**Coral resilience to unprecedented heat stress**

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Keywords: coral bleaching, El Niño, heat stress, climate change, resilience, *Symbiodinium*, symbiosis

**Summary**

**Main text**

Global coral bleaching is increasing, and the 2014-2017 event caused a catastrophic loss of corals around the globe. There was up to 95% mortality in some regions during the 1997/1998 El Niño event (Glynn 1993). The 2014-2017 global coral bleaching event caused coral bleaching across the world's oceans (Eakin 2016, Normile 2016), with 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). The 2015-2016 El Niño, superimposed on nearly-ubiquitous tropical ocean warming, instigated the third global coral bleaching event (@Eakin:2016vf).

The symbiosis between coral and their single-celled dinoflagellate symbionts, *Symbiodinium*, is the foundation of reef ecosystems, and a critical element of reef resilience [@Van\_Oppen2006-qf]. The coral holobiont responds to environmental conditions, and is the unit that interacts with the broader reef community [@Gates2011-zy], supporting reef diversity and function at a global scale. There is much genetic, functional, and response diversity within the *Symbiodinium* genus. *Symbiodinium* types, considered putative species [@Pochon2010-jm], have distinct geographic distributions, host associations, and environmental optima [@Fabina2012-mm]. There are functional differences between *Symbiodinium* 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]. Recent advances in next-generation sequencing techniques have revealed cryptic genetic diversity within symbiotic *Symbiodinium* [@Quigley2014-zj; @Arif2014-kx; @Green2014-az], and has allowed for long-term genetic and ecological comparisons of symbiont community structure [@Edmunds\_undated-fd].

Here, we provide the first evidence that corals have the capacity to regain their symbionts and recover from bleaching while still under intense thermal stress (Figure 1b, 2ab).

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]. 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, but functional differences such as photosynthetic efficiency and bleaching resistance are also present among *Symbiodinium* types within a single clade [@Sampayo2008-tw; @Kemp2014-xj]. Mechanisms of thermal tolerance vary among coral taxa due to the variability in symbiotic flexibility between symbiotic generalists (coral species that associate with several *Symbiodinium* partners through space and/or time) and specialitsts (coral species that consistently associate with one or a limited number of *Symbiodinium* types). Clade D *Symbiodinium* are considered heat-tolerant symbionts [@Stat2010-zg]. Furthermore, repopulation of a coral host with clade D symbionts after a bleaching event is proposed to be 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 a generalist coral species, but did not instigate similar changes in two specialist coral species [@Stat2013-qp]. However, there is a tradeoff 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].

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 the coral symbioses, leading to expulsion of all (or nearly all) *Symbiodinium* from the coral host tissue, leading to mortality [@Hoegh-Guldberg1999-rb]. Thermal stress can be exacerbated by other environmental stressors (Cooper et al 2011, BÃ©raud et al 2013, Maina et al 2008). 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). 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 while temperatures were still elevated.

Here we show that despite unprecedented heat stress, some corals exhibited resilience and survived. Our study location, Kiritimati Atoll (Christmas Island, Kiribati, Central Equatorial Pacific, Coordinates: 2, -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 DHW over a year-long bleaching event, demolishing most of the reef (@Baum\_inprep). Despite staggering losses caused by ocean warming, some corals have the capacity to be resilient to these increasingly frequent mass-bleaching events (Hughes et al 2017). Here, we assess coral symbiosis and survival during the massive 2015/2016 El Niño event. We tagged, sampled, and photographed the same coral colonies before, during, and immediately after the El Niño event. We assessed bleaching condition and survival for each coral colony, and used Illumina MiSeq ITS2 amplicon sequencing and 97% \*de novo\* OTU clustering to evaluate changes in *Symbiodinium* community structure. 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.

We document, for the first time, corals that were able to visually recover from bleaching, and to regain their *Symbiodinium* communities during the course of an extreme heat stress event. These corals (family Faviidae; *Platygyra* sp. and *Favites* sp.) were bleached within two months of the onset of warming, but had visibly recovered after 10 consecutive months of intense warming (Fig. 1).

Stochasticity in the rare *Symbiodinium* biosphere 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, and these rare types may be commensal (symbionts that pass through coral's holobiont with no harm or gain for either partner), parasitic ("cheaters", or 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), while other evidence supports the idea that the rare *Symbiodinium* biosphere is important for corals' response to climate change (Boulotte et al 2016), and that shifts in *Symbiodinium* community diversity may have a large influence on coral resilience (Baskett et al 2010). We show that after two months of heat stress, fully-bleached corals retained approximately the same *Symbiodinium* community as they had before the bleaching event. 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 recovered symbiosis with *Symbiodinium* types that were present in only a negligible amount before the bleaching event. This suggests that symbionts present in even very low abundances can play a critical role in coral survival and recovery.

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, rather than attempting to directly mitigate underlying climate stressorsbut see vanOppen et al. 2015 PNASetc.etc. 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. What is unclear is if local management can also influence coral resistance to heat stress, and if so via which mechanisms. 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 levelsHughes et al. 2017. –plus Emily’s paper showing protection in Kenya didn’t matter either –describe other studies that may have provided evidence that local protection does enhance resistance (Carilli? Etc) – but the mechanism was still unknown. –then a sentence describing what is known about how local protection influences *Symbiodinium* communities. –then BOOM! Our findings (evidence PLUS the mechanism because we rock)!!!

Notes:

-it has been unclear via what mechanism local protection would enhance coral resistance to heat stress – Here, we show that it does enhance coral resistance to heat stress \*\*AND\*\* we show the mechanism of how it does so.

-~90% mortality on KI (cite bleaching paper), but different mortality for some species

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).

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 some coral species may have the capacity to experience evolutionary rescue, defined as adaptation at a rate that allows an endangered population to survive the rate of environmental change (Orr & Unkless 2014, Carlson 2014). Our results suggest that the capacity for evolutionary rescue 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.

**Acknowledgements** Thanks to H. Putnam and J.R. Cunning for discussions about *Symbiodinium* and bioinformatics, J. Davidson for logistical and lab support, A. Eggers for molecular sequencing, and anyone else? DCC acknowledges scholarship support from an NSERC Vanier Canada Graduate Scholarship, as well as funding from the American Academy of Underwater Sciences, International Society for Reef Studies, National Geographic Young Explorers Grant, University of Victoria (UVic), and the Women Divers Hall of Fame, and equipment grants from Sea-Bird Electronics and Diver Alert Network. R.G. and J.K.B. acknowledge support from NSF RAPID (insert grant # here). DCC and JKB acknowledge funding from UVic’s Centre for Asia-Pacific Initiatives. JKB acknowledges support from the Packard Foundation, the Rufford Maurice Laing Foundation, an NSERC Discovery Grant, the Canadian Foundation for Innovation, and the University of Victoria.

**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 such coral from healthy – bleached – recovered, at the epicentre of the 2015-2016 El Niño event. a.** Degree Heating Weeks (DHW), on Kiritimati Island over the course of the 2015-2016 El Niño event. Corals are sensitive to temperatures warmer than 1°C above their normal highest summertime mean sea surface temperature (SST), known as the bleaching threshold. DHW shows how much heat stress has accumulated in an area over the past twelve weeks by summing any temperature exceeding the bleaching threshold during that period. Horizontal lines show expected bleaching severity levels: 4°C (yellow line), NOAA Coral Reef Watch (CRW) Bleaching Alert Level 1 (significant bleaching likely); 8°C (light orange line), Bleaching Alert Level 2 (widespread bleaching and mortality may occur); 12°C (dark orange line), ‘mass coral mortality’ expected to occur (Hoegh-Guldberg 2011); 24°C (dark red line) ‘not experienced by reefs yet’ (Hoegh-Guldberg 2011). Solid black line indicates *in situ* calculated DHW, and fill colors correspond to bleaching severity levels. Dashed vertical gray lines show the six sampling time points. **b.** Photographs of the same tagged *Platygyra* coral colony (#99), from the six time points (dashed grey lines), showing the initially healthy colony (i-ii) bleached after two months of heat stress (iv), ‘recovered’ to a normal brown colour after ten months of heat stress (v), and still alive six months post heat stress (vi).

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

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Figure 3 |

a. [Danielle to write this one: - will be the Constrained ordination plot showing groupings of *Symbiodinium* communities from individual *Platygyra* colonies, grouping into two distinct areas according to level of local disturbance….]; b. Bar plots showing *Symbiodinium*community composition for individual *Platygya* colonies at a single time point prior to the heat stress, from sites with high (top) and low (bottom) levels of local disturbance levels.]

Potentially fit the *Symbiodinium* network plot in here as two subpanels.

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

**Extended Data Figure 1 | Transition of individual tagged coral colonies on Kiritimati Island from healthy – bleached – recovered over the course 2015-2016 El Niño event.** Photographs of **a.** *Favites* pentagona, **b.** *Favia mathii*, **c.** Hydno??? taken prior to (i-iii), during (iv-v) and after (v) the the heat stress. Roman numerals (i-vi) align with those in Figure 1.

**Extended Data Figure 2 |** Potentially the rank abundance plot for Platy…..