**Coral resilience to unprecedented heat stress**

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**Summary**

Coral reefs, biologically diverse and economically important ecosystems which already live on the edge of their thermal tolerance [@Sampayo2016-vd], are under acute threat from gradual ocean warming and increasingly intense warming events [@Hughes2003-aj; @Hoegh-Guldberg2007-fh; @Baker2008-ky,@newhughespapers]. The 2015/16 El Niño was the worst warming event recorded on modern reefs in terms of severity and longevity [@Eakin:2016vf; @Heron2016-am, Claar et al PLOS ONE], yet despite massive coral mortality, some corals showed resilience to this extreme event (@Bauminprep). The response of corals to environmental stress is critically modulated by the structure and function of their diverse algal symbiont communities (*Symbiodinium* spp.), with some coral-*Symbiodinium* partnerships being much more heat tolerant than others (CITE, CITE). Identifying the mechanisms that underpin these functional differences may help us understand the capacity of corals to adapt to increasingly severe climate disturbances. Here, we track coral symbioses and survival at the epicenter of bleaching impact (Kiritimati, Central Pacific), and show, contrary to our current paradigm of coral bleaching and recovery dynamics (CITE?), that local human disturbance can influence coral susceptibility to bleaching-induced mortality, and that some corals have the capacity to re-establish symbiosis before heat stress subsides. Furthermore, we demonstrate potential mechanisms for coral survival and recovery, including the lack of preferential symbiont expulsion, and the effect of local human disturbance on pre-bleaching symbiont community structure and the probability of coral survival. These findings indicate that, even under unprecedented thermal stress, resilient coral-symbiont interactions allowed some corals to survive, providing some hope for coral reef persistence in the Anthropocene.

**Main text**

Coral bleaching, the breakdown of symbiosis between corals and their obligate photosynthetic symbionts [@Brown1997-mf], is increasing and threatening the foundation of reefs worldwide. The 2014-2017 global coral bleaching event instigated a catastrophic loss of corals across the world's oceans (Eakin 2016, Normile 2016). This event caused up to 75% bleaching on some reefs in Hawaii, and at least some level of bleaching across 93% of the Great Barrier Reef (Minton et al 2015, GBRMPA 2016, @hughesnewpaper). Superimposed on nearly-ubiquitous tropical ocean warming, the 2015/16 El Niño further amplified warming in the Central Pacific during this event (@Eakin:2016vf). Coral bleaching can lead to mortality, although corals can recover by regaining symbionts after the stress has abated [@Douglas2003-nr; @Stat2009-qq]. Despite staggering losses caused by ocean warming at a global scale, some corals have the capacity to be resilient to increasingly frequent mass-bleaching events (Hughes et al 2017).

The symbiosis between coral and their single-celled photosynthetic dinoflagellate symbionts, *Symbiodinium* spp. [@Muscatine1977-pn; @Rowan1992-lg], is the foundation of coral reef ecosystems, supporting reef diversity and function at a global scale. There is much genetic, functional, and response diversity within the genus *Symbiodinium* [@Rowan1992-lg, @Baker2003-ks; @Little2004-tm … more], prompting recent research exploring the efficacy of coral and *Symbiodinium* assisted evolution as an avenue for saving threatened reefs [Ruth and Madeline]. The *Symbiodinium* genus is divided into nine functionally distinct clades [@Stat2008-hk], and *Symbiodinium* associations can range from mutualistic to neutral to parasitic based on *Symbiodinium* type as well as environmental conditions [@Lesser2013-dj]. *Symbiodinium* “types” (a subdivision of clades), are considered putative species [@Pochon2010-jm], and have distinct geographic distributions, host associations, environmental optima [@Fabina2012-mm], and functional differences such as photosynthetic efficiency and bleaching resistance [@Sampayo2008-tw; @Kemp2014-xj]. TALK MORE ABOUT CORAL SYMBIOSES – ALGAE AND FUNGI (HOLOBIONT)

Here we show that despite the unprecedented heat stress that occurred during the 2015-2016 El Niño event, some corals exhibited resilience and survived (Figure 1). Our study location, Kiritimati Atoll (Christmas Island, Kiribati, Central Equatorial Pacific, Coordinates: 2.0, -157.4), was at the epicenter of this extreme El Niño event. Thermal anomalies were severe on Kiritimati, rapidly exceeding NOAA Coral Reef Watch's Coral Bleaching Alert Level 1 and Alert Level 2 thresholds, reaching an unprecedented (@Hoegh-Guldberg2011-sl) 25.7 Degree Heating Weeks (DHW) over a year-long bleaching event, demolishing most of the reef (Figure 1a, @Baum\_inprep). Here, we assess coral symbiosis and survival during this extreme event. We tagged, sampled, and photographed the same coral colonies before, during, and immediately after the El Niño event. We determined bleaching condition and survival for each coral colony, and used Illumina MiSeq ITS-2 amplicon sequencing and 97% *de novo* OTU clustering to evaluate changes in *Symbiodinium* community structure. We also quantified symbiont abundance by *Symbiodinium* clade using qPCR and symbiont-to-host cell ratios. To investigate mechanisms underlying the ability of these corals to not only survive a year of continuous heat stress, but to recover in the interim, we assessed the relationship between human disturbance, pre-bleaching *Symbiodinium* community structure, and coral survival, as well as the timing of *Symbiodinium* community shifts throughout this El Niño event.

Global climate change is superimposed on a suite of local stressors on coral reefs ranging from overfishing to pollution. Coral reef management has typically focused on minimizing local stressors, through marine protected areas that restrict fishing pressure or limiting agricultural runoff and sewage inputs [Mumby and Stenek 2008], rather than attempting to directly mitigate underlying climate stressors [but see vanOppen et al 2015, any of Terry Hughes’ papers]. Local management measures can significantly enhance reef recovery rates following bleaching events, for example, by protecting populations of herbivorous fishes which indirectly provision space for new coral recruits by mediating competition between coral and macroalgae [Mumby and Harborne 2010]. What is unclear is if, and via which mechanisms, local management might also influence coral resistance to heat stress. Coral bleaching and mortality on the Great Barrier Reef during the 2015-2016 El Niño event occurred irrespective of local protection, with no detectable differences across water quality or fishing pressure levels [Hughes et al. 2017]. Similarly, in Kenya, corals in unfished marine reserves fared no better than those on fished reefs during the 1997-98 El Niño event [Darling et al 2009]. Local disturbance may have an indirect effect on coral calcification rates and energy stores (Carilli et al 2017), although this study did not find a strong relationship between amount of local human disturbance and corals’ response to heat stress. describe other studies that may have provided evidence that local protection does enhance resistance (Carilli? Etc) – then a sentence describing what is known about how local protection influences *Symbiodinium* communities. –

Here, we show that it does enhance coral resistance to heat stress \*\*AND\*\* we show the mechanism of how it does so.

We show that corals living at different levels of local human disturbance had distinct symbiont communities that corresponded tightly to survivorship. This is in contrast to a recent study which concluded that particulate and dissolved nutrients do not reduce coral health at a colony scale (Rocker et al 2017).

The current paradigm of coral bleaching and resilience is that as environmental stress (such as warming) increases, corals begin to lose their obligate symbionts (*Symbiodinium*) and "bleach" [@Gates1992-ew; @Douglas2003-nr]. Thermal stress is the primary cause for coral bleaching, and extreme or long-lasting warming causes a complete breakdown of symbiosis, leading to expulsion of all (or nearly all) *Symbiodinium* from the coral host tissue, often leading to coral mortality [@Hoegh-Guldberg1999-rb]. During bleaching, there is a window for recovery, that is, a certain amount of time during which the warming must cease and conditions must return to normal so that the coral can regain its symbionts. If the window for recovery passes without amelioration of environmental conditions, the coral will starve and die. (Cunning et al 2016, Putnam et al 2017). The 2015-2016 El Niño caused prolonged thermal stress that exceeded most known coral tolerances, both in amplitude and duration (Hoegh-Guldberg 2011). Survival through such an extreme heat event provides an exceptional opportunity to understand how some corals can withstand intense heat stress, and how corals in general might survive long-term warming. Remarkably, we find that some coral colonies were able to survive this prolonged heat stress by regaining their symbionts after approximately 10 months of heat stress while temperatures were still elevated. Here, we provide evidence that corals have the capacity to not only survive, but to regain their symbionts and visibly recover from bleaching while still under intense thermal stress (Figure 1b, 2ab). These corals (Scleractinia family Merulinidae; *Platygyra* sp. and *Favites* *pentagona*) were bleached within two months of the onset of warming, but had visibly recovered after 10 consecutive months of intense warming (Fig. 1).

It is thought that corals may be able to survive thermal stress by changing their complement of symbionts to better suit environmental conditions. The adaptive bleaching hypothesis suggests that corals bleach to expel environmentally sub-optimal symbionts, followed by switching (picking up new symbionts from the environment) or shuffling (an internal change in dominant symbiont type or overall symbiont community structure) [@Buddemeier2004-se; @Buddemeier1993-sx; @Baker2001-vc; @Baker2003-ks, @Rossrecentpaper]. There is evidence for both *Symbiodinium* shuffling (Rowan 2004) and switching [@Boulotte2016-dy]. However, what remains unclear is if, and how frequently, bleaching events can actually be considered adaptive. Changes in symbiotic function have been demonstrated due to shifts in the dominant *Symbiodinium* clade. Clade D *Symbiodinium* are considered heat-tolerant symbionts [@Stat2010-zg]. Furthermore, repopulation of a coral host with clade D symbionts after a bleaching event has been proposed as a survival mechanism [@Berkelmans2006-rf; @Mieog2007-yy; @Silverstein2012-tm]. For example, one study showed that a history of thermal stress increased the prevalence of clade D *Symbiodinium* in one coral species, but did not instigate similar changes in two other coral species [@Stat2013-qp]. However, there is a trade-off to housing Clade D *Symbiodinium*, as corals that house clade D symbionts may have slower growth rates [@Little2004-tm] or lower capacity for energy storage [@Jones2011-nf]. TALK ABOUT HOW C IS MORE EVOLUTIONARILY ADAPTED (?). WHAT WE FOUND FOR C VS D

Stochasticity in the rare *Symbiodinium* biosphere (Quigley et al 2014) may build or weaken a coral's capacity for resilience. Corals commonly host background *Symbiodinium* types in low levels (Correa et al 2009), but sub-dominant *Symbiodinium* communities are often unstable (Coffroth et al 2010). Despite their small numbers, rare microbial species have been demonstrated to be disproportionally important to maintaining functional processes during environmental change in other systems (Shade et al 2014). The importance of rare *Symbiodinium* types is currently under debate. These rare types of symbionts may be commensal (neither harming nor providing gain for either partner), parasitic ("cheaters" (Yu 2001), opportunistic symbionts that take more than they give), or mutualistic (symbionts which support host function) (Parkinson et al 2015). Some research suggests that low-abundance *Symbiodinium* types have minimal functional significance to corals (Lee et al 2016). Other evidence supports the idea that shifts in *Symbiodinium* community diversity may have a large influence on coral resilience (Baskett et al 2010), and that the rare *Symbiodinium* biosphere is important for corals' response to climate change (Boulotte et al 2016). We show that after two months of heat stress, fully-bleached corals retained approximately the same *Symbiodinium* community which they had before the bleaching event (Figure 2a). This suggests that a wholesale breakdown of symbiosis occurred in bleached corals during this event, indicating a lack of preferential symbiont expulsion or exodus. Furthermore, some coral colonies changed *Symbiodinium* communities drastically upon recovery, and recovered symbiosis with *Symbiodinium* types that were present in only a negligible amount before the bleaching event (Figure 2b). This supports recent evidence suggesting that symbionts present in even very low abundances can play a critical role in coral survival and recovery (CITE recent papers).

There is increasing evidence for local adaptation in corals (Howells et al 2012, Logan et al 2013, Dixon et al 2015). Our results suggest that the capacity for coral resilience is tangibly related to local reef protection. Although massive bleaching events like this one will likely continue to cause catastrophic damage to coral reefs worldwide, mitigating local human disturbance can potentially help protect some coral species against a modest amount of ocean warming (paper showing improving local water quality increased bleaching resistance?).

Methods

**Study Location**

Kiritimati Atoll (Christmas Island), Kiribati, is located in the Central Equatorial Pacific (1.9N 157W), at the center of the El Niño 3.4 region (a region which is used to quantify El Niño presence and strength). Kiritimati has a strong gradient of human disturbance around the island, with the majority of the human population residing in three villages on the West side of the atoll. Human use, including subsistence fishing and waste water runoff, are densely concentrated in this area, while the North, East, and South regions of the island are minimally impacted (Watson et al 2016). During the 2015/2016 El Niño event, Kiritimati experienced 10 months of sustained temperature stress, causing a mass bleaching and mortality event (@BauminPrep).

**Temperature quantification**

Temperature loggers (SBE 56, Sea-Bird Scientific) were deployed around the island at 10-12m depth from 2011-2016 to measure *in situ* thermal stress. Corals are sensitive to temperatures warmer than 1°C above their normal highest summertime mean sea surface temperature (SST), known as the bleaching threshold. Temperature measurements were sub-sampled to a consistent 1-hour sampling grid, and then averaged to determine ‘half week’ temperature (similar to NOAA’s DHW product, https://coralreefwatch.noaa.gov/satellite/dhw.php). Next, hotspot values were calculated, where a hotspot is defined as when (half-weekly temperature) – (baseline temperature) is a positive number (baseline temperature is the long-term maximum monthly mean, 28.14°C). For degree heating week calculations (DHW), the value of a hotspot is included if it is >1°C (values of 0-1°C are discarded), with each of the 24 half-week cumulative hotspot measurements divided by two. DHW is calculated as a rolling sum over twelve weeks, demonstrating cumulative heat stress exceeding the bleaching threshold during that period. As temperature profiles are similar among sites, and not all sites had temperature data for the complete time period, DHW values were averaged across sites to create an island-wide *in situ* DHW metric.

**Coral tagging and sampling**

In August/September 2014, colonies of *Platygyra* sp. (n = 82) were tagged along a 60m transect at 10-12m depth at 15 different sites around Kiritimati Atoll. A photo was taken of each coral to record colony measurements and bleaching. The tagged coral colonies were resampled twice more before (January/February 2015, April/May 2015), once during (July 2015), and once near the end (March 2016) of the El Niño warming. Not all sites were visited during all field seasons, and some site surveys were only partially completed during some field seasons due to inclement weather conditions. Corals were sampled underwater using a small chisel, and stored in seawater on ice until preservation. Coral tissue samples were separated and half of the sample was preserved in Guanidinium buffer (50% w/v guanidinium isothiocyanate; 50 mM Tris pH 7.6; 10 µM EDTA; 4.2% w/v sarkosyl; 2.1% v/v-mercaptoethanol) and stored at 4°C until extraction for sequencing. The other half of the sample was preserved in SDS in DNA buffer and extracted using an organic extraction protocol for qPCR assays.

**Sample processing**

*DNA Extraction*

For the samples prepared for sequencing, DNA extraction was performed using a guanidinium-based extraction protocol [@Stat2009-qq; Cunning2017-sc; Cunning2015-mt] with the modification that the DNA pellet was washed with 70% ethanol three times rather than once. After extraction, DNA was cleaned using Zymo Genomic DNA Clean and ConcentratorTM -25 (Catalog Nos. D4064 & D4065) following the standard protocol (<http://www.zymoresearch.com/downloads/dl/file/id/638/d4064i.pdf>). DNA was measured using the dsDNA Qubit BR assay. Any samples that had concentrations below detection levels of this assay, were quantified using the dsDNA Qubit HS assay.

For the samples prepared for qPCR, DNA extraction was performed using an organic extraction method following [CITE HERE]. Briefly, …

**High-Throughput (MiSeq) Amplicon Sequencing**

*ITS-2 Amplicon*

The ITS-2 amplicon was chosen for high-throughput sequencing because it is currently the standard region used for identification and quantification of *Symbiodinium* taxa. Although ITS-2 is a multi-copy marker, it can be phylogenetically (LaJeunesse, 2001), functionally, and ecologically (Cunning et al 2017) informative. To minimize misinterpretation of intragenomic data, we conducted 97% within-sample OTU clustering. Instead of combining all sequences together into one fasta file and clustering together, we cluster each sample independently, and then collapse identical taxa across samples. As described in Cunning et al 2017, this approach increases the likelihood of collapsing intragenomic variation within a sample, while maintaining what is more likely to be biologically and ecologically relevant interspecific variation among samples.

*Library Preparation and Sequencing*

Library preparation for Illumina MiSeq ITS-2 amplicon sequencing was performed following the Illumina 16S Metagenomic Sequencing Library Preparation (Illumina protocol, Part # 15044223 Rev. B) with the following modifications:

* ITS primers (ITS-forward: 5’-TCG TCG GCA GCG TCA GAT GTG TAT AAG AGA CAG GTG AAT TGC AGA ACT CCG TC-3’ and ITS-reverse: 5’-GTC TCG TGG GCT CGG AGA TGT GTA TAA GAG ACA GCC TCC GCT TAC TTA TAT GCT T-3’ [@Stat2009-qq]) were used instead of the 16S primers
* PCR 1 annealing temp was 52°C, PCR 1 was performed in triplicate, and PCR product was pooled prior to bead clean.
* 60 µl SPRI beads were used for PCR 1 clean up
* PCR 1 bead clean up elution buffer volume varied depending on the Qubit concentration of initial gDNA. Changes were as follows:
  + gDNA concentrations with 1 ng/ µl (or less) were resuspended in 12.5 µl elution buffer
  + gDNA concentrations between 2 ng/ µl to 4 ng/ µl were resuspended in 42.5 µl elution buffer
  + gDNA concentrations of 5 ng/ µl were resuspended in 52.5 µl elution buffer

Samples were sequenced on the Illumina MiSeq platform with 2x300 paired-end read chemistry. A total of 289 samples were prepared for sequencing, and 282 of these samples were successfully amplified, sequenced, and used in downstream analyses.

**Quantitative-PCR**

*Primer Design*

Primer design for Symbiodinium (cite previous studies), clades C and D…

Primer design for *Platygyra daedalea*, choice of primers and validation… Pax-C primer; Forward 5’-GGATACCCGCGTCGACTCT-3’, reverse 5’-CCCTAAGTTTGCTTTTTATTGTTCCT, probe 5’-AATGCTAATTCAAGAATGGT-3’.

*Determination of Copy Number*

Describe process to determine copy number for C and D symbionts

*qPCR Parameters*

PCR conditions, machine used, etc…

Ct  ratios, calculation of S/H ratios

**Bioinformatics**

We conducted quality filtering of raw sequence reads (in fastq format) first using the iu-filter-quality-bokulich script implemented in Illumina-Utils [@Bokulich2013-cm; Eren2013-yg], followed by paired-end sequence merging via the iu-merge-pairs script (also in Illumina-Utils, [Eren2013-yg]), with a maximum mismatch of three bases between the forward and reverse reads. After quality filtering, sequence processing and identification was performed following all specifications of [@Cunning2017-sc]; chimeric sequences were removed, primers were trimmed, sequences from each sample were clustered independently at 97% similarity using UCLUST [@Edgar2010-zl] implemented in QIIME [@Caporaso2010-yl] and resulting OTUs were collapsed at 100% identity across samples, sequences were aligned using the Needleman-Wunsch global alignment algorithm (Biostrings package, [@Pages2017-ie]) in R [@R\_Development\_Core\_Team2008-sp], and *Symbiodinium* sequences were named using a reference database (Cunning et al 2015, Cunning et al 2017; reference database is archived, along with full bioinformatic pipeline at https://github.com/daniclaar/KI\_Platy).

The Phyloseq package [@McMurdie2013-hf] in R was used to store and analyze OTU tables, taxonomic information, and sample metadata. The phyloseq object was filtered to remove OTUs observed <5 times in the entire data set (n=33 OTUs removed and n=114 kept). The phyloseq object was further filtered to remove samples with very low sequence abundances due to amplification issues (<200 sequences, n=27 samples removed and n=262 kept). In 262 coral samples, there were a total of 1,977,124 sequences after quality filtering.

A *Symbiodinium* phylogenetic tree was built by aligning ITS-2 sequences from each clade separately (align\_seqs.py from QIIME, Caporaso et al 2011) using muscle (Edgar, 2004). After sequences were aligned within each clade, a distance matrix encompassing all sequences was created using nr28s-rDNA distances (divergence of the D1–D3 region of the 28S; Pochon and Gates 2010) to describe between-clade distances. A phylogenetic tree was created using upgma (R package phangorn v.2.2.0, Schliep 2011), and the resulting tree was imported into the phyloseq object before statistical analysis.

**Statistical Analysis**

All code for analyses is available on GitHub (https://github.com/daniclaar/KI\_Platy).

*Symbiodinium clade summary*

Sequences were summarized to show overall clade abundance across the coral populations by calculating the percent of sequences for each sampling date that were identified as *Symbiodinium* clades A, C, D, and G. Not all corals were sampled at all time points due to logistical constraints. Therefor, changes in the percent of sequences for each *Symbiodinium* clade (Fig 2) can be due to either changes in *Symbiodinium* communities associated with individual coral colonies or due to selective mortality during the bleaching event.

*Constrained ordination*

To assess the factors driving differences among *Symbiodinium* communities, a canonical analysis of principal coordinates (CAP) was performed. CAP is a constrained ordination method which allows for direct comparison of environmental variables and changes in *Symbiodinium* community composition by constraining ordination axes to linear combinations of the environmental variables. After exhausting all potential constrained axes, residual variability is addressed by fitting additional unconstrained axes (which represent linear variability which is caused by factors not included in the constrained axes. We conducted ordination with the function ‘ordinate’ (phyloseq, McMurdie and Holmes 2013), using weighted unifrac distances (Lozupone et al 2007), and included field season (timepoint during which each coral was collected), status (whether the coral survived the bleaching event (alive) or died (dead)), and local human disturbance level (very high, medium, low, and very low). After ordination, we conducted an ANOVA-like permutation test to determine if the defined model was significant (anova.cca, vegan package; Oksanen et al 2017). We confirm these results using an automatic stepwise model building tool to build and evaluate the significance of constrained axes using permutation P-values (ordistep tool, vegan package; Oksanen et al 2017). Furthermore, we tested the variance inflation factors (vif.cca, R package vegan) to test for redundant constraints, or for multicollinearity between model factors. Finally, we conducted two ANOVA-like permutation tests (anova.cca, R package vegan) to assess the significance of constraints by testing the full model as a whole, and the model terms individually.

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**Author Contributions**: D.C.C., R.D.G.., and J.K.B. planned the project, D.C.C., K.L.T. and J.K.B. collected the data and conducted lab analyses. D.C.C. conducted the bioinformatics and statistical analyses. More to come here on interpreting results, writing, editing……

**Author Information**: The authors declare no competing financial interests.

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**Figure 1 | Thermal stress experienced by corals, and the transition of one coral from healthy – bleached – recovered, at the epicentre of the 2015-2016 El Niño. a.** *In situ* temperature on Kiritimati (black) and bleaching threshold (red line). Color fill shows thermal thresholds: 4°C and 8°C (yellow; light orange), NOAA CRW Bleaching Alert Level 1 and 2; 12°C (dark orange), ‘mass coral mortality’ (Hoegh-Guldberg 2011); 24°C (red) ‘not experienced by reefs yet’ (Hoegh-Guldberg 2011). **b.** *Platygyra daedalea* coral, showing the initially healthy colony (i-ii) bleached after two months of heat stress (iv), ‘recovered’ after ten months of heat stress (v), still alive after heat stress (vi).

**[input figure 2 file here when we are ready to submit]**

**Figure 2 | Shift in *Symbiodinium* community composition from clade C to clade D dominance over the course of the 2015-2016 El Niño.** *Symbiodinium* community composition at each of five sampled time points for **i)** the entire pool of tagged coral colonies (solid lines, n=21-67 colonies per time point), and **ii)** a single representative tagged *Platygyra* colony (dashed lines).

**[input figure 3 file here when we are ready to submit]**

**Figure 3** **| Constrained ordination plot showing groupings of *Symbiodinium* communities from individual *Platygyra* colonies, grouping into two distinct areas according to level of local disturbance.** Ellipses show separation of the corals which survived the bleaching event (“Alive”, left side of plot) and those that did not (“Dead”, right side of plot). Values in square brackets show per cent variation explained by each constrained axis.

**[insert extended data figure 1 here]**

**Extended Data Figure 1 | Transition of individual tagged coral colonies on Kiritimati Island from bleached – recovered over the course 2015-2016 El Niño event.** Photographs of **i-iii.** *Platygyra* *ryukyuensis*, **iv-vi.** *Favites pentagona*, **vii-ix.** *Favia matthaii* (*Dipsastrea matthaii*) taken two months into the heat stress (July 2015, left column), at the conclusion of the heat stress (March 2016, right column), and after the heat stress (*iii* and *vi* November 2016, *ix* July 2017). Partial visual recovery was observed before the conclusion of the heat stress event, followed by an apparently healthy trajectory (*Platygyra ryukuensis*), partial recovery and persistence (*Favites pentagona)*, and partial persistence and extensive tissue mortality (*Dipsastrea matthaii*, note that this colony had small patches of living tissue on the lower sides of the colony).

**Extended Data Figure 2 |** Rank abundance plot for

**Extended Data Table 1 |** Indicator *Symbiodinium* taxa, significant at p<0.05 (multipatt analysis, indicspecies package, R) for *Platygyra* and *Favites pentagona* that either survived peak thermal stress (were alive in March 2016), or died during the bleaching event (tagged colonies identified with no living tissue). *Symbiodinium* communities were analyzed before the bleaching event (“Before”), two months into the bleaching event (“During”, July 2015), and with both time points pooled together (“All”).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | ***Platygyra* spp.** | | ***Favites pentagona*** | |
| Survived | Died | Survived | Died |
| Before | C1232 | D1\_multiple | N/A | N/A |
| During | C1232 | N/A | N/A | N/A |
| All | N/A | D1\_multiple | N/A | C1c/C45\_multiple |