



REPORT

Decadal stability of coral reef benthic communities on Palmyra Atoll, central Pacific, through two bleaching events

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Abstract The prevalence of coral bleaching due to thermal stress has been increasing on coral reefs worldwide. While many studies have documented how corals respond to warming, fewer have focused on benthic community responses over longer time periods or on the response of non-coral taxa (e.g., crustose coralline algae, macroalgae, or turf). Here, we quantify spatial and temporal changes in benthic community composition over a decade using image analysis of permanent photoquadrats on Palmyra Atoll in the central Pacific Ocean. Eighty permanent plots were photographed annually between 2009 and 2018 on both the wave-exposed fore reef (FR, 10 m depth, $n=4$ sites) and the wave-sheltered reef terrace (RT, 5 m depth, $n=4$ sites) habitats. The El Niño events of 2009–2010 and 2015–2016 resulted in acute thermal stress and coral bleaching was observed at both reef habitats during these events. Across 10 yr and two bleaching events, the benthic community structure on Palmyra shows evidence of long-term stability. Communities on the RT exhibited minimal change in percent cover of the dominant functional groups, while the FR had greater variability and minor declines in hard coral cover. There was also spatial variation in the trajectory of each site through time. Coral cover decreased at some sites 1 yr following both bleaching

events and was replaced by different algal groups depending on the site, yet returned to pre-bleaching levels within 2 yr. Overall, our data reveal the resilience of calcifier-dominated coral reef communities on Palmyra Atoll that have persisted over the last decade despite two bleaching events, demonstrating the capacity for these reefs to recover from and/or withstand disturbances in the absence of local stressors.

Keywords Long-term monitoring · Community structure · Benthic algae · Resilience · Climate change

Introduction

Coral reef ecosystems are declining globally due to the combined impacts of local and global stressors. In particular, mass bleaching events associated with rising ocean temperatures have continued to increase in both frequency and intensity (Hughes et al. 2017) with dire consequences for the persistence of coral reef ecosystems. Such events can cause reefs to shift from dominance by calcifying, reef-building taxa (e.g., corals and crustose coralline algae) to dominance by fleshy organisms such as turf and fleshy macroalgae (McCook et al. 2001; Smith et al. 2016). This may lead to a net negative calcium carbonate budget (Takeshita et al. 2016), the loss of structural complexity (Graham and Nash 2013), and the degradation of ecosystem services (Moberg and Folke 1999; Woodhead et al. 2019). Coral reef benthic communities are highly dynamic (Nyström et al. 2000) and long-term monitoring is required to tease apart natural mechanisms of change (e.g., competition) following large-scale disturbances such as temperature-induced bleaching.

Periods of high thermal stress can result in coral bleaching, subsequent partial or full colony mortality, decreases in live coral cover, and corresponding increases in turf or

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fleshy algal cover (Shulman and Robertson 1996; Ostrander et al. 2000; McClanahan et al. 2001; Ridgway et al. 2016; De Bakker et al. 2017). In some cases, there has been no significant mortality of hard corals after a bleaching event (Gleason 1993; Hardman et al. 2004). However, for many of these studies, reefs were surveyed up to 1 yr post-bleaching at most, with no further time points. Given that benthic organisms colonize open substrata on reefs at different rates (McClanahan et al. 2001; Diaz-Pulido and McCook 2002), longer-term perspectives before and after disturbance would allow for better indication of which ecosystem changes are transient or permanent.

Multi-year data sets from permanent sites are informative because a single time point does not reflect the successional trajectory of a given reef. However, there are not enough long-term studies of coral reef community composition which precisely track changes in entire benthic assemblages through time. Most large-scale regional or global monitoring efforts (Souter et al. 2020; Towle et al. 2022) typically measure coral cover alone or some other indicators of reef status through opportunistic sampling, which is certainly valuable but future efforts could implement a more holistic (i.e., assessing benthic community composition) and precise (e.g., using permanent plots) approach. Existing decadal studies incorporating all benthic functional groups have documented phase shifts from hard corals to either macroalgae (Done et al. 2007; Jones et al. 2020), cyanobacterial mats (De Bakker et al. 2017), or octocorals and sponges (Ruzicka et al. 2013; Reverter et al. 2021) following major bleaching events. Studies extending multiple years post-bleaching often found that there was a reversal back to a coral-dominated or other calcifying state (Done 1992; Adjeroud et al. 2009; Graham et al. 2015; Cruz-García et al. 2020). Overall, these data suggest that benthic community response varies depending on the duration of time since a disturbance event as well as the location, thermal severity, and ecological context (e.g., abundance of herbivores). Responses can also vary by habitat, site, depth, genus, and/or species within a given functional group (Muhandó and Mohammed 2002; Darling et al. 2013; Krishnan et al. 2018). Nevertheless, most studies evaluating the effects of warming on benthic community composition through time have reported losses in coral cover worldwide (see Supplementary Table 1 for specific examples).

The majority of coral bleaching studies to date have measured at least one other benthic component besides hard corals; usually these included algae, though the algal designations have been broad (Supplementary Table 1). Crustose coralline algae (CCA) and turf algae are often lumped into a single category (McClanahan 2000; Ridgway et al. 2016) or combined with bare space (Aronson et al. 2002) or macroalgae (Ostrander et al. 2000; Stuart-Smith et al. 2018). The studies that did not distinguish between algal groups noted

transitions from coral to algal-dominated states and assumed a negative correlation between corals and algae (Ostrander et al. 2000; Stuart-Smith et al. 2018). Given that algae are a highly diverse (i.e., taxonomically, morphologically, and ecologically) assemblage of primary producers that are naturally abundant on reefs, it is important to understand how different algal functional groups respond to thermal stress and what role they may play independently as benthic coral reef communities change over time.

CCA are encrusting, calcifying red algae that provide settlement cues for larval corals (Harrington et al. 2004) and serve as reef builders that cement the reef framework (Setchell 1930). Notably, CCA have been found to be sensitive to thermal stress (Anthony et al. 2008; Martin and Gattuso 2009; Short et al. 2015). In contrast, turf algae are a heterogeneous consortium of largely fleshy, short filamentous algae, juvenile macroalgae, or cyanobacteria (Adey and Steneck 1985; Harris et al. 2015). They opportunistically and rapidly occupy open space following coral bleaching or disease outbreaks (Diaz-Pulido and McCook 2002) because they are fast-growing and can thrive under conditions not optimal for corals (McClanahan 1997). Finally, macroalgae can be further classified as fleshy or calcareous taxa. Fleshy macroalgae can be harmful to corals via abrasion, shading, and/or the release of dissolved organic carbon, allelochemicals, or pathogens (McCook et al. 2001; Rasher and Hay 2010; Barott and Rohwer 2012). Calcareous macroalgae vary in their interaction with corals but are generally more benign (Brown et al. 2020). However, responses of fleshy and calcareous macroalgae can be mixed, species-specific, and/or fluctuate seasonally. Further, these responses cannot be expected to be uniform across reefs experiencing varying degrees of anthropogenic stressors.

Here, we use a decade-long time series of benthic community data from eight permanent monitoring sites across two reef habitats on Palmyra Atoll to investigate coral reef benthic dynamics in an ecosystem with minimal local stressors through two bleaching events. Using image analysis of permanent photoquadrats, we examined (i) how key functional groups changed following each bleaching event, (ii) the stability of reef builders (i.e., corals and CCA) relative to fleshy algae (i.e., turf and fleshy macroalgae) through time, and (iii) interannual and decadal variation of benthic community composition. These data provide valuable insight on natural benthic community dynamics and their response to thermal stress.

Methods

Study site

Palmyra Atoll National Wildlife Refuge (5.89° N, 162.08° W) is a remote atoll in the Northern Line Islands, located approximately 1300 km south of Hawai'i (Fig. 1). Palmyra

was temporarily inhabited and modified by the US Navy during the World War II era, which involved lagoon dredging and causeway construction. Since 2001, however, it has been federally protected within the Pacific Remote Islands Marine National Monument and therefore provides a natural laboratory to study the effects of global change on benthic community dynamics in the presence of high herbivory (Hamilton et al. 2014) and the absence of local stressors (Sandin et al. 2008; Braun et al. 2009; Williams et al. 2010; Fox et al. 2019b).

Four permanent monitoring sites were established in each of Palmyra's primary reef habitats: the wave-exposed fore reef (FR, 10 m depth) and the shallower, more wave-protected western reef terrace (RT, 5 m depth). At each site, ten permanent plots (90 cm × 60 cm) were marked along a 50 m transect (Supplementary Fig. 1). Photographs of the individual plots (i.e., "photoquadrats") were collected by divers using a Canon G-series camera attached to a PVC tripod to maintain fixed distance from and orientation to the substrate. Sites were visited at least once per year in the late summer or early fall between 2009 and 2018.

Benthic community analysis

We used quantitative image analysis to determine the total planar area of benthic organisms within each photoquadrat (Supplementary Fig. 1). In Adobe Photoshop (Creative Cloud), we digitized the borders of live hard corals, soft corals, and algal patches within each quadrat and identified them to the finest possible taxonomic resolution, which were later pooled by functional group. We used Photoshop's image analysis tool to convert pixel counts to planar area measurements (cm²) based on the dimensions of the photoquadrat frame (90 cm × 60 cm).

Temperature history

We estimated monthly mean sea surface temperature (SST) on Palmyra throughout the duration of this study using both in situ sensors and NOAA's 0.25° daily Optimum Interpolation Sea Surface Temperature (OISST v2.0). In situ measurements were made using SeaFET and SeapHOx sensors (Bresnahan et al. 2014), via the thermistor in the DuraFet III combination electrode (SeaFET) or the Seabird Electronics SBE37 microcat (SEapHOx). Temperature data were collected every 30 min in at least one site per habitat, from which monthly means were generated and combined with satellite measurements (Fig. 2; Supplementary Fig. 2). Coral

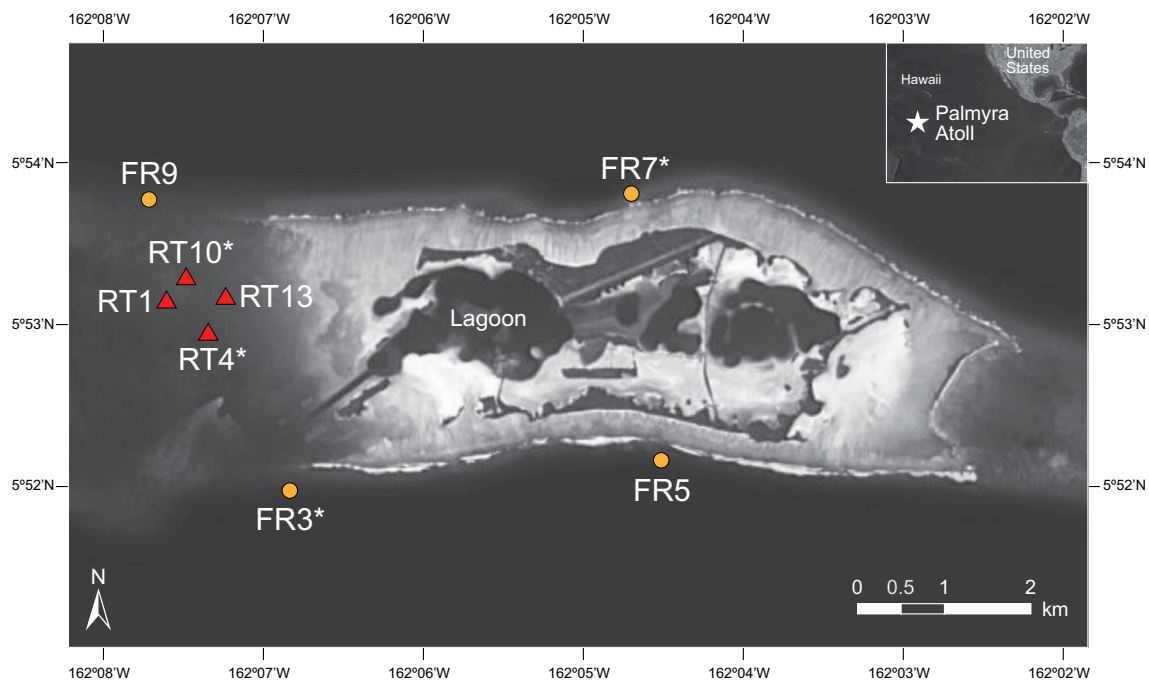


Fig. 1 Map of the eight monitoring sites surrounding Palmyra Atoll, with an overview of the broader geographical area at the top right. Red triangles represent the RT (5 m depth) sites, and orange circles

represent the FR (10 m depth) sites. Sites denoted with a star indicate locations of sensor deployments

bleaching occurred during two marine heatwaves (i.e., prolonged periods of thermal stress) associated with El Niño Southern Oscillation events in 2009–2010 and 2015–2016 (Williams et al. 2010; Fox et al. 2019b). Cumulative thermal stress was quantified as Degree Heating Weeks (DHW) using the NOAA Coral Reef Watch program 50 km product (Liu et al. 2014), which indicates that DHWs on Palmyra reached 9.1 °C weeks by late November 2009 and 11.9 °C weeks by early October 2015 (https://coralreefwatch.noaa.gov/data3/50km/vs/timeseries/vs_ts_PalmyraAtoll.txt). Bleaching was observed during both heatwaves but was more widespread in 2015 (Williams et al. 2010; Fox et al. 2019b).

Statistical analysis

All analyses were conducted in R software version 3.6.3 (R Core Team 2018). Temporal changes in benthic community composition were quantified within individual quadrats and summarized at the site level ($n = 10$ quadrats per site). We used non-metric multidimensional scaling (nMDS, via *metaMDS* in *vegan* for R; Oksanen et al. 2019) based on Bray–Curtis dissimilarity to visualize the trajectories of benthic community composition at each site through time. We did not transform percent cover data due to the absence of rare species (Clarke et al. 2006). We then performed a three-way permutational multivariate analysis of variance (PERMANOVA) with 9999 unrestricted permutations (*adonis* in *vegan*; Anderson 2001; Oksanen et al. 2019) to determine whether similarity in multivariate community composition varied across time, habitats, and/or sites nested within habitat. Habitat (two levels: FR and RT) and time (ten levels, one for each yearly time point) were treated as fixed factors, whereas site (eight levels) was considered a random factor. We also tested for possible interactions between factors to see whether sites and/or habitats were changing differently over time. Repeated measures were not incorporated because we used site level as opposed to quadrat-level data.

To investigate short-term changes in benthic communities following bleaching, we calculated the mean difference in

percent cover values for each functional group, by quadrat at each site, 1 yr after the respective bleaching events (i.e., 2010 and 2016). We ran two-tailed t tests to determine which sites experienced significant changes in benthic cover post-bleaching. We used two-tailed t tests rather than planned contrasts within sites because we evaluated whether changes in cover were significantly less than or greater than zero, as opposed to whether paired values differed between years. For sites where hard coral cover declined, we plotted the benthic community composition (in terms of mean percent cover data averaged across quadrats, by site) at all available time points, within 2 yr of each bleaching event.

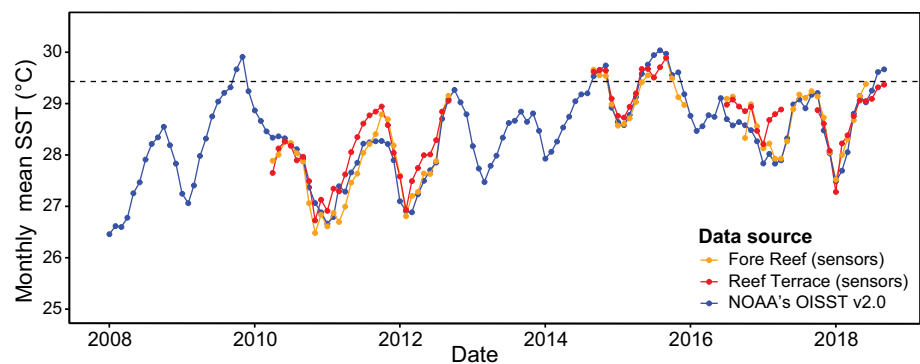
We quantified net change in percent cover from 2009 to 2018, for each benthic functional group as well as for reef builders and fleshy algae, by subtracting initial (i.e., at the 2009 time point) from final (2018 time point) values by quadrat and then calculating the mean differences and 95% confidence intervals by site. We ran a two-way analysis of variance (ANOVA) for each functional group separately to test whether these net differences varied by habitat and/or site. We then compared net differences through two-tailed t tests to identify which sites experienced significant changes not overlapping zero (e.g., an increase or decrease in functional group percent cover) across the 10 yr.

Results

Benthic community structure through time

The composition of benthic coral reef communities across sites on Palmyra is distinct between habitats and sites over time (Fig. 3). Between 2009 and 2018, average hard coral cover was $33.3 \pm 0.8\%$ (mean \pm SE) on the FR (Fig. 3a) and $49.2 \pm 0.9\%$ on the RT (Fig. 3f). Coral cover was generally stable through time on the terrace but exhibited a gradual decline on the FR between 2009 and 2018. While coral cover recovered at the terrace sites after the 2015 bleaching event, it continued to decline on the FR, particularly at FR3 (Fig. 3b). A significant habitat by time interaction

Fig. 2 Temperature history from Palmyra's fore reef and reef terrace in the past decade, as measured by both in situ sensors (with data averaged by habitat type) and satellites, via NOAA's Optimum Interpolation Sea Surface Temperature. The dashed horizontal line at 29.4 °C represents the estimated bleaching threshold for Palmyra (Fox et al. 2019b)



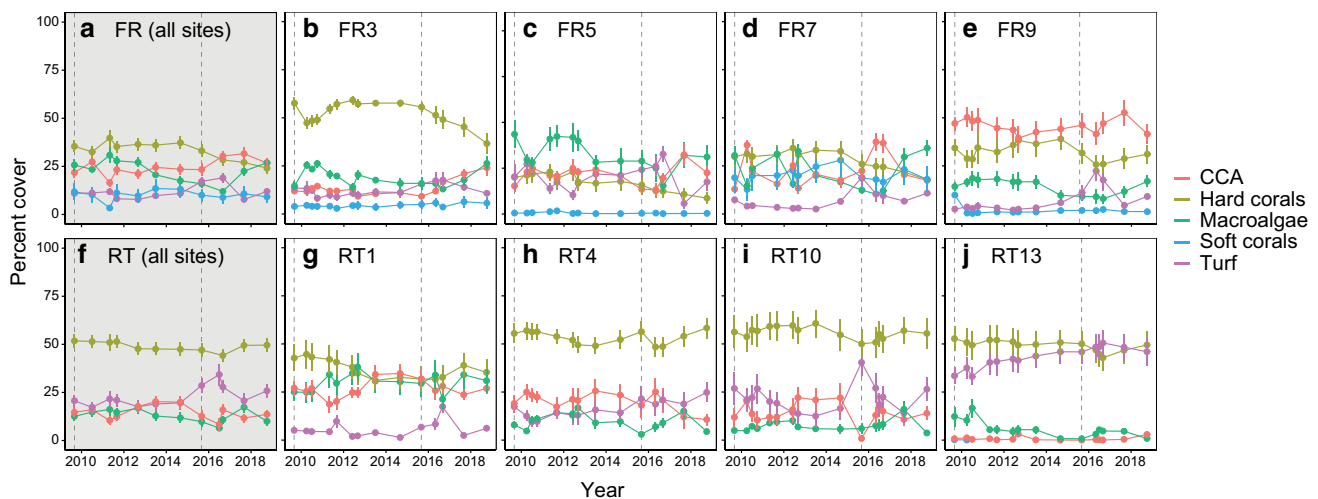


Fig. 3 Percent cover (mean \pm SE) over time by habitat (a, f) or site (b–e, g–j) on Palmyra for each benthic functional group. Dashed vertical lines indicate bleaching events in 2009 and 2015

(PERMANOVA, $p < 0.001$; Supplementary Table 2) suggests that despite site-level variability, each habitat is changing differently over time (Supplementary Fig. 3). Further, it seems that site is a better predictor for benthic community response than year or habitat, explaining 32.0% of the variation ($R^2 = 0.320$; Supplementary Table 2).

The nMDS (Fig. 4) showed that the sites were each characterized by a unique assemblage of benthic organisms (e.g., primarily CCA at FR9 or primarily turf at RT13) as well as individualized trajectories. There was more overlap

among the RT sites (Fig. 4b) as compared to the FR sites (Fig. 4a), suggesting that benthic composition is more similar among the different terrace sites than the FR sites. Despite the 10-yr time span, the community assemblage at each site remained relatively consistent through time (i.e., the lines representing sites generally occupy the same region in theoretical two-dimensional space).

The hard coral community on Palmyra's RT was dominated by table *Acropora* and encrusting *Montipora* spp., while the FR had more taxonomic diversity but less hard

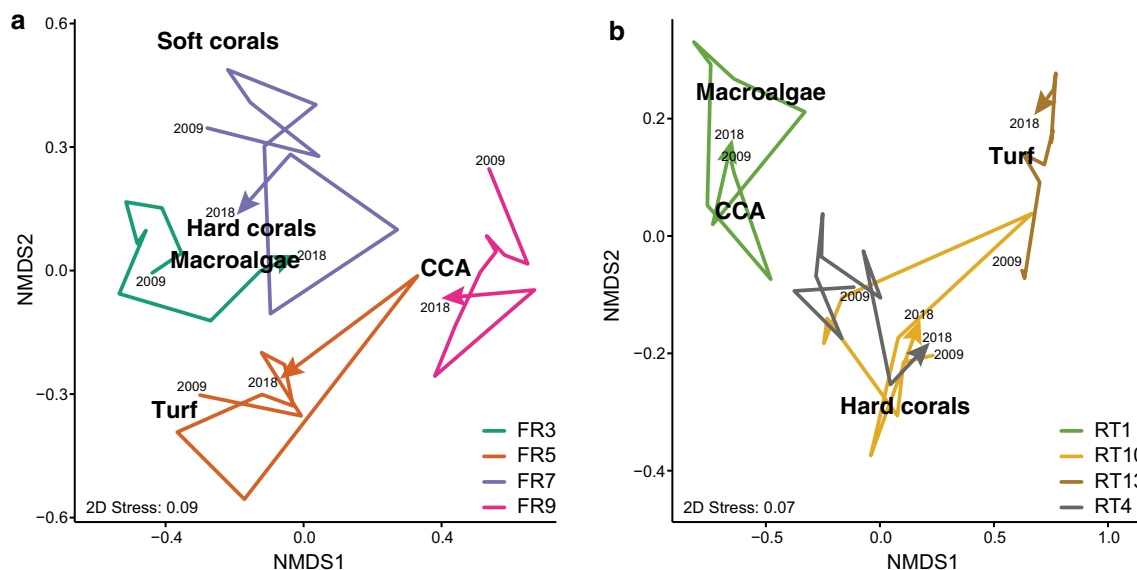


Fig. 4 Non-metric multidimensional scaling (nMDS) based on Bray–Curtis dissimilarity measures of benthic functional group composition through time for sites within a fore reef and b reef terrace

habitats. Colored lines terminating in an arrowhead represent the trajectory of each site from 2009 to 2018

coral cover overall. Soft corals (mainly *Sinularia* spp. and *Lobophytum* spp.) only occurred on the FR (especially FR7, Fig. 3d) with an overall average of $10.0 \pm 1.0\%$ cover (Fig. 3a). Macroalgae were also more abundant on the FR, accounting for $21.8 \pm 0.6\%$ of the benthos (Fig. 3a) compared to $12.9 \pm 0.6\%$ on the RT (Fig. 3f). The most abundant macroalgal species were *Halimeda* spp., *Lobophora* spp., and members of the *Peyssonneliaceae* complex. CCA were most abundant on the FR, accounting for over a quarter of the benthos ($25.7 \pm 0.7\%$; Fig. 3a), compared to the RT ($15.3 \pm 0.7\%$; Fig. 3f). In contrast, turf algal cover was higher on the terrace ($21.9 \pm 0.9\%$; Fig. 3f) relative to the FR ($11.5 \pm 0.5\%$; Fig. 3a). Of all benthic functional groups, macroalgae and turf were the most variable through time.

Almost all sites on Palmyra were dominated by reef builders as opposed to fleshy algae (Fig. 5). At one site on the RT (RT10), the cover of reef builders declined from 2014 to 2015 from 76.8 ± 15.8 to $50.9 \pm 7.9\%$, while the cover of fleshy algae rose from 16.6 ± 5.7 to $40.7 \pm 6.9\%$, but by 2018, they returned to their pre-disturbance levels (Fig. 5i). An increase in fleshy algae and corresponding decrease in reef builders was also observed to a lesser extent at both FR9 (Fig. 5e) and RT1 in 2016 (Fig. 5g) but was similarly temporary. Ultimately, there is no indication of a shift from reef builders to fleshy algal dominance. Overall, the FR (Fig. 5a) had $57.4 \pm 9.1\%$ reef builder cover and $13.4 \pm 3.6\%$ fleshy algal cover, while the RT (Fig. 5f) had $64.3 \pm 10.3\%$ reef builder cover and $28.1 \pm 5.9\%$ fleshy algal cover.

Responses of benthic communities to thermal stress

Coral cover did not change at five out of eight sites and declined at the remaining three sites (FR3, FR9, and RT13) by an average of $6.1 \pm 1.6\%$ (Fig. 6a; Supplementary Table 3) in the year following the 2009 bleaching event. This free space was colonized by different algal functional groups depending on the site (macroalgae at FR3, CCA at FR9, and turf at RT13) but in all cases, the sites returned to the former pre-bleaching levels of coral cover within 2 yr (Fig. 7a–c). One year after the 2015 bleaching event, hard coral cover declined at three of the same sites as documented in 2009–2010 as well as at an additional site, RT4, by $6.8 \pm 0.4\%$ on average (Fig. 6e; Supplementary Table 3). This space transitioned to CCA at FR3, turf algae at FR9, macroalgae and turf at RT13, and CCA and macroalgae at RT4 (Fig. 7d–g). Within 2 yr, baseline coral cover was once again restored at all sites except for one (FR3; Fig. 7d).

Net change in benthic cover over a decade

Between 2009 and 2018, benthic communities on Palmyra exhibited habitat-specific dynamics, and net trajectories varied among sites (Supplementary Table 4). Coral cover decreased at three of the four FR sites (FR3, FR5, and FR7) by $14.4 \pm 2.6\%$ but remained constant on the shallow RT (Fig. 8a; Supplementary Table 5). Cover of CCA and macroalgae remained constant at all sites except FR3, where they slightly increased (Fig. 8b, c; Supplementary Table 5). Turf cover also slightly increased at FR9 (Fig. 8d) but there were no significant net changes at any other sites. The abundance of reef builders decreased at three of the FR sites (FR3, FR7, and FR9) by $9.4 \pm 0.7\%$ on average, but did not change significantly on the terrace. Fleshy algal cover increased at

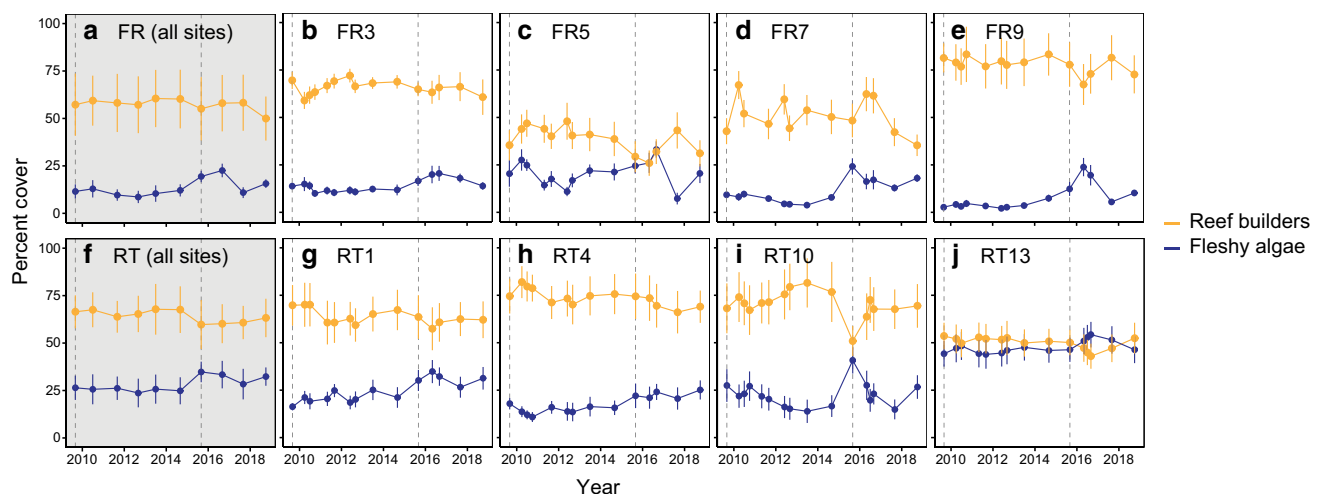
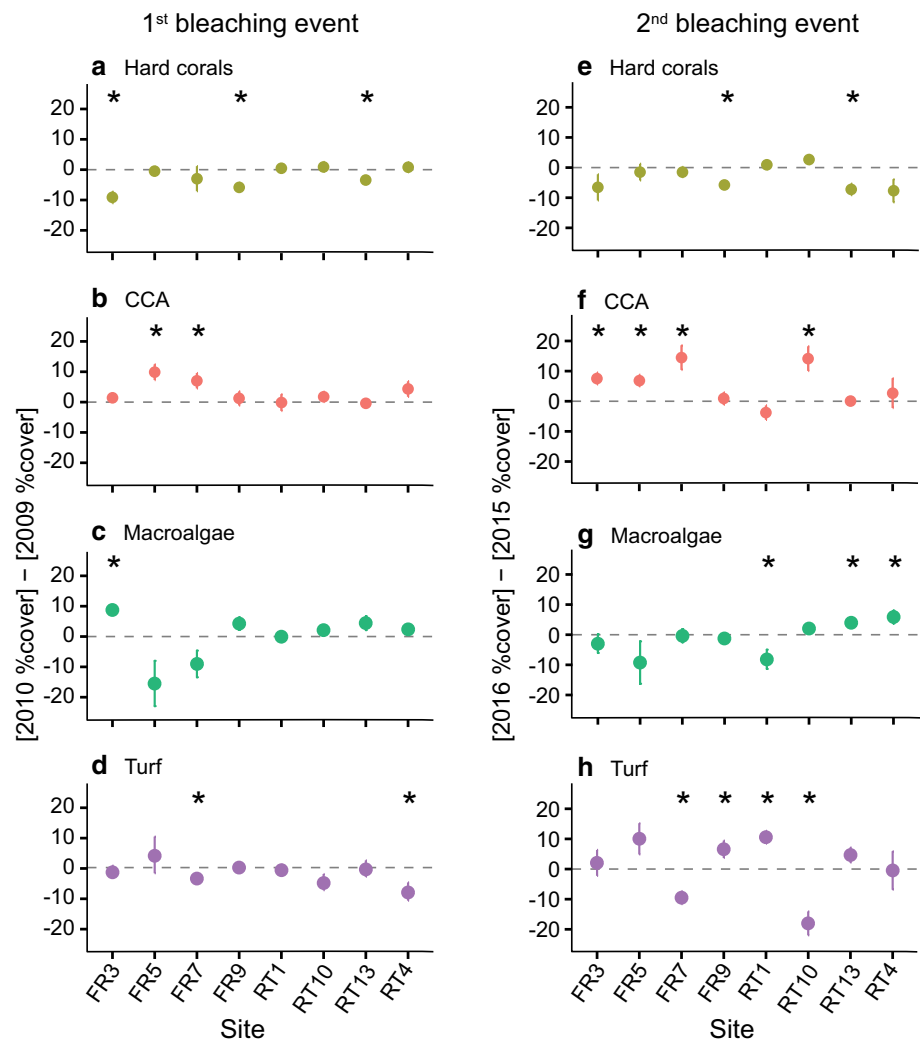


Fig. 5 Percent cover (mean \pm SE) over time by habitat (a, f) or site (b–e, g–j) on Palmyra for reef builders (i.e., hard corals and CCA) and fleshy algae (i.e., turf and fleshy macroalgae). Dashed vertical lines indicate bleaching events in 2009 and 2015

Fig. 6 Changes in percent cover (mean \pm SE) by site for each major benthic group, 1 yr following the first (a–d) and second (e–h) bleaching events in 2009 and 2015. Significance symbols for sites whose net change is different than zero ($p < 0.05$ according to two-tailed t tests; Supplementary Table 3) are shown. Dashed horizontal lines indicate no change



two FR sites (FR7 and FR9) by $8.2\% \pm 0.7\%$ on average, and one terrace site (RT1; Supplementary Table 5) but did not change at the remaining sites.

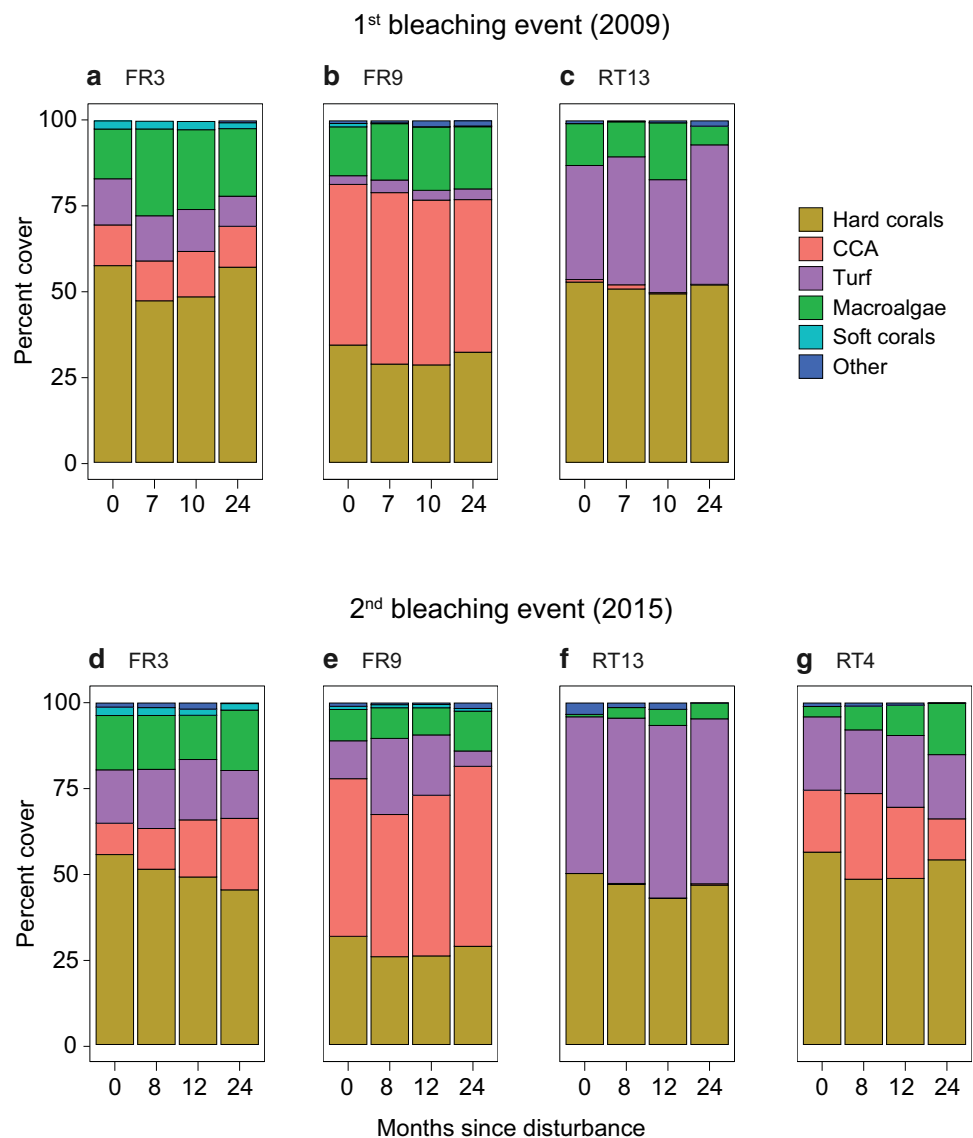
Discussion

Marine heatwaves are increasing in frequency and magnitude (Oliver et al. 2018; Smale et al. 2019) with widespread declines in coral cover (Ridgway et al. 2016; De Bakker et al. 2017; Stuart-Smith et al. 2018) and devastating consequences for coral reefs globally (Hughes et al. 2018), yet some coral communities are able to resist and/or recover (Adjeroud et al. 2009; Cruz-García et al. 2020; Fox et al. 2021). Here, we quantified the spatial and temporal dynamics of benthic coral reef communities on Palmyra Atoll, which have remained largely unchanged on a decadal scale despite two El Niño-associated bleaching events. These findings, based on 80 permanent plots from two distinct reef

habitats, demonstrate the resilience of Palmyra's reefs at least up until the present time.

Long-term monitoring of coral communities at multiple sites allowed us to detect site-specific patterns of bleaching-induced mortality as well as evidence of recovery which is often not apparent in other studies (Supplementary Table 1). Coral cover declined on Palmyra at three out of eight sites 1 yr post-bleaching in 2009 and those same sites declined again after the 2015 event, along with an additional site. This indicates that these sites may be more susceptible to bleaching than the others. Two of the sites that declined in coral cover are most proximate to the dredged channel that flushes lagoonal water out to the open coast (Rogers et al. 2017). While lagoon outflow may provide heterotrophic resources that can augment coral nutrition and facilitate their recovery (Fox et al. 2019a), high turbidity of these waters can reduce light available for photosynthesis and surface waters may also be warmer than surrounding oceanic waters. Williams et al. (2010) found that exposure to turbidity was the single best predictor of bleaching on Palmyra during the 2009 event

Fig. 7 Bar plots of benthic community composition for up to 2 yr following the 2009 (a–c) and 2015 (d–g) bleaching events at sites that declined in hard coral cover. Note that x-axis values correspond to months since the thermal disturbance (e.g., “0” is at the time of bleaching)



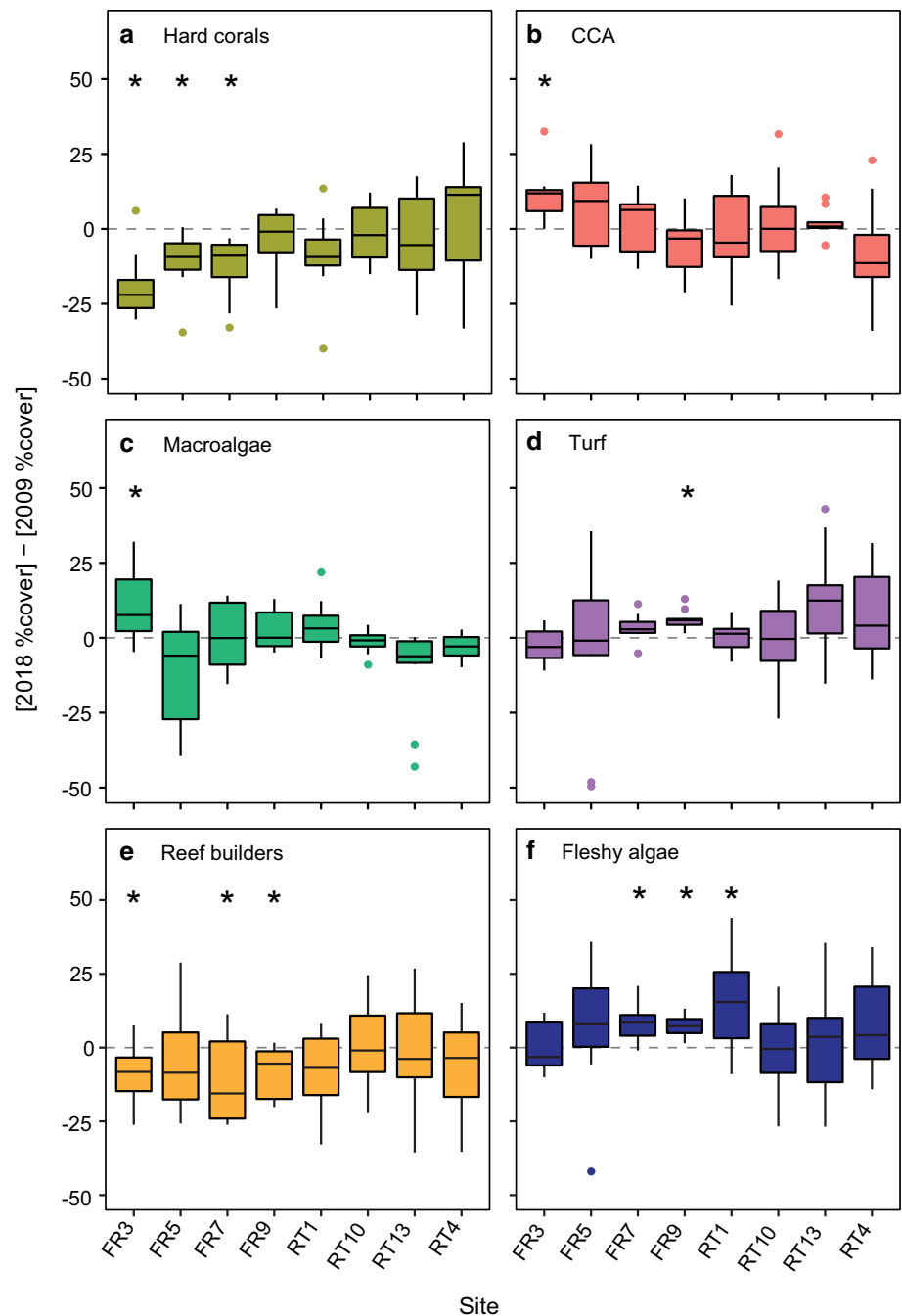
and this was directly tied to lagoonal outflow. Interestingly, although these sites suffered some mortality following the bleaching events, they were able to recover quickly, which suggests that a link to the lagoon during “normal” conditions may positively influence coral growth rates (e.g., via heterotrophic feeding).

Incorporating key algal functional groups in our study provided further insight into benthic successional dynamics. Turf algae are known to be the first to colonize after disturbances and persist for up to 2.5 yr (Diaz-Pulido and McCook 2002) while CCA are less competitive and slower growing (Adey and Vassar 1975; McClanahan 1997). However, since herbivores will preferentially feed on turf algae (Vermeij et al. 2010; Hamilton et al. 2014; Kelly et al. 2016), CCA can dominate in the presence of high herbivory (Steneck and Dethier 1994; Littler et al. 2006). On Palmyra, declines in coral cover were followed by increases in turf, macroalgae,

and/or CCA within 1 yr depending on the site, but at almost all of these sites, coral cover returned to pre-bleaching levels after 2 yr. Intense grazing by herbivores on Palmyra (Edwards et al. 2014; Hamilton et al. 2014) may have led to calcifier dominance and coral recovery on shorter time scales (Fox et al. 2019b). Ultimately, over the 10 yr time span, there was minimal net change in any benthic functional group.

Despite the general stability of Palmyra’s reefs, we found a gradual decline in coral cover at three of the FR sites, which has accelerated since 2015. The rate of this decline at some sites suggests it is not directly driven by bleaching-associated mortality but rather by a more recent change in the system. This may be due to an ongoing outbreak of crown-of-thorns sea star (COTS) on the FR that was first observed in 2017 (personal observation). Another potential cause of decline is invasion by the corallimorph, *Rhodactis*

Fig. 8 Box plots of the distributions of net changes in percent cover of major benthic groups, by site, between only the initial and final time points (September 2009 and October 2018). Mean values and 95% confidence intervals are provided in Supplementary Table 5. Significance symbols for sites whose net change is different than zero ($p < 0.05$ according to two-tailed t tests) are shown. Dashed horizontal lines indicate no change



howesii, which is an aggressive competitor to corals (Work et al. 2008; Chadwick and Morrow 2011) that has continued to increase in abundance at certain sites on Palmyra, particularly FR5 (Carter et al. 2019).

Spatial variability in benthic community structure across the FR is also known to be driven by wave energy and strong upwelling or downwelling events, which are modulated by reef slope and bathymetry (Gove et al. 2015; Williams et al. 2018). Here, we show that the two western-most FR sites were dominated by hard corals or a combination of corals and CCA, while the two centrally located sites had a more

even distribution across different functional groups with higher percent cover of soft corals, macroalgae, and turf algae. The shallower RT sites are less wave-exposed (Gove et al. 2015), physically closer to one another, and are generally more similar to one another in benthic community composition than FR sites.

Throughout the decade, there was less coral mortality and higher recovery observed at RT sites in comparison with FR sites. Because of the shallow and wave-protected nature of the RT habitat, sites here undergo more diurnal variability in temperature than the FR sites (Fox et al. 2019b) as well

as large diel fluctuations in pH and dissolved oxygen (Take-shita et al. 2016; Cyronak et al. 2020). The regular exposure of corals at these sites to changes in temperature may have pre-acclimated them to warmer conditions, and perhaps as such, they experience less bleaching and mortality than corals at the FR sites (Donner 2011; Safaie et al. 2018). Previous studies have shown that Palmyra's FR communities appear to be less resistant to bleaching and post-bleaching mortality than at the terrace (Fox et al. 2019b). While we did not measure bleaching responses specifically, our results corroborate these observations. Differential responses by habitat or sites have also been mentioned in previous studies (McClanahan 2000; McClanahan et al. 2001; Muhando and Mohammed 2002; Done et al. 2007; Guest et al. 2016). Here, the significant interaction between habitat and time (Supplementary Table 2; Supplementary Fig. 3) indicates that these communities are changing differently over time. This variation is likely related to site-specific differences in oceanographic conditions.

On Palmyra, benthic reef communities at all sites surveyed aside from one were dominated by reef builders. Notably, the site with a more even distribution of fleshy algae and reef builders (RT13) is the site most proximate to the lagoon, where sedimentation or access to higher concentrations of inorganic nutrients may have resulted in more fleshy algal cover. Dominance by reef builders at the majority of sites studied here suggests that Palmyra's reefs are in a state of net calcification and growth (Goreau 1963; Perry et al. 2017). Reef builders such as CCA promote coral recruitment and regrowth, whereas turf and other fleshy algae can prevent coral settlement, inhibit growth, or otherwise harm corals (Birrell et al. 2005; Price 2010; Barott and Rohwer 2012). Past studies consisting of single snapshot or baseline surveys have shown similar abundance of reef-building organisms on remote and/or uninhabited islands across the Pacific, while more impacted or populated islands tend to be dominated by fleshy algae (Knowlton and Jackson 2008; Sandin et al. 2008; Smith et al. 2016).

Interestingly, we noticed some cases of substantial macroalgal decline (e.g., up to 50% within a single quadrat at FR5) following both bleaching events. This was largely attributed to the calcareous algae, *Halimeda* spp., which account for much of the macroalgal community on Palmyra. Due to their high growth, calcification, and rapid turnover rates, they contribute significantly to carbonate production on coral reefs (Rees et al. 2007). Additionally, they are holocarpic, releasing all of their gametes during reproduction and dying thereafter (Hillis-Colinvaux 1980). Since little is known about sexual reproduction in tropical green algae (Clifton 2013), it is unclear whether thermal stress triggered their reproduction and subsequent mortality. Nevertheless, if *Halimeda* populations are indeed sensitive to warm-water

events, this could have negative implications for overall reef carbonate budgets, highlighting a research gap.

While Palmyra's reefs did experience warming and consequent bleaching, these events were not nearly as extreme as those experienced by other reefs in the central Pacific. For example, at the uninhabited Jarvis Island, where maximum accumulated thermal stress was 22.25 DHWs (Vargas-Angel et al. 2019), in contrast to 11.9 DHWs on Palmyra (Fox et al. 2019b), catastrophic losses in coral cover of up to 95% were reported following the 2015–2016 bleaching event (Barkley et al. 2018). Similarly, Kiritimati Atoll experienced unprecedented thermal stress exceeding 25–30+ DHWs between 2015 and 2016 (Claar et al. 2019) and consequently, over 80% coral mortality occurred (Baum et al., unpublished data). Howland, Baker, and Kanton Islands experienced substantially less thermal stress during this event (NOAA Coral Reef Watch) and had reductions in coral cover of only around 30% at Howland and Baker with little discernable mortality at Kanton (Brainard et al. 2018). Thus, not surprisingly, bleaching-related mortality across this region seems to be strongly correlated to the degree of thermal stress experienced at a given location, among other factors. While we report evidence of stability in Palmyra's benthic reef communities, we must interpret these trends within the context of Palmyra's thermal history. If more extreme and/or frequent bleaching events affect Palmyra in the future, the consequences are as of yet unknown.

In conclusion, the results of a decade of monitoring on Palmyra's coral reefs reveal remarkable resilience despite two El Niño-associated bleaching events. It is unclear whether the resistance and recovery observed here are due to the lack of local human impacts, acclimation and/or adaptation, or the degree of thermal exposure relative to other more-impacted locations. Nonetheless, Palmyra's reefs provide a unique opportunity to better understand benthic community dynamics and successional trajectories in the face of global change. This data set is not only a testament to Palmyra's resilience, but also a backdrop from which to consider the adaptation and acclimation potential of coral reef communities.

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Declarations

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

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