Differential recovery from mass coral bleaching on naturally extreme reef environments in NW Australia

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Abstract

Coral reefs are severely threatened by climate change and recurrent mass bleaching events, highlighting the need for a better understanding of the factors driving recovery and resilience both at the community and species level. While temperature variability has been shown to promote coral heat tolerance, it remains poorly understood how this influences coral recovery capacity. Similarly, few studies have investigated how the presence of cryptic species influences bleaching and recovery responses. Using an integrated ecological, physiological and genomic approach, we examined the recovery of both coral communities and their dominant species from the 2016 mass bleaching event in the macrotidal Kimberley region, NW Australia. We show that recovery of coral communities inhabiting adjacent but environmentally contrasting reef habitats differed dramatically following unprecedented bleaching in 2016. Both intertidal (thermally extreme) and subtidal (thermally moderate) habitats experienced extensive bleaching (72-81%), but subtidal coral communities had a greater percentage of severely bleached corals than the intertidal community (76% versus 53%). Similarly, subtidal *Acropora aspera* corals suffered much greater losses of chlorophyll *a* than intertidal conspecifics (96% versus 46%). The intertidal coral community fully recovered to its pre-bleaching configuration within six months, whereas the adjacent subtidal suffered extensive mortality (68% loss of live coral cover). Despite the presence of three cryptic genetic lineages in the dominant coral species, the physiological response of *A. aspera* was independent of host cryptic genetic diversity. Furthermore, both intertidal and subtidal *A. aspera* harbored symbionts in the genus *Cladocopium* (previously clade C). Our findings highlight the important role of tidally-controlled temperature variability in promoting coral recovery capacity, and we propose that shallow reef environments characterized by strong environmental gradients may generally promote coral resilience to extreme climatic events. Thermally variable reef environments may therefore provide important spatial refugia for coral reefs under rapid climate change.

Introduction

Tropical coral reefs are biodiversity hotspots that provide income and resources to millions of people worldwide (Moberg and Folke, 1999); however, they are in serious decline globally due to climate change and a wide range of other stressors (Hughes et al., 2017, 2018, 2019). As recurrent mass bleaching events progressively reduce the recovery time available to coral reefs (Hughes et al., 2018), there is an urgent need to better understand the mechanisms and drivers that promote rapid recovery from extreme climatic events (Graham et al., 2011; Gouezo et al., 2019), both on the community and species level.

Reef-building corals often exist over strong environmental gradients and are characterized by wide variation in thermal tolerance (Bay and Palumbi, 2014; Palumbi et al., 2014; Dixon et al., 2015; Kenkel et al., 2015b), although their bleaching thresholds are typically only 1-2°C above their local maximum summer temperatures. Thermal tolerance can vary across latitudes and regional scales (Coles et al., 1976; Berkelmans and van Oppen, 2006; Riegl et al., 2011; Howells et al., 2013) but also over much smaller spatial gradients (<10 km), including thermally distinct habitats within a single reef (Palumbi et al., 2014; Kenkel et al., 2015a; Schoepf et al., 2015b; Barshis et al., 2018). While much attention has recently focused on how these different thermal environments shape the heat tolerance and bleaching resistance of corals (McClanahan et al., 2005; Castillo et al., 2012; Palumbi et al., 2014; Kenkel et al., 2015a; Schoepf et al., 2015b; Louis et al., 2016; Barshis et al., 2018; Safaie et al., 2018), it is poorly understood how high-frequency environmental variability influences coral recovery capacity, particularly at the species level. This is despite the fact that coral community studies have shown that recovery can be highly heterogeneous (Hoogenboom et al., 2017) and habitat-specific (McClanahan and Maina, 2003; Golbuu et al., 2007; Le Nohaïc et al., 2017), for example due to differences in local environmental conditions and community composition. In addition, specific biological traits, such as the type of algal symbionts, often play an important role in influencing bleaching resistance and recovery (Stat and Gates, 2011; Putnam et al., 2012; Grottoli

et al., 2014b; Silverstein et al., 2015). Finally, unrecognized species diversity can mask differences in functional ecology, including microhabitat distributions and bleaching resistance (Boulay et al., 2014; Rose et al., 2017), and although it is increasingly being recognized that many coral species may in fact consist of several cryptic species (Knowlton, 1993; Souter, 2010; Ladner and Palumbi, 2012; Warner et al., 2015), this is rarely considered in studies investigating coral responses to and recovery from bleaching.

Thermally variable and extreme reef environments, such as back-reef environments and tide-dominated reefs (Brown et al., 2000; Palumbi et al., 2014; Schoepf et al., 2015b; Camp et al., 2018), have provided important insights into the mechanisms underlying coral heat tolerance. Therefore, these systems also have the potential to advance our understanding of how corals living in such environments recover from heat stress events. Here, we examined the divergent recovery responses of coral communities in adjacent reef habitats following an unprecedented mass bleaching event in the macrotidal Kimberley region in NW Australia in 2016 (Le Nohaïc et al., 2017; Gilmour et al., 2019). Shallow coral reefs in this region are subject to tidally-induced (up to 12 m tidal range), extreme environmental gradients (e.g. temperature, light and aerial exposure) that fluctuate strongly across multiple temporal and spatial scales (Dandan et al., 2015; Schoepf et al., 2015b). Using an integrated ecological, physiological and genomic approach, we compared the recovery capacity of two reef habitats with distinct environmental conditions at low tide (Fig. 1): (i) an environmentally extreme and thermally variable intertidal pool where corals regularly get exposed to air and have a naturally elevated heat tolerance, and (ii) a thermally moderate subtidal reef with less heat-tolerant corals (Dandan et al., 2015; Schoepf et al., 2015b). We combined reef-wide ecological surveys with physiological and genetic tissue analyses of the dominant coral species, *Acropora aspera*, to explore drivers of recovery capacity.

Material and Methods

Study site

Our study site was located at Shell Island (Shenton Bluff), Cygnet Bay, in the macrotidal Kimberley region of NW Australia (Fig. 1a). Shell Island has a tidal range of ~8 m, which creates extreme environmental gradients across small spatial scales resulting in a mosaic of environmentally different habitats depending on tidal exposure (Dandan et al., 2015; Schoepf et al., 2015b). The intertidal environment (16°28′ 45.8″ S, 123°2′ 41.3″ E) is a small shallow pool (ca. 200 × 100 m, Fig. 1a) that becomes isolated from the surrounding waters of King Sound during low tide (min. depth ~20-30 cm, average depth ~3 m, max. depth ~7 m). Although the pool retains at least 20-30 cm of water during spring low tides, the upper parts of coral colonies growing there regularly get exposed to air for up to several hours. The associated slack water period lasts for up to 4 hours, with corals experiencing a combination of stagnant flow conditions, high light levels (up to 2400 µmol m^{-2} s^{-1}) and short-term maximum temperatures of up to 37°C (Dandan et al., 2015; Schoepf et al., 2015b). In contrast, the nearby subtidal environment (16°28′ 46.8″ S, 123°2′ 36.6″ E; within 200-300 m of the intertidal; min. depth 0 cm, average depth ~4 m, max. depth ~8 m) represents a less extreme environment (Fig. 1a) where corals experience maximum light levels of up to 1800 µmol m^{-2} s^{-1} and more moderate temperatures, although average temperatures in the subtidal are the same as in the intertidal. Corals in the subtidal environment are typically not exposed to air during low tides, except during the most extreme spring low tides (i.e., only a few days per year). Short-term maximum temperatures (Fig. 1) as well as daily temperature variability differ strongly between intertidal and subtidal, with intertidal corals being exposed to up to 7°C daily temperature variability, whereas subtidal corals only experience up to 3°C daily variability (Schoepf et al., 2015b). Both intertidal and subtidal environments feature diverse coral communities dominated by branching *Acropora* spp. (Le

123 Nohaïc et al., 2017); however, intertidal corals have a higher heat tolerance than subtidal corals
124 (Schoepf et al., 2015b; Le Nohaïc et al., 2017).

125 **Reef-wide coral health surveys and environmental monitoring**

126 In the austral summer of 2016, a marine heatwave associated with strong El Niño conditions
127 caused unprecedented mass bleaching in NW Australia, including the Kimberley region (Le Nohaïc
128 et al., 2017; Gilmour et al., 2019; but see Richards et al., 2019). To quantify coral recovery and
129 mortality following this bleaching event, reef-wide coral health surveys were conducted at Shell
130 Island six months after peak bleaching from 18-21 October 2016 using the same methods that were
131 used by Le Nohaïc et al. (2017) to assess coral health prior to and during peak bleaching (13-17
132 January and 6-9 April 2016, respectively). Surveys were conducted along six randomly positioned,
133 15 m transects in each of the intertidal and subtidal environments. High-resolution photos of a 50×50
134 cm quadrat were taken every 0.5–1 m along the transect line. Photo-quadrats were analyzed using the
135 software (Trygonis and Sini, 2012). Hard corals were scored using the following four health
136 categories as a categorical bleaching score (McClanahan et al., 2004): unbleached/healthy (H),
137 moderately bleached (M: <50% of the colony bleached or colony pale), severely bleached (S: >50%
138 bleached), and dead (D).

139 From September 2015 until October 2016, water temperature, water level and
140 photosynthetically active irradiance were recorded in both intertidal and subtidal environments.
141 Water temperature was recorded every 15 minutes by HOBO U22 v2 temperature loggers (±0.2°C) in
142 both intertidal and subtidal environments. To assess cumulative heat stress, we calculated the days
143 when daily average temperature exceeded the local maximum monthly mean (MMM) temperature
144 over the previous 12 weeks from 1 September 2015 until 18 October 2016 and then accumulated the
145 positive temperature anomalies from these days. This value was then divided by 7 to calculate the
146 metric “w>MMM”, which can easily be compared to NOAA’s degree heating week (DHW) product,

except that our metric calculates the sum of all positive temperature anomalies exceeding the local MMM, whereas DHW only represents the sum of the positive temperature anomalies exceeding the local MMM by more than 1°C. This new metric "w>MMM" was developed because it provides more realistic estimates of heat stress at our study site than NOAA's DHW methodology (Le Nohaïc et al., 2017); however, in contrast to Le Nohaïc et al. (2017) we here chose to rename the metric to avoid confusion with the widely used DHW terminology. Bleaching thresholds for both intertidal and subtidal corals were previously experimentally established to be ~32°C (Schoepf et al., 2015b), ~1°C above the local MMM of 30.827 °C from NOAA's 5-km virtual station North Western Australia (version 2).

Water level was monitored continuously over the same time period at both sites using HOBO U20-001-02-Ti water level loggers (±0.05%) and RBR virtuoso water level loggers (±0.05%). Downwelling planar photosynthetically active irradiance (PAR) was measured at each site for a few days over a spring tide at three time periods in 2016 (12-17 January, 6-8 and 10-12 April, 17-20 October) using Odyssey light loggers. No light data are available from January 2016 due to the logger malfunctioning. Each of the Odyssey loggers was calibrated under water against a factory-calibrated LiCor PAR sensor. All loggers were deployed on tripods approximately 20 cm above the benthos.

Physiological analyses

In addition to the community surveys, we also tagged 5-10 visibly healthy and pale/bleached colonies of the dominant coral species at our study site, *A. aspera*, which is widespread on shallow reef habitats in both the Kimberley (Richards et al., 2015) and Indo-Pacific. Corals were tagged in both intertidal and subtidal environments during peak bleaching (April 2016) using cattle tags epoxied to the coral (Z-Spar). The health status of all tagged colonies was assessed in April 2016 and after 7 months of recovery in November 2016 using the Coral Watch® Coral Health Chart where a

change of two units in brightness indicates a significant change in symbiont density and chlorophyll *a* content (Siebeck et al., 2006). Colonies were considered either "healthy" (brightness scale 3.6-6) or "bleached" (brightness 1-3.5). Four branch tips (~3 cm) were collected from the upper part of all tagged colonies in April and November 2016 for physiological and genetic analyses (see below). However, by November 2016, several of the (mostly bleached) tagged colonies had died or could not be relocated, which led to reduced sample sizes for this time point (Table S1). Corals were collected using exemption #2549 from the Western Australia Department of Fisheries.

Corals were stored at -80°C prior to processing. To quantify bleaching, chlorophyll *a* concentration was determined spectrophotometrically (Jeffrey and Humphrey, 1975) and used as a proxy for bleaching susceptibility. Tissue was removed from the first branch tip using an airbrush and separated into animal and symbiont fraction via centrifugation (2x 10 min at 3000 g). Chlorophyll *a* from the symbiont fraction was extracted in 100% acetone in the dark at 4°C for 24 hours and the concentration determined spectrophotometrically (Jeffrey and Humphrey, 1975) and then standardized to surface area. Surface area was calculated using the relationship between skeletal mass (x, in g) and the respective computer tomography (CT)-determined surface area (y, in cm^2) of *A. aspera* skeletons from our study site ($y = 9.4871 \cdot x^{0.7729}$, n=6, R^2=0.99).

Genetic analyses

To determine if the presence of morphologically cryptic genetic lineages within our dataset influenced bleaching and recovery responses across the two reef habitats, we used an ultra-low-coverage whole genome sequencing approach to generate genotype matrices. We generated Illumina compatible shotgun libraries using Nextera DNA Library Prep Kits as in Therkildsen and Palumbi (Therkildsen and Palumbi, 2017), which offers a cost effective approach to generating whole genome libraries. Thirty-two individuals (16 from each environment) were individually barcoded and

194 sequenced on a NextSeq Illumina platform using a 300-cycle kit. We used BOWTIE2 to map reads to
195 the *A. aspera* mitochondrial genome (NCBI reference sequence: NC_022827). Mitochondrial
196 sequence reads were filtered for variant sites with a minor allele frequency greater than 0.05 and with
197 a minimum base and mapping quality of 10. Duplicate reads were removed with SAMTOOLS (Li et
198 al., 2009). We identified variant sites using a genotype likelihood approach in ANGSD (Korneliussen
199 et al., 2014) and used the resulting covariance matrix to carry out a principle components analysis
200 (PCA) in R. We also explored clustering of the data using NGSADMIX (Skotte et al., 2013) to
201 identify admixture proportions among samples assigned to predefined clusters, restricting our
202 analyses to loci scored in >95% of individuals. Finally, to identify any differences in symbiont
203 communities between environments, we used BLASTn to map merged paired-end reads from the
204 library to the GeoSymbio ITS2 database (Franklin et al., 2012).

205 **Statistical analyses**

206 *Coral health surveys.* Coral health and community composition was analyzed using
207 Permutational Multivariate Analysis of Variance (PERMANOVAs). Prior to multivariate statistical
208 analysis, count data were converted to percent abundance and square root transformed. The four
209 health categories (UB, M, S, D) across all coral genera were statistically tested for differences
210 between environments (intertidal, subtidal) and time points (January, April and October 2016) using
211 two-way PERMANOVAs, the Bray-Curtis similarity index and 9999 permutations. Transects served
212 as replicates. Additional one-way PERMANOVAs were conducted to (1) test the effect of time on
213 coral health across all genera in the intertidal and subtidal, respectively, and (2) to compare intertidal
214 and subtidal at the recovery time point (Oct). Post-hoc pairwise comparisons were calculated, with *p*-
215 values adjusted using the sequential Bonferroni correction. Principal Component Analysis (PCA) was
216 used to visualize the data. The software PAST was used for the PERMANOVA and PCA analyses
217 (Hammer et al., 2001).

Physiological analyses. Since three cryptic genetic lineages were identified (see Results), the effect of genetic lineage on coral chlorophyll *a* concentration was assessed using generalized linear mixed model (GLMM) analysis. GLMM analyses were conducted for (1) corals from all three lineages, and (2) corals from the two main lineages only, to see if the small sample size of the third lineage (n=3) affected the robustness of this analyses. As there was no significant effect of genetic lineage on chl*a* concentration in either case (Table S2), further statistical analysis to test for the effect of environment, health and time on chl*a* concentration was conducted for corals pooled from all three lineages (see below). However, chl*a* data for the dominant lineage only are also presented in the Supplementary Material to facilitate comparison (Fig. S2). Prior to GLMM analysis of the chlorophyll *a* data, the distribution of the residuals was visually assessed and the data were square root transformed to meet assumptions associated with GLMM analysis.

GLMM analysis was then also used to test for the effect of health (healthy and bleached as determined in April 2016), environment (intertidal, subtidal) and time (April, November 2016) on chl*a* concentration. Tukey adjusted *p*-values were used for post hoc tests when main effects were significant. When a significant interaction was observed, multiple pair-wise comparisons were conducted using Tukey adjusted *p*-values. Differences between healthy and bleached corals in their respective environments were tested *a priori*. GLMM analyses were performed using SAS. *P*-values ≤ 0.05 were considered significant.

Results

Recovery responses of intertidal versus subtidal coral communities

Coral community health surveys conducted before, during and six months after the 2016 bleaching event revealed strong differences in survival and recovery across small spatial scales

241 (hundreds of meters) (Fig. 1, Table 1). The intertidal coral community suffered 72% bleaching (± 5
242 SE; moderately and severely bleached corals combined) but mostly recovered within six months with
243 little mortality (9% ± 5 SE) (Fig. 2). In stark contrast, the large majority of the bleached subtidal
244 coral community ultimately died (71% ± 11 SE) (Fig. 2), although being separated by only 200-300
245 meters and experiencing a similar though slightly higher degree of bleaching (81% ± 4 SE versus
246 72% ± 5 SE for intertidal). Thus, live coral cover in the intertidal was maintained at essentially pre-
247 bleaching levels (6% proportional decrease in coral cover), whereas in the subtidal it dropped by
248 68%, resulting in a degraded reef dominated by dead *Acropora* spp. corals that differed significantly
249 from its pre-bleaching state (Fig. 2a, Table 1).
250 Despite the different recovery responses, intertidal and subtidal coral communities had a
251 similar composition prior to bleaching and experienced similar levels of heat stress exposure. Both
252 reef environments were strongly dominated by healthy *Acropora* spp. corals prior to bleaching (Fig.
253 2a); thus, the bleaching and recovery response of this genus largely determined the overall recovery
254 trajectory within each environment. Similarly, heat stress in both reef environments accumulated
255 along a similar trajectory, reaching 4.5 and 4.3 w>MMM in the intertidal and subtidal during peak
256 bleaching, respectively (April 2016; Fig. 1b, c). w>MMM values ultimately peaked in early May
257 2016 with 5.8 and 6.2 W>MMM in the intertidal and subtidal, respectively, and declined in a similar
258 manner in both environments as temperatures seasonally decreased throughout autumn and winter
259 (Fig. 1b, c). However, daily temperature variability was generally much greater in the intertidal
260 compared to the subtidal, with temperatures reaching short-term maxima of up to 38.1°C in the
261 intertidal, yet only 33.8°C in the subtidal (Fig. 1b, c).
262 Light levels across spring tides were not consistently higher or more variable in the intertidal
263 as this depended on season (Fig. S1), even though average water depth is generally ~1m lower in the
264 intertidal compared to the subtidal (IT: 3.07 m ±1.82 SD, max = 6.77 m; ST: 4.07 m ±1.89, max =
265 7.89 m). In April 2016, both intertidal and subtidal corals experienced average daily light intensities

266 of ~500 µmol m^{-2} s^{-1} (IT: 514 ±519, ST: 541 ±571), and maximum light intensities of 1990 and 2115
267 µmol m^{-2} s^{-1}, respectively (Fig. S1a). In October 2016, intertidal and subtidal corals experienced
268 similar but slightly lower average light intensities of ~400 µmol m^{-2} s^{-1} than in April (IT: 442 ±426,
269 ST: 406 ±388), and maximum light intensities were also lower with 1573 and 1357 µmol m^{-2} s^{-1},
270 respectively (Fig. S1b).

271 **Cryptic genetic diversity and symbiont genus of tagged *A. aspera* corals**

272 Using a low-coverage whole genome sequencing approach, we mapped 36,717,172 reads
273 from 32 *A. aspera* colonies (mean 1,112,642 reads per sample) to the *A. aspera* complete
274 mitochondrial genome. Based on 79 variable sites spread across the mitogenome, we identified three
275 distinct genetic lineages in our dataset (Fig. 3a); however, all three lineages co-occurred in intertidal
276 and subtidal environments and were comprised of both bleached and healthy coral colonies (Fig. 3b).
277 Furthermore, the chlorophyll *a* concentration of the *A. aspera* complex was not significantly
278 influenced by host genetic lineage (Table S2). We therefore analyzed the effects of environment,
279 health and time on chlorophyll *a* concentration pooled across all lineages (see below). Mapping raw
280 reads to a list of dominant symbiont genera identified that all *A. aspera* colonies in both habitats were
281 dominated by symbionts from the genus *Cladocopium* (previously clade C; LaJeunesse et al., 2018).
282 Due to the low coverage and short reads recovered from the shotgun dataset, however, we could not
283 further resolve *Cladocopium* to ITS2 types.

284 **Chlorophyll *a* concentrations and survival of tagged *A. aspera* corals**

285 Tissue samples collected during and seven months after bleaching revealed that the
286 physiological bleaching and recovery response of *A. aspera* was characterized by significant
287 interactive effects of environment, health status and time (Table S3). Although coral community
288 health surveys showed a relatively similar overall extent of bleaching for both reef habitats,

289 chlorophyll *a* analyses revealed that intertidal *A. aspera* bleached less severely than subtidal *A.*
290 *aspera*, losing only 46% of their area-normalized chlorophyll *a* concentration compared to 96% in
291 subtidal corals (Fig. 4a). This relatively higher bleaching resistance was also observed in the
292 community-wide surveys as reflected in the lower percentage of severely bleached corals (53%) in
293 the intertidal coral community compared to the subtidal community (76%) (Fig. 2b).
294 Survival of tagged *A. aspera* differed strongly between environments, with 83% (n=5) of
295 bleached colonies surviving in the intertidal, yet only one bleached colony (20%, n=1) surviving in
296 the subtidal, thus strongly mirroring the trends observed in the coral community surveys (Fig. 2).
297 However, among the surviving colonies, chlorophyll *a* concentrations of previously bleached corals
298 were no longer significantly lower compared to the healthy coral and had, thus, fully recovered 7
299 months after peak bleaching in both intertidal and subtidal environments (Fig. 4b).
300

301 **Discussion**

302 As coral reefs face more frequent mass bleaching events and reduced recovery times (Hughes
303 et al., 2017, 2018), attention has increasingly focused on how different thermal environments shape
304 the bleaching resistance of corals (McClanahan et al., 2005; Castillo et al., 2012; Palumbi et al.,
305 2014; Kenkel et al., 2015a; Schoepf et al., 2015b; Louis et al., 2016; Barshis et al., 2018; Safaie et al.,
306 2018). However, how recovery from heat stress events is influenced by environmental variability has
307 received much less attention, especially on the species level. We show here that strong environmental
308 variability associated with a naturally extreme, macrotidal reef site not only increases coral heat
309 tolerance as has been shown previously (McClanahan and Maina, 2003; Oliver and Palumbi, 2011;
310 Palumbi et al., 2014; Schoepf et al., 2015b; Safaie et al., 2018), but also promoted rapid recovery of
311 coral communities from mass bleaching.

312 **Thermally variable reef habitats promote rapid recovery from mass bleaching**

313 Bleaching and recovery responses of coral communities in adjacent reef habitats differed
314 strongly across fine-scale but extreme environmental gradients following unprecedented mass
315 bleaching in the macrotidal Kimberley region of NW Australia in 2016. Both intertidal and subtidal
316 reef habitats experienced extensive, severe bleaching during peak heat stress (Le Nohaïc et al., 2017),
317 with 72% and 81% of corals bleached, respectively (Fig. 2b). However, the subtidal coral community
318 had a greater percentage of severely bleached corals than the intertidal community (76% versus
319 53%), indicative of lower heat tolerance as observed in previous experimental work (Schoepf et al.,
320 2015b). These differences in community-wide heat tolerance were further corroborated by the
321 physiological analyses of tagged *Acropora aspera* corals, the dominant coral species at our study site:
322 bleached subtidal corals lost 96% of their area-normalized chlorophyll *a* concentration compared to
323 their healthy-looking counterparts, whereas intertidal bleached corals lost only 46% of their
324 chlorophyll *a* concentration (Fig. 4).
325 Surveys conducted six months after peak bleaching further revealed dramatic differences in
326 survival and recovery. The intertidal coral community was able to fully recover to its pre-bleaching
327 health configuration within six months and only lost 6% of live coral cover (Fig. 2, Table 1). In
328 contrast, the subtidal community only 200-300 meters away suffered extensive mortality (71%), loss
329 of live coral cover (-68%) and reduced framework complexity driven by death and overgrowth of
330 branching *Acropora* corals, resulting in a significantly different community configuration compared
331 to pre-bleaching (Fig. 2, Table 1). The markedly distinct recovery responses contradict results from a
332 meta-analysis finding no evidence for reef zone impacting recovery rates (Graham et al., 2011) but
333 are consistent with other studies showing habitat-dependent reef recovery. For example, thermally
334 variable Kenyan reef habitats suffered less mortality and changes in community composition than
335 thermally less variable habitats after the 1998 bleaching event (McClanahan and Maina, 2003).
336 Similarly, sheltered bays in Palau suffered less mortality and recovered better from the 1998 and
337 2010 bleaching events than other habitats due to naturally higher temperatures and lower light levels

(Golbuu et al., 2007; van Woesik et al., 2012). Our findings also agree with recent experimental work showing that two genera of intertidal Kimberley corals (*Acropora* and *Dipsastraea*) had a higher bleaching resistance and survival rate than their subtidal counterparts (Schoepf et al., 2015b). Given that the two habitats experienced similar heat stress exposure and were both dominated by heat-sensitive *Acropora* corals (Le Nohaïc et al., 2017), this points to the more extreme environmental conditions, particularly greater daily temperature fluctuations (Oliver and Palumbi, 2011; Schoepf et al., 2015b; Safaie et al., 2018) and/or high light levels (Brown et al., 2000, 2002) in the intertidal, playing a key role in promoting coral heat tolerance (Schoepf et al., 2015b) and recovery capacity (this study). Since our findings are consistent with those from other reefs characterized by environmental variability (McClanahan and Maina, 2003; Golbuu et al., 2007; van Woesik et al., 2012), we propose that strong, fine-scale environmental gradients may be significant drivers of coral recovery from mass bleaching.

The 2016 bleaching event is the first documented mass bleaching event in the inshore Kimberley region (Le Nohaïc et al., 2017; Gilmour et al., 2019), highlighting that global warming is increasingly also impacting remote coral populations with naturally high stress tolerance (Dandan et al., 2015; Schoepf et al., 2015b), although some areas seem to have escaped bleaching (Richards et al., 2019). This bleaching event coincided with an extremely unusual and dry wet season in the Kimberley (Le Nohaïc et al., 2017), high local night-time temperatures (Richards et al., 2019) and the most extreme tides of the year; thus, it is likely that the presumably increased light and UV stress as well as aerial exposure contributed to the extensive mortality observed in the more heat-sensitive subtidal corals. However, the high survival and rapid recovery of the intertidal community is expected to enhance the longer-term recovery of the subtidal coral community via recruitment, even though we note that bleaching can have negative impacts on coral reproduction (e.g. Szmant and Gassman, 1990).

Limited influence of host cryptic genetic diversity and symbiont genus on recovery responses

Our study showed that the divergent recovery responses of intertidal and subtidal coral communities were not significantly influenced by the presence of cryptic genetic diversity in the host of the dominant coral species, *Acropora aspera.* We identified three cryptic genetic lineages in our dataset that cannot be distinguished based on morphology; however, neither lineage was associated with a specific habitat nor displayed particular susceptibility/resistance during bleaching. This is in contrast to other cryptic coral species found to have different environmental niches and/or stress tolerance (Boulay et al., 2014; Rose et al., 2017). We caution, however, that two of the three lineages were represented in only a small number of samples. Environmentally extreme habitats may favor cryptic species diversity because evolving under extreme conditions can constrain morphological change, thus resulting in morphological stasis (Bickford et al., 2007). Therefore, our study adds macrotidal reef environments to a growing list of extreme environments, such as underwater karst (Lefebure et al., 2006) or deep-sea environments (Vrijenhoek et al., 1994), which support significant cryptic species diversity.

Corals from the *Acropora aspera* complex from both intertidal and subtidal habitats harbored symbionts from the broadly distributed genus *Cladocopium*, which is consistent with other work at our study site (Schoepf et al., 2015b) and in the north Kimberley region (Thomas et al., 2014). However, these findings differ from other thermally extreme reef habitats, such as the back-reef pools in American Samoa, where higher proportions of *Durusdinium* symbionts (LaJeunesse et al., 2018) were found in the pool with higher and more variable temperatures (Palumbi et al., 2014). The genus *Cladocopium* comprises many physiologically diverse species, which are often locally adapted to a range of environmental conditions (Fisher et al., 2012; LaJeunesse et al., 2018), including high temperatures (Howells et al., 2011). It is therefore possible that intertidal and subtidal corals in our study hosted different species of *Cladocopium*, and/or that shifts in dominant symbiont genus or

386 species occurred during recovery (Grottoli et al., 2014b; Silverstein et al., 2015). However, a growing
387 body of literature suggests that resistance to high temperatures (though not light) can be strongly
388 mediated by the coral host (Baird et al., 2008) and is, thus, often (but not always) independent of the
389 symbiont (Barshis et al., 2010, 2018; Bellantuono et al., 2012; Palumbi et al., 2014). Analysis of
390 finer-scale symbiont dynamics at greater taxonomic and temporal resolution was beyond the scope of
391 this study, but our findings provide a framework for future research investigating this topic.

392 **Conclusion**

393 In summary, we show here that strong daily temperature fluctuations promoted rapid recovery
394 of an intertidal coral community from mass bleaching and return to pre-bleaching configurations in a
395 macrotidal, shallow reef system. Our integrated ecological, physiological and genomic approach
396 revealed that the divergent responses of intertidal and subtidal reef habitats to the 2016 bleaching
397 event were largely independent of host cryptic genetic diversity and association with certain
398 symbiont genera. This suggests that the presence of tidally-induced strong environmental gradients at
399 our study site led to local adaptation and/or acclimatization of the coral holobiont to the different
400 environmental conditions in the intertidal and subtidal reef habitat. We caution, however, that we did
401 not resolve symbiont type to species level and two of the three cryptic lineages were only represented
402 in a small number of samples. Furthermore, we were not able to investigate any signals of local
403 adaptation in the nuclear genome since our study focused on the mitogenome. Future research is
404 needed to investigate other traits associated with increased recovery capacity, such as high levels of
405 energy reserves (Grottoli et al., 2014a; Schoepf et al., 2015a) or heterotrophic plasticity (Grottoli et
406 al., 2006; Connolly et al., 2012), as well as the evolutionary and possible genetic mechanisms
407 underlying the higher bleaching resilience of intertidal corals.

408 While the macrotidal reef site investigated here represents a naturally extreme environment,
409 such thermally extreme reef habitats have significantly advanced our understanding of the

mechanisms underlying climate change resilience (e.g. Palumbi et al., 2014). Furthermore, improved recovery from bleaching has also been observed in other reefs with higher or more variable temperatures (McClanahan and Maina, 2003; Golbuu et al., 2007; van Woesik et al., 2012), although temperatures on those reefs are much less extreme than at our study site. Our findings therefore highlight the important role that tidally-controlled temperature variability can play in promoting coral heat tolerance (Schoepf et al., 2015b; Safaie et al., 2018) and we propose that shallow reef environments characterized by strong environmental gradients may generally promote the resilience of local coral populations to extreme climatic events. They may therefore provide critical refugia and spatial resilience to recurrent mass bleaching events, while also providing stocks of stress-resilient coral populations that could be targeted for new management approaches (Morikawa and Palumbi, 2019; Schoepf et al., 2019).

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author Contributions

VS designed the experiments and conducted the field work. MJ analysed the coral health surveys and conducted the physiological analyses. LT and NW conducted the genetic analyses. VS, MJ and LT conducted the statistical analyses. All authors provided feedback and contributed to the final manuscript.

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Tables

Table 1. Permutational multivariate analyses of variance (PERMANOVA) testing for the effect of environment and time on coral health across all surveyed coral genera. *P*-values ≤0.05 are highlighted in bold.

	Factor	***df***	***F*-value**	***p*-value**	**Pairwise comparisons (*p*-value)**
Two-way PERMANOVA	Environment	1	4.35	**0.0038**	
	Time	2	17.45	**0.0001**	
	Interaction	2	3.39	**0.0009**	See below
One-way PERMANOVA Intertidal	Time	2	7.27	**0.0001**	Jan vs April: **0.0007** Apr vs Oct: **0.0020** Jan vs Oct: 0.2206
One-way PERMANOVA Subtidal	Time	2	16.13	**0.0001**	Jan vs April: **0.0014** Apr vs Oct: **0.0020** Jan vs Oct: **0.0037**
One-way PERMANOVA October	Environment	1	8.54	0.0024	IT ≠ ST

Figures

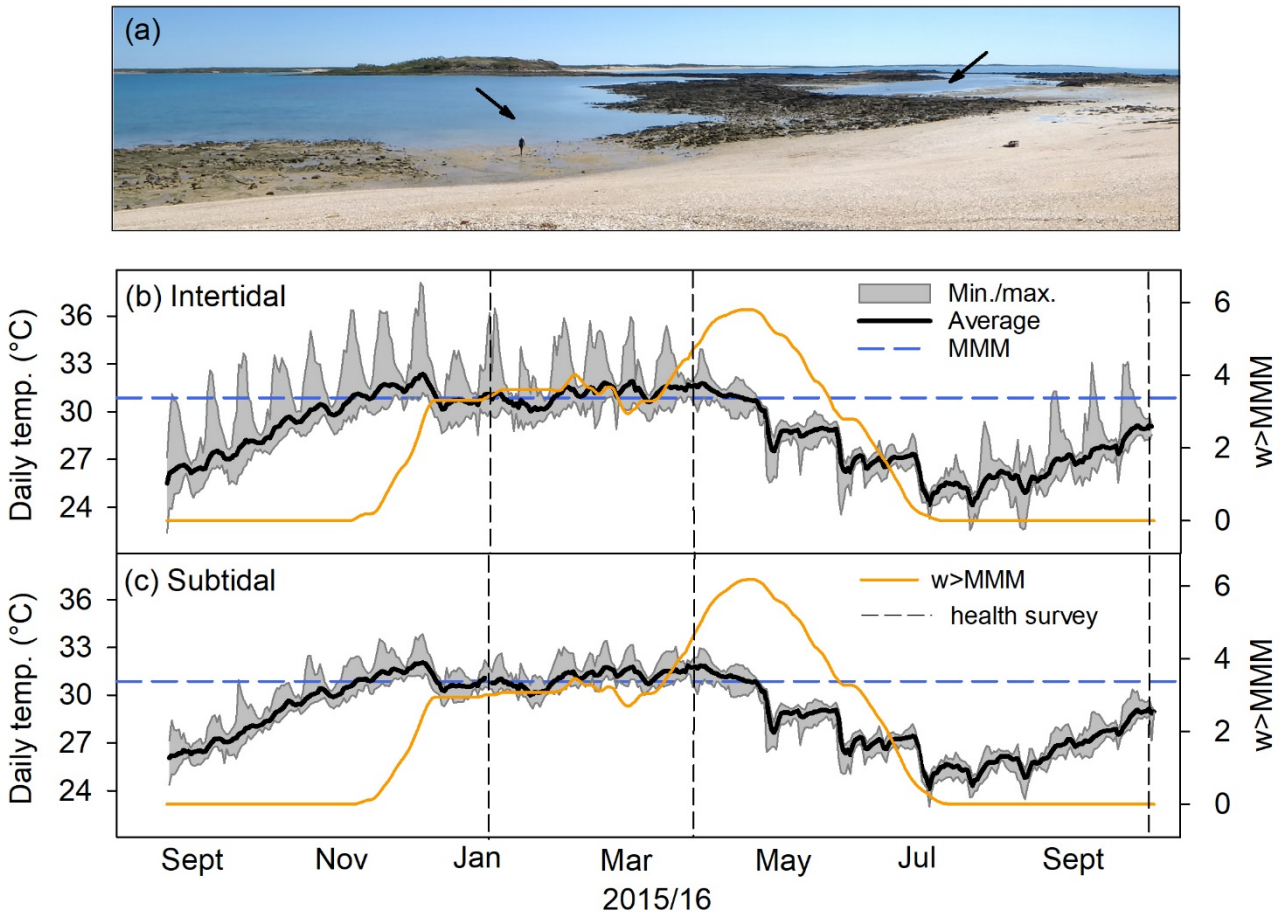
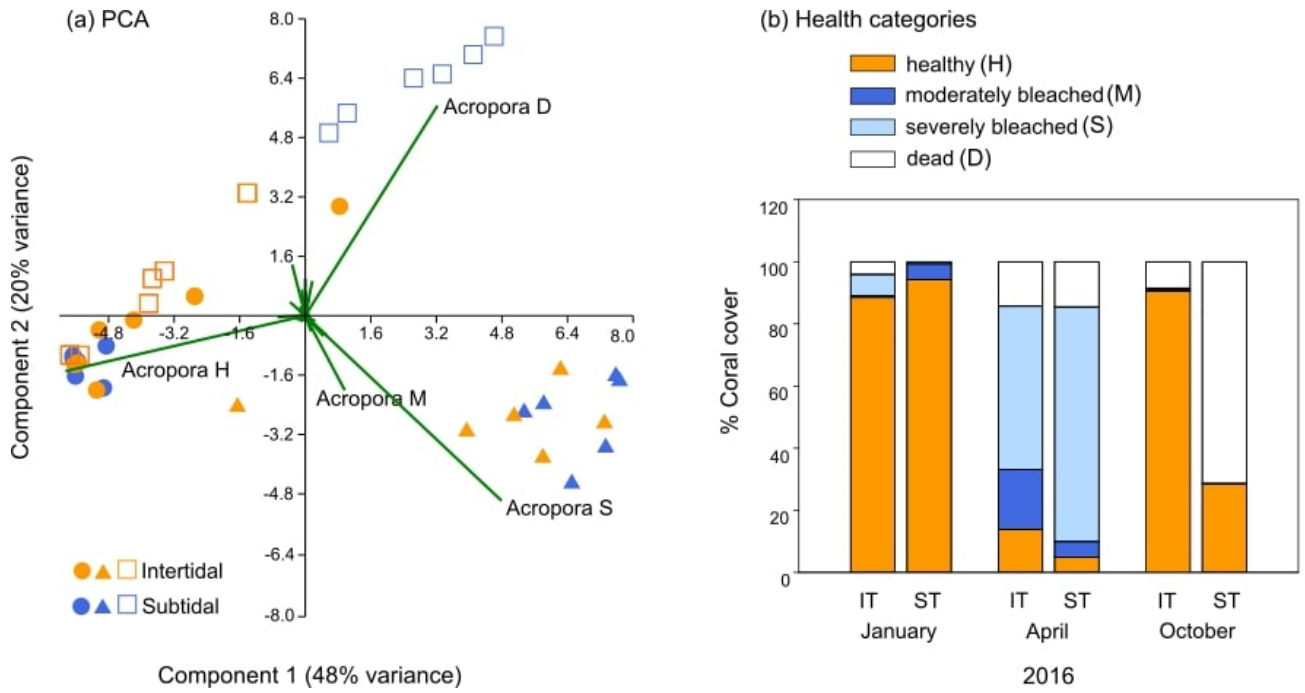


Figure 1. Temperature and heat stress exposure at intertidal and subtidal environments. (a) The subtidal (arrow centre left) and intertidal (arrow upper right) at Shell Island, Kimberley region at mid- to low tide. **(b)** Daily average, minimum and maximum temperature in the intertidal from 1 September 2015 – 18 October 2016. The blue dashed lines show the local maximum monthly mean (MMM) temperature. Orange solid lines indicate cumulative heat stress above the local MMM (w>MMM; see Methods). Vertical dashed lines indicate when coral health was assessed in reef-wide surveys. **(c)** Same as in (b) but for the subtidal.



464
465

466 **Figure 2. Changes in reef-wide coral health over time based on coral health surveys. (a)**

467 Principal components analysis (PCA) of coral health across all hard coral genera in the intertidal (IT)

468 and subtidal (ST) before (January, ●), during (April, ▲) and 6 months after (October, □) a bleaching

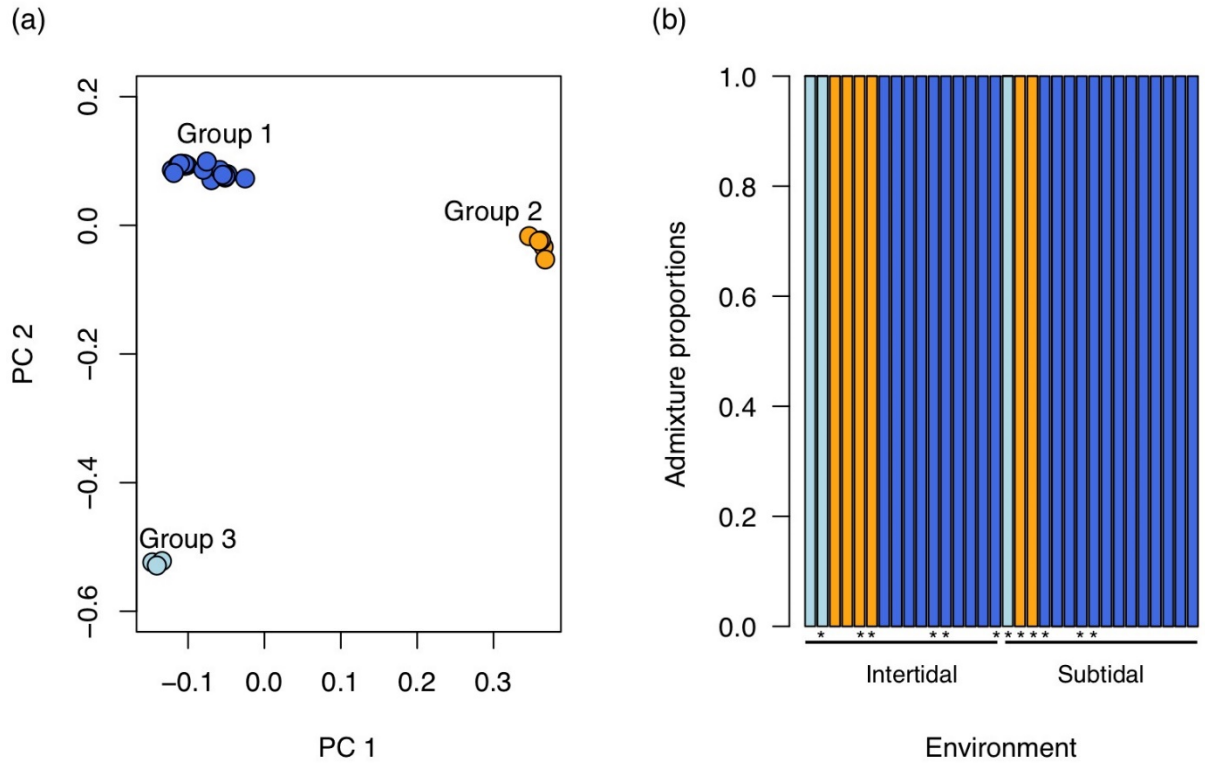
469 event in 2016. Vectors represent the dominant coral genus *Acropora* and its associated health status

470 (see below) because it had the greatest influence on overall coral health. **(b)** Percent coral cover that

471 was healthy (H), moderately bleached (M), severely bleached (S) or dead (D) at the same time points.

472 Data for January and April 2016 are also included in Le Nohaïc et al. (2017).

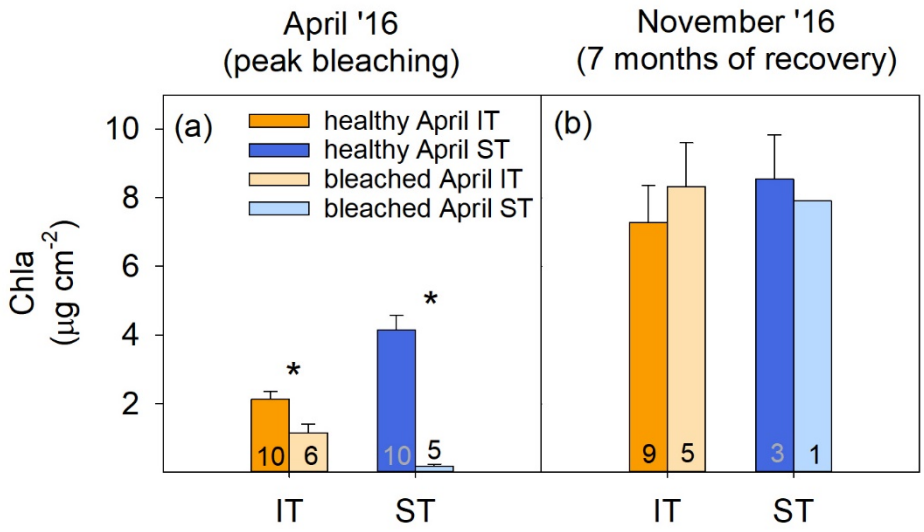
473



474

475 **Figure 3. Cryptic genetic diversity in the *Acropora aspera* species complex on Shell Island,**
476 **Kimberley. (a)** Principle components analysis and **(b)** admixture plot showing the presence of three
477 distinct genetic lineages in colonies that were tagged during peak bleaching (April 2016). Asterisks
478 indicate corals that "bleached" (see Methods).

479



480

481 **Figure 4. Coral physiology.** Chlorophyll *a* concentration of intertidal (IT) and subtidal (ST)

482 *Acropora aspera* (all genetic lineages) in **(a)** April and **(b)** November 2016. Asterisks indicate

483 significant differences between healthy and bleached/recovering corals within a specific environment

484 and time point. Numbers indicate sample size per treatment. Note that only one of the tagged

485 bleached subtidal corals survived.

486

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Supplementary Material

1 **Supplementary Figures and Tables**

2 **Supplementary Tables**

3 **Supplementary Table S1. Sample sizes for physiological analyses (area-normalized chlorophyll**
4 ***a* concentration) for corals from (a) all genetic lineages and (b) the dominant lineage only.** Coral
5 fragments were collected during and after the natural bleaching event in April and November 2016,
6 respectively.

7

	Intertidal		Subtidal	
	healthy	bleached/recovered	healthy	bleached/recovered
(a) All genetic lineages				
April 2016	10	6	10	5
Nov. 2016	9	5	3	1
(b) dominant genetic lineage only				
April 2016	7	3	10	2
Nov. 2016	6	2	3	0

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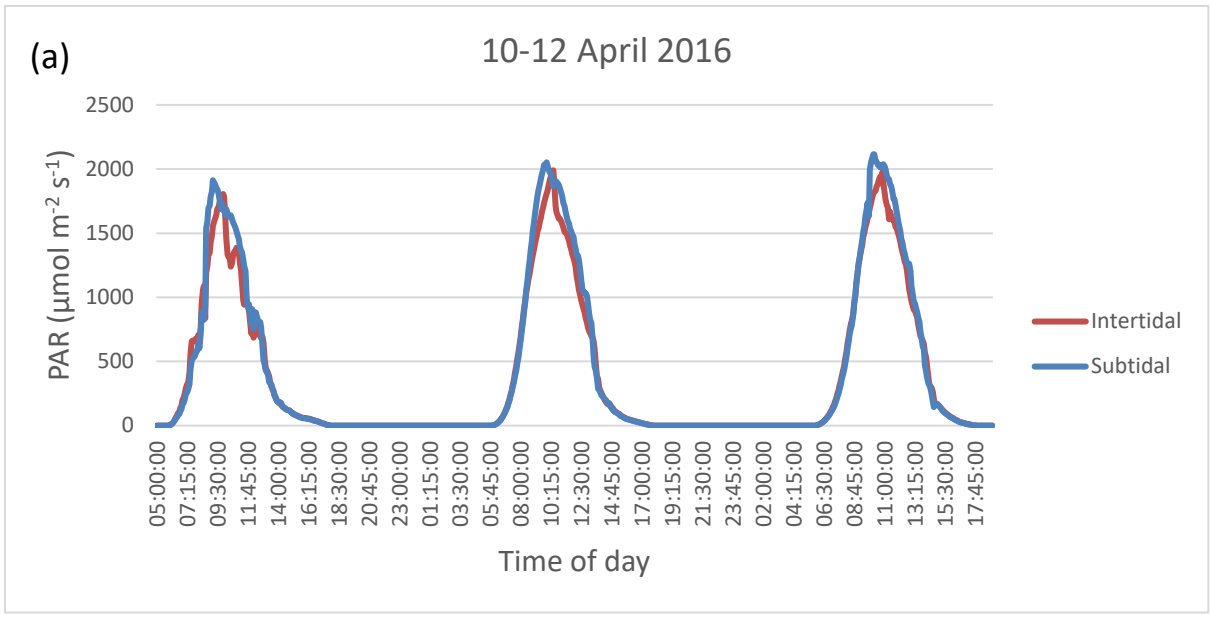
Supplementary Table S2. Generalized linear mixed model (GLMM) analyses testing the effect of genetic lineage on chlorophyll *a* concentration measured on intertidal and subtidal *Acropora aspera* corals collected in April and November 2016. Num df = numerator degrees of freedom, den df = denominator degrees of freedom.

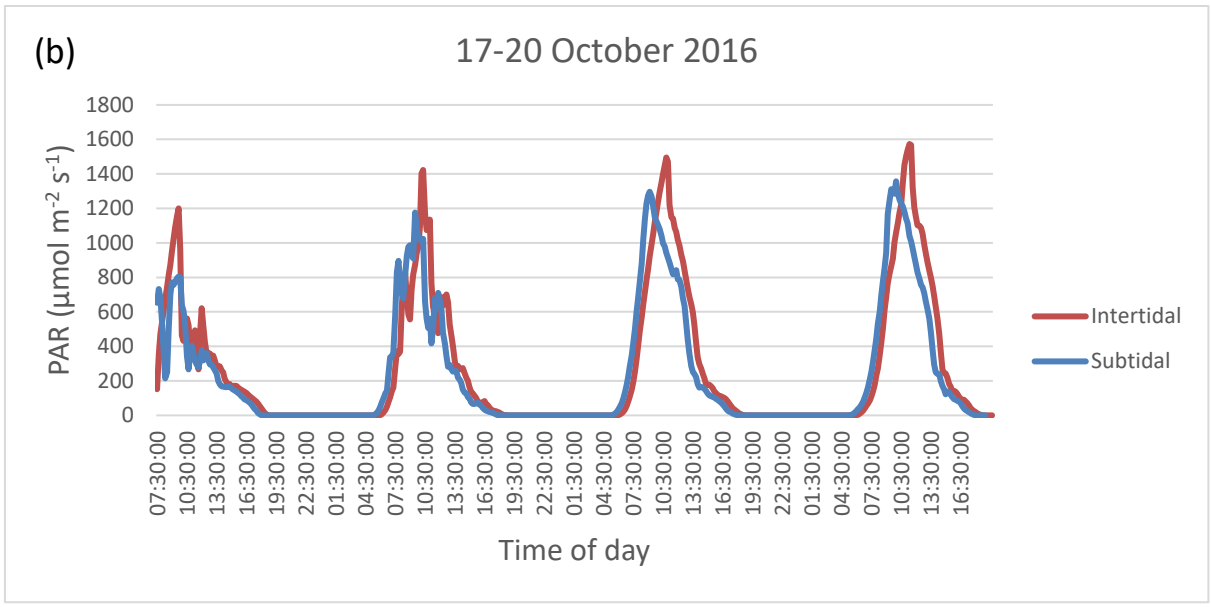
Analysis	Factor levels	Num df	Den df	*F*-statistic	*p*-value
All lineages included	1, 2, 3	2	46	0.29	0.7462
Two dominant lineages only	1, 2	1	42	0.39	0.5338

Supplementary Table S3. Generalized linear mixed model (GLMM) analyses testing the effect of environment, health and time on chlorophyll *a* concentration of *Acropora aspera* from all genetic lineages and the dominant lineage only. Post hoc Tukey tests results are given when main effects (but no interaction terms) were significant. Effects with *p*-values ≤0.05 are highlighted in bold. Num df = numerator degrees of freedom, den df = denominator degrees of freedom. Note that the three-way interaction could not be assessed for the dominant lineage corals because none of the tagged bleached subtidal corals from lineage 1 survived.

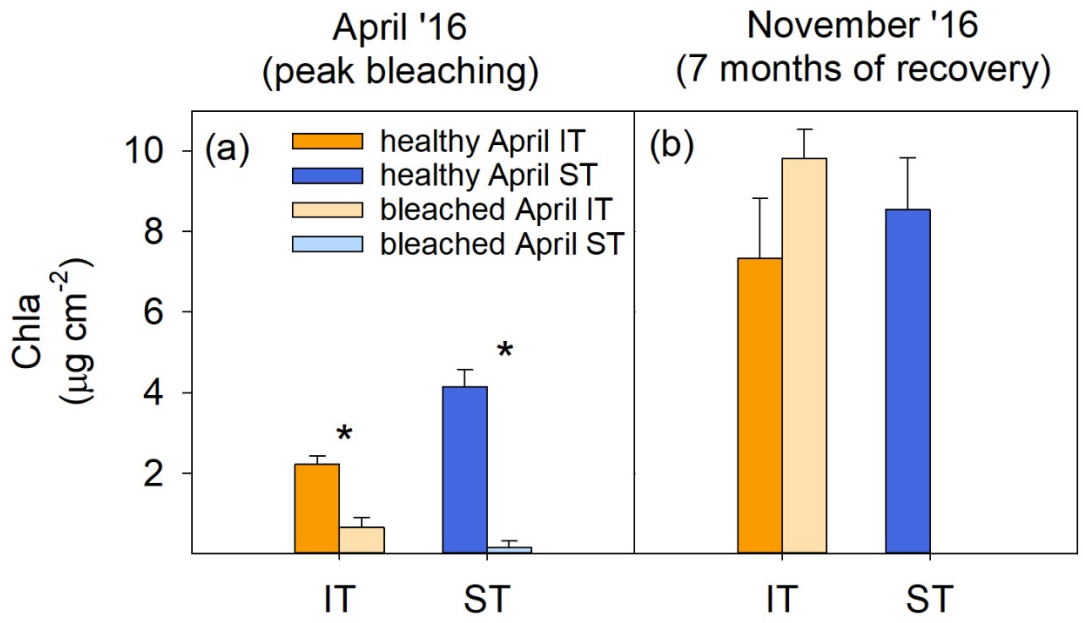
Var.	Effect	Num df	Den df	*F*-statistic	*p*-value	Tukey
all lineages	Env.	1	41	0.77	0.3845	
	Health	1	41	27.31	**<0.0001**	
	Env. * health	1	41	12.94	**0.0009**	
	Time	1	41	131.15	**<0.0001**	
	Env. * time	1	41	2.73	0.1064	
	Health * time	1	41	30.67	**<0.0001**	
	Env. * health * time	1	41	8.70	**0.0052**	See text
dominant lineage	Env.	1	26	1.61	0.2160	
	Health	1	26	42.99	**<0.0001**	
	Env. * health	1	26	16.80	**0.0004**	See text
	Time	1	26	71.53	**<0.0001**	
	Env. * time	1	26	1.02	0.3216	
	Health * time	1	26	13.52	**0.0011**	See text
	Env. * health * time	0	.	.	.	

1.1 Supplementary Figures





Supplementary Figure S1. Photosynthetically active radiation (PAR) measured in the intertidal and subtidal over a spring tide in **(a)** April and **(b)** October 2016.



Supplementary Figure S2. Coral physiology for the dominant genetic lineage. Area-normalized chlorophyll *a* concentration of intertidal (IT) and subtidal (ST) *Acropora aspera* (lineage 1 only) in **(a)** April and **(b)** November 2016. Asterisks indicate significant differences between healthy and bleached/recovering corals within a specific environment and time point. Note that none of the tagged bleached subtidal corals from lineage 1 survived.