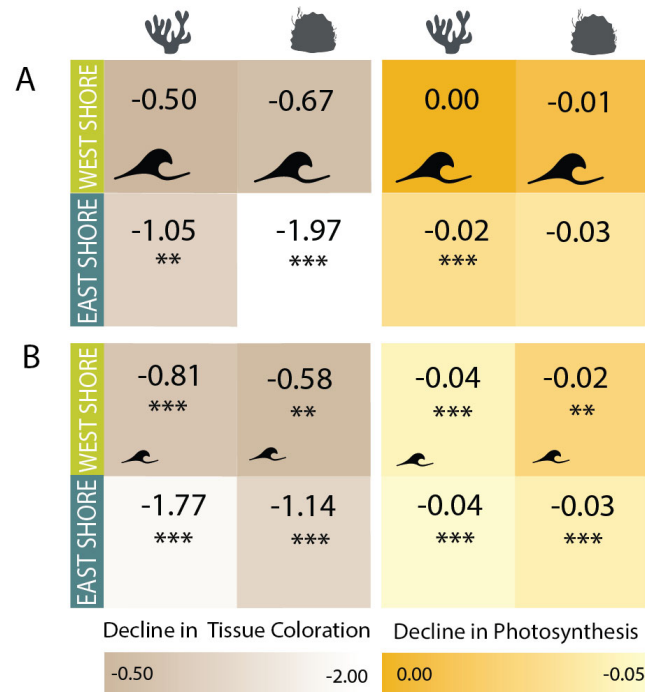
220 **Figure 2 Seasonal difference of environmental variability at the study sites.** Temperature records
221 served as a proxy for environmental variability in the study sites. This variability was generated by
222 large amplitude internal waves, a potential stimulus for coral stress-hardening. (A) A time series
223 depicts that internal waves on the western shores (light green) induced strong temperature anomalies
224 during March to April. The eastern shore (dark green) remained mostly sheltered from this stimulus.
225 (B) Fairly constant temperatures, with almost similar dynamics on both island shores, were
226 characteristic for the second part of the year (October to November), the season of stimulus absence.
227 During this time, the western and eastern shores featured more similar conditions. (C) The median
228 temperatures are indicated by circles and the average positive and negative diurnal anomalies from the
229 median are displayed as whiskers for both island shores and seasons.

230 Stress responses to short-term heat stress assays

231

232 Overall, the bleaching score and photosynthetic efficiency data indicated that stress levels after the
233 short-term heat stress assay were highest in corals from the eastern, stimulus-sheltered site, as reflected
234 in the lighter color tones in the heatmap, where effect sizes are visualized (Figure 3). This becomes
235 clear, as the largest and significant declines in the two variables, tissue coloration and photosynthesis,
236 were recorded in east shore corals irrespective of the season. Corals from the west shore did not show
237 any significant signs of stress when tested during stimulus presence (Figure 3A), but significant declines
238 of the two variables were noted, when corals were tested during stimulus absence (Figure 3B). Here
239 effect sizes of the heat stress treatment were fairly small (< 0.9) for tissue coloration, indicating a mild
240 stress response. In comparison, the large stress responses measured for the east shore corals were in the
241 effect size range of 1.05 - 1.97 (for the tissue coloration). Interestingly, the decline in photosynthesis of
242 the west-shore corals during stimulus absence was comparable to the decline of photosynthesis in corals
243 from the east shore.

244



245

246 **Figure 3 Summary of thermal stress levels of corals under experimental heat exposure compared**
 247 **between their sites of origin and seasons.** Stress levels of corals assessed in short-term heat stress
 248 assays during the (A) season of stimulus presence (April) and the (B) season of stimulus absence
 249 (November) are visualized. Lighter tones indicate higher stress levels. Colors represent the effect sizes
 250 determined using Cohen's d metric as the mean differences of measurements between the heat treatment
 251 and ambient control group of the heat stress assays. Negative values and lighter color tones indicate
 252 decreases of the bleaching score (brown tones) and the decline in photosynthetic efficiency (yellow
 253 tones) as a result of heat stress. Significant effects are marked as $p < 0.001$ ***, < 0.01 **,
 254 < 0.05 * as obtained from the post hoc tests of generalized linear mixed models. Dark green=
 255 eastern sheltered shore; light green = western exposed shore; the size of the wave icon indicates the
 256 magnitude of internal wave impact on the reef as a stress-hardening stimulus.

257

258 Bleaching responses

259 Across the seasons the bleaching score of corals from the eastern sheltered reef strongly declined under
 260 the acute heat exposure during the heat stress assay, as indicated by significant loss of tissue coloration
 261 ($29\text{ }^{\circ}\text{C}$ group vs. $34\text{ }^{\circ}\text{C}$ group, $p < 0.001$, Figure 4 A-D, Tables S3-4 and S6). Negative effect sizes
 262 were largest in these east-shore corals, i.e., -1 to -2, which was mostly 2 to 4-fold larger, compared to those
 263 of corals from the western reef (i.e., effect sizes of 0 to -0.8). In contrast, the stress responses of
 264 westshore corals differed between the seasons. Overall, their bleaching score did not decline in response
 265 to heat stress, when assessment was conducted during the season of stimulus presence (Figure 4 A, C,
 266 Table S6). However, during the second half of the year (i.e., stimulus absence season), tissue coloration
 267 of corals from the western shore slightly declined under experimental heat exposure with rather small,
 268 but measurable, differences between the heat and ambient temperature control group (Figure 4 B, D,
 269 Table S6). A small but significant decrease of the bleaching score was recorded ($p < 0.001$, Figure 3 B,

270 D). Further, a small-scale decline in the bleaching score was recorded for *Porites* sp. assessed during
271 both seasons with effect sizes were around ~ 0.6 (*n.s.* under stimulus presence and $p < 0.01$ under
272 stimulus absence, Figure 4 C-D, Table S4, S6).

273

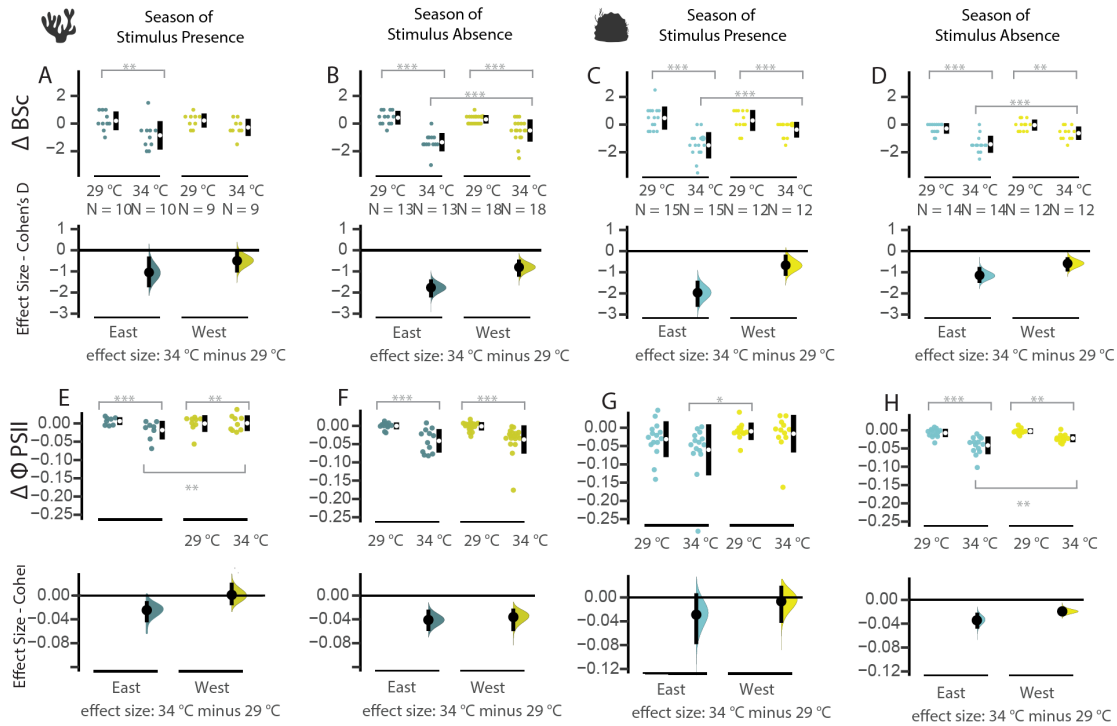
274 Declines in photosynthetic efficiency

275 Across the two seasons, photosynthetic efficiency decreased significantly after the heat stress exposure
276 in almost all coral fragments after heat exposure (29 °C group vs. 34 °C group, $p < 0.001$, Figure 4 E-
277 H, Tables S3, S5, S8), except for *Porites* sp. assessed during the season of stimulus presence (*n.s.*,
278 Figure 4 G, Table S8). Despite a significant response of almost all corals, the declines of photosynthetic
279 efficiency measured by effect size were larger in corals from the eastern reef, i.e., -0.02 to -0.03,
280 compared to corals from the western reef, i.e., mostly 0 or -0.01 (e.g., $p < 0.01$, Figure E and H).

281

282

283



284

285 **Figure 4 Symbiont loss and photosynthetic efficiency change of corals under experimental heat**
 286 **exposure compared between their sites of origin and seasons.** Estimation plots compare the effects
 287 of acute experimental heat exposure (“29°C” vs. “34°C”) on (A - D) the loss of coral tissue coloration
 288 (bleaching score = “BSc”) and (E - H) the photosynthetic efficiency of coral microalgal symbionts
 289 (quantum efficiency of electron transport = $\Delta\Phi$ PSII). Data is shown for the corals *Pocillopora* sp.
 290 (“branching” coral icon) and *Porites* sp. (“massive” coral icon) during the two seasons of stress-
 291 hardening stimulus presence and absence. The data is presented as a Δ -value of the measured
 292 variables (i.e., the decline of values between the start and end of stress exposure). Negative values
 293 indicate the loss of pigments and microalgal symbiont cells from the coral tissues or the decline of
 294 photosynthetic efficiency as a result of heat stress. Swarm plots show raw data points (first and third
 295 row) and Cumming Estimation plots (second and fourth row) depict the effect sizes as the mean
 296 differences between the experimental groups using Cohen’s d and a 95% confidence interval.
 297 Significant differences between the stress responses within the groups are indicated by connecting
 298 lines ($p < 0.001$ ***, < 0.01 ** , < 0.05 * obtained from the post hoc tests of generalized linear mixed
 299 models). Vertical error bars = 95% CI; N = individuals per treatment group.

300 Discussion

301 This study investigated the dynamics of coral thermal resistance in relation to a seasonally changing
 302 priming stimulus of internal waves in the Thai Andaman Sea. Our data revealed that colonies from two
 303 coral species, *Porites* sp. and *Pocillopora* sp., that were exposed to high environmental variability
 304 generated by internal waves, were mostly immune to acute heat stress treatments. In contrast, their
 305 conspecifics from sheltered shores with low environmental variability demonstrated thermal sensitivity
 306 under these treatments. Importantly, we showed that stress-hardening through environmental variability
 307 can exist under a stimulus comprising low temperature pulses (down to $\sim 26.5^\circ\text{C}$ and minima of 24°C)

308 that fluctuate at large amplitudes ($\sim 3^{\circ}\text{C}$ ranging between $0.7 - 5.4^{\circ}\text{C}$). Secondly, we found that the
309 thermal resistance of corals from exposed reefs persisted throughout the year in presence and in absence
310 of the internal wave stimulus. However, thermal stress resistance levels appeared to fade slightly during
311 the season when the stimulus was absent. Surprisingly, the dynamics of thermal stress resistance were
312 very similar in both coral species, *Pocillopora* sp. and *Porites* sp. despite representing a naturally
313 thermo-sensitive and a robust coral ecotype, respectively (Brown and Phongsuwan 2012; Schmidt et al.
314 2012; Jain et al. 2023). In the following we discuss these new insights about environmental priming,
315 while considering the regional context of the Thai Andaman Sea, and with regard to designing efficient
316 preconditioning treatments that can enhance coral thermal resistance for coral reef conservation.

317 Pulses of cooler temperatures and large amplitudes of variation provide a stress-hardening
318 stimulus for corals in the Thai Andaman Sea

319 Various organisms, including corals (Rivest et al. 2017; Hackerott et al. 2021)), are known to be more
320 stress-tolerant, when previously exposed to environmental variability (Nicotra et al. 2010; Li et al. 2014;
321 Hilker et al. 2016; Hilker and Schmülling 2019). However, the underlying environmental drivers that
322 induce environmental variability and generate such “stress-hardening regimes” in coral reefs differ
323 between habitat types and reef locations. Since temperature is a major determinant of coral reef
324 distribution and warming poses a threat to corals (Hoegh-Guldberg 1999; Kleypas et al. 1999), it has
325 been commonly used as a proxy to characterize reefs and quantify their environmental variability
326 (Leichter et al. 1996; Oliver and Palumbi 2011a; Wall et al. 2012; Kenkel et al. 2015). In this regard,
327 the most commonly investigated stimuli for stress hardening were elevated and/or fluctuating
328 temperatures that are a feature of shallow reef flats, tidal pool sites or lagoon-type habitats (Palumbi et
329 al. 2014; Camp et al. 2016, 2017). In these locations, corals experience temperature conditions that
330 often exceed the local bleaching thresholds during midday which provide “training periods” for more
331 severe heat wave conditions. It seems intuitive that corals exposed to such conditions, occurring in short
332 term-intervals, “learn” to cope with the environmental stress of elevated temperatures that would
333 usually lead to massive bleaching events.

334 Notably, the environmental variability regime in our study sites was induced by internal waves and can
335 be so far considered a unique scenario, as it differs from the other locations where environmental
336 priming has been typically investigated. In our study area, reef sites on the western shores of the islands
337 were exposed to the physical forces of internal waves, which create the remarkable difference in
338 environmental conditions between the exposed, western reef sites and the sheltered, eastern sites
339 (Schmidt et al. 2012; Wall et al. 2012, 2015). Internal waves in the Andaman Sea transport cooler waters
340 from the depths to the reefs, significantly increasing the amplitude of temperature variation on western
341 island shores. Other than in reef flat or tidal pool sites where others have investigated environmental
342 priming, internal waves at our study sites provided stimuli of lower rather than higher temperatures.
343 Irrespective of this thermal difference, we report that corals exposed to internal waves were able to cope
344 better with short-term acute heat stress conditions than corals living without the stimulus of internal
345 waves. We propose that the specific amplitude of variability ($\sim 3\text{-}5^{\circ}\text{C}$) in our west-shore study sites and
346 the lowest temperatures, likely reaching lower thermal threshold (minima of 24°C), might be equally
347 relevant for environmental priming, as established for fluctuating temperatures that temporarily
348 transgress upper thermal thresholds (Oliver and Palumbi 2011a).

349 Indeed, short pulses of cold water have been shown to induce an acute stress response in corals, but
350 corals could more easily acclimatize to the cooling treatment in comparison to the heat treatment where
351 coral health slowly declined (Roth et al. 2012). In another study, corals performed slightly better under
352 a cooler but “sublethal” temperature compared to the ambient corals, being able to build up more mass
353 and energy reserves (Nielsen et al. 2020). Based on these reports and our new insights, we propose that

354 the effects of low temperature pulses deserve to be further investigated, as they could offer a stress-
355 hardening regime that might emerge as more efficient than the application of high temperature pulses.
356 This could entail accumulation of heat stress when thermal thresholds are exceeded, leading to a
357 negative effect.

358 To date, findings supporting the effect of environmental priming regimes on coral thermal tolerance are
359 equivocal. While most studies indicate that a “challenging” thermal history or preconditioning regime
360 (of thermal variability or elevated baseline temperature) enhances thermal tolerance of corals
361 (McClanahan et al. 2005; Bellantuono et al. 2012b; Palumbi et al. 2014; Buerger et al. 2015; Schoepf
362 et al. 2015; Kenkel and Matz 2016; DeMerlis et al. 2022; Brown et al. 2023), some report neutral or
363 negative results, including cases where corals ended up less stress resistant compared to the control
364 group (Putnam and Edmunds 2011; Camp et al. 2016; Schoepf et al. 2019; Henley et al. 2022). It has
365 been suggested that such preconditioning treatments must have exerted too much stress on the corals
366 with the consequence of having drained their energy reserves, hence did not contribute to stress-
367 hardening but rather had a contrary effect (Hackerott et al. 2021; Wong et al. 2021). As such, regimes
368 of variability at elevated temperatures can be difficult to implement. We often have a limited
369 understanding of the thermal performance curve of corals, in particular in regard to their species- and
370 location-specific thermal optimum, as well as to their upper critical temperature (Sinclair et al. 2016;
371 Hillebrand et al. 2020). This impedes the determination of an effective environmental regime that can
372 achieve a positive effect of stress-hardening. Considering our knowledge about the effects of cooler
373 temperature on corals and the results in our study, we conclude that cold-stress could be an effective
374 tool to stress-harden corals, as it can successfully trigger metabolic flexibility without the effect of stress
375 accumulation through depletion of energy reserves or taxing coral symbionts.

376 Seasonality of the stimulus and the durability of the environmental priming effect

377 Internal wave activity is seasonal in the shallow reef habitat of the Andaman Sea (Schmidt et al. 2012;
378 Wall et al. 2012). During the first part of the year internal waves expose corals to cold, deep water at
379 regular intervals. At that time, the western shore is usually hit by the waves and thus the stimulus is at
380 its peak, creating the largest environmental differences between the western and the sheltered, eastern
381 shore. Later in the year, internal wave impact dwindles and consequently the environmental conditions
382 on both island shores, east and west, become very similar. We took advantage of this seasonality in the
383 Andaman Sea region to explore the effects of the presence and absence of a variable stimulus. To date,
384 the persistence of a stress-hardening effect in corals has hardly been considered in great detail and
385 remains to be investigated (Klepac and Barshis 2022). Our results showed that the positive effect on
386 thermal resistance had prevailed even in the absence of the stimulus. However, we observed a slight,
387 but measurable decline of stress resistance during the season of stimulus absence. This speaks for the
388 case that the effect of stress-hardening is lasting, but could slowly fade in the complete absence of the
389 priming stimulus. Our observation aligns with the finding that bleaching thresholds of corals decreased
390 seasonally, e.g., during the cooler winter season, when thermal challenges of the summer time were
391 absent (Berkelmans and Willis 1999). Similarly, this has been the case for one Caribbean coral species
392 (Scheufen et al. 2017), however, the same study found that other coral species did not follow this
393 seasonality. The latter agrees with several other cases which have shown that corals maintained their
394 stress resistance levels after transplantation from a high variability reef to an aquarium or site with more
395 stable conditions (Morikawa and Palumbi 2019; Schoepf et al. 2019; Marhoefer et al. 2021). Also, the
396 effect of various thermal preconditioning treatments (variable and stable) had a measurable effect on
397 coral thermal tolerance four months later (Drury et al. 2022). Notably, Morikawa and Palumbi (2020)
398 have observed the permanence of stress resistance across coral taxa in their coral nursery hosting
399 resilient corals from high variability sites for two consecutive years.

400 Disentangling covariates of variable environmental priming regimes

401 Reef sites that are exposed to internal waves have an important advantage over the typically investigated
402 intertidal and lagoon-type coral habitats. They represent a reef habitat with all typical physicochemical
403 features of an ocean-facing reef slope and can be compared to similar reefs that are sheltered from the
404 impact of internal waves. This provides a setting where the effects of reef site-specific characteristics
405 are accounted for and effects induced by the variability regime can be studied in isolation. In contrast,
406 tidal pools and lagoons are habitats that are fundamentally different from the typical coral reef. Extreme
407 light intensities and elevated salinities are characteristic for these shallow sites (Yates et al. 2014). Yet,
408 these sites are often compared to control sites located in a proper reef slope habitat, which does not
409 allow to disentangle the sole effect of the variability experienced in these sites. Still, it is important to
410 consider that corals in our study were not solely challenged by temperature fluctuations caused by the
411 internal waves. The deep-water brought into the reefs by internal waves is also typically rich in
412 inorganic nutrients and particulate matter. Both can be either beneficial or challenging for corals and
413 microalgal symbionts (Risk 2014). On one hand, the increase in nutrient sources could be valuable for
414 corals and contribute to their resilience (Ferrier-Pagès et al. 2000; Meunier et al. 2022). On the other
415 hand, particle loads may reduce light penetration and reduce photosynthetic output of microalgal
416 symbionts (Anthony et al. 2007). In addition, sediment particles typically threaten to smother corals
417 (Tuttle et al. 2020) that will need to spend energy on mucus production to free their tissues from these
418 sediments. Depending on the amount of nutrients introduced by internal waves and the requirements of
419 the corals, increases in inorganic nutrients and particulates can lead to a nutrient imbalance that can
420 threaten the intricate balance between host and algal symbiont (Wiedenmann et al. 2012; Rådecker et
421 al. 2015; Morris et al. 2019). Similarly, a slightly lower pH and oxygen-depleted seawater carried by
422 internal waves (Schmidt et al. 2012; Wall et al. 2012) may pose a stressor to corals and challenge their
423 performance (Chan and Connolly 2013; Alderdice et al. 2021). To better understand how co-variation
424 of these variables influences coral physiology and stress-hardening in the Andaman Sea, holistic
425 surveys will be needed that assess and consider a diversity of physico-chemical variables. However,
426 this is not only important when studying internal wave sites. Co-fluctuating variables exist in all types
427 of high variability reef sites, including tidal pools, reef flats, and lagoons in proximity to seagrass or
428 mangroves (Ruiz-Jones and Palumbi 2015; Camp et al. 2016). To explain some of the ambiguous
429 findings of coral stress-hardening studies, future research will need to explore the effects of co-varying
430 variables, as they may play a role in modulating the effects of stress-hardening.

431

432 Considerations for the design of efficient stress-hardening regimes

433 Studies of stress-hardening in corals through thermal variability regimes have sparked the idea of
434 instrumentalizing this phenomenon to improve coral thermal stress resistance during climate change. It
435 is anticipated that simulation of a stress-hardening stimulus can be used to enhance thermal tolerance
436 of corals for the purpose of conservation and restoration of coral reefs (Middlebrook et al. 2008;
437 Bellantuono et al. 2012b). The phenomenon, however, is still poorly understood and some findings
438 remain equivocal. While many studies have reported positive effects of a variable environment on the
439 stress tolerance in corals (Doering et al. 2021; Oliver and Palumbi 2011b; Buerger et al. 2015; Wong et
440 al. 2021; DeMerlis et al. 2022; Brown et al. 2023), a few have not reported any improvements or rather
441 observed declines in stress tolerance. Negative reports are likely due to stress-buildup during the
442 preconditioning process (Hackerott et al. 2021), which can occur when a variability regime becomes
443 too challenging (Putnam and Edmunds 2011; Camp et al. 2016; Schoepf et al. 2019; Klepac and Barshis
444 2020; Henley et al. 2022). Also, dynamic interaction of all covariates present in the respective study
445 sites can act as confounding factors and influence the outcomes of preconditioning (as laid out in the

446 chapter above), but most importantly, the “priming dosage” will be decisive for the success of the
447 method. Fine-scale differences in the amplitude and frequency of variation employed (Klepac and
448 Barshis 2022; Brown et al. 2023), the average temperature in the preconditioning regime, as well as the
449 duration of the exposure (Bellantuono et al. 2012a; Hackerott et al. 2021; Martell 2023) deserve careful
450 consideration. In some studies that have failed to observe a positive effect, environmental variability in
451 the reef sites or treatments might have been too small in comparison to the ambient regime in order to
452 elicit a measurable effect on corals. For instance, the variability ranges of the study sites in (Camp et al.
453 2016), only differed by $\sim 1 - 2^{\circ}\text{C}$, which might be too small of a difference to pinpoint any effect (Rivest
454 et al. 2017). Only a few efforts so far have set out to systematically identify optimal priming regimes.
455 Early surveys and experiments have found that heat tolerance was correlated with the magnitude of
456 variability, as corals from the tidal pool with the highest variability appeared to be most resistant to heat
457 (Palumbi et al. 2014). Several recent study designs have allowed us to gain insights at a higher resolution
458 and have found that an intermediate variability regime might likely be the most effective for stress-
459 hardening of corals. For instance, corals living in sites of intermediate variability on Heron Island in the
460 Great Barrier Reef (Brown et al. 2023) or in the moderately variable pools of the well-known study
461 sites in American Samoa (Klepac and Barshis 2022), have outperformed conspecifics that had
462 experienced lower or higher variability. Most recent findings suggest that exposure to thermal
463 variability at a rather low average mean temperature, or involving cooling rather than heat pulses, could
464 be more efficient than variability at a higher average temperature, as it has led to better stress-hardening
465 results in corals (Drury et al. 2022). Future studies will be needed to further refine our understanding of
466 how environmental priming regimes work, which will lead to the design of efficient preconditioning
467 protocols.

468 On a last note, it still remains to be elucidated whether and at which cost(s) stress-hardened corals
469 acclimate to perform well under challenging environmental regimes. Trade-offs will be an important
470 aspect of future investigations. Conservation and restoration efforts that aim to apply preconditioning
471 strategies to stress-harden corals will need to evaluate whether the gain in thermal resistance is related
472 to any critical trade-offs. At our study sites in the Andaman Sea, resistance of west-shore corals might
473 be coupled with a lower reef framework building capacity that was reported from these sites earlier
474 (Schmidt et al. 2012; Wall et al. 2012). This calls for detailed investigations into the calcification
475 capacity of these resistant corals. Recent study focussing on trade-offs (Wong et al. 2021) have found
476 that corals from high variability sites or long-term high-temperature treatments, had either a lower
477 metabolic capacity, lower growth rates, or lower reproductive potential compared to the control groups
478 from stable or ambient habitats or treatments. Overall, efforts aimed at increasing thermal tolerance of
479 corals will need a holistic approach to the subject. For the development of new interventions, it will be
480 essential to carefully assess cost-benefits and evaluate each new method and its potential ecological
481 consequences.

482 Conclusion

483 We showed that two coral species that occupy different ecological niches were receptive to the same
484 environmental priming of cooling pulses, which improved their thermal stress resistance to acute short-
485 term heat stress. A cold-water priming pulse can induce stress-hardening effectively. It might be a safer
486 option compared to the implementation of high temperature peaks in variability regimes used as
487 preconditioning treatments as heat-stress accumulation is avoided. Our study also showed that a
488 temporary priming exposure can induce a stress-hardening effect, which, however, is likely to fade in
489 longer absence of the stimulus, suggesting that a reapplication of a preconditioning treatment will be
490 necessary. Most importantly, the ideal dosage and length of thermal variability exposure in a
491 preconditioning treatment will need to be determined. Eventually, the enhancement of stress resistance

492 traits is likely to come at the cost of other traits. Therefore, research into the trade-offs that accompany
493 thermal resistance gain in corals will be crucial in order to understand the capacity and limitations of
494 corals to resist future thermal stress.

495

496 Acknowledgments

497 We acknowledge the team of the research unit Marine Ecology at Phuket Marine Biological Center
498 for field logistics and support during the set up of coral experimental facilities. We thank M.
499 Heckwolf, K. Bimson, L. Niewendieck, M. Suwareh, and V. Conrad for field assistance. We thank F.
500 Wendt for advice regarding aquarium equipment. This research was funded by the DFG (German
501 National Science Foundation) excellence initiative “Future Ocean” (# CP1782) awarded to AR. A.R.
502 further supported by funding of the Helmholtz Institute for Functional Marine Biodiversity at the
503 University of Oldenburg, Niedersachsen, Germany. HIFMB is a collaboration between the Alfred-
504 Wegener-Institute, Helmholtz-Center for Polar and Marine Research, and the Carl-von-Ossietzky
505 University Oldenburg, initially funded by the Ministry for Science and Culture of Lower Saxony and
506 the Volkswagen Foundation through the “Niedersächsisches Vorab” grant program (grant number
507 ZN3285).

508

509 Permissions

510 Research in Thailand was conducted under the permit of the National Research Council of Thailand
511 (NRCT # 0002/632), and corals were collected under the collection permission of CITES (export #
512 AC.0510.6/0017 and # AC.0510.6/022; import # DE E-04829/18 and # DE E-01510/19).

513

514 Authors’ contributions

515 AR conceived the study. AR and TD designed the experiment. TD, AR, MW conducted coral
516 experiments. AR, MW, LP, and TR performed coral collection. TD, NP, MW, AR performed the data
517 analysis. AR generated data visualization. AR, MW, TD wrote and edited the manuscript. Field
518 facilities and logistics were provided by LP, TR and the PMBC team. The authors read and approved
519 the final manuscript.

520

521 Declarations

522 The authors declare that they have no competing interests.

523

524 Corresponding author

525 Correspondence to: anna.roik@hifmb.de

526

527

528 References

- 529 Ainsworth TD, Heron SF, Ortiz JC, Mumby PJ, Grech A, Ogawa D, Eakin CM, Leggat W (2016) Climate
530 change disables coral bleaching protection on the Great Barrier Reef. *Science* 352:338–342
- 531 Alderdice R, Suggett DJ, Cárdenas A, Hughes DJ, Kühl M, Pernice M, Voolstra CR (2021) Divergent
532 expression of hypoxia response systems under deoxygenation in reef-forming corals aligns with bleaching
533 susceptibility. *Glob Chang Biol* 27:312–326
- 534 Alexander G, Hancock JR, Huffmyer AS, Matsuda SB (2022) Larval thermal conditioning does not improve
535 post-settlement thermal tolerance in the dominant reef-building coral, *Montipora capitata*. *Coral Reefs*
536 41:333–342

- 537 Anthony KRN, Connolly SR, Hoegh-Guldberg O (2007) Bleaching, energetics, and coral mortality risk: Effects
538 of temperature, light, and sediment regime. *Limnol Oceanogr* 52:11
- 539 Barshis DJ, Ladner JT, Oliver TA, Seneca FO, Traylor-Knowles N, Palumbi SR (2013) Genomic basis for coral
540 resilience to climate change. *Proc Natl Acad Sci U S A* 110:1387–1392
- 541 Bellantuono AJ, Granados-Cifuentes C, Miller DJ, Hoegh-Guldberg O, Rodriguez-Lanetty M (2012a) Coral
542 thermal tolerance: tuning gene expression to resist thermal stress. *PLoS One* 7:e50685
- 543 Bellantuono AJ, Hoegh-Guldberg O, Rodriguez-Lanetty M (2012b) Resistance to thermal stress in corals
544 without changes in symbiont composition. *Proceedings of the Royal Society B: Biological Sciences*
545 279:1100–1107
- 546 Berkelmans R, Willis BL (1999) Seasonal and local spatial patterns in the upper thermal limits of corals on the
547 inshore Central Great Barrier Reef. *Coral Reefs* 18:219–228
- 548 Brown B, Dunne R, Goodson M, Douglas A (2002) Experience shapes the susceptibility of a reef coral to
549 bleaching. *Coral Reefs* 21:119–126
- 550 Brown BE (1997) Coral bleaching: causes and consequences. *Coral Reefs* 16:S129–S138
- 551 Brown B, Phongsuwan N (2012) Delayed mortality in bleached massive corals on intertidal reef flats around
552 Phuket, Andaman Sea, Thailand. *Phuket Marine Biological Center Research Bulletin* 48:43–48
- 553 Brown KT, Martynek M, Barott KL (2023) Maximal coral thermal tolerance is found at intermediate diel
554 temperature variability. *bioRxiv* 2023.03.27.534434
- 555 Buerger P, Schmidt GM, Wall M, Held C, Richter C (2015) Temperature tolerance of the coral *Porites lutea*
556 exposed to simulated large amplitude internal waves (LAIW). *J Exp Mar Bio Ecol* 471:232–239
- 557 Camp EF, Nitschke MR, Rodolfo-Metalpa R, Houlbreque F, Gardner SG, Smith DJ, Zampighi M, Suggett DJ
558 (2017) Reef-building corals thrive within hot-acidified and deoxygenated waters. *Sci Rep* 7:2434
- 559 Camp EF, Smith DJ, Evenhuis C, Enochs I, Manzello D, Woodcock S, Suggett DJ (2016) Acclimatization to
560 high-variance habitats does not enhance physiological tolerance of two key Caribbean corals to future
561 temperature and pH. *Proc R Soc B* 283:20160442
- 562 Chan NCS, Connolly SR (2013) Sensitivity of coral calcification to ocean acidification: a meta-analysis. *Glob*
563 *Chang Biol* 19:282–290
- 564 Darling ES, Alvarez-Filip L, Oliver TA, McClanahan TR, Côté IM (2012) Evaluating life-history strategies of
565 reef corals from species traits. *Ecol Lett* 15:1378–1386
- 566 DeMerlis A, Kirkland A, Kaufman ML, Mayfield AB, Formel N, Kolodziej G, Manzello DP, Lirman D,
567 Traylor-Knowles N, Enochs IC (2022) Pre-exposure to a variable temperature treatment improves the
568 response of *Acropora cervicornis* to acute thermal stress. *Coral Reefs* 41:435–445
- 569 Dilworth J, Caruso C, Kahkejian VA, Baker AC, Drury C (2021) Host genotype and stable differences in algal
570 symbiont communities explain patterns of thermal stress response of *Montipora capitata* following thermal
571 pre-exposure and across multiple bleaching events. *Coral Reefs* 40:151–163
- 572 Doering T, Wall M, Putschim L, Rattanawongwan T, Schroeder R, Hentschel U, Roik A (2021) Towards
573 enhancing coral heat tolerance: a “microbiome transplantation” treatment using inoculations of
574 homogenized coral tissues. *Microbiome* 9:102
- 575 Drury C, Dilworth J, Majerová E, Caruso C, Greer JB (2022) Expression plasticity regulates intraspecific
576 variation in the acclimatization potential of a reef-building coral. *Nat Commun* 13:4790
- 577 Epstein HE, Smith HA, Torda G, van Oppen MJH (2019) Microbiome engineering: enhancing climate resilience
578 in corals. *Front Ecol Environ*
- 579 Evensen NR, Fine M, Perna G, Voolstra CR, Barshis DJ (2021) Remarkably high and consistent tolerance of a
580 Red Sea coral to acute and chronic thermal stress exposures. *Limnol Oceanogr* 9999:Ino.11715–Ino.11715

- 581 Ferrier-Pagès C, Gattuso JP, Dallot S, Jaubert J (2000) Effect of nutrient enrichment on growth and
582 photosynthesis of the zooxanthellate coral *Stylophora pistillata*. *Coral Reefs* 19:103–113
- 583 Foo SA, Byrne M (2016) Chapter Two - Acclimatization and Adaptive Capacity of Marine Species in a
584 Changing Ocean. In: Curry B.E. (eds) *Advances in Marine Biology*. Academic Press, pp 69–116
- 585 Fox MD, Cohen AL, Rotjan RD, Mangubhai S, Sandin SA, Smith JE, Thorrold SR, Dissly L, Mollica NR,
586 Obura D (2021) Increasing coral reef resilience through successive marine heatwaves. *Geophys Res Lett*
587 48:
- 588 Genty B, Briantais J-M, Baker NR (1989) The relationship between the quantum yield of photosynthetic
589 electron transport and quenching of chlorophyll fluorescence. *Biochimica et Biophysica Acta (BBA) -*
590 *General Subjects* 990:87–92
- 591 Glynn PW (1991) Coral reef bleaching in the 1980s and possible connections with global warming. *Trends Ecol*
592 *Evol* 6:175–179
- 593 Guest JR, Baird AH, Maynard JA, Muttaqin E, Edwards AJ, Campbell SJ, Yewdall K, Affendi YA, Chou LM
594 (2012) Contrasting Patterns of Coral Bleaching Susceptibility in 2010 Suggest an Adaptive Response to
595 Thermal Stress. *PLoS One* 7:e33353
- 596 Hackerott S, Martell HA, Eirin-Lopez JM (2021) Coral environmental memory: causes, mechanisms, and
597 consequences for future reefs. *Trends Ecol Evol* 36:1011–1023
- 598 Hawkins TD, Warner ME (2017) Warm preconditioning protects against acute heat-induced respiratory
599 dysfunction and delays bleaching in a symbiotic sea anemone. *J Exp Biol* 220:969–983
- 600 Henley EM, Bouwmeester J, Jury CP, Toonen RJ, Quinn M, Lager CVA, Hagedorn M (2022) Growth and
601 survival among Hawaiian corals outplanted from tanks to an ocean nursery are driven by individual
602 genotype and species differences rather than preconditioning to thermal stress. *PeerJ* 10:e13112
- 603 Hilker M, Schmülling T (2019) Stress priming, memory, and signalling in plants. *Plant Cell Environ* 42:753–
604 761
- 605 Hilker M, Schwachtje J, Baier M, Balazadeh S, Bäurle I, Geiselhardt S, Hincha DK, Kunze R, Mueller-Roeber
606 B, Rillig MC, Rolff J, Romeis T, Schmülling T, Steppuhn A, van Dongen J, Whitcomb SJ, Wurst S, Zuther
607 E, Kopka J (2016) Priming and memory of stress responses in organisms lacking a nervous system. *Biol*
608 *Rev Camb Philos Soc* 91:1118–1133
- 609 Hillebrand H, Jacob U, Leslie HM (2020) Integrative research perspectives on marine conservation. *Philos*
610 *Trans R Soc Lond B Biol Sci* 375:20190444
- 611 Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world’s coral reefs. *Mar*
612 *Freshwater Res* 50:839
- 613 Ho J, Tumkaya T, Aryal S, Choi H, Claridge-Chang A (2019) Moving beyond P values: data analysis with
614 estimation graphics. *Nat Methods* 16:565–566
- 615 Howells EJ, Abrego D, Liew YJ, Burt JA, Meyer E, Aranda M (2021) Enhancing the heat tolerance of reef-
616 building corals to future warming. *Science Advances* 7:eabg6070–eabg6070
- 617 Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML,
618 Bridge TC, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison H, Hobbs J-PA, Hoey AS,
619 Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett M, Schoepf V, Torda G, Wilson SK
620 (2018) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* 359:80–83
- 621 Jackson C, da Silva J, Jeans G (2012) The generation of nonlinear internal waves. *Oceanography* 25:108–123
- 622 Jain T, Buapet P, Ying L, Yucharoen M (2023) Differing Responses of Three Scleractinian Corals from Phuket
623 Coast in the Andaman Sea to Experimental Warming and Hypoxia. *J Mar Sci Eng* 11:403
- 624 Kenkel CD, Almanza AT, Matz MV (2015) Fine-scale environmental specialization of reef-building corals
625 might be limiting reef recovery in the Florida Keys. *Ecology* 96:3197–3212

- 626 Kenkel CD, Matz MV (2016) Gene expression plasticity as a mechanism of coral adaptation to a variable
627 environment. *Nature Ecology & Evolution* 1:0014
- 628 Klepac CN, Barshis DJ (2020) Reduced thermal tolerance of massive coral species in a highly variable
629 environment. *Proc Biol Sci* 287:20201379
- 630 Klepac CN, Barshis DJ (2022) High-resolution in situ thermal metrics coupled with acute heat stress
631 experiments reveal differential coral bleaching susceptibility. *Coral Reefs* 41:1045–1057
- 632 Kleypas JA, McManus JW, Menez LAB (1999) Environmental Limits to Coral Reef Development: Where Do
633 We Draw the Line? *American Zoology* 39:146–159
- 634 Leichter JJ, Wing SR, Miller SL, Denny MW (1996) Pulsed delivery of subthermocline water to Conch Reef
635 (Florida Keys) by internal tidal bores. *Limnol Oceanogr* 41:1490–1501
- 636 Li X, Cai J, Liu F, Dai T, Cao W, Jiang D (2014) Cold priming drives the sub-cellular antioxidant systems to
637 protect photosynthetic electron transport against subsequent low temperature stress in winter wheat. *Plant*
638 *Physiol Biochem* 82:34–43
- 639 Majerova E, Carey FC, Drury C, Gates RD (2021) Preconditioning improves bleaching tolerance in the reef-
640 building coral *Pocillopora acuta* through modulations in the programmed cell death pathways. *Mol Ecol*
641 *mec.15988–mec.15988*
- 642 Marhoefer SR, Zenger KR, Strugnell JM, Logan M, van Oppen MJH, Kenkel CD, Bay LK (2021) Signatures of
643 Adaptation and Acclimatization to Reef Flat and Slope Habitats in the Coral *Pocillopora damicornis*.
644 *Frontiers in Marine Science* 8:
- 645 Martell HA (2023) Thermal priming and bleaching hormesis in the staghorn coral, *Acropora cervicornis*
646 (Lamarck 1816). *J Exp Mar Bio Ecol* 560:151820
- 647 Marzonie MR, Bay LK, Bourne DG, Hoey AS, Matthews S, Nielsen JJV, Harrison HB (2023) The effects of
648 marine heatwaves on acute heat tolerance in corals. *Glob Chang Biol* 29:404–416
- 649 Maynard JA, Anthony KRN, Marshall PA, Masiri I (2008) Major bleaching events can lead to increased thermal
650 tolerance in corals. *Mar Biol* 155:173–182
- 651 McClanahan TR, Maina J, Moothien-Pillay R, Baker AC (2005) Effects of geography, taxa, water flow, and
652 temperature variation on coral bleaching intensity in Mauritius. *Mar Ecol Prog Ser* 298:131–142
- 653 Meunier V, Bonnet S, Camps M, Benavides M, Dubosc J, Rodolfo-Metalpa R, Houlbrèque F (2022) Ingestion
654 of Diazotrophs Makes Corals More Resistant to Heat Stress. *Biomolecules* 12:
- 655 Middlebrook R, Hoegh-Guldberg O, Leggat W (2008) The effect of thermal history on the susceptibility of reef-
656 building corals to thermal stress. *J Exp Biol* 211:1050–1056
- 657 Morikawa MK, Palumbi SR (2019) Using naturally occurring climate resilient corals to construct bleaching-
658 resistant nurseries. *Proc Natl Acad Sci U S A* 201721415
- 659 Morris LA, Voolstra CR, Quigley KM, Bourne DG, Bay LK (2019) Nutrient Availability and Metabolism
660 Affect the Stability of Coral-Symbiodiniaceae Symbioses. *Trends Microbiol* 27:678–689
- 661 Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P, Purugganan MD,
662 Richards CL, Valladares F, van Kleunen M (2010) Plant phenotypic plasticity in a changing climate.
663 *Trends Plant Sci* 15:684–692
- 664 Nielsen JJV, Kenkel CD, Bourne DG, Despringhere L, Mocellin VJL, Bay LK (2020) Physiological effects of
665 heat and cold exposure in the common reef coral *Acropora millepora*. *Coral Reefs* 39:259–269
- 666 Oliver TA, Palumbi SR (2011a) Do fluctuating temperature environments elevate coral thermal tolerance? *Coral*
667 *Reefs* 30:429–440
- 668 Oliver TA, Palumbi SR (2011b) Many corals host thermally resistant symbionts in high-temperature habitat.
669 *Coral Reefs* 30:241–250

- 670 Osborne AR, Burch TL (1980) Internal solitons in the Andaman Sea. *Science* 208:451–460
- 671 Palumbi SR, Barshis DJ, Traylor-Knowles N, Bay RA (2014) Mechanisms of reef coral resistance to future
672 climate change. *Science* 344:895–898
- 673 Penin L, Vidal-Dupiol J, Adjeroud M (2013) Response of coral assemblages to thermal stress: are bleaching
674 intensity and spatial patterns consistent between events? *Environ Monit Assess* 185:5031–5042
- 675 Putnam HM, Edmunds PJ (2011) The physiological response of reef corals to diel fluctuations in seawater
676 temperature. *J Exp Mar Bio Ecol* 396:216–223
- 677 Putnam HM, Gates RD (2015) Preconditioning in the reef-building coral *Pocillopora damicornis* and the
678 potential for trans-generational acclimatization in coral larvae under future climate change conditions. *J*
679 *Exp Biol* 218:2365–2372
- 680 Rådecker N, Pogoreutz C, Gegner HM, Cárdenas A, Roth F (2021) Heat stress destabilizes symbiotic nutrient
681 cycling in corals. *Proc Natl Acad Sci U S A* 118:e2022653118–e2022653118
- 682 Rådecker N, Pogoreutz C, Voolstra CR, Wiedenmann J, Wild C (2015) Nitrogen cycling in corals: the key to
683 understanding holobiont functioning? *Trends Microbiol* 23:490–497
- 684 R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical
685 Computing, Vienna, Austria
- 686 Risk MJ (2014) Assessing the effects of sediments and nutrients on coral reefs. *Current Opinion in*
687 *Environmental Sustainability* 7:108–117
- 688 Rivest EB, Comeau S, Cornwall CE (2017) The Role of Natural Variability in Shaping the Response of Coral
689 Reef Organisms to Climate Change. *Curr Clim Change Rep* 3:271–281
- 690 Roth MS, Goericke R, Deheyn DD (2012) Cold induces acute stress but heat is ultimately more deleterious for
691 the reef-building coral *Acropora yongei*. *Sci Rep* 2:240
- 692 Ruiz-Jones LJ, Palumbi SR (2015) Transcriptome-wide Changes in Coral Gene Expression at Noon and
693 Midnight Under Field Conditions. *Biol Bull* 228:227–241
- 694 Sawall Y, Nicosia AM, McLaughlin K, Ito M (2022) Physiological responses and adjustments of corals to
695 strong seasonal temperature variations (20–28°C). *J Exp Biol* 225:
- 696 Scheufen T, Krämer WE, Iglesias-Prieto R, Enriquez S (2017) Seasonal variation modulates coral sensibility to
697 heat-stress and explains annual changes in coral productivity. *Sci Rep* 7:4937
- 698 Schmidt GM, Phongsuwan N, Jantzen C, Roder C, Khokiattiwong S, Richter C (2012) Coral community
699 composition and reef development at the Similan Islands, Andaman Sea, in response to strong
700 environmental variations. *Mar Ecol Prog Ser* 456:113–126
- 701 Schmidt GM, Wall M, Taylor M, Jantzen C, Richter C (2016) Large-amplitude internal waves sustain coral
702 health during thermal stress. *Coral Reefs* 1–13
- 703 Schoepf V, Carrion SA, Pfeifer SM, Naugle M, Dugal L, Bruyn J, McCulloch MT (2019) Stress-resistant corals
704 may not acclimatize to ocean warming but maintain heat tolerance under cooler temperatures. *Nat*
705 *Commun* 10:4031
- 706 Schoepf V, Sanderson H, Larcombe E (2022) Coral heat tolerance under variable temperatures: Effects of
707 different variability regimes and past environmental history vs. current exposure. *Limnol Oceanogr*
708 67:404–418
- 709 Schoepf V, Stat M, Falter JL, McCulloch MT (2015) Limits to the thermal tolerance of corals adapted to a
710 highly fluctuating, naturally extreme temperature environment. *Sci Rep* 5:17639
- 711 Siebeck UE, Marshall NJ, Klüter A, Hoegh-Guldberg O (2006) Monitoring coral bleaching using a colour
712 reference card. *Coral Reefs* 25:453–460

- 713 Sinclair BJ, Marshall KE, Sewell MA, Levesque DL, Willett CS, Slotsbo S, Dong Y, Harley CDG, Marshall DJ,
714 Helmuth BS, Huey RB (2016) Can we predict ectotherm responses to climate change using thermal
715 performance curves and body temperatures? *Ecol Lett* 19:1372–1385
- 716 Sully S, Burkepile DE, Donovan MK, Hodgson G, van Woesik R (2019) A global analysis of coral bleaching
717 over the past two decades. *Nat Commun* 10:1264
- 718 Tanou G, Fotopoulos V, Molassiotis A (2012) Priming against environmental challenges and proteomics in
719 plants: Update and agricultural perspectives. *Front Plant Sci* 3:216
- 720 Tuttle LJ, Johnson C, Kolinski S, Minton D, Donahue MJ (2020) How does sediment exposure affect corals? A
721 systematic review protocol. *Environmental Evidence* 9:1–7
- 722 Wall M, Putschim L, Schmidt GM, Jantzen C, Khokiattiwong S, Richter C (2015) Large-amplitude internal
723 waves benefit corals during thermal stress. *Proceedings of the Royal Society of London B: Biological*
724 *Sciences* 282:20140650
- 725 Wall M, Schmidt GM, Janjang P, Khokiattiwong S, Richter C (2012) Differential Impact of Monsoon and Large
726 Amplitude Internal Waves on Coral Reef Development in the Andaman Sea. *PLoS One* 7:e50207
- 727 Whitman DW, Agrawal AA (2009) What is phenotypic plasticity and why is it important? Whitman DW,
728 Ananthakrishnan TN (Eds.), *Phenotypic Plasticity of Insects*.
- 729 Wiedenmann J, D'Angelo C, Smith EG, Hunt AN, Legiret F-E, Achterberg EP (2012) Nutrient enrichment can
730 increase the susceptibility of reef corals to bleaching. *Nat Clim Chang* 3:160–164
- 731 Wong KH, Goodbody-Gringley G, Putron SJ, Becker DM, Chequer A, Putnam HM (2021) Brooded coral
732 offspring physiology depends on the combined effects of parental press and pulse thermal history. *Glob*
733 *Chang Biol* gcb.15629–gcb.15629
- 734 Wyatt ASJ, Leichter JJ, Toth LT, Miyajima T, Aronson RB, Nagata T (2019) Heat accumulation on coral reefs
735 mitigated by internal waves. *Nat Geosci* 13:28–34
- 736 Yates KK, Rogers CS, Herlan JJ, Brooks GR, Smiley NA, Larson RA (2014) Diverse coral communities in
737 mangrove habitats suggest a novel refuge from climate change. *Biogeosciences* 11:4321–4337
- 738 Ziegler M, Seneca FO, Yum LK, Palumbi SR, Voolstra CR (2017) Bacterial community dynamics are linked to
739 patterns of coral heat tolerance. *Nat Commun* 8:14213