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Key Points:

- An 18-year record of coral cover spanning three strong El Niño heatwaves reveals a weakening impact of thermal stress over time
- Coral communities recovered from the catastrophic 2002/2003 heatwave suffered lower mortality in 2015/2016 despite a doubling of thermal stress
- A decoupling of coral mortality and thermal stress suggests repopulation by thermally tolerant survivors may aid adaptation to ocean warming

Supporting Information:

Supporting Information may be found in the online version of this article.

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Increasing Coral Reef Resilience Through Successive Marine Heatwaves

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Abstract Ocean warming is causing declines of coral reefs globally, raising critical questions about the potential for corals to adapt. In the central equatorial Pacific, reefs persisting through recurrent El Niño heatwaves hold important clues. Using an 18-year record of coral cover spanning three major bleaching events, we show that the impact of thermal stress on coral mortality within the Phoenix Islands Protected Area (PIPA) has lessened over time. Disproportionate survival of extreme thermal stress during the 2009–2010 and 2015–2016 heatwaves, relative to that in 2002–2003, suggests that selective mortality through successive heatwaves may help shape coral community responses to future warming. Identifying and facilitating the conditions under which coral survival and recovery can keep pace with rates of warming are essential first steps toward successful stewardship of coral reefs under 21st century climate change.

Plain Language Summary Mass bleaching events caused by warming oceans and intensifying marine heatwaves have killed millions of corals globally. In the central equatorial Pacific, coral reefs experienced three extreme heatwaves within 15 years, providing valuable insights into the mechanisms that could facilitate coral survival under global warming. We examined an 18-year record of coral cover in the Phoenix Islands Protected Area (PIPA) to track the community response to each event. In the 2002/2003 heatwave, coral communities across PIPA were decimated, with some reefs experiencing near complete mortality. Strong recovery followed and in 2009/2010, a heatwave of similar magnitude caused minimal mortality. The 2015/2016 heatwave was the strongest on record, exposing PIPA's coral communities to twice the thermal stress of 2002/2003. Yet coral mortality during this event was disproportionately low. An examination of 11 environmental metrics that may have modulated the impacts of extreme heat revealed no consistent explanation. Rather, our results support the hypothesis that the survival of thermally tolerant colonies in 2002/2003 and localized recruitment, facilitated recovered communities with greater thermal tolerance than those that inhabited the reefs two decades ago. Understanding and promoting the conditions that facilitate coral recovery and adaptation would enhance our ability to foster coral reef survival.

1. Introduction

Marine heatwaves have increased in frequency and magnitude with devastating consequences for ocean ecosystems (Smale et al., 2019). Tropical reef-building corals have been particularly hard hit, with significant global declines linked to thermal stress (Hughes et al., 2018). As the oceans continue to warm, model projections of coral reef futures have become increasingly dire (van Hooidonk et al., 2016).

Yet, amidst widespread declines are indications that some coral populations have the ability to survive rising sea surface temperatures (SST) (Romero-Torres et al., 2020; Sully et al., 2019). Survivors of extreme, recurrent bleaching events (Barkley et al., 2018), corals thriving in chronically hot environments (Palumbi et al., 2014; Shamberger et al., 2014), and resilience to multiple heatwaves (Obura et al., 2018; Romero-Torres et al., 2020) indicate that adaptation, enabled by extensive genetic architecture associated with acclimatization and adaptation to thermal stress (Bay et al., 2017; Fuller et al., 2020; Palumbi et al., 2014),

is possible. But critical questions remain. Can such adaptations occur at the spatial scales required for the survival of entire coral populations (Romero-Torres et al., 2020) and how will they modify survival projections under future warming (Bay et al., 2017; Logan et al., 2014)?

Directional selection of naturally tolerant individuals by extreme events can rapidly increase the frequency of resilient genotypes and facilitate population-level adaptation to environmental stress (Coleman et al., 2020; Coleman & Wernberg, 2020; De Wit et al., 2014). A role for directional selection in the survival of coral reefs under climate change has been proposed (Baird & Maynard, 2008), but evidence of this occurring at large scales is limited. Here we show, using an 18-year record of coral cover from the Phoenix Islands Protected Area (PIPA) (Figure 1), that changes in the mortality response of diverse coral communities through three successive bleaching events are inconsistent with environmental drivers and instead suggest the possibility for population-level shifts in thermal tolerance that are facilitated by directional selection and enhanced by highly localized recruitment (Wood et al., 2014).

We conducted surveys across four of the Phoenix Islands (Kanton, Rawaki, Orona, Nikumaroro) spanning 4° of latitude within the remote central equatorial Pacific (CEP). Monitoring sites established at 10–15 m depth on leeward fore reefs were surveyed in 2000, 2002, 2005 (Obura & Mangubhai, 2011), 2009, 2012, 2015, and 2018 (Figure 2a, Table S1). Over this period, three strong El Niño's, each 6 years apart, fueled SST anomalies +2–3°C across PIPA for several consecutive months (Figure 1a).

2. Materials and Methods

2.1. Experimental Design

The Phoenix Islands Protected Area (PIPA), Kiribati is a UNESCO World Heritage Site encompassing 408,250 km² of ocean and eight small islands that collectively contain 34 km² of reef area (Obura, 2011) in the central equatorial Pacific (Figure 1). These reefs harbor some of the most isolated coral populations in the Pacific with the distance between the surveyed islands ranging from 150 to 375 km and the nearest islands beyond PIPA are 500–1,200 km away. To assess temporal changes in coral communities we compiled long-term monitoring data from four islands within PIPA: Kanton (2.80°S, 171.64°W), Rawaki (3.72°S, 170.71°W), Orona (4.52°S, 172.18°W), and Nikumaroro (4.68°S, 174.52°W) (Figure 1). Of these islands, only Kanton is inhabited by a small caretaker population (~50 people). Monitoring sites across the leeward fore reef slopes (10–15 m depth) of each island were established in 2000 and 2002 (Obura et al., 2011) and have been re-surveyed during five subsequent expeditions in 2005, 2009, 2012, 2015, and 2018 (Figure S1). Sites were spaced approximately ~1 km apart to minimize spatial autocorrelation of benthic communities that occurs at distances <500 m on central Pacific reefs (Gove et al., 2015). A total of 30 unique locations were surveyed and eight sites distributed across all islands have estimates of coral cover from immediately before and 2-years after the major El Niño associated bleaching events in 2002/2003, 2009/2010, and 2015/2016 (Figure S1, Table S1). Widespread evidence of community bleaching during each El Niño is confirmed based on the presence of high-density stress bands of massive *Porites* corals across PIPA (Mollica et al., 2019).

We combined published mean coral cover estimates from 2002 and 2005 (Obura & Mangubhai, 2011) with photoquadrat survey data from 2009 to 2018. Surveys were conducted following Pacific monitoring protocols using two 25 m transects separated by 5 m and laid parallel to the reef edge. Photoquadrats (0.76 m²) were taken every 2 m on alternating sides of the transect ($n = 24$ – 26 photos per site) (Smith et al., 2016). Mean coral cover was determined using manually classified images based on 100 randomly stratified points per image (one point randomly placed within each cell of a 10 × 10 grid to ensure complete coverage) in the programs Photogrid 1.0 (survey years 2009–2015) and Coral Net (survey year 2018) (Beijbom et al., 2012, 2015). Live coral was identified to genus.

Coral cover on uninhabited central Pacific Islands is fairly stable on decadal scales with the largest changes occurring with El Niño associated bleaching events (Brainard et al., 2018; Fox et al., 2019). In addition to their protected status and minimal local human impacts, the Phoenix Islands are infrequently impacted by cyclones and have no documented outbreaks of Crown-of-Thorns sea stars (Mangubhai et al., 2019). Thus, we are confident that our estimates of coral mortality are predominantly associated with bleaching induced mortality during each El Niño. We estimated coral mortality as the change in coral cover from several months prior to widespread bleaching during each El Niño to approximately 2 years after the bleaching

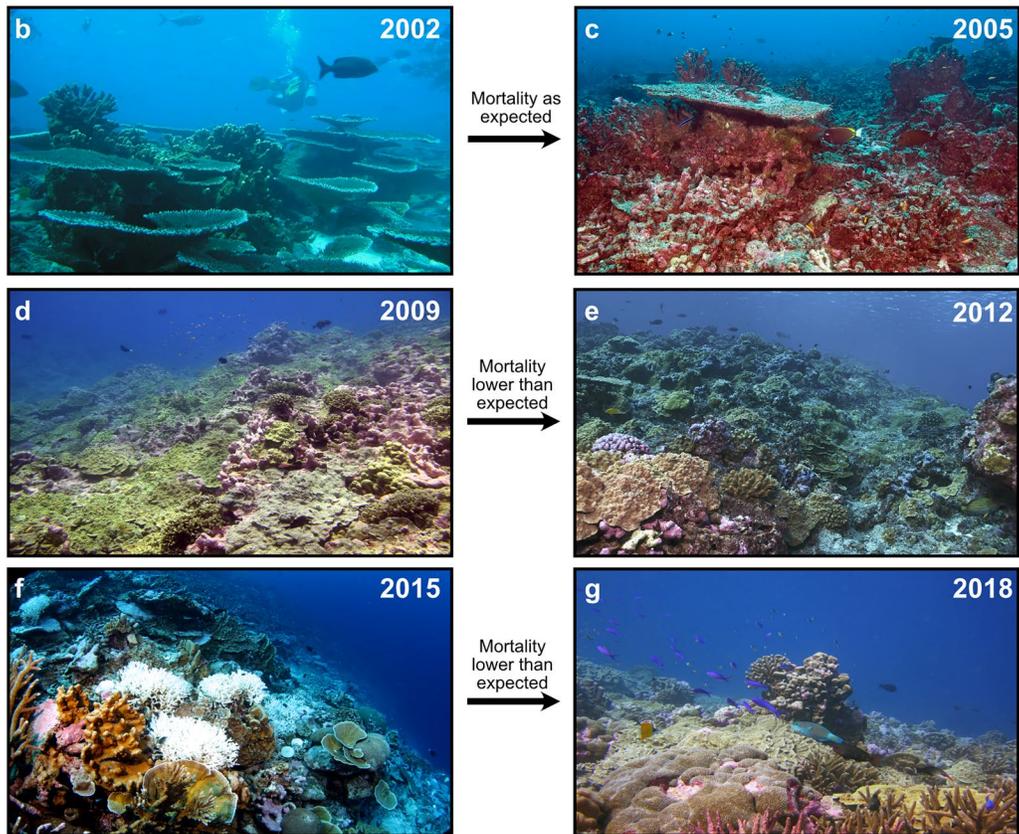
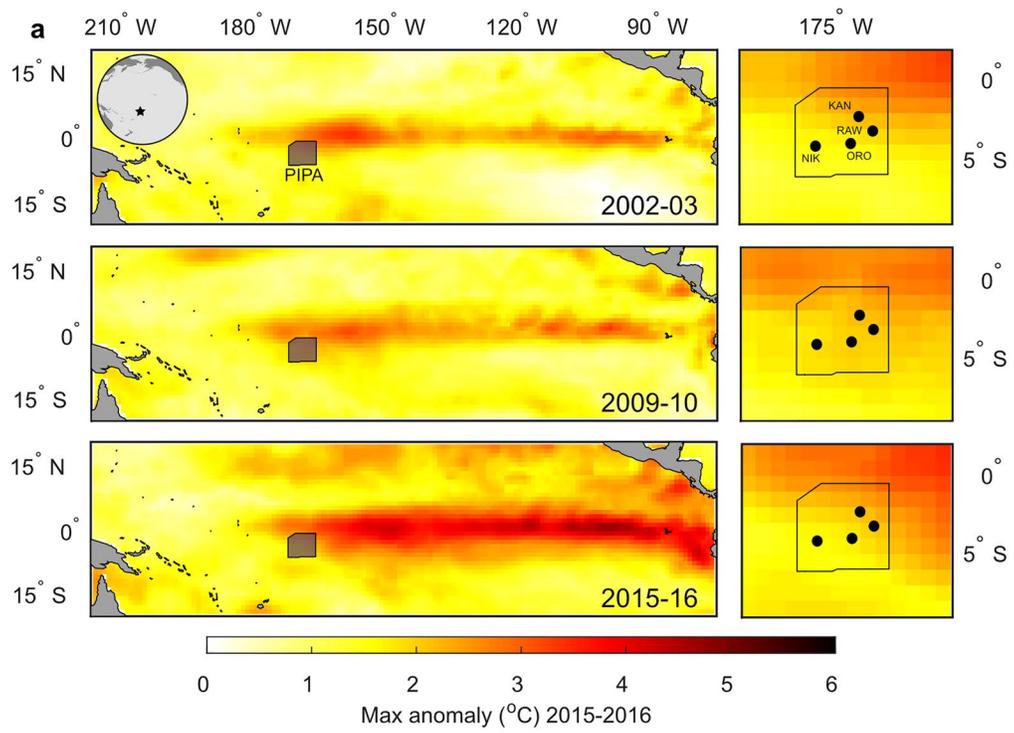


Figure 1.

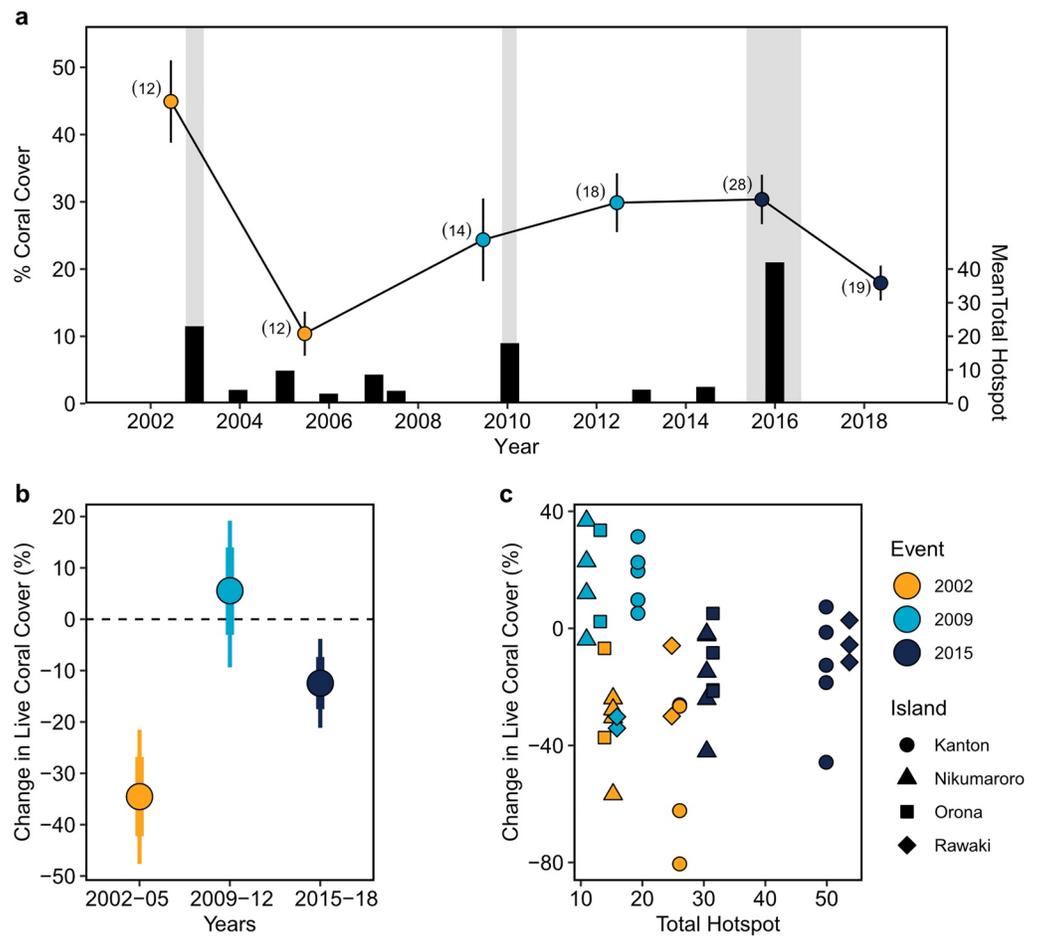


Figure 2. Long-term monitoring across the Phoenix Islands Protected Area (PIPA) reveals evidence for increasing thermal tolerance of coral communities following mass mortality during the 2002 El Niño. (a) Long-term trends in mean coral cover (\pm SE) with the number of survey sites for each time point shown in parentheses. The total hotspot is plotted as black bars to illustrate the relative magnitude of cumulative thermal stress across PIPA during each major El Niño and the width of each gray bar depicts the length of time where degree heating weeks exceeded 4°C-weeks. (b) Estimated change in live coral cover during each event. Thick and thin bars denote 75% and 95% CI, respectively. (c) Change in coral cover as a function of total hotspot values for all survey sites across PIPA reveals no relationship between coral mortality and increased thermal stress.

event ended. Mortality was estimated as both the direct change in percentage live coral cover and as the proportional loss of coral cover per site relative to the percent cover prior to the bleaching event. We used a non-parametric bootstrapping procedure to generate conservative confidence intervals around our estimates of coral mortality to accurately describe changes in coral cover across PIPA during each event. We included coral cover from all sites surveyed during a given expedition to maximize the variability in our estimates and account for differences in sample sizes through time (Figure 2, Table S1). Despite spatial heterogeneity at the site level, island-specific patterns of mean coral cover mirrored the broader pattern observed across PIPA showing decreased mortality through time (Figures 2a and S2). For each year, we randomly sampled (with replacement, n = survey sites per time period) mean coral cover from all islands and sites and calculated the mean average change in coral cover across El Niño (2002/2003, 2009/2010, 2015/2016). This

Figure 1. A history of thermal stress and coral survival in the Phoenix Islands through three major El Niño heatwaves. (a) Maximum sea surface temperature anomalies across the Pacific with the boundary of the Phoenix Islands Protected Area (PIPA), Kiribati shown (box). More detailed spatial and temporal patterns of thermal stress surrounding PIPA are shown in the adjacent plots. Each island in the study is identified by the first three letters of its name. Images of coral change across each heatwave: Kanton experienced high mortality in 2002–2005 (b, c). Low mortality was observed between 2009 and 2012 (d, e). Despite unprecedented thermal stress and extensive bleaching mortality was lower than expected between 2015 and 2018 (f, g). Photos: (b, c) D. Obura; (d) R. Rotjan; (e) M. Priest; (f) B. Zgliczynski; (g) M. Fox.

process was repeated 10,000 times to create a distribution of PIPA-wide estimates of change in coral cover during each bleaching event. From these distributions, we estimated the 75 and 95% confidence intervals around the mean decline in coral cover (Figure 2b) and the proportional loss of coral cover (reported in text) to compare the differential responses across the bleaching events. For detailed methods on the analysis of coral community structure and in situ validation of satellite SST measurements, and additional imagery from PIPA through time see Supporting Information S1.

2.2. Quantification of Thermal Stress

We quantified 3 metrics of thermal stress to compare the magnitude and duration of temperature stress to the coral populations during each El Niño. We used daily satellite SSTs from the AVHRR Pathfinder version 5.3, 4 km nighttime only data set (November 1981–December 2016) (Casey et al., 2010). Temporal gaps in weekly averaged Pathfinder \ SSTs were filled using mean-adjusted values from the IGOSS OIv2 $1^\circ \times 1^\circ$ resolution data set (Mollica et al., 2019; Reynolds et al., 2002). SSTs were obtained from the grid cells nearest each sampling site and averaged together ($n = 3$ for all islands except Rawaki, $n = 1$). Weekly mean SSTs were used to quantify the maximum temperature achieved during each bleaching event to ensure conservative estimates that are temporally aligned with the period of peak thermal stress and less subject to short-term temperature spikes or missing data from finer resolution SST data products. Degree Heating Weeks (DHWs) were quantified using two methods, the traditional NOAA's Coral Reef Watch DHW where a bleaching threshold is defined as 1°C above the mean monthly maximum SST (MMM) (Liu et al., 2003) and the percentile method (Mollica et al., 2019). Percentile DHWs more accurately reflect thermal stress in regions where seasonal variability is not dominant, such as the CEP, because it accounts for the strong interannual-variability (Mollica et al., 2019). Rather than the threshold temperature of $\text{MMM}+1^\circ$, which can over-estimate thermal stress in the CEP, the percentile method considers the full distribution of temperatures experienced by corals during ENSO neutral years between 1982 and 2012 in order to account for peak temperatures occurring at different times of the year and uses the 94.4th percentile temperature as the threshold value (Mollica et al., 2019). We also calculated total hotspot (TH) as an index of cumulative thermal stress using the percentile-based threshold temperature, which reflects the total number of weeks during which SSTs exceeded the 94.4th percentile temperature during each El Niño (Mollica et al., 2019).

Temporal patterns of SST can influence the severity of coral bleaching. Specifically, a short warming event prior to the onset of peak thermal stress can boost coral thermal tolerance and protect against bleaching (Ainsworth et al., 2016). This temporal pattern results in a bimodal distribution of temperatures that can be described by the bimodality coefficient of SSTs during the 90 days prior to peak temperature (McClanahan et al., 2019). Bimodality coefficient values >0.55 suggest bimodality and support the hypothesis that a pre-bleaching warming event may have occurred (McClanahan et al., 2019). We tested for the presence of protective warming events by calculating the bimodality coefficient of weekly SSTs at each island for the 90 days prior to peak temperature during each El Niño using the *mousetrap* package in R (Kieslich et al., 2019). We found no evidence that protective warming events influenced our observed mortality patterns (Figure S6). Only Rawaki in 2015 exhibited a weakly bimodal pattern of temperature (coefficient = 0.58) and for all other islands bimodality coefficient values were below 0.55 for all El Niño events (range = 0.25–0.52). We also considered differences in the rates of warming (Fong & Glynn, 2001) and cooling as well as patterns of cloud cover and solar irradiance between events (Supporting Information S1).

2.3. Statistical Analysis

All statistical analyses were conducted using R 3.5.0 (R Core Team, 2020). We quantified the effect of peak temperature, thermal stress, SST bimodality, cloud cover, and irradiance on site-specific declines in live coral cover using linear mixed effects models. The small geographic area of PIPA and the distinct zonal gradient of environmental conditions during El Niño events in the CEP caused high collinearity between our environmental variables. Therefore, each predictor was examined individually to determine which had the greatest influence patterns of coral mortality. The monitoring site was nested within the island as a random effect to account for geographic variation and repeated sampling through time. All models were analyzed using the *lme4* package (Bates et al., 2015) and assumptions of normality and homogeneity of variance were satisfied based on visual assessment of the residuals. We tested for significant effects of each factor on coral

cover decline by calculating standardized effect sizes with bootstrapped confidence intervals using the *jtools* package, which provides a more conservative estimate of error (Long & Long, 2018). To account for multiple comparisons, family wise error rates were maintained at $\alpha = 0.05$ using the Holm-Bonferroni method. Overall, we found no significant effect of peak temperature, thermal stress, SST bimodality, or cloud cover on patterns of coral mortality (Figure S6) and all metrics showed similarly poor explanatory power (Table S2).

We used principal components regression to examine the relationship between the collinear environmental predictors and the potential for interactive effects on coral mortality (Figure S9). Scores of the orthogonal principal components were used as explanatory variables in the linear mixed effects model framework described above. Metrics of cloud cover and degree heating weeks were positively correlated (Figure S9a), which is common in this region during El Niño (Mollica et al., 2019). To simplify the PCA, we removed cloud cover and used mean irradiance as a measure of potential light stress during El Niño events and achieved similar separation (Figure S9b, Table S3). We considered all principal components of this model ($n = 5$) as potentially significant explanatory variables and sequentially removed individual components based on the least significant contribution to model fit (Graham, 2003). The best fit model was selected using Akaike Information Criteria corrected for small sample sizes (AICc) using the *MuMIn* package (Barton, 2020) (Table S4). The best fit model included principal components 1 and 3 and explained 17% of the variation in our observed patterns of coral mortality.

3. Results and Discussion

In 2002/2003, the first El Niño of the 21st century brought levels of thermal stress to PIPA's coral communities that were at the time, unprecedented in the instrumental record. Total hotspot (TH) or the total number of weeks above the bleaching threshold, the most accurate metric of cumulative thermal stress for central Pacific reefs (Mollica et al., 2019), exceeded 20°C-weeks, resulting in widespread coral bleaching across PIPA (Figures 1a, 2a and 2b). The proportional loss of coral cover across the four islands was 76.4% [95% CI: 59.1–89.3] at 10–15 m depth, reducing average coral cover from 44.9% (± 6.1 SE) to 10.4% (± 3.3) by 2005. Mortality was widespread but patchy survivorship was observed (Alling et al., 2007; Obura & Mangubhai, 2011). With the isolated PIPA islands being predominantly self-recruiting (Wood et al., 2014), these thermally tolerant survivors were likely the most important source of new recruits that bolstered the subsequent recovery.

The growth of these surviving colonies and successful recruitment of juveniles combined with an absence of local human impacts enabled a steady recovery post 2005. Benthic surveys in June 2009 showed coral cover had doubled from 10.4% to 24.4% (± 6.2) within 4 years (Figure 2a) (Stone et al., 2009). Six months later, ocean warming associated with the 2009/2010 central Pacific El Niño peaked across PIPA. Average TH exceeded 15°C-weeks, raising concerns about widespread coral bleaching and mortality across the already diminished reefscape (Figures 1 and 3). However, surveys conducted in 2012, 2 years after the El Niño, revealed that mean coral cover across PIPA had increased by 5.7% [95% CI: -9.3 to 19.0] to 30.4% (± 3.7), returning the reefs to ~68% of the mean pre-2002 coral cover (Figures 1d, 1e, 2a and 2b).

In 2015, a so-called “Super El Niño” erupted across the tropical Pacific, resulting in prolonged SST anomalies exceeding 3°C (Figure 1). In PIPA, levels of thermal stress (average TH = 39°C-weeks) far exceeded those of 2002/2003 and 2009/2010, setting a new record for the region (NOAA ERSST.v5) (Figures 1–3). During surveys conducted in September 2015, 2 months prior to peak thermal stress, moderate levels of bleaching were recorded across all islands (Mangubhai & Rotjan, 2015), and based on the magnitude of thermal stress, catastrophic coral mortality was expected. However, this was not the case. In May 2018, 2 years after the El Niño subsided, the relative reduction in coral cover during 2015/2016 was estimated to be 40.0% [95% CI: 15.5–59.8], approximately half that of 2002/2003 (Figures 1c and 1g, Figure 2b), despite double the thermal stress. Inter- and intra-island variability in coral recovery trajectories was observed but not unexpected given the unique geomorphology and community compositions across locations. The reduced sensitivity of corals to the extreme thermal stress observed over the three heatwaves, however, was consistent across PIPA (Figure S2).

The magnitude and duration of thermal stress (e.g., DHW, TH) are the principal abiotic factors used to predict bleaching and mortality. However, the severity of coral responses can be modulated by a variety of

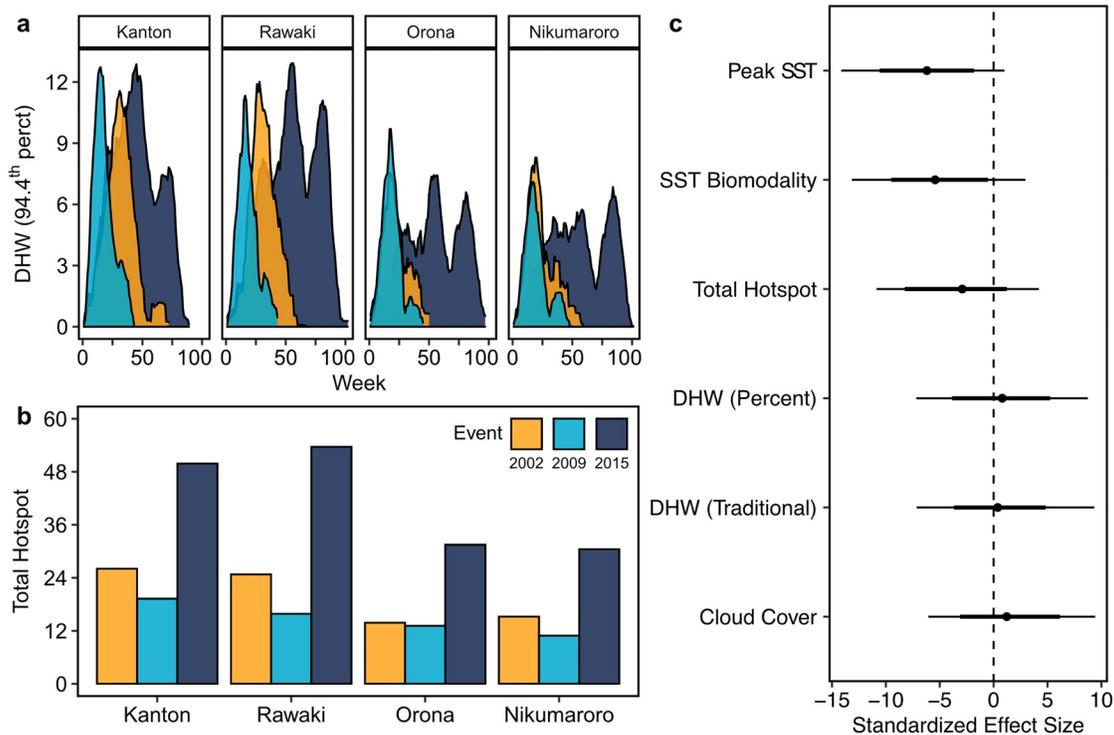


Figure 3. Thermal stress patterns across the Phoenix Islands during three major El Niño's reveal that the 2015 event was unprecedented and that environmental conditions during each event are poor predictors of coral mortality. Islands are arranged by increasing distance from the equator (increasing latitude). (a) Degree heating week (DHW) time series for each event calculated using the percentile method, which more accurately estimates thermal stress in the central equatorial Pacific than traditional DHWs. (b) Cumulative thermal stress is estimated as the total hotspot, which is the total time above the bleaching threshold during each event. (c) Individually estimated effect sizes for five metrics of thermal stress known to influence coral bleaching and mortality. Points represent mean values, thick and thin bars denote 75% and 95% CIs, respectively. All effect sizes are mean-centered and standardized by 1 SD to account for differences in predictor scales.

environmental conditions (McClanahan et al., 2019) or by adaptation to thermal stress by coral populations over time (Morikawa & Palumbi, 2019). We examined the possibility that environmental factors specific to each heatwave caused an apparent decoupling of coral mortality from thermal stress by comparing 11 metrics, including thermal stress, SST variability, cloud cover, irradiance, and their interactions against site-level estimates of coral mortality using linear mixed effects models and principal component analysis.

Our analysis confirmed that the thermal stress imposed on PIPA during the 2015/2016 heatwave was substantially greater than both 2002/2003 and 2009/2010 (Figures 3a and 3b), yet none of the environmental metrics evaluated explained more than 6% of the variation in our data (Peak SST, $r^2 = 0.06$) (Figures 3c and S6, Table S2) and the combined effects of thermal stress and irradiance explained less than 20% (principal component regression best fit model, $r^2 = 0.17$) (Figure S9, Tables S3 and S4). In the central equatorial Pacific, El Niño events are associated with increased cloud cover (Mollica et al., 2019), which can mitigate the effects of extreme heat (Donner & Carilli, 2019). However, our analysis showed that that variation in cloud cover and/or irradiance between the three heatwaves did not influence the observed coral mortality patterns (Figures S6–S9, Tables S2–S4). In other words, the inconsistent mortality outcomes from one El Niño to the next could not be explained by modulating environmental factors specific to each event (Figures 2c and 3c), highlighting the possible contribution of shifting thermal thresholds facilitated by adaptation through directional selection (Coleman & Wernberg, 2020).

We also evaluated if the rate of temperature rise contributed to inconsistent coral mortality outcomes by analyzing five temporal windows ranging from 4 to 72 weeks prior to peak SSTs (Figure S4). The rate at which temperatures increase during heatwaves can affect coral mortality (Fong & Glynn, 2001) but no consistent differences in the rate of warming across PIPA were identified between each of the three El Niño's

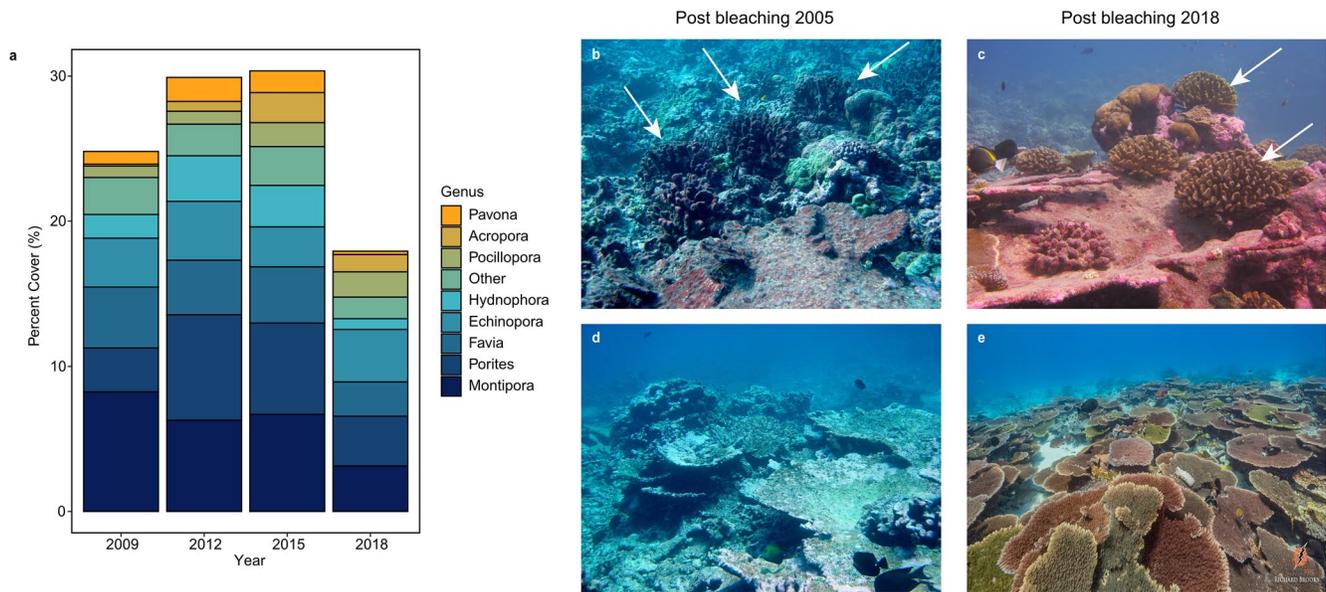


Figure 4. The most common coral genera of Phoenix Islands Protected Area (PIPA) have remained consistent across multiple heatwaves. (a) The proportional cover of each of the eight most common coral genera across PIPA has remained stable since 2009. All other taxa are pooled into the “Other” category. The historically important reef-builders in PIPA were *Pocillopora* spp. and *Acropora* spp., which experienced near-complete mortality from 2002 to 2005, dead colonies of *Pocillopora* (b white arrows) and *Acropora* (d) on Kanton’s fore reef in 2005. In stark contrast, these same genera exhibited much higher survivorship at the same locations during the 2015 bleaching event and have increased in relative abundance since 2009. Large *Pocillopora* colonies (c white arrows) and abundant *Acropora* colonies (e) provide evidence of unexpectedly high survival during 2015. Photos: (b, d) D. Obura; (c) M. Fox; (e) R. Brooks.

that corresponded with mortality outcomes. Similarly, no consistent differences were found in the rate of temperature decrease 4–12 weeks after the peak SST was attained (Figure S5).

By ruling out environmental factors, we hypothesize that the diminishing effect of thermal stress on coral mortality over three successive heatwaves is at least partly associated with an increase in the baseline thermal tolerance of PIPA’s coral communities between 2002 and 2018. Specifically, high mortality in 2002/2003, followed by no observable mortality response to the slightly weaker heatwave in 2009/10, and disproportionately low mortality in 2015/2016, the strongest heatwave on record, suggests that thermally tolerant survivors of the 2002/03 event and their progeny repopulated PIPA’s reefs, elevating the baseline thermal threshold above that required to resist the heat stress of 2009/10 and substantially reduce bleaching and mortality in 2015/2016.

Extreme events can weed out thermally sensitive coral species, shifting communities toward dominance by stress-tolerant taxa (Donner & Carilli, 2019). Such shifts can lead to increased resistance to future bleaching events but may compromise diversity and the recovery rates of coral populations (Yadav et al., 2018). In PIPA, we found no evidence for fundamental shifts in the relative abundance of the most common genera across our monitoring sites through time (PERMANOVA: Island \times Time, $p = 0.21$, Figure S10) (Figure 4a). While relative abundances exhibit some temporal fluctuation within islands, the most common genera remain consistent with those observed in surveys conducted nearly 50 years ago (Jokiel & Maragos, 1978). *Acropora* and *Pocillopora* suffered the highest mortality in 2002/03 and current populations remain below historical levels. However, these key reef-builders appear to be on a trajectory toward recovery (Figure 4a) and provide a compelling example of increased thermal thresholds. For instance, in 2004, only eight living *Pocillopora* colonies were found within six 80 m² sites on Kanton’s leeward fore reef (Alling et al., 2007) and the *Acropora* population was nearly extirpated (Alling et al., 2007; Obura & Mangubhai, 2011). Yet in 2018, *Pocillopora* and *Acropora* colonies were common across Kanton (Figures 4b–4e, Supporting Information S1) with abundances at their highest levels since pre-bleaching 2002. Much like the coral communities of the fore reef, the *Acropora* community of Kanton’s lagoon was devastated in 2002 (Alling et al., 2007; Obura & Mangubhai, 2011) but has recovered and exhibited disproportionate survival during the subsequent El Niños (Mangubhai et al., 2018). Collectively, our observations suggest the increased thermal tolerance in

PIPA is not associated with a shift to more tolerant taxa but rather, with an increase in the thermal thresholds of PIPA coral populations as a whole.

The recovery of remote reef systems strongly depends on the growth and reproduction of surviving colonies (Gilmour et al., 2013). Consequently, directional selection toward increased thermal tolerance of coral populations is likely enhanced in exceptionally isolated regions like PIPA, where larval immigration is highly restricted by distance (Wood et al., 2014). While larval dispersal models cannot rule out external larval supply to PIPA, the isolated reefs off the coast of Western Australia provide helpful context when considering the distance at which coral populations become meaningfully isolated. Scott Reef and the Houtman Abrolhos are ~250 km from their nearest neighboring reef system and rely heavily on local recruitment (Gilmour et al., 2013; Markey et al., 2016). In comparison, the closest reefs to PIPA are 2–5× more distant and the total reef area in PIPA is nearly 20× smaller than Scott Reef (Obura, 2011; Oppen et al., 2011) further reinforcing the likelihood that these coral communities are highly self-recruiting over the timescales of relevance here. Finally, larvae that do arrive from off-equatorial reefs have a lower probability of surviving the climatological extremes of the central equatorial Pacific (Mollica et al., 2019).

Coral populations naturally harbor a diversity of thermally adapted alleles and genotypes (Bay et al., 2017; Torda et al., 2017) that constitute the genetic material required for directional selection to increase the thermal tolerance of populations through selective mortality of thermally sensitive genotypes (Coleman et al., 2020; Coleman & Wernberg, 2020). Whole colony mortality is not the only means of achieving increased thermal tolerance through selection (Maynard et al., 2008). Some corals exhibit multiple genotypes within a single colony (Schweinsberg et al., 2014), which could be selected upon by partial mortality. Transgenerational plasticity can also enable coral acclimatization through successive generations and may occur through multiple mechanisms (Liew et al., 2020; Torda et al., 2017). Collectively, these processes offer viable pathways for genetic adaptation at the population level, providing opportunities for corals to adapt to climate change. Our observations from PIPA, consistent with a handful of similar observations from other isolated reef systems (Head et al., 2019; Obura et al., 2018), lend support that such processes are likely occurring over ecologically relevant spatial scales and at rates compatible with survivorship of ocean warming. Identifying existing genetic datasets that can be leveraged to help test this hypothesis is an essential next step. Given the need for samples that span multiple bleaching events, strategic collaboration and coordination with existing sample collections may provide important baselines for comparison following future events.

Nevertheless, coral adaptation to thermal stress likely has temporal and physiological limits. With each selection event genotypic diversity is reduced (Coleman & Wernberg, 2020), which can impede successful adaptation if genetic diversity or population growth rates are low (Bay et al., 2017). Additionally, projected increases in heatwave frequency and/or magnitude could overwhelm coral adaptation in some regions (Barkley et al., 2018). The adaptive potential of reef systems over the long-term will therefore be influenced strongly by population connectivity, genetic diversity (Bay et al., 2017), and the frequency of resilient genotypes (Morikawa & Palumbi, 2019; Shamberger et al., 2014), superimposed on spatial patterns of heatwave exposure and projected warming trends.

4. Conclusions

Our observations from PIPA offer an important contrast to the expectation that coral mortality will continue to increase with increasing thermal stress. Instead, we find compelling evidence that the relationship between coral mortality and thermal stress is evolving in this region, consistent with the *hypothesis* that thermal thresholds of isolated coral populations increased within a period of 18 years and facilitated unexpectedly high survival rates in the face of unprecedented thermal stress. While our observations raise key questions, they also highlight the inherent capacity of coral populations for adaptation and recovery and suggest that efforts to optimize this capacity should be a key component of coral reef management planning. These include identifying and protecting thermally tolerant populations, optimizing connectivity between these source populations and neighboring reefs, and strategic use of these populations in coral propagation and restoration efforts. Ultimately, however, coral adaptation and proactive management alone

are insufficient to prevent coral reef decline. Reversing global warming trends, therefore, remains essential for the survival of coral reefs.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

All data and code associated with this study are archived at Zenodo and available at <http://doi.org/10.5281/zenodo.5140344>. All files are also available through the Biological and Chemical Oceanography Data Management Office. <https://www.bco-dmo.org/>.

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