Limited coral mortality following acute thermal stress and widespread bleaching on Palmyra Atoll, central Pacific

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REPORT

Limited coral mortality following acute thermal stress and widespread bleaching on Palmyra Atoll, central Pacific

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Abstract During 2015–2016, an El Niño and associated warm water event caused widespread coral bleaching across the equatorial Pacific. Here, we combine 8 yr of benthic monitoring data from permanent photoquadrats with remotely sensed and in situ temperature measurements to assess the impact of the warming event on benthic communities at Palmyra Atoll. We quantified bleaching prevalence across two distinct reef habitats using the best available data. On the fore reef ($\sim$ 10 m depth), we quantified bleaching severity within 100–200 m^2 large-area plots using the custom visualization and analysis software, *Viscore*. On the reef terrace ($\sim$ 5 m depth), we used 95 focal colonies across three species that have been monitored annually since 2014. The 2015–2016 warm water event was the most extreme such event recorded on Palmyra in the past several decades with a maximum cumulative heat stress (degree heating weeks) of 11.9 °C-weeks. On the fore reef, 90% of live coral cover exhibited some degree of bleaching (32% severe bleaching). On the shallow reef terrace, bleaching was observed in 93% of the focal colonies across all species. Overall, coral cover declined 9% on the fore reef from 2014 to 2017, whereas coral cover did not change on the terrace. These contrasting results may be associated with typical daily temperature ranges on the terrace that are three times greater than on the fore reef. Permanent photoquadrats showed that turf algae initially colonized skeletons of recently dead corals but transitioned to crustose coralline algae within a year. Collectively, our study emphasizes that comprehensive monitoring of benthic communities over time combined with in situ temperature data can provide taxonomically precise trajectories of community change during and following thermal stress.

Topic Editor Morgan S. Pratchett

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Introduction

Coral reef ecosystems are sensitive to global change, and the increasing frequency of mass bleaching events associated with ocean warming poses one of the greatest threats to their persistence (Hughes et al. 2018a). During 2014–2016, a strong El Niño Southern Oscillation (ENSO)

Published online: 04 April 2019

event caused pantropical increases in sea surface temperature (SST), resulting in the longest and most severe global coral bleaching event on record (Eakin et al. 2016). The prolonged heat stress associated with this warm water event generated four times more coral bleaching and mortality on the Great Barrier Reef (GBR) than previous mass bleaching events in 1998 and 2002 (Hughes et al. 2017). Studies examining the impacts of bleaching events on coral reef assemblages have generally shown that these events not only lead to community-wide reductions in coral cover but may also lead to shifts in coral community structure that fundamentally alter these ecosystems (Loya et al. 2001; Hughes et al. 2018b). While many coral reefs across the Pacific have experienced widespread bleaching and mortality during the last three mass bleaching events (Baker et al. 2008; Obura and Mangubhai 2011; Guest et al. 2012; Barkley and Cohen 2016; Couch et al. 2017; Hughes et al. 2018a), information regarding post-bleaching trajectories of community change is known for only a handful of localities. Because the remote Pacific harbors some of the least disturbed reef ecosystems on the planet (Smith et al. 2016), the region provides a unique opportunity to examine how reefs recover from severe coral bleaching in the absence of local stressors.

The symbiosis between reef-building corals and *Symbiodinium* spp. is sensitive to temperature change (Brown 1997), though the sensitivity shows spatial, temporal and taxonomic specificity. Bleaching susceptibility and subsequent mortality can be highly variable among individual coral colonies due to differences in endosymbionts (Berkelmans and van Oppen 2006; Cunning et al. 2016), species-specific physiology (Baird and Marshall 2002; Grottoli et al. 2014) and coral gene expression (Barshis et al. 2013). Moreover, corals have high levels of phenotypic and genotypic plasticity and are capable of enhancing thermal tolerance based on habitat variability and history of thermal exposure (Thomas et al. 2018). The development of thermal stress tolerance can occur at multiple spatial scales (e.g., colonies, patch reefs, islands and regions), but appears to be most strongly influenced by the magnitude and frequency of daily temperature fluctuations (Donner 2011; Safaie et al. 2018). Once bleached, subsequent mortality or the ability of corals to recover may depend on environmental factors such as the duration and magnitude of the warm water event (Hughes et al. 2018b), background nutrient levels (Wiedenmann et al. 2012), the availability of heterotrophic food resources (Grottoli et al. 2006) or local oceanographic conditions such as upwelling or internal waves (Wall et al. 2015; Barkley et al. 2018). The interaction among these factors results in a broad range of potential outcomes within and among reefs following thermal stress of similar magnitudes (Eakin et al. 2010; Donner 2011). Our understanding of coral responses to

warm water events, both with short-term impacts and longer-term community responses (e.g., recovery or shifts to new states), is founded on the collection of robust data describing both environmental context and community structure through time.

Satellite and aerial surveys provide robust estimates of bleaching severity at island and regional scales (Hughes et al. 2018a) but can be problematic for tracking community responses following bleaching disturbances, particularly in heterogeneous environments (Hedley et al. 2016). The stark shifts in color associated with bleaching are highly amenable to observation through remotely sensed data products, but the subtle shifts in taxonomy associated with coral recovery or ecological succession following disturbances are observed with precision only with in situ approaches. When conducted with a randomized design, in situ approaches such as transect point intercept or photoquadrat image collection (with associated data extraction) provide overviews of shifts in mean composition of benthic habitats through time. Such in situ methods, especially those with larger areal coverage (i.e., photo-based methods), can be employed with spatial consistency through time, providing a powerful approach for understanding how corals respond individually to disturbances such as bleaching events (Connell 1997). While detailed, multi-year, in situ studies of community response to bleaching events are necessary to identify mechanisms that infer resilience or promote recovery, such studies are time-consuming and are relatively rare (Kayanne et al. 2002; van Woesik et al. 2011; Edmunds et al. 2014; Couch et al. 2017).

When coral bleaching results in full or partial colony mortality, the successional trajectories of newly exposed skeletal surfaces will likely influence the ability of corals to recolonize these spaces. The few studies that have tracked the fate of coral skeletons following bleaching-induced mortality have found that biofilms containing diatoms and other microalgae are often the first to settle and after a few days to weeks, a mixed community of filamentous turf algae and cyanobacteria then colonize (Diaz-Pulido and McCook 2002; Mullen et al. 2017). As succession continues, specific trajectories become associated with local conditions (e.g., level of herbivory, nutrient availability, sediment load, etc.) (Nyström et al. 2000). For example, crustose coralline algae (CCA) eventually outcompete algal turfs when grazing rates are high (Smith et al. 2010). Because CCA are generally less aggressive competitors with corals than turfs or macroalgae (Barott et al. 2012) and because CCA are known to enhance coral larval settlement (Morse et al. 1988; Harrington et al. 2004; Tebben et al. 2015), it is likely that coral regrowth will be more rapid in communities where CCA and herbivory are abundant. The general lack of data tracking the post-

bleaching trajectory of multiple benthic functional groups makes it difficult to predict if, when, and how a given system is likely to recover.

Here, we combine in situ and remotely sensed temperature measurements with 8 yr of benthic monitoring data from two reef habitats to assess the impact of the 2015 bleaching event at Palmyra Atoll. The combination of high-resolution temperature measurements with our long-term small and large-area benthic imagery monitoring efforts before, during and after the bleaching event in 2015 provide an opportunity to examine coral recovery trajectories at a location with minimal human impacts and naturally high rates of herbivory (Edwards et al. 2014; Hamilton et al. 2014). Our objectives were to (1) determine the magnitude and duration of thermal stress on Palmyra during 2015, (2) quantify the bleaching prevalence using large-area imaging on the fore reef and with monitored colonies on the shallower reef terrace, (3) quantify change in live coral cover between 2014 and 2017 in both reef habitats, and (4) document temporal changes in benthic community structure before, during and after the bleaching event. Collectively, our results document the impacts of the 2015 El Niño event on the benthic community of Palmyra and shed light on important ecological processes that may facilitate the recovery of coral communities following bleaching-induced mortality.

Methods

Study location

Palmyra Atoll is a National Wildlife Refuge within the Pacific Remote Islands National Marine Monument, located approximately 1600 km south of Oahu, HI. Palmyra's coral reef ecosystem remains relatively undisturbed by local human impacts, and the reef communities have been closely studied for more than a decade (Sandin et al. 2008). Despite severe bleaching and mortality on coral reefs around the world, the coral communities on Palmyra remain largely intact (Smith et al. 2016). Thriving stands of *Acropora* were reported on Palmyra's reef terrace in 1985 suggesting the 1982–1983 El Niño did not induce significant mortality on the local coral communities (Brainard et al. 2010). These same *Acropora* stands are believed to have bleached and died during 1997–1998, but qualitative recovery was evident in some locations by the early 2000s (Brainard et al. 2010). Quantitative surveys in 2009 detected mild bleaching when mean water temperatures exceeded the bleaching threshold, but temperatures remained lower than levels recorded in 2015 (Williams et al. 2010). Our permanent photoquadrat transects were installed prior to any significant bleaching or bleaching-

related mortality in 2009. Data from this time period reveal a slight decline in mean coral cover on the fore reef by 2010 (37–34%) but no change on the reef terrace, suggesting this warming event did not result in significant coral mortality.

In situ sensors

SeaFET and SeapHOx sensors (Bresnahan et al. 2014) were deployed at two sites on the reef terrace (5 m depth) and two sites on the fore reef (10 m depth) between 2010 and 2016. Coverage of the four sites throughout this study (2014–2016) is summarized in ESM Fig. S1. Temperature data were collected every 30 min using either the thermistor in the Durafet III combination electrode (SeaFET, T_{DFET}) or the Seabird Electronics SBE37 microcat (SeapHOx, T_{SBE37}) depending on which instrument was deployed. The two temperature records were combined to obtain better spatiotemporal coverage across Palmyra. The T_{SBE37} is the more accurate of the two temperature sensors ($\pm$ 0.01 °C); SeaFETs only measure T_{DFET}, whereas the SeapHOx measures both T_{DFET} and T_{SBE37}. Thus, SeapHOx deployments provide an assessment of the accuracy of T_{DFET}. The mean difference between T_{DFET} and T_{SBE37} was 0.21 $\pm$ 0.12 °C, based on 14 SeapHOx deployments at Palmyra; this offset was applied to T_{DFET} from SeaFETs. Since both T_{DFET} and T_{SBE37} were used to create the in situ temperature data set, we estimate the accuracy of the overall time series to be $\pm$ 0.12 °C.

Mean nighttime temperature on the fore reef and reef terrace sites was strongly correlated between 2010 and 2016 ($r = 0.93$). Thus, we quantified accumulated thermal stress as degree heating weeks (DHW) (Liu et al. 2014) using nighttime temperatures from the reef terrace which represented the longest contiguous time series (ESM Fig. S1). We estimated a bleaching threshold temperature specific to Palmyra using remotely sensed SST measurements described as follows.

Daily temperature ranges were determined for all days between 2010 and 2016 with measurements from at least one site in each habitat. The daily maximum and minimum temperatures were subtracted to determine the overall range. Daily range was binned into 0.1 °C intervals, and the number of days in a given range was enumerated by habitat.

Remotely sensed SST

We calculated a Palmyra-specific bleaching threshold, defined as 1° above the maximum monthly mean (MMM), using the NOAA's Pathfinder Version 5.2 SST (PFV5.2), daily 0.0417° Geo-Polar Blended Night-only product from 1985 to 2012 (http://coastwatch.pfeg.noaa.gov/erddap/

griddap/nodcPH2sstn1day.html) (Gove et al. 2013; Liu et al. 2014). Poor-quality data (quality value < 4) were excluded, and data from pixels within or intersecting Palmyra's 30 m isobaths and the next three most proximate pixels (to increase temporal data coverage, $n = 6$ pixels total) were spatially averaged (Kilpatrick et al. 2001; Gove et al. 2013). Climatologically, the warmest months on Palmyra are between July and November and the MMM of 28.43 °C is consistently during October. Thus, the bleaching threshold can be considered 29.43 °C based on 27 yr of historical data (ESM Fig. S2). To extend our remotely sensed SST measurements to the decade surrounding the 2015 bleaching event, we used the global 0.1° degree spatial resolution (10 km), monthly day/night composite SST data from the Advanced Very High Resolution Radiometer instrument aboard NOAA's Polar Operational Environmental Satellites (POES) (http://coast watch.pfeg.noaa.gov/erddap/griddap/erdAGsstamday_LonPM180.html). We quantified monthly SST during the four-month window of maximum thermal stress in 2015 (June–September) for each year from 2004 to 2015 to assess how the warming was around Palmyra in 2015 compared to the previous years. Finally, to determine whether SST measurements at $\sim$ 10 km resolution are relevant to the water temperatures corals experience on the reefs of Palmyra, we used Pearson's correlation to examine the relationship between monthly mean SST from the POES satellite with those calculated from our in situ sensors using all available data across both reef habitats.

Benthic community surveys

Temporal changes in benthic cover

Changes in benthic community structure were determined with permanent photoquadrat plots (0.63 m^2) along 50 m transects on Palmyra's fore reef (10 m depth, $n = 4$ sites) and western reef terrace (5 m depth, $n = 4$ sites) (ESM Fig. S1) (Smith et al. 2016). Along each transect, plots were spaced 5 m apart ($n = 10$ photos per site) and photographed annually during September/October from 2009 to 2017 (with the addition of a single time point in May 2016) using a Canon G-series camera with a 2:3 aspect ratio. Using point count software, Photogrid 1.0, we generated 100 stratified random points to determine percent cover in the first image of the time series for each permanent plot. We then replicated the x, y pixel location of these points in subsequent images in the time series, allowing us to track change at fixed locations through time. Atoll-wide trends in benthic community structure were determined using the site-level means for each habitat and benthic category ($n = 4$ sites).

To determine the impact of the warm water event on the benthos, we compared changes in the percent cover of live coral, crustose coralline algae (CCA) and turf algae from 2014 to 2017. We selected these three functional groups, as coral and CCA are key reef builders and thus changes in their relative abundance directly impact the capacity for reef growth on Palmyra (Smith et al. 2016). Further, filamentous turf algae are among the first colonizers of recently dead coral skeletons (Diaz-Pulido and McCook 2002), and therefore, change in turf cover provides a useful proxy for recent coral mortality. Together, these groups comprise more than 70% of the benthos in both habitats around the time of the bleaching event.

To estimate percent change in each functional group across both reef habitats, we used a nonparametric bootstrapping procedure. For each functional group across each time step, we calculated the difference in percent cover for each of the ten plots at each site. We then randomly sampled (with replacement) the calculated differences at each site, calculated a site-specific mean of differences and finally calculated one estimate of island-wide mean difference as the average of site-specific means. By repeating this process 10,000 times, we created a distribution of island-level differences in percent cover for each functional group at each time step. We determined changes in the percent cover of each functional group between time periods to be significant if 95% quantile ranges did not overlap zero.

Bleaching prevalence on fore reef: large-area imaging

Bleaching prevalence of the coral communities on Palmyra's fore reef was determined by analyzing large-area imagery collected from 200 m^2 plots (except for FR9, where only 100 m^2 could be analyzed) along the 10 m isobath of the fore reef habitat between September 22 and October 03, 2015. These plots partially overlap the permanent photoquadrat transects described above and, importantly, include on the order of 10^4 individual coral colonies (Edwards et al. 2017), allowing us to accurately relate bleaching prevalence to the observed patterns of change in benthic community structure from the photoquadrat analysis.

Plot establishment and raw imagery collection follow methods described by Edwards et al. (2017), with the exception that images were processed to create dense three-dimensional (3D) models of each plot using the structure-from-motion (SfM) software Agisoft Photoscan Pro 1.3.5 (Agisoft LLC., St. Petersburg, Russia) (Burns et al. 2015). Three-dimensional models were exported as dense point clouds from Photoscan into the custom visualization and image analysis platform Viscore (Petrovic et al. 2014; Naughton et al. 2015) (electronic supplementary materials:

Viscore and the virtual point intercept approach). Viscore is a software environment for the organization, visualization and the analysis of digital representations of natural habitats, enabling the development and application of tools and workflows for performing virtual fieldwork. Designed with an emphasis on the use of massive 3D point clouds and the associated raw imagery, Viscore enables researchers to systematically collect any number of measurements that could have been collected in situ, with the exception of physical samples. The *Virtual Point Intercept* extension in Viscore was used to estimate bleaching prevalence using a sample of 4000 stratified random points within each plot (except 2000 points in the 100 m² plot at FR9). Each point landing on coral was designated to genus, and the bleaching level of each colony was designated into four discrete categories (Guest et al. 2012) based on visual assessment on the entire colony: (1) healthy, (2) partially bleached (colony noticeably pale or < 50% loss of pigmentation), (3) mostly bleached (50–95% loss of pigmentation), (4) completely bleached (no visible pigmentation and no algal overgrowth). As such, we present bleaching prevalence data as portion of cover of a given taxa assigned to one of the specific bleaching categories. For example, *Porites spp.* occupied a mean of 3.92% of the benthos on Palmyra's fore reef and of this 3.92% we designated a mean of 78.70% as partially bleached.

Rather than limiting the point count analysis workflow to rely solely on the reconstructed 3D models, Viscore provides access to the most detailed source of information—the raw imagery—with 3D representation providing spatial organization and context. Using estimates of camera position, orientation and lens parameters calculated during the alignment and sparse cloud reconstruction steps in Photoscan, Viscore allows the user to interactively fetch all images associated with any given location in the composite 3D model. This enables the use of numerous, rather than single, images when making taxonomic and bleaching status assignments for each of the random points. Importantly, in cases where the entire colony is not visible in the collection of images associated with a given point or when additional perspectives are needed, Viscore allows access to images of adjacent areas using a simple spatial query. Readers are encouraged to refer to the electronic supplementary materials: *Viscore and the virtual point intercept approach* for additional information regarding the capabilities of the Viscore platform and details of the approach described here.

Bleaching prevalence on reef terrace: focal colonies

In 2014, we established nine replicate 3 m × 3 m plots (9 m²) at the Longliner site on the shallow reef terrace as part of a restoration experiment (ESM Fig. S1). In 2014, plots were cleared entirely of benthic organisms and 3–4 colonies each of *Acropora acuminata* ($n = 28$), *Montipora capitata* ($n = 32$) and *Pocillopora damicornis* ($n = 35$) were outplanted into each plot (total colonies $n = 95$). Colonies in each plot were photographed annually from 2014 to 2016 in September/October, and each colony was assigned one of the bleaching categories described above. The presence or absence of bleaching-induced mortality (complete or partial) from 2014 to 2015 was determined visually for each colony. The species-specific response to the thermal stress in 2015 and subsequent recovery in 2016 are reported as the proportion of the total colony number for each species.

Results

Temperature measurements

In situ nighttime temperature on Palmyra's reef terrace (30.30 °C) and fore reef (29.88 °C) peaked in September 2015, at 0.87 °C and 0.45 °C, respectively, above the island-specific bleaching threshold (29.43 °C) (Fig. 1a, c). Peak daytime temperatures were 30.98 °C on the reef terrace in September and 30.01 °C on the fore reef. Remotely sensed and in situ monthly mean SST between 2010 and 2016 were strongly correlated for the terrace ($r = 0.96$, $p < 0.01$, $n = 47$) and fore reef ($r = 0.95$, $p < 0.01$, $n = 48$) habitats. This indicates that the temperature environment was similar across the atoll (Fig. 1a) and provides confidence that satellite measurements reliably track nearshore temperatures (above 10 m depth) at a monthly scale. As such, the temperatures observed between June and September are likely the most extreme experienced by corals in either habitat since 2004 (Fig. 1b). Accumulated thermal stress was greatest between July and September 2015 (DHW = 11.9 °C-weeks), and nighttime mean SST on Palmyra's reef terrace was at, or above, the bleaching threshold for 23 consecutive weeks between May and October 2015 (Fig. 1 c, d). Palmyra's shallower reef terrace is more thermally variable than the fore reef at 10 m depth. Daily temperature ranges on the reef terrace exceeded 1 °C 27% of the time (Fig. 2), while temperature ranges on the fore reef only exceeded 1 °C on 1% of all days measured between 2010 and 2016. Overall, the mean daily temperature range on the reef terrace (0.81 °C) was 3.24 times greater than on the fore reef (0.25 °C).

Benthic community surveys

Data from long-term permanent photoquadrats showed that on the fore reef from 2014 to 2015, coral cover declined by 4.8% (median, 95% quantile range: − 7.9 to − 2.0%), turf
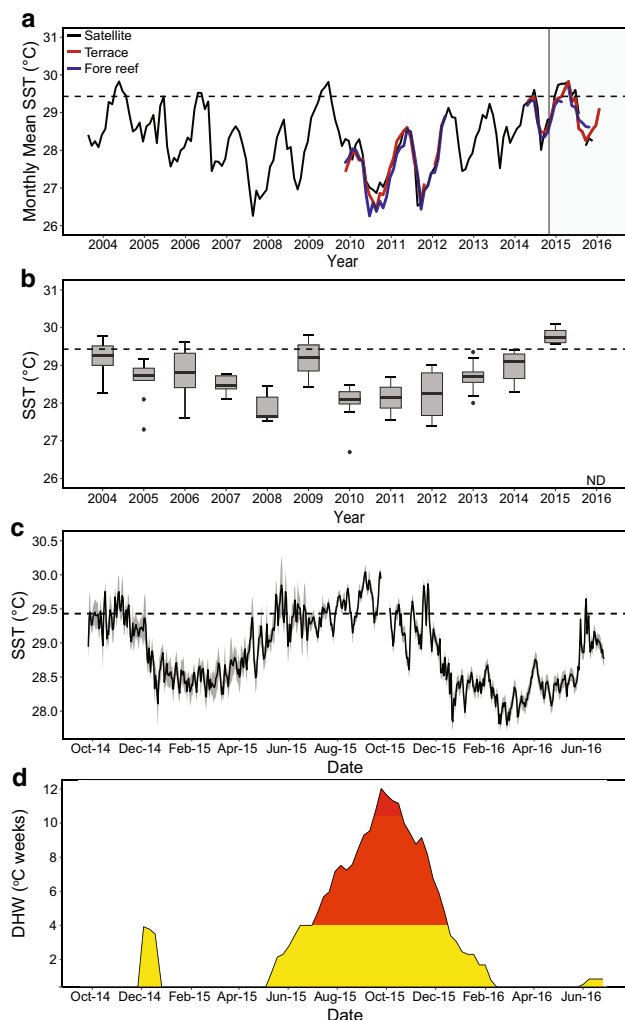
Fig. 1 Sea surface temperature (SST) on Palmyra Atoll. **a** Remotely sensed SST (NOAA POES data: 2004–2016) and in situ temperatures from both reef habitats (2010–2016). The gray box indicates the time period in **c**. **b** Box plots for remotely sensed monthly mean SST during June–September ($n = 12$ measurements per year). The dashed line represents the Palmyra-specific bleaching threshold 29.43 °C. **c** In situ nighttime SST on Palmyra's reef terrace from 2014 to 2016. Shating represents ± 1SD. **d** Degree heating weeks (DHW) calculated from in situ nighttime temperature data on the reef terrace **c**
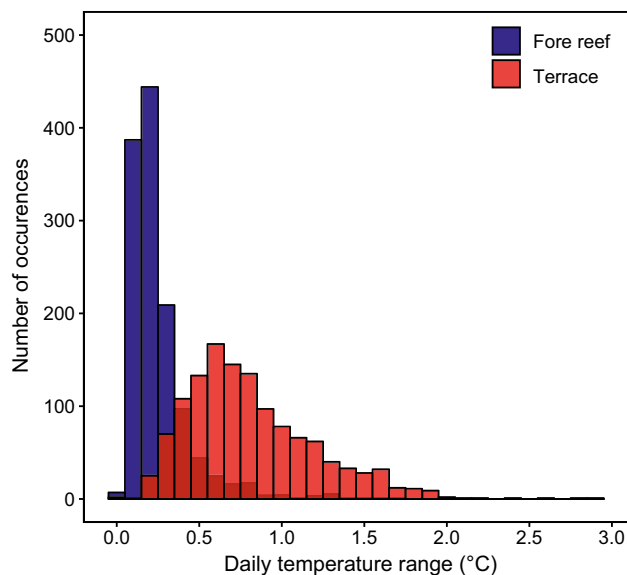

Fig. 2 Daily temperature range for each reef habitat on Palmyra for 3.5 yr of paired daily measurements from 2009 to 2016. Measurements were recorded every 30 min, and the range was defined as the maximum recorded temperature minus the lowest temperature in a 24-h period. The histogram represents the total number of days recorded at a given temperature range throughout the length of the record. Mean temperature range (± SD) for the fore reef was 0.25 ± 0.19 °C and 0.81 ± 0.46 °C for the reef terrace

algae increased by 10.5% (6.7–15.4%) and CCA cover declined by 1.8% (− 3.9–0.5%) (Fig. 3a, b). Coral cover continued to decline from 2015 to 2016 by 3.5% (− 6.9 to − 0.4%). However, the trend in algal functional groups shifted as turf cover decreased by 8.5% (− 12.8 to − 4.2%), while CCA cover increased by 8.0% (5.1–11.1%) (Fig. 3a, b). From 2016 to 2017, turf cover continued to decline by 7.8% (− 11.7 to − 4.5%), and there was no significant change in coral or CCA cover, − 1.0% (− 3.5–2.0%) and − 0.3% (− 4.5–4.8%), respectively. Overall, from 2014 to 2017, there was significant decline in coral cover by 9.1% (− 13.1 to − 5.1%) and turf cover by

5.7% (− 8.2 to − 3.1%) and a significant increase in the cover of CCA by 6.0% (2.6–9.8%) (Fig. 3a, b).

On the reef terrace, there was no significant change between annual time steps or overall from 2014 to 2017 for coral or CCA cover. For turf cover, there was significant change across annual time steps only in 2016–2017 (− 7.7% [− 10.2 to − 4.6%]). Overall, from 2014 to 2017, turf cover declined 11.8% (− 16.1 to − 7.6%) (Fig. 3c, d).

Using large-area imaging across 700 m^2 of Palmyra's fore reef habitat, total coral cover was 25.7% and, of this, 89.9% exhibited some degree of bleaching. The severity of bleaching was moderate, with 58.4% of all coral cover being partially bleached (< 50% of colony bleached). Colonies that were completely and mostly bleached accounted for 12.1% and 19.4% of the total coral cover, respectively. However, only 10.1% of all coral cover showed no obvious sign of bleaching (Fig. 4). The three most abundant coral genera on Palmyra's fore reef are *Montipora*, *Pocillopora* and *Porites* (Edwards et al. 2017). Of these, *Montipora* was the most thermally sensitive, with 22.0% of the total cover of *Montipora* found to be completely bleached. *Porites* and *Pocillopora* were predominantly partially bleached. *Pocillopora* had the largest percentage of unbleached colonies (19.7%) (Fig. 4).

Of the 95 focal colonies on the shallow reef terrace, 92.6% of colonies exhibited some degree of bleaching by October 2015. Despite extensive bleaching, virtually all

Fig. 3 Change in key benthic taxa from 2009 to 2017. **a** and **c** Mean changes (± 1 SE) in coral, CCA and turf algal cover in both habitats. **b** and **d** Bootstrapped mean percent cover change in each functional group between years. Error bars denote bootstrapped 95% CI of the mean. Bars not overlapping zero (dashed line) indicate a significant change ($p < 0.05$). Gray boxes indicate the cumulative change from 2014 to 2017. Note that in addition to annual surveys, a survey was conducted in May 2016 to assess community changes within the first six months following the bleaching event
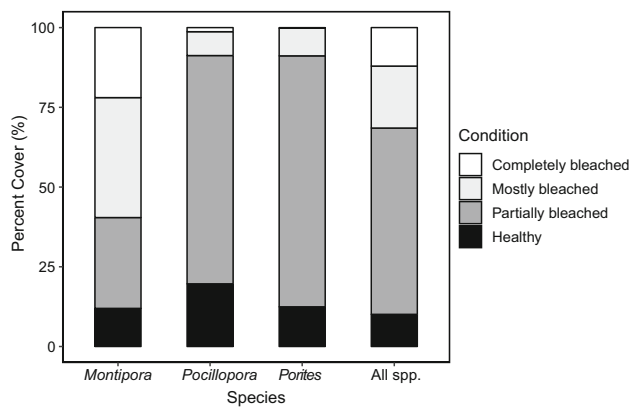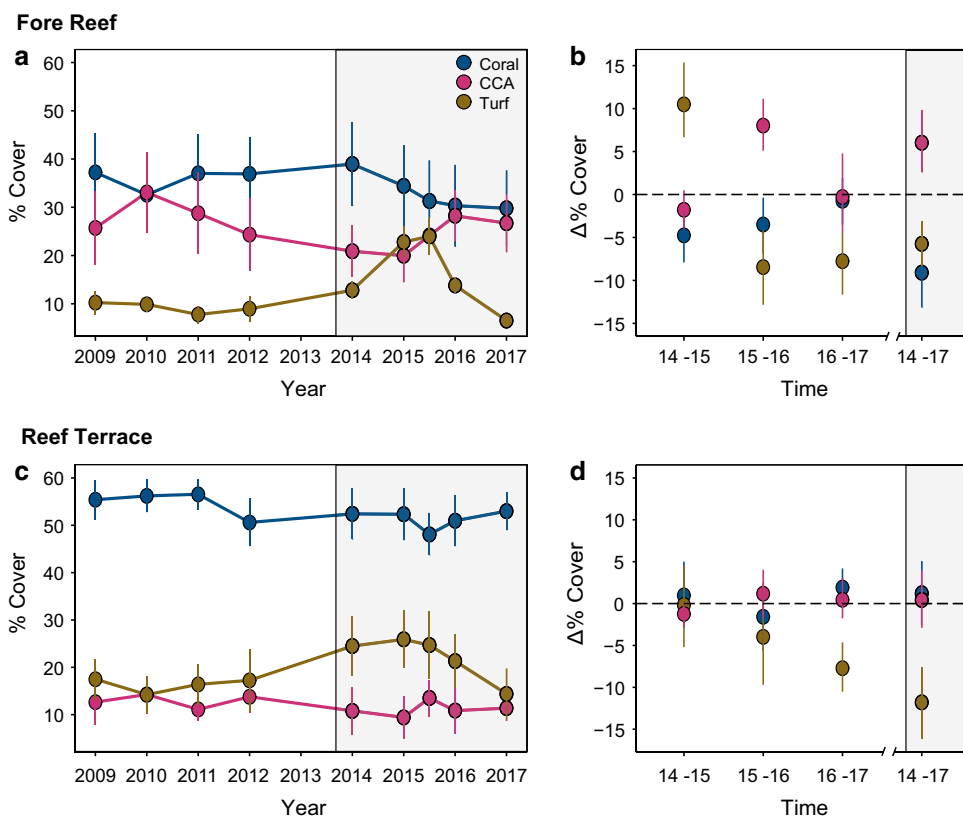

Fig. 4 Bleaching prevalence on the fore reef of Palmyra Atoll. Bleaching prevalence is reported as the relative percent cover per bleaching category of the total percent cover by hard coral or a particular genus. The three most abundant genera on Palmyra are massive *Porites* sp., *Pocillopora* spp., and encrusting *Montipora* spp. The bleaching categories are: (1) healthy, (2) partially bleached (colony noticeably pale or < 50% of colony bleached), (3) mostly bleached (50–95% of colony bleached) and (4) completely bleached (no visible pigmentation and no algal overgrowth)

colonies and none died completely. Partial mortality was observed in 37.9% of all colonies (ESM Table S1) and occurred in 51.4% of all *P. damicornis* colonies. *Montipora capitata* was the most thermally sensitive of the three focal species with 31.3% of all colonies being completely bleached in 2015.

Discussion

The 2015–2016 warm water event at Palmyra produced an accumulated heat stress of 11.9 °C-weeks and moderate levels of bleaching (89.9% of total coral cover on the fore reef and almost all focal colonies exhibited some degree of bleaching); notably, the bleaching resulted in low levels of coral mortality (e.g., median loss of 9.1% coral cover on the fore reef). Total DHW on Palmyra were below maximum values observed during other mass bleaching events on the GBR (15 °C-weeks) and in the Caribbean (17 °C-weeks) (Eakin et al. 2010; Hughes et al. 2017). However, compared to the reported 27% decline in coral cover on reefs experiencing > 8 °C-weeks on the GBR (Hughes et al. 2018b), the magnitude of morality observed at Palmyra was strikingly low. Despite a substantial amount of thermal stress, the majority of corals on Palmyra's fore reef (58%) were partially bleached (< 50% loss of

corals fully recovered (90.5%). Whole colony mortality was low overall (6.3%) but highest (14.3%) in *P. damicornis* (ESM Table S1). While all 28 *A. acuminata* colonies bleached, partial mortality was observed in only 25.0% of

pigmentation), while 32% of colonies bleached severely (almost complete loss of pigmentation). This suggests that the lower mortality observed on Palmyra is partly attributable to lower bleaching severity for a similar level of thermal stress compared to corals on the GBR. Coral mortality on Palmyra was also substantially lower than on other central Pacific Islands (e.g., Jarvis Island), where extreme thermal stress resulted in almost complete coral mortality (Barkley et al. 2018). Perhaps most importantly, we show that where coral mortality was observed, initial settlement by algal turfs was rapidly replaced by CCA. Coral cover subsequently stabilized or returned to pre-bleaching levels within 24 months likely due to clonal regrowth of colonies that suffered partial mortality (Furby et al. 2017). Given the predicted increase in the frequency and magnitude of bleaching events (Hughes et al. 2018a), the remarkable stability of the coral community on Palmyra represents an important case study for investigating drivers of resistance and resilience to thermal stress events in the Pacific.

Sea surface temperatures during June–September 2015 represent the warmest conditions corals have experienced on Palmyra during the satellite era. The historical SST measurements from the Pathfinder V5.2 (1985–2012) product indicate the temperatures measured during 2015 are among the warmest and most persistently stressful temperatures experienced by coral populations on Palmyra in at least the past three decades. These measurements indicate that temperatures on Palmyra were slightly warmer and persisted for a longer duration than during the El Niño event of 2009, which resulted in 9.1 DHW by the end of November (Coral Reef Watch 50 km, Palmyra Atoll http://www.ospo.noaa.gov/data/cb/TS_vs/vs_ts_PalmyraAtoll.txt) and caused substantial but less extensive bleaching (Williams et al. 2010). Limited historical observations suggest *Acropora* communities on Palmyra's reef terrace suffered significant mortality during 1997–1998 but successfully recovered (Brainard et al. 2010). Interestingly, despite the moderate bleaching in 2009 and elevated thermal stress in 2015–2016, the mortality following 2015 was not much greater than that observed following 2009 (Fig. 3a). Given that these events were separated by only 6 yr, many of the same colonies were likely affected by both warm water events. Our results provide evidence consistent with the hypothesis that surviving corals will suffer reduced physiological impacts after exposure to successive bleaching events, suggesting increased resistance via adaptive processes within the coral holobiont (Buddemeier and Fautin 1993; Guest et al. 2012; Logan et al. 2014; McClanahan 2017).

Levels of mortality following warm water events are also linked with bleaching severity (Baird and Marshall 2002; Hughes et al. 2017; Barkley et al. 2018), taxon-specific susceptibilities (Loya et al. 2001; Guest et al. 2016; Muir et al. 2017; Mizerek et al. 2018) and the magnitude of thermal stress (DeCarlo et al. 2017; Claar et al. 2018; Hughes et al. 2018b). We show that 89% of total coral cover on the fore reef was represented by colonies with some level of bleaching, with 32% of cover represented by mostly or completely bleached colonies. Consistent with observations from the warm water event of 2009 (Williams et al. 2010), *Montipora* was most susceptible to bleaching with > 66% of cover within this genus mostly or completely bleached. Branching species, particularly corals in the genus *Acropora*, are widely known to suffer the greatest levels of bleaching and subsequent mortality following warm water events (Hoegh-Guldberg and Salvat 1995; Loya et al. 2001). The results presented here largely support these findings, with severe bleaching (> 50% loss of pigmentation) in 90% of the total *Acropora* cover on the fore reef and in all 28 focal colonies of *A. acuminata* on the reef terrace. Contrary to these previous findings and the high levels of bleaching observed here, only limited partial mortality was observed in the focal *Acropora* colonies. On the shallow reef terrace, of our 95 coral colonies from three species monitored over the course of the warm water event, only three colonies did not display any sign of bleaching and 42 colonies were mostly or completely bleached. Despite this, mortality of focal colonies was extremely limited (4 of 95 across species) and we did not observe any change in overall coral cover in this thermally variable habitat (Fig. 3d). The low levels of mortality on the shallow, diurnally variable reef terrace habitat (Fig. 2) support other observations that more extreme daily variation in temperature may promote bleaching resistance in coral populations worldwide (Donner 2011; Safaie et al. 2018).

Elevated levels of energy reserves prior to the onset of thermal stress associated with the availability of allochthonous heterotrophic resources may also prevent coral death and facilitate recovery (Grottoli et al. 2006; Grottoli and Rodrigues 2011). Overall, we observed considerable heterogeneity in the bleaching response of most corals to the warm water event. On the reef terrace, similar proportions of focal colonies were either unaffected by the warm water event or suffered complete mortality. Similarly, on the fore reef we saw variation in levels of bleaching both within and among coral taxa. Recent work from Palmyra and other central Pacific islands has shown that corals take advantage of heterotrophic resources to the extent that they are available, with some degree of spatial variation in the levels of uptake (Fox et al. 2018; Williams et al. 2018). Palmyra's lagoonal waters are known to contain an abundance of phytoplankton and zooplankton that regularly flush onto the reef terrace habitat (Rogers et al. 2017) and, to a lesser extent, the fore reef. These disparities in resource availability associated with local

scale hydrodynamics may help to explain some of the variability in bleaching recovery observed here. Ultimately, the coral communities on Palmyra's reefs offer a unique opportunity to assess biophysical couplings that may drive spatial variation in coral survival following bleaching.

Contrary to our observations on Palmyra, the nearby Northern Line Islands of Kiritimati and Jarvis experienced extreme thermal stress in excess of 29.0 and 35.8 °C-weeks, respectively, more than twice than that observed on Palmyra (Barkley et al. 2018; Brainard et al. 2018; Hughes et al. 2018a). This unprecedented thermal stress led to significant coral mortality (80–95%) in the region (Barkley et al. 2018; Magel et al. 2019). Corals at Palmyra experienced widespread, but moderate, bleaching during a shorter duration of thermal stress over this same time period. Notably, despite over 30% of coral colonies on the fore reef exhibiting severe bleaching, overall mortality remained fairly low. Unlike on Jarvis where extreme heat stress persisted into early 2016 (Barkley et al. 2018), SST on Palmyra declined rapidly between October and December 2015 immediately after peak heat stress and the bleaching observations reported here. Thus, the timing of the regional cooling may have helped minimize coral mortality on Palmyra by alleviating thermal stress before widespread mortality could occur. Conversely, the extended thermal stress at Jarvis and failed resurgence of upwelling conditions that reduced primary production and heterotrophic resource availability likely drove the drastic reduction in coral cover observed there (Brainard et al. 2018). Caution must be taken in directly comparing DHW between these locations due to the inherent interannual variability in SST's in this region. However, these regional findings reinforce that extreme thermal stress can erode the bleaching resistance conveyed to corals of the central Pacific by regional oceanographic variability (Donner 2011) and highlights the vulnerability of this region to future ENSO events (Yeh et al. 2009).

The results presented here make use of data collected at extensive temporal and spatial scales. The photoquadrat time series used in this analysis includes 80 permanent plots that have been imaged on an annual basis since 2009. While randomized surveys allow for more broad-scale assessment of community structure, an understanding of the fate of individual benthic organisms can only be obtained through systematic sampling of permanent locations. By using permanent plots and fixed points in image analysis, we were able to observe direct responses to the warm water event in the context of nearly a decade of monitoring. These temporally replicated data were complemented by the use of large-area imaging and SfM-based techniques, that are being used in greater frequency to produce highly accurate digital archives and extract information from imagery collected in situ (Pizarro et al. 2009; Petrovic et al. 2014; Burns et al. 2015; Murfitt et al. 2017). Here, we analyzed the products from SfM and large-area imaging with the novel visualization and analytical software platform Viscore, a platform that uses 3D models to leverage the highest resolution data available—the raw imagery (ESM). The approach used here not only allowed us to census thousands of individual coral colonies, but unlike other image-based approaches, allowed us to view each coral colony from multiple angles and exposures. This new approach helps maximize the the amount of time that can be spent on image collection over large areas during bleaching events by allowing for quantification of bleaching severity and benthic change in the laboratory with the aid of numerous images and perspectives of individual corals (ESM).

Our long-term monitoring data revealed a critical element of coral recovery that has received little attention historically—a transition between turf algal and CCA cover in the months and years following the bleaching event. CCA is an important component of healthy reef ecosystems that facilitates coral settlement, contributes to reef development by cementing together dead coral skeletons and is an important indicator of reef health (Smith et al. 2016). While turf algae are often the first benthic group to colonize recently dead coral skeletons (Diaz-Pulido and McCook 2002), the proliferation of CCA following coral mortality may help facilitate recovery, as CCA tends to be an inferior competitor with coral relative to other algal groups (Barott et al. 2012). Within months of the warm water event, coral cover declined, with concomitant increases in turf algae. However, by May of 2016, the losses in coral cover were compensated by an increase in the cover of CCA, thus resulting in a rapid maintenance of benthic coverage by reef-building taxa. By September 2016, turf cover had begun to decline in both habitats, coral cover on the terrace had returned to 2015 levels, replacing the temporary increase in CCA, and losses in coral cover on the fore reef had stabilized. Prior to 2015, turf algal cover on Palmyra's fore reef was stable, indicating that the spike in turf cover occurred in response to coral mortality following the bleaching event. The maintenance of reef-builder cover following the bleaching event on Palmyra is somewhat unexpected given reports highlighting loss of calcifying organisms and the proliferation of fleshy algae from bleached reefs globally (Hughes et al. 2010).

The shift from turf to CCA may be the result of intense grazing pressure associated with relatively high biomass of herbivorous fishes on Palmyra (Edwards et al. 2014; Hamilton et al. 2014). Previous studies have demonstrated the importance of herbivores in preventing reefs from

becoming algal-dominated (Hughes et al. 2007; Graham et al. 2015), yet these studies have primarily considered the role of herbivores in regulating macroalgal populations. Our results suggest that the control of turf algal proliferation following coral mortality may be one of the primary drivers in the divergent responses of fished and un-fished reefs following bleaching events. Herbivory may aid in reef recovery not simply by reducing turf cover but by keeping turf communities tightly cropped and therefore facilitating growth of CCA. While local management efforts cannot prevent a given reef from bleaching, our results suggest that the presence of healthy herbivore populations likely contributes to recovery trajectories following coral mortality.

The response of Palmyra's coral communities to the 2015–2016 thermal stress event provides an important counterpoint to other locations that documented widespread coral mortality. Our data illustrate that some reefs can resist high levels of mortality and a shift toward algal dominance following coral bleaching. Such locations provide valuable baselines for studying drivers of resistance and resilience to thermal stress events in the Pacific. Despite suffering two bleaching events separated by just 6 yr, the coral communities at Palmyra have demonstrated remarkable stability. Our data suggest that the combination of adaptation, a naturally variable thermal environment and the ability of CCA to rapidly colonize space following coral mortality has resulted in resilient coral communities at Palmyra. Other remote and uninhabited locations across the central equatorial Pacific have shown similar patterns in the past, but unfortunately the magnitude of the 2015–2016 event exceeded the bleaching resistance of corals on these reefs, resulting in extensive mortality (Barkley et al. 2018). Regional oceanographic variability was an important driver in the differential responses of coral communities across the central Pacific during 2015. As the frequency and magnitude of warm water events are predicted to increase, the coral communities at Palmyra may represent an increasingly important source of coral recruits for other reefs in this region. Connecting patterns of basin-scale oceanography with in situ temperature measurements and quantitative, long-term assessments of coral reef benthic communities are necessary to enhance predictions of spatial variation in coral reef survival in the Anthropocene.

Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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