Title

Spatial and Temporal Ecology of Corals and Algae on Palmyra Atoll, Central Pacific Following Thermal Disturbance

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Publication Date

2022

UNIVERSITY OF CALIFORNIA SAN DIEGO

Spatial and Temporal Ecology of Corals and Algae on Palmyra Atoll, Central Pacific Following Thermal Disturbance

A dissertation submitted in partial satisfaction of the requirements
for the degree Doctor of Philosophy

in

Marine Biology

by

Adi Khen

Committee in charge:

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2022

The dissertation of Adi Khen is approved, and it is acceptable in quality and form for publication on microfilm and electronically.

University of California San Diego

2022

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ACKNOWLEDGEMENTS

First and foremost, I would like to acknowledge my advisor, Dr. Jennifer E. Smith, for providing me with opportunities to succeed; her support has proven invaluable throughout my professional career. I am sincerely thankful to my dissertation committee for their guidance over the years. I would also like to acknowledge my mentor, Dr. Levi S. Lewis, whose critical yet constructive feedback has helped me grow as a scientist and person. My research project could not have been completed without the dedicated team of Smith and Sandin lab members, staff, alumni, and volunteers. The Scripps Graduate Office and Center for Marine Biodiversity and Conservation provided administrative and educational support. Finally, this work was generously funded by the Beyster family and National Science Foundation.

Chapter 1, in part, is currently being prepared for submission for publication of the material. Khen, Adi; Wall, Christopher B; Smith, Jennifer E. The dissertation author was the primary investigator and author of this material.

Chapter 2, in full, is a reprint of the material as it appears in Coral Reefs 2022. Khen, Adi; Johnson, Maggie D; Fox, Michael D; Clements, Samantha M; Carter, Amanda L; Smith, Jennifer E, Springer, 2022. The dissertation author was the primary investigator and author of this paper.

Chapter 3, in part, is currently being prepared for submission for publication of the material. Khen, Adi; Fox, Michael D; Johnson, Maggie D; Smith, Jennifer E. The dissertation author was the primary investigator and author of this material.

Chapter 4, in part, is currently being prepared for submission for publication of the material. Khen, Adi; Johnson, Maggie D; Fox, Michael D; Smith, Jennifer E. The dissertation author was the primary investigator and author of this material.

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Khen A, Johnson MD, Fox MD, Clements SM, Carter AL, Smith JE (2022) Decadal stability of coral reef benthic communities on Palmyra Atoll, central Pacific, through two bleaching events. Coral Reefs:1-13

Khen A, McCormick LR, Steinke C, Rouse GW, Zerofski PJ (2022) First known observations of brooding, development, and hatching of fertilized eggs for the North Pacific bigeye octopus, *Octopus californicus*. Ecology and Evolution 12:e9481

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ABSTRACT OF THE DISSERTATION

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by

Adi Khen

Doctor of Philosophy in Marine Biology

University of California San Diego, 2022

Professor Jennifer Smith, Chair

Coral reefs are valuable ecosystems that provide billions of dollars globally in ecological goods and services, but they are facing widespread degradation due to climate change. This dissertation provides insights into the dynamics of coral bleaching and recovery, responses of other key taxa such as algae, and broader ecological implications for coral reef communities in the context of thermal stress. Chapter 1 of the dissertation synthesizes results from past studies on coral bleaching: while bleaching severity was highly variable as expected, this was complicated by inconsistent response metrics and the fact that bleaching measurements are often taken at different timing with respect to the onset of thermal stress. By standardizing existing observations, this chapter allows for inter-study comparison of coral bleaching susceptibility by genus, morphology, and/or region. Chapter 2 uses a time series of underwater imagery taken yearly for the past decade from two habitats on Palmyra Atoll to quantify the cover of reef-building corals, crustose coralline algae, macroalgae, turf, and other invertebrates. One year after each of the thermal anomalies in 2009 and 2015, some sites experienced reductions in coral cover which were replaced by turf or crustose coralline algae. However, across the entire decade, benthic community structure changed minimally at the functional group level, with greater stability at the reef terrace as compared to the fore reef. Chapter 3 of the dissertation tracks the growth, discoloration (i.e., lack of pigmentation), partial or whole-colony mortality, survival, and/or regrowth of individual coral colonies on Palmyra. This chapter explores which species were more sensitive or tolerant than others when exposed to thermal stress, and whether a colony's level of discoloration at the time of warming corresponds to its fate one year later. Finally, Chapter 4 evaluates the long-term effects of increased seawater temperatures on benthic algae. This chapter investigates the abundance of fleshy and calcareous algae on Palmyra's reef habitats over time, and suggests that a major macroalgal genus, *Halimeda* spp., showed evidence of temperature sensitivity. Long-term monitoring data sets from Palmyra can be used to establish baseline information for the conservation and restoration of more-threatened reefs at risk of decline.

CHAPTER 1: Standardization of Coral Bleaching Measurements Highlights the Variability in Genus, Morphology, and Region-Specific Responses

Adi Khen; Christopher B. Wall; Jennifer E. Smith

ABSTRACT

Marine heatwaves and regional coral bleaching events have become more frequent and severe across the world's oceans over the last several decades due to global climate change. Observational studies have documented spatiotemporal variation in the responses of reef-building corals to thermal stress within and among taxa across geographic scales. Although many tools exist for predicting, detecting, and quantifying coral bleaching, certain limitations often make it difficult to compare results among studies. For this review, we compiled over 1,500 bleaching observations representing 86 reef-building coral genera and 260 species of all morphological groups from a total of 62 peer-reviewed scientific articles, encompassing three broad geographic regions: the Atlantic, Indian, and Pacific Oceans. While bleaching severity was found to vary by genus and morphology, we found that genera and morphologies both responded differently to bleaching across regions. These patterns were complicated by the fact that (i) methods and response metrics were inconsistent across studies; (ii) observations were taken at different ecological scales (i.e., individual colony-level vs. population or community-level); and (iii) surveys were taken at different times with respect to the onset of thermal stress and the chronology of bleaching events. To improve cross-study comparisons, we recommend that future surveys should prioritize measuring bleaching in the same individual coral colonies over time and incorporate the severity and timing of warming into their analyses. By reevaluating and

standardizing the ways in which we quantify coral bleaching, we propose that scientists will be able to track responses to marine heatwaves with increased rigor, precision, and accuracy.

INTRODUCTION

Reviewing the Causes and Consequences of Coral Bleaching

Reef-building corals are important ecosystem engineers for tropical coral reefs. Corals exist in a mutualistic symbiosis with photosynthetic dinoflagellate symbionts (Symbiodiniaceae) which support coral nutrition and growth (Muscatine and Porter 1977). However, environmental stress can push this symbiosis into a state of dysbiosis, with the coral losing its symbionts in a process termed “coral bleaching.” Bleaching increases a coral’s vulnerability to disease and colony fragmentation, and can reduce coral growth or reproduction (Baird and Marshall 2002). Under prolonged duration (weeks to months) and/or increased magnitude of thermal stress, bleaching can lead to coral mortality (Cook et al. 1990). However, corals can recover from bleaching once non-stressful conditions are restored (Jones and Yellowlees 1997). During this period of dysbiosis and post-stress recovery, corals can compensate for the lack of symbiont-derived nutrition by feeding on suspended particles and plankton (i.e., heterotrophy; Grottoli et al. 2006; Palardy et al. 2008) or rely on the consumption of energy reserves, such as lipids, to sustain metabolism (Porter et al. 1989; Grottoli et al. 2004; Rodrigues and Grottoli 2007; Wall et al. 2019). Ultimately, corals surviving bleaching events can regain their endosymbiont communities by incorporating new Symbiodiniaceae symbionts into their tissues from environmental reservoirs (Fitt et al. 1993) or through the repopulation of symbionts remaining within coral tissues (Baker 2003). To better understand the dynamics of coral bleaching and recovery and the individual, local, or regional factors contributing to bleaching susceptibility, we need more precise colony-level data incorporating the severity of warming and the reef's surrounding environment.

Many environmental triggers can result in coral bleaching (e.g., reduced salinity [Goreau 1964; Van Woesik et al. 1995], decreased sea water temperature [Muscatine et al. 1991; Gates et al. 1992], solar radiation [Lesser et al. 1990; Brown et al. 1994], and bacterial infection [Kushmaro et al. 1996]; see Brown 1997). However, widespread coral bleaching events are largely due to marine heatwaves that cause anomalously high seawater temperatures and are driven by global climate change (Spalding and Brown 2015; Heron et al. 2016; Hughes et al. 2017). Mass coral bleaching events in particular occur in areas of high accumulated heat stress, where sea surface temperatures (SST) have exceeded the bleaching threshold for multiple consecutive weeks. Mass coral bleaching was first described in scientific literature in 1984, following the severe El Niño-Southern Oscillation (ENSO) event from 1982-1983 (Glynn 1984). As of 2011, regional bleaching has been documented over 7,000 independent times worldwide (ReefBase; Donner et al. 2017). In the span of the past few decades, bleaching has been reported in nearly every location where coral reefs exist across the globe (Donner et al. 2017; Fig. 1.1). In an effort to catalog these bleaching events and their consequences, a historical coral bleaching database has been compiled (https://simondonner.com/bleachingdatabase/) which is currently the most comprehensive archive of bleaching records publicly available. This archive combines observations compiled by the non-profit global information system, ReefBase (http://www.reefbase.org), with reports from researchers and reef managers. For instance, the Great Barrier Reef predominantly suffered from the 2002 bleaching event while the 2005 event was centralized on the Caribbean (Fig. 1.2). Three global bleaching events were observed across all tropical oceans in 1998, 2010, and 2015. The 2015 global coral bleaching event lasted for an unprecedented three successive years of bleaching (2014-2017) in some locations and hit nearly every major tropical region on Earth (Eakin et al. 2019; Fig. 1.3). Altogether, this has allowed for geographic explorations of patterns in bleaching prevalence.

Coral Bleaching Assessment Methods

Current methods for assessing bleaching usually involve satellite remote sensing, aerial surveys, underwater surveys, or image analysis of transects or quadrats. While all of these methods contribute to our knowledge of bleaching severity, they operate under varying levels of taxonomic and spatial resolution (reviewed in van Woesik et al. 2022; Fig. 1.4) and present their own advantages and disadvantages. Satellite remote sensing, while informative and large-scale (e.g., 50 km or 5 km resolution), only captures emergent reefs and relies on predictions from temperature metrics rather than *in situ* bleaching data (Liu et al. 2014). Other complications with remote-sensing include cloud cover and the fact that bleached corals can have a similar spectral signature as sand (Elvidge et al. 2004). Moreover, satellites can only provide bleaching forecasts whereas aerial surveys conducted via aircrafts (Hughes et al. 2017) or small unmanned drones (Levy et al. 2018) can map entire reefs but quantify bleaching on a reef-wide basis. However, new technologies such as fluid lensing (Chirayath and Earle 2016), which uses water-transmitting wavelengths to passively image underwater objects, are now being developed to improve the use of remote sensing tools and could potentially deliver centimeter-resolution data at regional scales. Similarly, airborne mapping combined with laser-guided imaging spectroscopy and deep learning models (Asner et al. 2020) can provide regional-scale quantitative estimates of reef condition.

Underwater surveys (i.e., SCUBA/snorkel surveys, tow-boards) offer the opportunity to make direct observations but are more time-intensive and vary in scale from focal colony assessments to towed-diver surveys at the community or reefscape level. Alternative approaches for surveying entire reef communities are diver-led surveys at the tens-of-meter scale (i.e., point-intercept and transects), which can give insights into population or colony-level bleaching responses. Corals are often categorized as “bleached,” “unbleached,” or another qualitative bleaching group (McClanahan et al. 2004) rather than quantifying percent of color change relative to an unaffected (i.e., non-bleached) conspecific colony, although this can be subject to observer bias (Siebeck et al. 2006). A color reference card (Siebeck et al. 2006; Bahr et al. 2020) can also be used to visually compare coral pigmentation *in situ* to “healthy” representatives, however, these color references require extensive local ground-truthing to capture the range of color for healthy and bleached corals in a specific region (Bahr et al. 2020). Image analysis, in which bleached areas within photoquadrats taken during underwater surveys are digitally traced using computer software (e.g., Neal et al. 2017), is arguably the most precise, yet this method can be time-consuming (Williams et al. 2019). Image analysis is also traditionally small-scale at the colony level, which does not always represent the population or community as a whole. Recent machine learning initiatives, such as exclusively-automatic bleaching detection, are now being attempted by the XL Catlin Seaview Survey (https://www.catlinseaviewsurvey.com/). Other automated classification programs such as CoralNet (Beijbom et al. 2015, https://coralnet.ucsd.edu/), have not yet been achieved to a sufficient level of taxonomic resolution and cannot measure bleaching within colonies (Bryant et al. 2017). In the future, a combination of human-validated, computer-annotated image analysis will likely optimize efficiency and allow for thorough examination of how corals bleach over time on an individual colony basis. While bleaching observations of all scales have merit, in order to predict regional or taxonomic responses more accurately, it is also important to acknowledge underlying physical, biological, or contextual factors.

Coral Bleaching Resistance and Reef Resilience

It is generally accepted that corals have different susceptibilities to bleaching based on taxonomy (Marshall and Baird 2000), life history strategy (Darling et al. 2013), morphology (Loya et al. 2001; van Woesik et al. 2012), colony size class (Shenkar et al. 2005), symbiont type and/or density (Berkelmans and van Oppen 2006), as well as any other distinguishing characteristics. ‘Weedy’ genera (i.e., ones that are fast-growing, opportunistic, and able to dominate post-disturbance, such as *Acropora* or *Pocillopora* spp.) may be more sensitive to bleaching yet quicker to regain their pre-bleaching cover following substantial losses (Darling et al. 2013; McClanahan et al. 2014). Morphology is also thought to play a role, though results are often contradictory. For instance, massive (i.e., mounding) corals show high (Marshall and Baird 2000) or low (Williams et al. 2010) resistance to thermal bleaching. Branching corals may experience more bleaching-related mortality than massive or encrusting corals (Marshall and Baird 2000; Hoegh-Guldberg and Salvat 1995), presumably because the thinner tissues of branching corals expose symbionts to higher light intensities (Loya et al. 2001). Larger colonies with more tissue area could hypothetically have an advantage over smaller colonies during bleaching due to their higher symbiont densities, although some studies indicate otherwise (Shenkar et al. 2005; Brandt 2009; Wagner et al. 2010). Tissue biomass may also correlate with symbiont density, as species with lower tissue biomass have been found to experience increased mortality following bleaching (Thornhill et al. 2011).

Additionally, it has long been known that certain symbionts may be more stress-tolerant and that symbiont-switching may serve as an adaptive function for corals (Baker 2003). The "Adaptive Bleaching Hypothesis" (Buddemeier and Fautin 1993) suggests that bleaching is adaptive and that after bleaching, corals may replace their symbionts ("symbiont-switching") with more heat-resistant varieties in order to withstand future heat stress. There is experimental evidence of this, albeit short-term (i.e., less than a year; see Toller et al. 2001). For instance, if coral bleaching was not severe, recovering corals maintained the same symbiont species post-treatment; however, corals whose symbionts had been depleted post-bleaching were repopulated with new symbiont taxa for up to nine months later (Toller et al. 2001). Other than symbiont-switching, corals may undergo symbiont-shuffling, in which colonies change the relative abundance of their existing symbionts (Baker 2003). Other studies have found a high degree of specificity among coral-Symbiodiniaceae associations in the long term (Thornhill et al. 2006; Stat et al. 2009; Lee et al. 2016), implying that the uptake of new symbionts with different stress tolerance may be transient (Coffroth et al. 2010), particularly for adult corals (but see: Scharfenstein et al. 2022; Boulotte et al. 2016). Further, some coral taxa exhibit higher flexibility in their *Symbiodinium* assemblages than others (Goulet 2006; Putnam et al. 2012) and individual colonies may have their own 'Symbiodiniaceae signature' (Rouzé et al. 2019). The dynamics of these symbioses are also affected by environmental regimes (Baker et al. 2013) and the symbionts' physiological traits (Wong et al. 2021), making it difficult to predict post-bleaching recovery or mortality based only on changes in symbiont communities.

Physical factors such as location (Sully et al. 2019), reef habitat type (Wagner et al. 2010), human population density (Sandin et al. 2008), and/or environmental variability (Jokiel and Brown 2004; Bahr et al. 2017) may also affect bleaching outcomes, along with prior bleaching history (Brown et al. 2002; Pratchett et al. 2013). Depth is thought to provide a refuge for corals from solar heating and light (Smith et al. 2014; Baird et al. 2018), but this does not always confer resistance to bleaching, as has been seen in both the Caribbean (Neal et al. 2014) and Pacific (Venegas et al. 2019). Resistance to thermal stress can be defined as the ability of individual corals to avoid bleaching or survive post-bleaching (West and Salm 2003). Factors that reduce thermal stress (e.g., cold-water upwelling; Goreau et al. 2000), enhance water flow and flush out toxins (Nakamura and Van Woesik 2001), and decrease light stress (e.g., shading from cloud cover [Mumby et al. 2001] or light absorption by dissolved organic matter [Anderson et al. 2001]) can determine bleaching resistance.

While resistance pertains to the ability to withstand or not be harmed by disturbance, resilience is a reef's ability to return to its previous state of biodiversity and abundance following disturbance (West and Salm 2003). The speed at which this occurs, along with the magnitude of disturbance, can also be considered when defining resilience (Nyström et al. 2000; Gunderson 2000). Ecosystem resilience is determined by either intrinsic (e.g., larval production capacity and recruitment success, or the presence of herbivorous grazers [Roff and Mumby 2012; Heenan and Williams 2013]) or extrinsic (e.g., effective management and protection [Salm and Coles 2001; Mellin et al. 2006]) factors. Some remote, protected reefs such as the Phoenix Islands in the central Pacific have shown evidence of increased resilience following successive heatwaves, possibly due to adaptive thermal tolerance and localized recruitment by surviving colonies (Fox et al. 2021). However, the 2016 heatwave also caused severe (>50%) mortality throughout the most remote sections of the Great Barrier Reef (Hughes et al. 2018) and in protected areas of the Northwestern Hawaiian Islands (Couch et al. 2017), where the human impacts that may further exacerbate thermal stress (e.g., urbanization, nutrient pollution) or degrade reef ecosystem function (e.g., overfishing) are largely absent.

Thus, in the context of global climate change, there are perhaps no refugia where corals are not threatened by marine heatwaves and regional bleaching events. By the year 2050, bleaching is predicted to occur annually for all reefs globally (Donner et al. 2005). By 2100 with a rise in global sea surface temperature of about 3 ºC (Pörtner et al. 2019) under the Intergovernmental Panel on Climate Change's high greenhouse gas emissions future scenario, most reefs worldwide are projected to decrease in coral cover by over 40% (Sully et al. 2022). Post-bleaching recovery, however, might be more influenced by local stressors (e.g., overfishing, pollution, sedimentation, or coastal development), the absence of which may facilitate the recovery of corals with more heat-adapted Symbiodiniaceae symbionts (see Claar et al. 2020) and reduce the extent of bleaching. While mitigating local stressors can potentially minimize climate impact (Donovan et al. 2020; but see: Bruno et al. 2019), local and global stressors could also act synergistically to magnify post-bleaching mortality (Donovan et al. 2021). In order to gain a better understanding of trends in coral bleaching and recovery, there is a need to synthesize studies that have quantified responses from multiple scales, regions, taxa, and/or morphologies. In this paper we address the various ways in which these data were collected or reported and use a standardization approach to compare data across studies.

METHODS

Using pre-defined search terms in Google Scholar and Web of Science (e.g., "coral bleaching," "bleaching severity," "bleaching index," "mass bleaching") we selected studies that quantified coral bleaching response at the population or colony level. Our literature review consisted of 62 published scientific studies; in total, there were over 1,500 bleaching observations from 86 coral genera and 260 species. For each study, we recorded the geographic location, reef habitat and depth, mass bleaching event(s) experienced, time of sampling with regard to the bleaching event as noted by the authors, and the study's bleaching response metric (e.g., % of total colonies bleached or Bleaching Index, developed by McClanahan in 2004). For each individual observation, we recorded the genus and species name as noted in the original study, the current taxonomic name (updated against the World Register of Marine Species, https://www.marinespecies.org/), the general morphology or growth form for that taxon, and the quantified bleaching response according to the original study. Since coral taxa often have more than one morphology (sometimes even within the same colony), morphological classifications were not mutually exclusive both among and within studies.

Each study-specific bleaching observation was assigned a relative bleaching severity category (i.e., from "none" to "severe"). This bleaching severity category was based on the quantified bleaching response reported in each study. Most commonly, >80% bleaching was considered "severe," 60-80% was "high," 40-60% was "moderate," and <40% was "low." However, given that each study used a different response metric and/or established a new metric *ad hoc*, these rating scales inevitably differed (e.g., Bleaching Index >40 was "high," 20-40 was "moderate," and <20 was "low"). For that reason, our bleaching severity category was relative to other taxa in that particular study to allow for adequate comparison across studies. These were later converted to numerical scores for each bleaching severity category as follows: 0 = none, 1 = low, 2 = moderate, 3 = high, and 4 = severe.

Of all studies that quantified coral bleaching by taxon, 10 were from the Atlantic Ocean, 14 were from the Indian Ocean, and 37 were from the Pacific Ocean; there was only one study from the Red Sea. Results for bleaching severity, represented by the adjusted numerical severity scores, were then plotted by region, genus, and/or morphology. Since more than half of the studies did not identify corals to species, we did not have enough information to visualize bleaching severities on a taxonomic resolution finer than the genus level.

For statistical analysis, we conducted two separate two-way analyses of variance (ANOVA) with Type-II sum of squares using the *car* package in R software version 3.6.3 (Fox and Weisberg 2018; R Core Team 2018) to determine how bleaching severity varied by (i) region and/or genus, and (ii) region and/or morphology. We tested for interactions between each pair of factors to see whether genera or morphologies bleached differently in different regions. Assumptions of normality and homogeneity of variance were checked by plotting model residuals. Multiple comparisons via the Tukey post-hoc method were used to identify genera or morphologies for which mean bleaching severity varied significantly by region. A three-way ANOVA with region, genus, and morphology as factors was not possible since not all morphologies were represented in all genera. Also, we only used a subset of the data since not all genera or morphologies exist in all regions, which otherwise would have led to an unbalanced design. We did not include data from the Red Sea due to lack of observations.

RESULTS

Variability in How Bleaching Was Measured by Study

71.0% of studies (44 out of 62; Table 1.1) assessed bleaching via rapid *in situ* surveys either by snorkelers, SCUBA divers, or tow-board; whereas 16.1% of studies (10 out of 62; Table 1.1) used exclusively image analysis methods, either on a small scale (e.g., quadrats) or larger scale (e.g., transects, mosaics, or photostations). 4.8% of studies (3 out of 62; Table 1.1) used exclusively video analysis, while the remaining 8.1% used a combination of *in situ* surveys and image or video analysis methods.

Bleaching response metrics were widely inconsistent across studies (Table 1.2). For 56.5% of studies (35 out of 62; Table 1.2), colonies were categorized as either completely bleached, mostly bleached, somewhat bleached, pale, “affected by bleaching,” or other *ad hoc* categories as denoted by authors. These studies used the proportion of colonies that fell within each category to quantify bleaching prevalence for a given genus and/or species. A similar approach used by 24.2% of studies (15 out of 62; Table 1.2) involved scoring colonies by their bleaching severity category (0% bleached, 0-20% bleached, 21-50% bleached, etc.) and calculating a weighted mean for each taxon representing bleaching index (also known as “BI,” Bleaching Response, or Bleaching Mortality Index, adapted from McClanahan 2004). Alternatively, rather than categorizing the bleaching state of an entire colony, 4.8% of studies (3 out of 62; Table 1.2) estimated the percentage of surface area tissue within a colony that appeared bleached, although these detailed, within-colony observations were much less common. 12.9% of studies (8 out of 62; Table 1.2) used qualitative observations (e.g., “*Acropora* was more impacted than *Porites*”) based on descriptions from the field. One study (Knipp et al. 2020) compared the Coral Watch health scores of individual colonies (via the color reference card from Siebeck et al. in 2006) against SST anomalies at the time of bleaching in order to rank taxa by their “cross-correlation coefficient.” To our knowledge, this is the only study to integrate regional thermal stress data into measurements of coral color.

54.8% of studies (34 out of 62; Table 1.3) designated bleaching observations only to coral genus rather than to the genus and species level. Given that coral taxonomy is complicated, rather arbitrary, and continually changing (Veron 2011), even species-specific studies sometimes grouped certain taxa by genus or species complex (e.g., the *Montastraea annularis* species complex comprising *M. annularis, M. faveolata, and M. franksi*, which have since been moved to *Orbicella*). In terms of sampling time frame, observations were taken anywhere between immediately at the onset of bleaching (25.8% of studies), to weeks (29.0% of studies) or months (14.5% of studies) later, and up to a year post-bleaching (4.8% of studies; Table 1.4), although some of these studies also measured recovery or mortality. 25.8% of studies (16 out of 62; Table 1.4) had observations of coral bleaching at multiple time points before, during, or after the mass bleaching event.

Variability in How Corals Responded by Region, Genus, and/or Morphology

The majority of bleaching observations were from the Pacific (n = 1,034 observations) followed by the Indian (n = 253) and Atlantic (n = 220) Oceans, whereas the Red Sea lacked sufficient observations (n = 16). A two-way ANOVA for the effects of region and genus showed that bleaching severity varied significantly by genus but not by region (Table 1.5). However, there was a significant interaction indicating that genera bleached differently in different regions. *Acropora* was more bleached in the Indian and Pacific than it was in the Atlantic, while *Favia* was relatively more bleached in the Atlantic than the Pacific or Indian (Fig. 1.5). Similarly, a two-way ANOVA for the effects of region and morphology detected significant differences by morphology but not by region, with a significant interaction between region and morphology (Table 1.6). Encrusting, massive/encrusting, and plating morphologies were more severely bleached in the Atlantic compared to the Pacific or Indian Oceans (Fig. 1.6). There was often a large spread of bleaching responses by genus or morphology within regions.

DISCUSSION

The frequency and magnitude of coral bleaching worldwide is increasing with the progression of climate change (Hughes et al. 2017; Baker et al. 2008). While the field of coral reef ecology has advanced considerably in the last few decades, bleaching responses are still challenging to predict on a smaller scale (i.e., taxon or colony-level). Variability in bleaching responses is to be expected since corals have distinct bleaching thresholds related to temperature fluctuations in a given location (Carilli et al. 2012). Responses may also be driven by factors such as high human influence and proximity to urban areas (Sandin et al. 2008; Smith et al. 2016), although the relationship between isolation from local stressors and coral reef resilience has been contested (Baumann et al. 2022). Further, while corals with a history of bleaching may be more acclimatized to warmer temperatures (DeCarlo et al. 2019; Coles et al. 2018) or exhibit local adaptation (Barshis 2015), climate change is interfering with the potential for coral adaptive mechanisms to support physiological resilience and thermal tolerance (Ainsworth et al. 2016). Indeed, cumulative and repeated thermal stress events can turn coral taxa previously deemed ‘winners’ into ‘losers’ (Grottoli et al. 2014), and responses at the population or community level can be related to the severity of prior bleaching events (Fox et al. 2021; Wall et al. 2021).

There are several projections of coral reef futures under global warming (Pandolfi et al. 2011), such as a >40% decline in coral cover by 2100 (Sully et al. 2022); however, bleaching responses cannot be expected to be uniform across regions or among all coral species (Guest et al. 2012). Rather, a half century of bleaching studies continues to emphasize that bleaching and recovery are complex processes that cannot be easily generalized. Comparing measurements from quantitative bleaching surveys can reveal possible taxonomic or morphological patterns, including findings of the present study that not only does bleaching severity vary by genus or morphology, but that coral genera and morphologies bleach differently by geographic region. Nevertheless, it is important to note that not all genera or morphologies are present equally in all regions, and that each region experiences a unique suite of environmental conditions.

It can be difficult to standardize results from observational studies on coral bleaching due to inconsistencies in available data, as discussed by Grottoli et al. (2021) for experimental studies. For example, when quantifying bleaching, studies have reported bleaching "prevalence" (e.g., Williams et al. 2010), "susceptibility" (Chou et al. 2016; Dalton et al. 2020), "sensitivity" (Darling et al. 2013), "frequency" (Montano et al. 2010), or "severity" (Guest et al. 2016), yet these metrics are not necessarily interchangeable. Moreover, percent bleaching can refer to either the tissue area that is bleached within a single colony (Glynn et al. 2001; Montano et al. 2010) or the proportion of total colonies displaying signs of bleaching as opposed to those that were unaffected (Bruno et al. 2001; Miller et al. 2011; Caroll et al. 2017). Thus, there is a need to consolidate not only our methods for measuring bleaching but also our terminology and bleaching response metrics. Given that *in situ* observations are commonly taken after the onset of bleaching (Table 1.4), the timing of surveys can also confound our interpretations of results (Claar and Baum 2019).

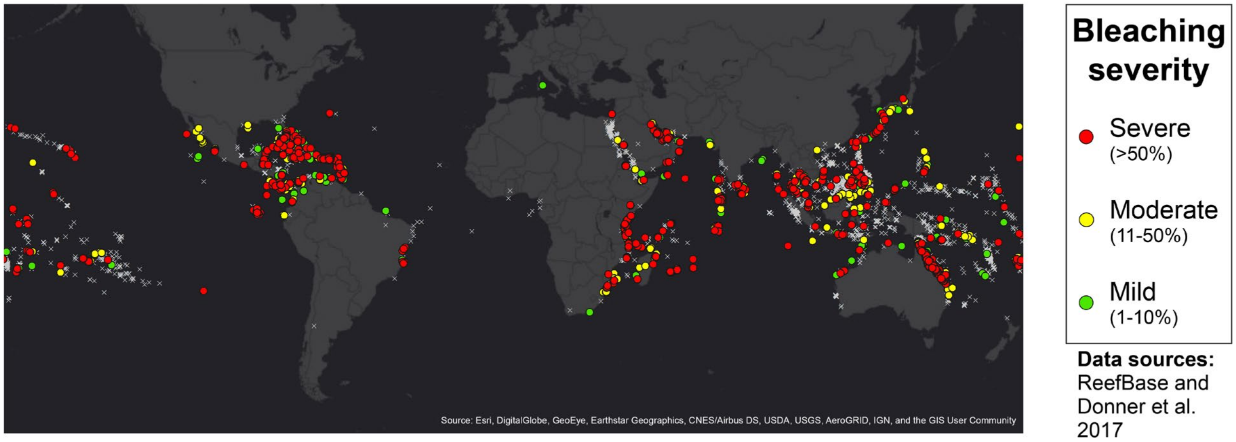
Additionally, since bleaching incidence is more often observed in areas of higher accumulated thermal stress (Fig. 1.3), it may be necessary to take into account the magnitude and duration of thermal stress when considering bleaching responses. Such analyses are for the most part unprecedented (but see: Knipp et al. 2020, in which coral color was cross-correlated with temperature data) and would lend themselves to more accurate inter-study comparison. We also need to account for prior bleaching history and environmental legacies (Brown et al. 2000; Bahr et al. 2017; Wall et al. 2021), since thermal adaptation and resilience has been demonstrated in some cases (Coles et al. 2018; Logan et al. 2014; Palumbi et al. 2014; Guest et al. 2012). For an even more nuanced perspective of bleaching, it is important to continue monitoring the same individual coral colonies in the long term.

In conclusion, while coral responses to thermal stress can vary by genus or morphology, with some genera or morphologies bleaching more severely in some regions than others, the ways in which bleaching is being measured and reported can obscure specific findings. Most studies do not identify corals to the species level, take repeated observations from before, during, and after a bleaching event, nor track individual colonies through time (but see: Ritson-Williams and Gates 2020). Standardized bleaching response metrics that incorporate the intensity of thermal stress and other contextual factors (e.g., local stressors) would be more useful in determining bleaching susceptibility, and will improve comparability across studies. However, it should be noted that this is inherently difficult since corals exist in different systems experiencing distinct combinations of local and global stressors, and comparing one reef to another may not always be appropriate. Still, disentangling some of these discrepancies will lead to a better understanding of coral bleaching and recovery dynamics and allow for more effective protection of coral reefs in the face of climate change.

ACKNOWLEDGMENTS

Adi Khen was supported by the National Science Foundation Graduate Research Fellowship and the Beyster Family Fellowship in Conservation and Biodiversity.

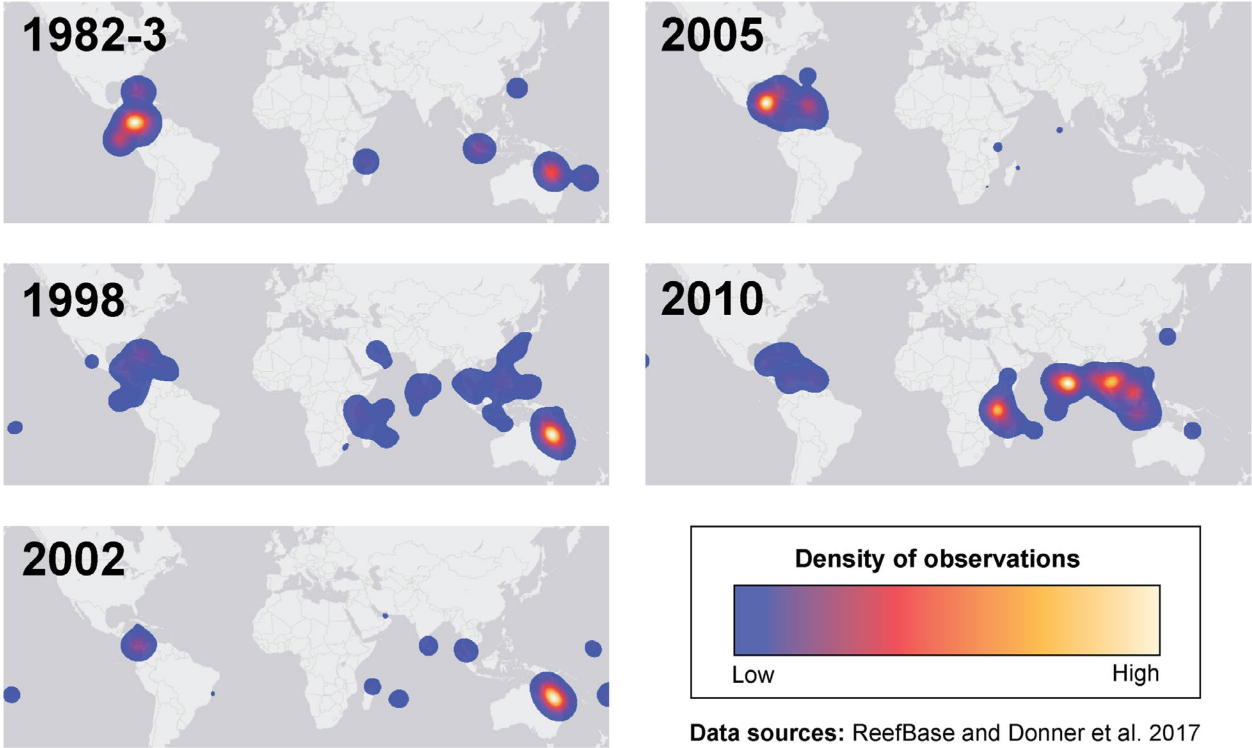
Chapter 1, in part, is currently being prepared for submission for publication of the material. Khen, Adi; Wall, Christopher B; Smith, Jennifer E. The dissertation author was the primary investigator and author of this material.



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

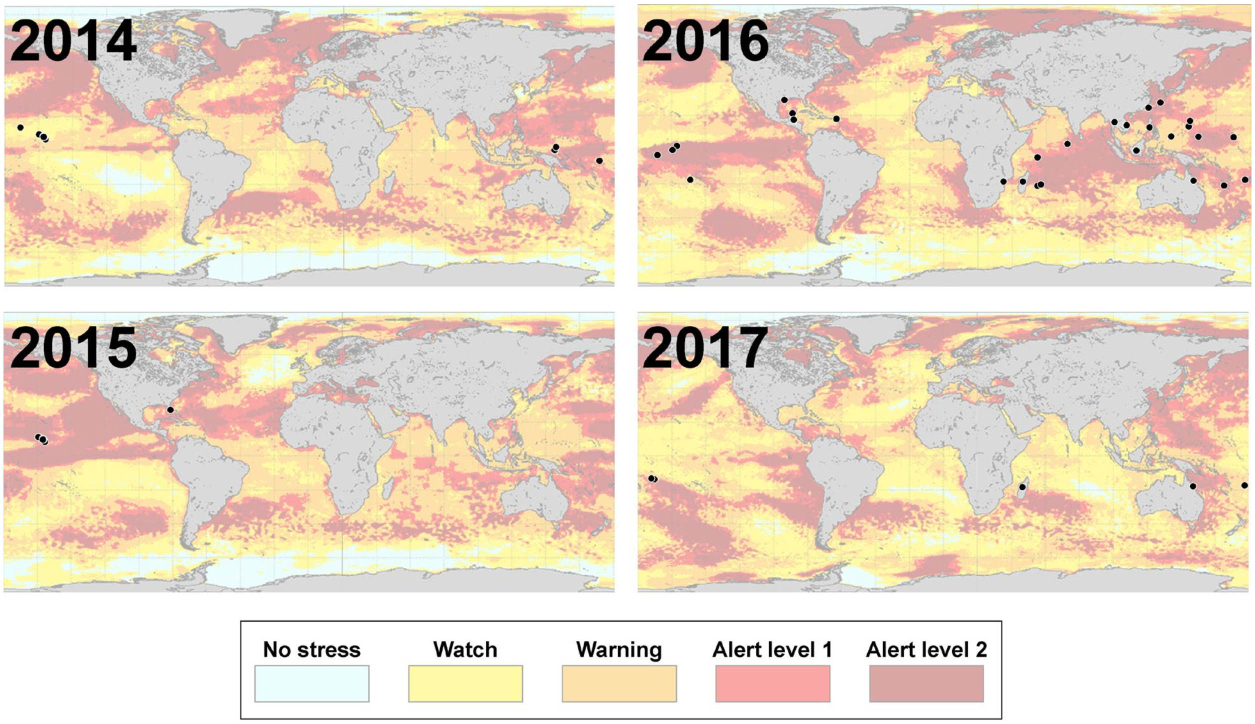
Data sources: ReefBase and Donner et al. 2017

Figure 1.1: World map showing the location and severity of mass coral bleaching events from 1963 to 2011 (Donner et al. 2017). Colored circles indicate bleaching severity and light gray crosses indicate documented locations where coral reefs exist (ReefBase)



Data sources: ReefBase and Donner et al. 2017

Figure 1.2: Heatmaps showing the spatial distributions of each major bleaching event between 1982 and 2010



Data sources: NOAA Coral Reef Watch and Eakin et al. 2017

Figure 1.3: Maps showing over 75 total locations worldwide, represented by black circles, affected by the third-ever global coral bleaching event lasting between 2014 and 2017 (Eakin et al. 2019). Each map is overlaid with maximum heat stress in that respective year from NOAA's Coral Reef Watch satellite data

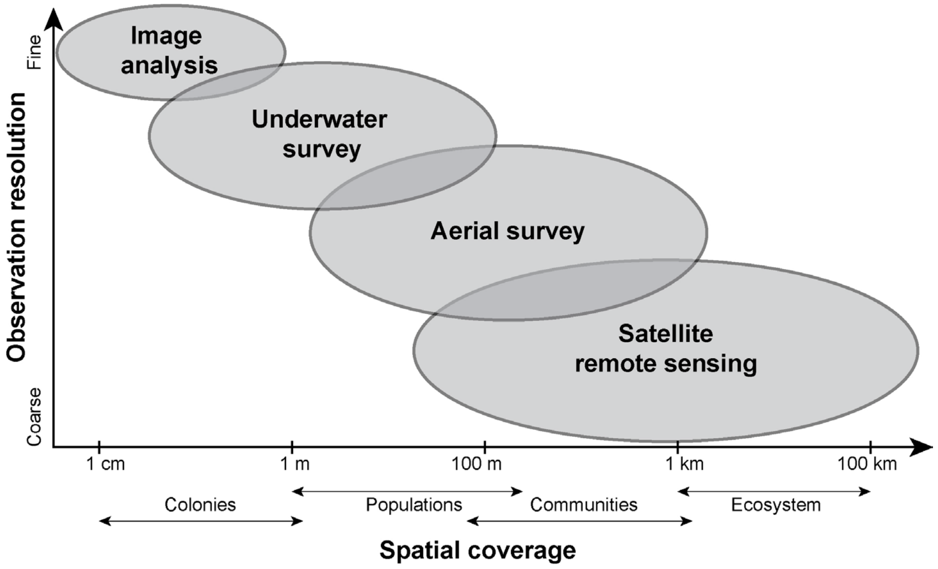


Figure 1.4: Diagram comparing different methods for measuring coral bleaching in terms of their spatial coverage and observation resolution (e.g., image analysis allows for the precise measurement of colony-specific bleaching but is limited spatially, whereas remote sensing is more expansive yet limited taxonomically)

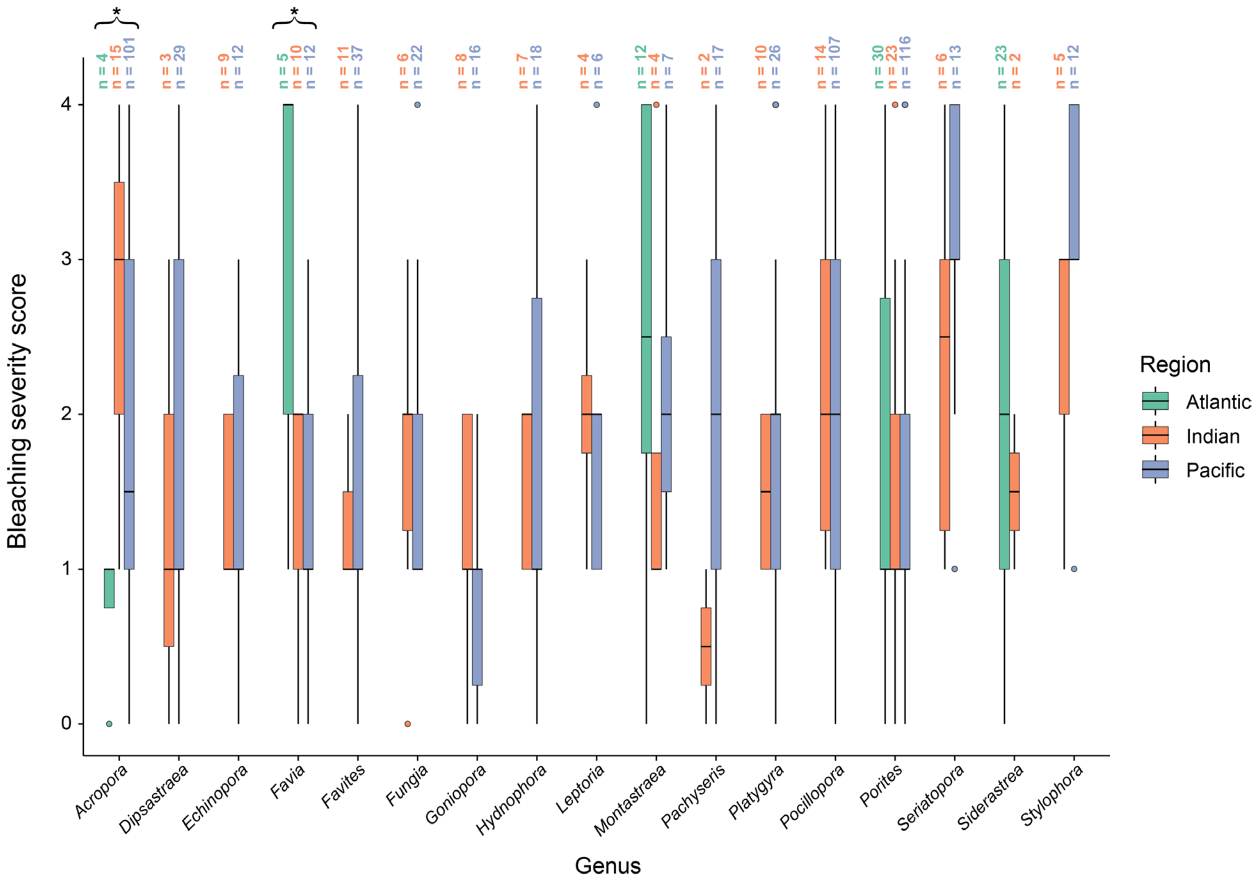


Figure 1.5: Boxplots showing the distribution of bleaching severity scores for each common coral genus across the Atlantic, Indian, and Pacific Oceans (0 = none, 1 = low, 2 = moderate, 3 = high, 4 = severe). The total number of observations by genus and region is provided above each box. Asterisks indicate genera for which mean bleaching severity varied significantly by region

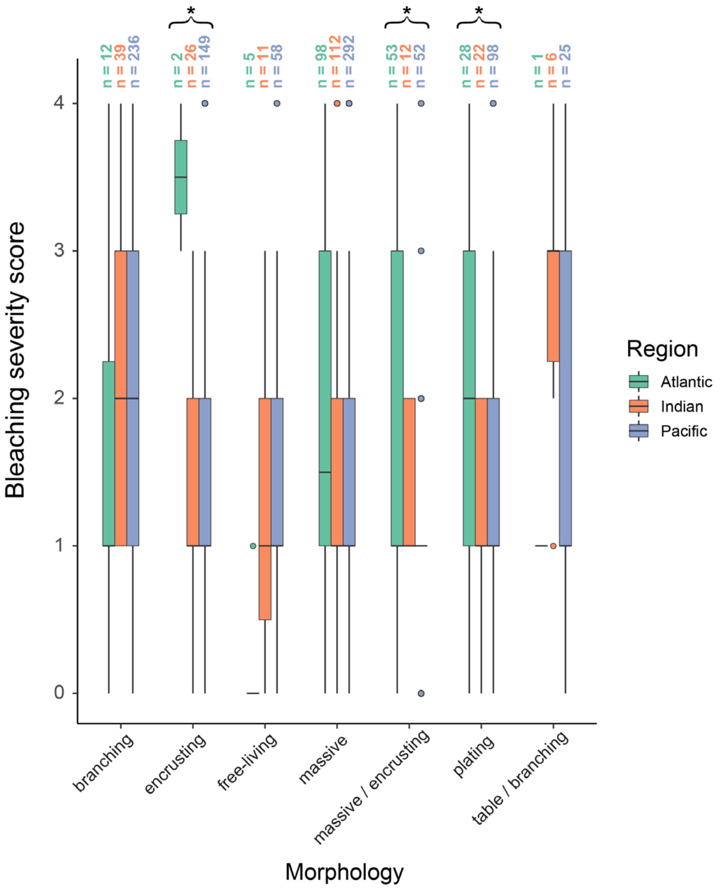


Figure 1.6: Boxplots showing the distribution of bleaching severity scores for each common coral morphology across the Atlantic, Indian, and Pacific Oceans (0 = none, 1 = low, 2 = moderate, 3 = high, 4 = severe). The total number of observations by genus and morphology is provided above each box. Asterisks indicate morphologies for which mean bleaching severity varied significantly by region

Table 1.1: Method of determining coral bleaching by study

Method	References
***In situ* surveys**	Bonilla 2001; Bruno et al. 2001; Clark et al. 2009; Couch et al. 2017; Dalton et al. 2020; Darling et al. 2013; Davies et al. 1997; Eriksson et al. 2012; Gleason 1993; Glynn et al. 2001; Guest et al. 2012; Guest et al. 2016; Hussain and Ingole 2020; Jiménez et al. 2001; Jokiel and Brown 2004; Kayanne et al. 2002; Kim et al. 2019; Knipp et al. 2020; Lang et al. 1992; Lenihan et al. 2008; Li et al. 2012; Loya et al. 2001; Marshall and Baird 2000; McClanahan 2004; McClanahan et al. 2005; McClanahan et al. 2007; McField 1999; Miller et al. 2011; Monroe et al. 2018; Montano et al. 2010; Muñiz-Castillo and Arias-González 2021; Obura 2001; Obura et al. 2018; Oxenford et al. 2008; Paulay and Benayahu 1999; Pengsakun et al. 2019; Quimpo et al. 2020; Rodgers et al. 2017; Sakai et al. 2019; Sebastián et al. 2009; Stimson et al. 2002; Thinesh et al. 2019; Vargas-Ángel et al. 2011; Williams et al. 2010
Image analysis— small scale (e.g., quadrats)	Chou et al. 2016; Jones 2008; Matsuda et al. 2020; Ng et al. 2020; Valino et al. 2021
Image analysis— large scale (e.g., transects or mosaics)	Gintert et al. 2018; Johnston et al. 2019; Raymundo et al. 2019; Teixeira et al. 2019; Tkachenko and Soong 2017
Video analysis	Carroll et al. 2017; Frade et al. 2018; Ritson-Williams and Gates 2020
Combination of *in situ* surveys and analysis	Hédouin et al. 2020; Hoegh-Guldberg and Salvat 1995; Morgan et al. 2017; Porter et al. 2021; Spencer et al. 2000

Table 1.2: Coral bleaching response metric by study

Response metric	References
Proportion of total colonies completely or partially bleached, pale, and/or otherwise affected; "bleaching prevalence"	Carroll et al. 2017; Chou et al. 2016; Clark et al. 2009; Couch et al. 2017; Davies et al. 1997; Frade et al. 2018; Gintert et al. 2018; Hédouin et al. 2020; Hoegh-Guldberg and Salvat 1995; Hussain and Ingole 2020; Jiménez et al. 2001; Johnston et al. 2019; Jones 2008; Kayanne et al. 2002; Lenihan et al. 2008; Lang et al. 1992; Li et al. 2012; Marshall and Baird 2000; Matsuda et al. 2020; McField 1999; Miller et al. 2011; Monroe et al. 2018; Obura 2001; Obura et al. 2018; Oxenford et al. 2008; Quimpo et al. 2020; Raymundo et al. 2019; Reyes-Bonilla 2001; Rodgers et al. 2017; Ritson-Williams and Gates 2020; Sakai et al. 2019; Teixeira et al. 2019; Thinesh et al. 2019; Vargas-Ángel et al. 2011; Williams et al. 2010
Bleaching Index (BI) developed by McClanahan; calculated as $[0c_1+1c_2+2c_3+3c_4+4c_5+5c_6]/5$ where c_1 through c_6 are bleaching categories by colony	Dalton et al. 2020; Darling et al. 2013; Guest et al. 2012; Guest et al. 2016; Kim et al. 2019; McClanahan 2004; McClanahan et al. 2005; McClanahan et al. 2007; Morgan et al. 2017; Muñiz-Castillo and Arias-González 2021; Ng et al. 2020; Pengsakun et al. 2019; Porter et al. 2021; Sebastián et al. 2009; Valino et al. 2021
Qualitative (based on field observations)	Bruno et al. 2001; Eriksson et al. 2012; Jokiel and Brown 2004; Loya et al. 2001; Paulay and Benayahu 1999; Spencer et al. 2000; Stimson et al. 2002; Tkachenko and Soong 2017
Within-colony condition assessments for % pale, bleached, dead, etc. area	Gleason 1993; Glynn et al. 2001; Montano et al. 2010

Table 1.3: Level of taxonomic resolution by study

Level of resolution	References
Genus-specific	Carroll et al. 2017; Chou et al. 2016; Dalton et al. 2020; Darling et al. 2013; Davies et al. 1997; Eriksson et al. 2012; Frade et al. 2018; Gleason 1993; Guest et al. 2012; Guest et al. 2016; Hédouin et al. 2020; Hoegh-Guldberg and Salvat 1995; Hussain and Ingole 2020; Kayanne et al. 2002; Kim et al. 2019; Li et al. 2012; Marshall and Baird 2000; McClanahan 2004; McClanahan et al. 2005; McClanahan et al. 2007; Monroe et al. 2018; Montano et al. 2010; Morgan et al. 2017; Obura et al. 2018; Porter et al. 2021; Quimpo et al. 2020; Sebastián et al. 2009; Spencer et al. 2000; Teixeira et al. 2019; Thinesh et al. 2019; Tkachenko and Soong 2017; Valino et al. 2021; Vargas-Ángel et al. 2011; Williams et al. 2010
Species-specific	Bruno et al. 2001; Clark et al. 2009; Couch et al. 2017; Gintert et al. 2018; Glynn et al. 2001; Jiménez et al. 2001; Johnston et al. 2019; Jokiel and Brown 2004; Jones 2008; Knipp et al. 2020; Lang et al. 1992; Lenihan et al. 2008; Loya et al. 2001; Matsuda et al. 2020; McField 1999; Miller et al. 2011; Muñiz-Castillo and Arias-González 2021; Ng et al. 2020; Obura 2001; Oxenford et al. 2008; Paulay and Benayahu 1999; Pengsakun et al. 2019; Raymundo et al. 2019; Reyes-Bonilla 2001; Rodgers et al. 2017; Ritson-Williams and Gates 2020; Sakai et al. 2019; Stimson et al. 2002

Table 1.4: Sampling time frame with regard to the bleaching event, by study

Time of observation	References
During the event	Chou et al. 2016; Frade et al. 2018; Glynn et al. 2001; Hédouin et al. 2020; Hoegh-Guldberg and Salvat 1995; Jokiel and Brown 2004; Kim et al. 2019; Lenihan et al. 2008; McClanahan et al. 2007; Muñiz-Castillo and Arias-González 2021; Paulay and Benayahu 1999; Pengsakun et al. 2019; Quimpo et al. 2020; Teixeira et al. 2019; Valino et al. 2021; Williams et al. 2010
Shortly after (within weeks)	Couch et al. 2017; Gleason 1993; Guest et al. 2016; Hussain and Ingole 2020; Johnston et al. 2019; Jones 2008; Li et al. 2012; Marshall and Baird 2000; McClanahan et al. 2005; Monroe et al. 2018; Obura 2001; Oxenford et al. 2008; Rodgers et al. 2017; Ritson-Williams and Gates 2020; Sebastián et al. 2009; Spencer et al. 2000; Tkachenko and Soong 2017; Vargas-Ángel et al. 2011
After (>2 months later)	Bruno et al. 2001; Carroll et al. 2017; Davies et al. 1997; Eriksson et al. 2012; Lang et al. 1992; Obura et al. 2018; Raymundo et al. 2019; Reyes-Bonilla 2001; Sakai et al. 2019
Far after (~6 months to one year later)	Guest et al. 2012; Miller et al. 2011; Stimson et al. 2002
Continual (before, during, and/or after)	Clark et al. 2009; Dalton et al. 2020; Darling et al. 2013; Gintert et al. 2018; Jiménez et al. 2001; Kayanne et al. 2002; Knipp et al. 2020; Loya et al. 2001; Matsuda et al. 2020; McClanahan 2004; McField 1999; Montano et al. 2010; Morgan et al. 2017; Ng et al. 2020; Porter et al. 2021; Thinesh et al. 2019

Table 1.5: Statistical output from a two-way ANOVA for the effects of region and genus on bleaching severity, as well as their interaction. Only genera present in most or all regions were included. Significant (p <0.05) factors are bolded

Source	Df	SumSqs	F value	Pr(>F)
Region	2	2.21	0.947	0.388
Genus	16	97.32	5.225	**<0.001**
Region * Genus	19	38.59	1.745	**0.026**
Residuals	651	757.79		

Table 1.6: Statistical output from a two-way ANOVA for the effects of region and morphology on bleaching severity, as well as their interaction. Only morphologies present in most or all regions were included. Significant (p <0.05) factors are bolded

Source	Df	SumSqs	F value	Pr(>F)
Region	2	3.61	1.476	0.229
Morphology	6	46.74	6.373	**<0.001**
Region * Morphology	8	25.50	2.607	**0.008**
Residuals	672	821.46		

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CHAPTER 2: 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 (10 m depth, n = 4 sites) and the wave-sheltered reef terrace (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 ten years and two bleaching events, the benthic community structure on Palmyra shows evidence of long-term stability. Communities on the reef terrace exhibited minimal change in percent cover of the dominant functional groups, while the fore reef 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 one year following both bleaching events and was replaced by different algal groups depending on the site, yet returned to pre-bleaching levels within two years.

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.

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 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 one year 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 (Muhando and Mohammed 2002; Darling et al. 2013; Krishnan et al. 2018). However, most studies evaluating the effects of warming on benthic community composition through time have reported losses in coral cover worldwide (see Supp. 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 (Supp. 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 heterogenous 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 ºN, 162.08 ºW) is a remote atoll in the Northern Line Islands, located approximately 1,300 km south of Hawaiʻi (Fig. 2.1). Palmyra was temporarily inhabited and modified by the U.S. 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 x 60 cm) were marked along a 50 m transect (Supp. Fig. 2.1). Photos 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 (Supp. Fig. 2.1). 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 (cm^2) based on the dimensions of the photoquadrat frame (90 cm x 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. 2.2; Supp. Fig. 2.2). Coral 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 ºC-weeks by late November 2009 and 11.9 ºC-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: fore reef and reef terrace) 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, one year 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 two years 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 ten years.

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. 2.3). Between 2009 and 2018, average hard coral cover was 33.3 ± 0.8% (mean ± SE) on the fore reef (Fig. 2.3a) and 49.2 ± 0.9% on the reef terrace (Fig. 2.3f). Coral cover was generally stable through time on the reef terrace but exhibited a gradual decline on the fore reef between 2009 and 2018. While coral cover recovered at the reef terrace sites after the 2015 bleaching event, it continued to decline on the fore reef, particularly at FR3 (Fig. 2.3b). A significant habitat by time interaction (PERMANOVA, $p < 0.001$; Supp. Table 2.2) suggests that despite site-level variability, each habitat is changing differently over time (Supp. Fig. 2.3). Further, it seems that site is a better predictor for benthic community response than year or habitat, explaining 32.0% of the variation ($R^2 = 0.320$; Supp. Table 2.2).

The nMDS (Fig. 2.4) 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 reef terrace sites (Fig. 2.4b) as compared to the fore reef sites (Fig. 2.4a), suggesting that benthic composition is more similar among the different terrace sites than the fore reef sites. Despite the ten-year 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 reef terrace was dominated by table *Acropora* and encrusting *Montipora* spp., while the fore reef had more taxonomic diversity but less hard coral cover overall. Soft corals (mainly *Sinularia* spp. and *Lobophytum* spp.) only occurred on the fore reef (especially FR7, Fig. 2.3d) with an overall average of 10.0 ± 1.0% cover (Fig. 2.3a). Macroalgae were also more abundant on the fore reef, accounting for 21.8 ± 0.6% of the benthos (Fig. 2.3a) compared to 12.9 ± 0.6% on the reef terrace (Fig. 2.3f). The most abundant macroalgal species were *Halimeda* spp., *Lobophora* spp., and members of the Peyssonneliaceae complex. CCA were most abundant on the fore reef, accounting for over a quarter of the benthos (25.7 ± 0.7%; Fig. 2.3a), compared to the reef terrace (15.3 ± 0.7%; Fig. 2.3f). In contrast, turf algal cover was higher on the reef terrace (21.9 ± 0.9%; Fig. 2.3f) relative to the fore reef (11.5 ± 0.5%; Fig. 2.3a). 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. 2.5). At one site on the reef terrace (RT10), the cover of reef builders declined from 2014 to 2015 from 76.8 ± 15.8% to 50.9 ± 7.9%, while the cover of fleshy algae rose from 16.6 ± 5.7% to 40.7 ± 6.9%, but by 2018, they returned to their pre-disturbance levels (Fig. 2.5i). An increase in fleshy algae and corresponding decrease in reef builders was also observed to a lesser extent at both FR9 (Fig. 2.5e) and RT1 in 2016 (Fig. 2.5g) but was similarly temporary. Ultimately, there is no indication of a shift from reef builders to fleshy algal dominance. Overall, the fore reef (Fig. 2.5a) had 57.4 ± 9.1% reef builder cover and 13.4 ± 3.6% fleshy algal cover, while the reef terrace (Fig. 2.5f) had 64.3 ± 10.3% reef builder cover and 28.1 ± 5.9% fleshy algal cover.

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 (Supp. Table 2.4). Coral cover decreased at three of the four fore reef sites (FR3, FR5, and FR7) by 14.4% ± 2.6% but remained constant on the shallow reef terrace (Fig. 8a; Supp. Table 2.5). Cover of CCA and macroalgae remained constant at all sites except FR3, where they slightly increased (Fig. 8b,c; Supp. Table 2.5). 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 fore reef sites (FR3, FR7, and FR9) by 9.4% ± 0.7% on average, but did not change significantly on the reef terrace. Fleshy algal cover increased at two fore reef sites (FR7 and FR9) by 8.2% ± 0.7% on average, and one reef terrace site (RT1; Supp. Table 2.5) 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, show 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 (Supp. Table 2.1). Coral cover declined on Palmyra at three out of eight sites one year 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 and this was also 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 years (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 one year depending on the site, but at almost all of these sites, coral cover returned to pre-bleaching levels after two years. 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 ten year 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 fore reef 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 fore reef that was first observed in 2017 (pers. obs.). Another potential cause of decline is invasion by the corallimorph, *Rhodactis 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 fore reef 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 fore reef 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 reef terrace 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 fore reef sites.

Throughout the decade, there was less coral mortality and higher recovery observed at reef terrace sites in comparison to fore reef sites. Because of the shallow and wave-protected nature of the reef terrace habitat, sites here undergo more diurnal variability in temperature than the fore reef sites (Fox et al. 2019b) as well as large diel fluctuations in pH and dissolved oxygen (Takeshita 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 fore reef sites (Donner 2011;

Safaie et al. 2018). Previous studies have shown that Palmyra's fore reef communities appear to be less resistant to bleaching and post-bleaching mortality than at the reef 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 (Supp. Table 2.2; Supp. Fig. 2.3) further demonstrates 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 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 2015-2016 (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.

ACKNOWLEDGMENTS

We thank the staff of The Nature Conservancy, U.S. Fish and Wildlife Service, and the Palmyra Atoll Research Consortium (PARC) for their logistical support and access to the refuge. This publication is PARC contribution #162. We thank Gareth Williams, Brian Zgliczynski, Clinton Edwards, and Stuart Sandin for their assistance with fieldwork. We thank Karina Arzuyan, Marie Diaz, Sarah Romero, Kyle Conner, Shelley Hazen, and Kailey Ramsing for their help with image digitization. Adi Khen was supported by the National Science Foundation Graduate Research Fellowship and the Beyster Family Fellowship in Conservation and Biodiversity. Funding for this work was generously provided by the Scripps Family Foundation, the Bohn Family, and the Gordon and Betty Moore Foundation.

Chapter 2, in full, is a reprint of the material as it appears in Coral Reefs 2022. Khen, Adi; Johnson, Maggie D; Fox, Michael D; Clements, Samantha M; Carter, Amanda L; Smith, Jennifer E, Springer, 2022. The dissertation author was the primary investigator and author of this paper.

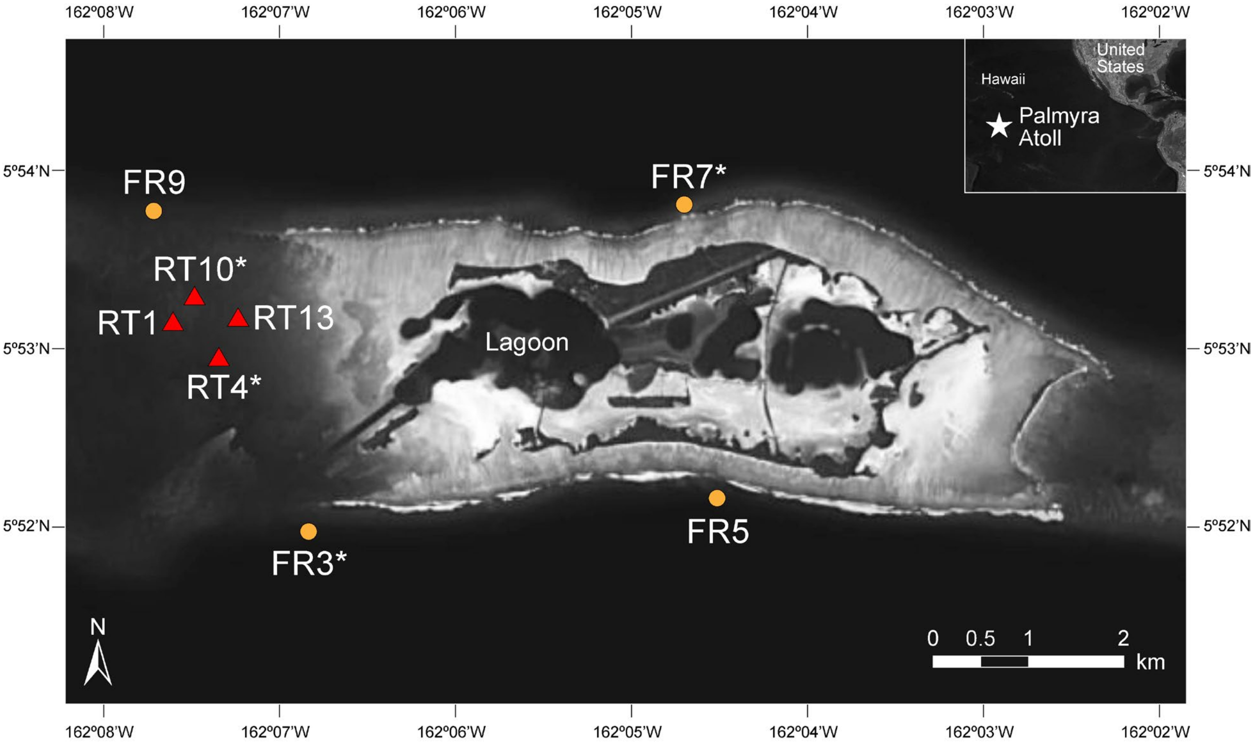


Figure 2.1: Map of the eight monitoring sites surrounding Palmyra Atoll, with an overview of the broader geographic area at the top right. Red triangles represent the Reef Terrace (RT; 5 m depth) sites, and orange circles represent the Fore Reef (FR; 10 m depth) sites. Sites denoted with an asterisk indicate locations of sensor deployments

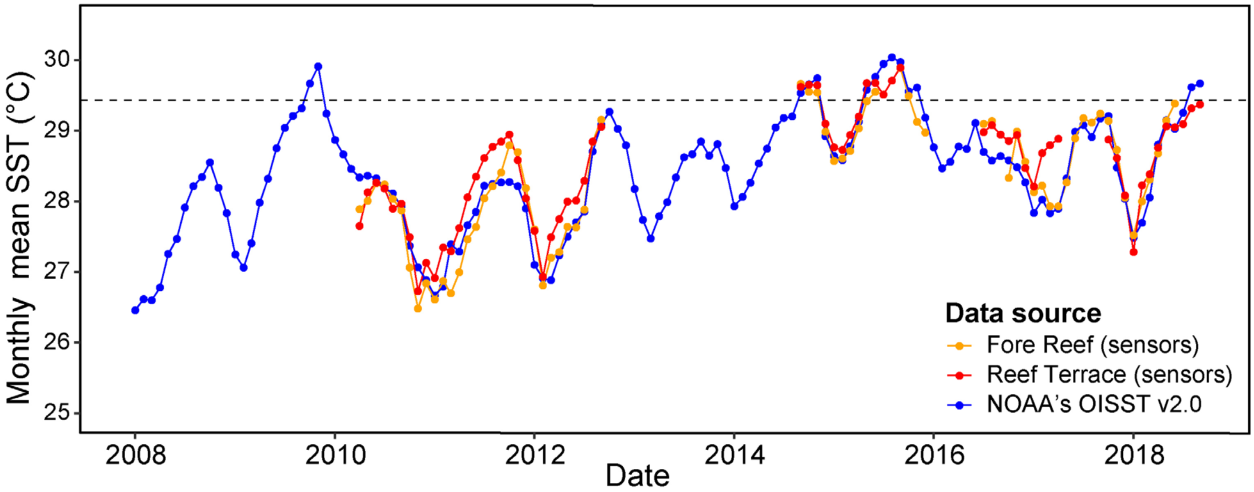


Figure 2.2: Temperature history from Palmyra's Fore Reef and Reef Terrace in the past decade, as measured by both *in situ* sensors (with data averaged by habitat type) and satellites, via NOAA's Optimum Interpolation sea surface temperature (SST). The dashed horizontal line at 29.4 ºC represents the estimated bleaching threshold for Palmyra (Fox et al. 2019b)

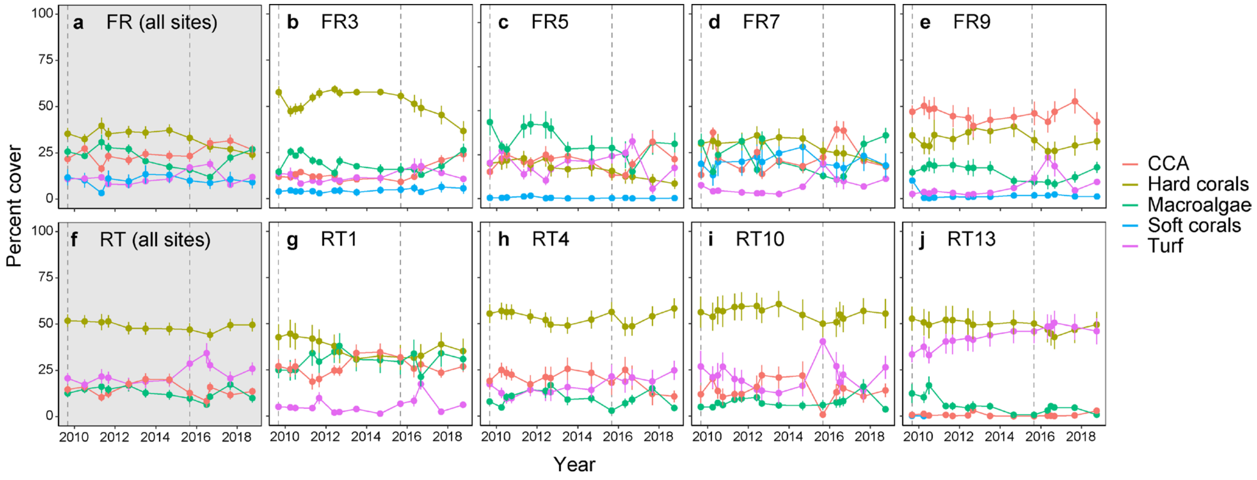


Figure 2.3: Percent cover (mean ± SE) over time by habitat **(a,f)** or site **(b-e; g-j)** on Palmyra for each benthic functional group. Dashed vertical lines indicate bleaching events in 2009 and 2015

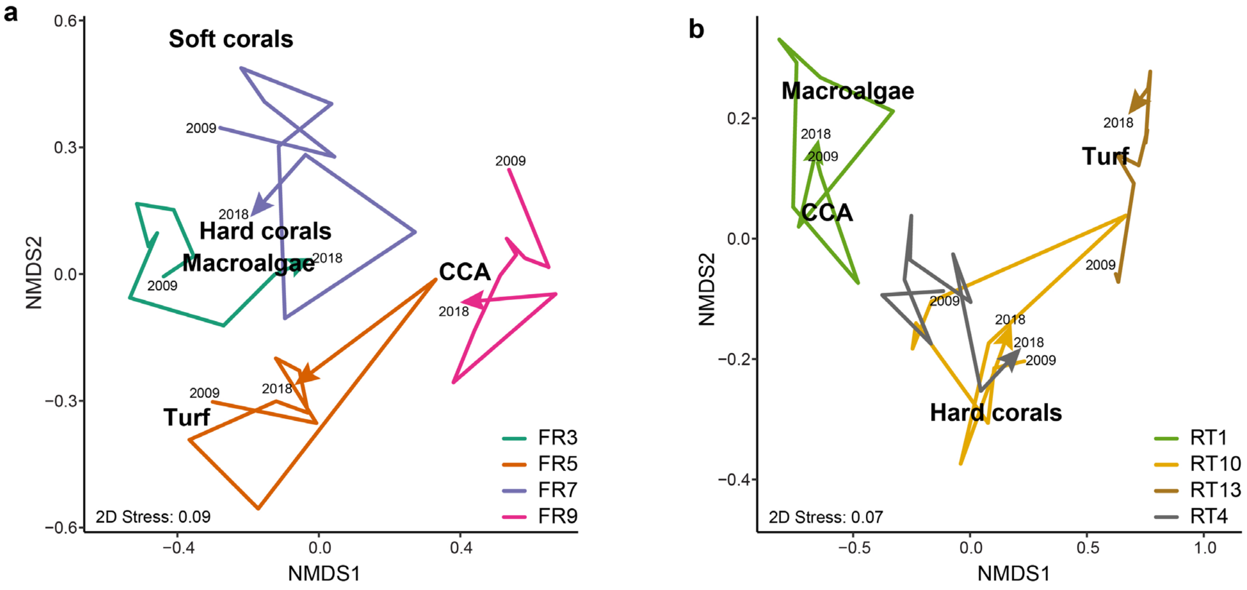


Figure 2.4: Non-metric multidimensional scaling (nMDS) based on Bray-Curtis dissimilarity measures of benthic functional group composition through time for sites within **(a)** Fore Reef and **(b)** Reef Terrace habitats. Colored lines terminating in an arrowhead represent the trajectory of each site from 2009 to 2018

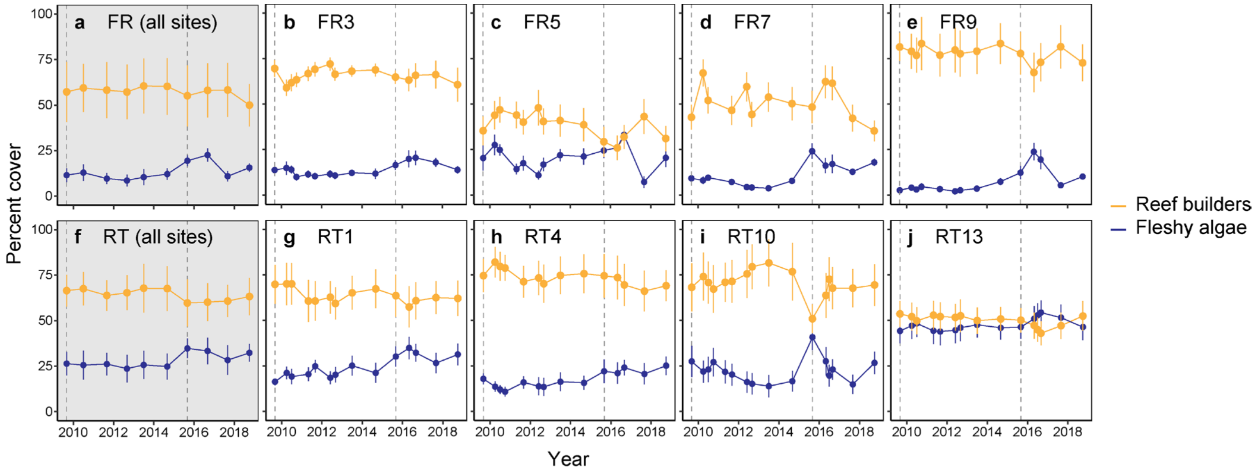


Figure 2.5: Percent cover (mean ± SE) over time by habitat **(a,f)** or site **(b-e; g-j)** on Palmyra for reef builders (i.e., hard corals and CCA) and fleshy algae (i.e., turf and fleshy macroalgae). Dashed vertical lines indicate bleaching events in 2009 and 2015

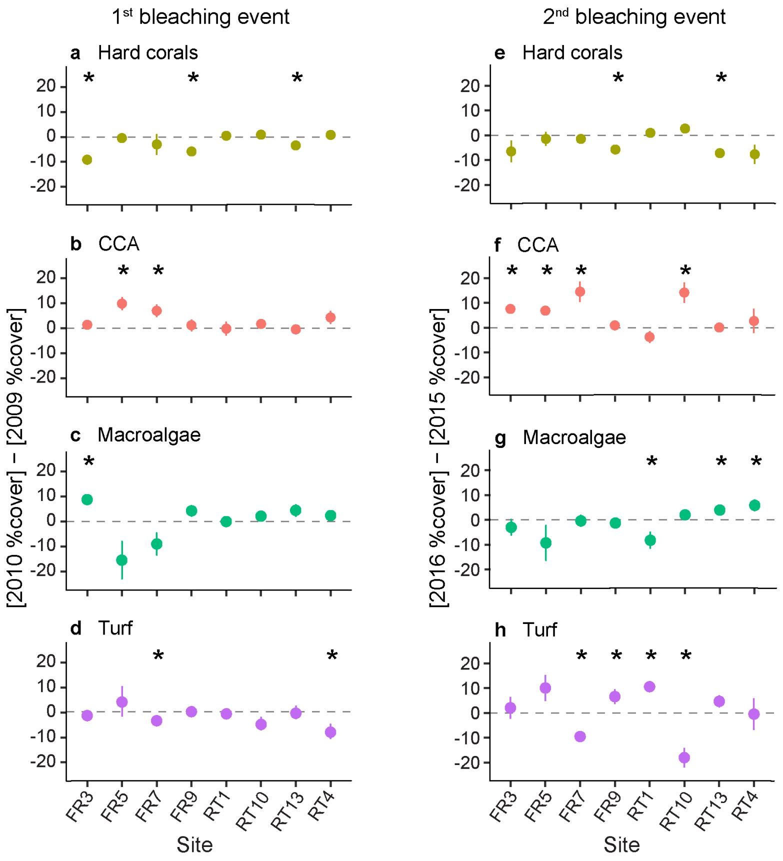


Figure 2.6: Changes in percent cover (mean ± SE) by site for each major benthic group, one year following the first **(a-d)** and second **(e-h)** bleaching events in 2009 and 2015. Significance symbols for sites whose net change is different than zero (p <0.05 according to two-tailed t-tests; Supp. Table 2.3) are shown. Dashed horizontal lines indicate no change

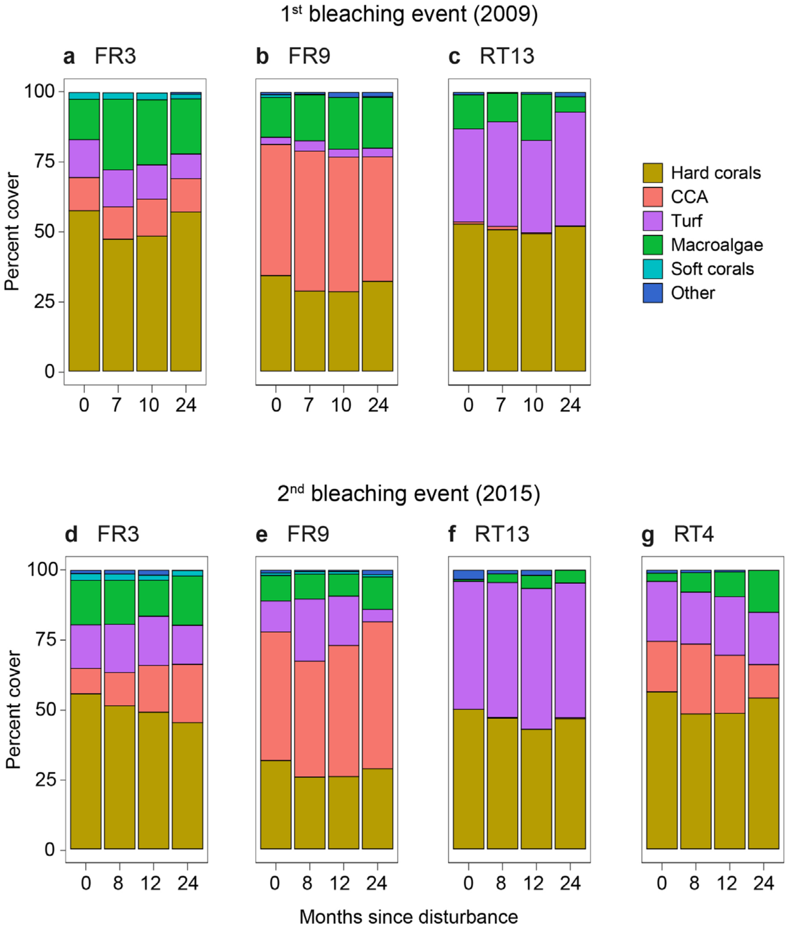


Figure 2.7: Bar plots of benthic community composition for up to two years following the 2009 **(a-c)** and 2015 **(d-g)** bleaching events at sites that declined in hard coral cover. Note that x-axis values correspond to months since the thermal disturbance (e.g., "0" is at the time of bleaching)

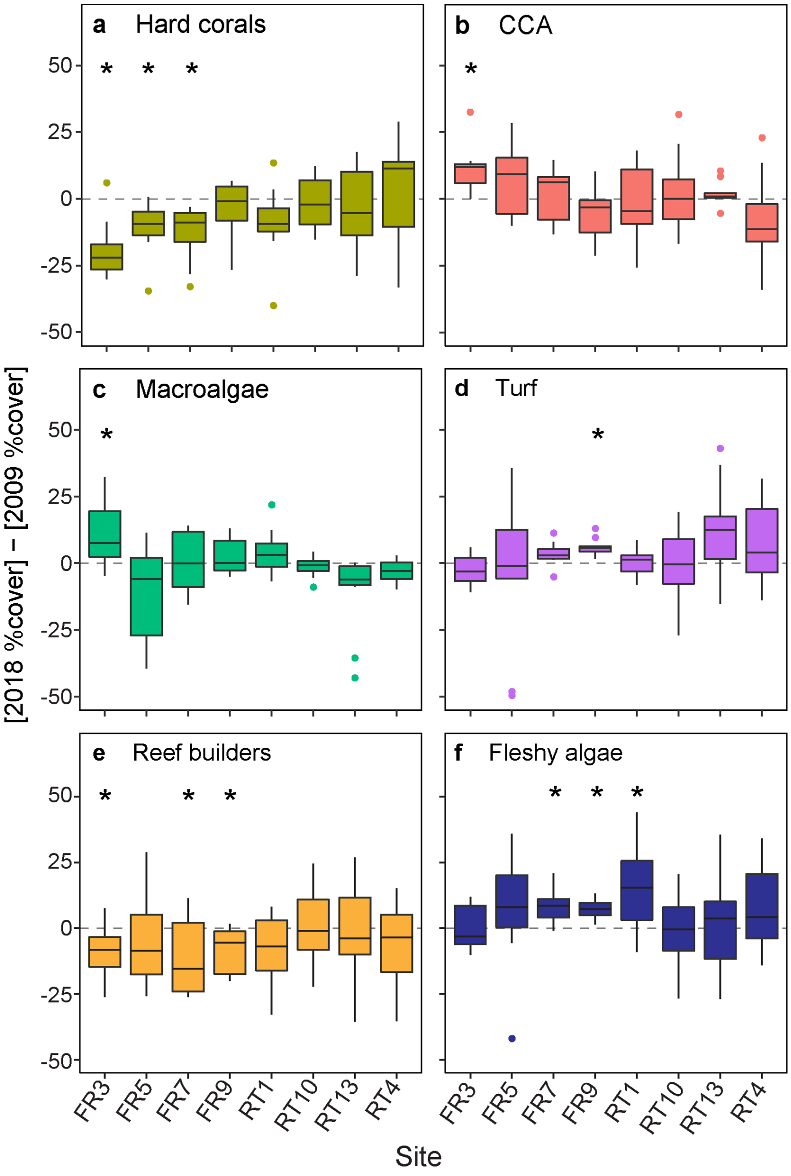
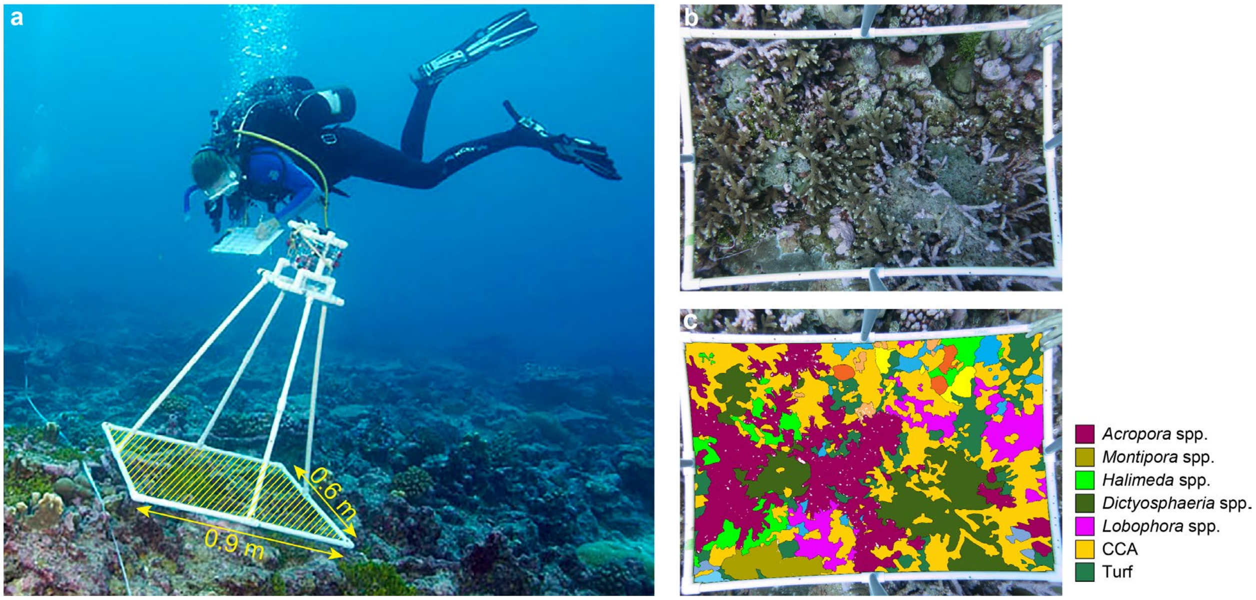
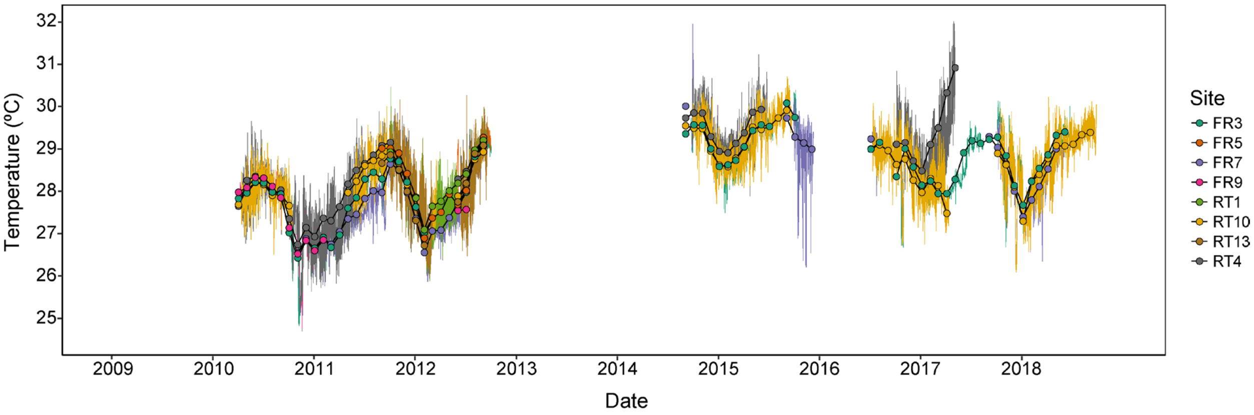


Figure 2.8: Box plots of the distributions of net changes in percent cover of major benthic groups, by site, between only the initial and final time points (September 2009 and October 2018). Mean values and 95% confidence intervals are provided in Supp. Table 2.5. Significance symbols for sites whose net change is different than zero ($p < 0.05$ according to two-tailed t-tests) are shown. Dashed horizontal lines indicate no change

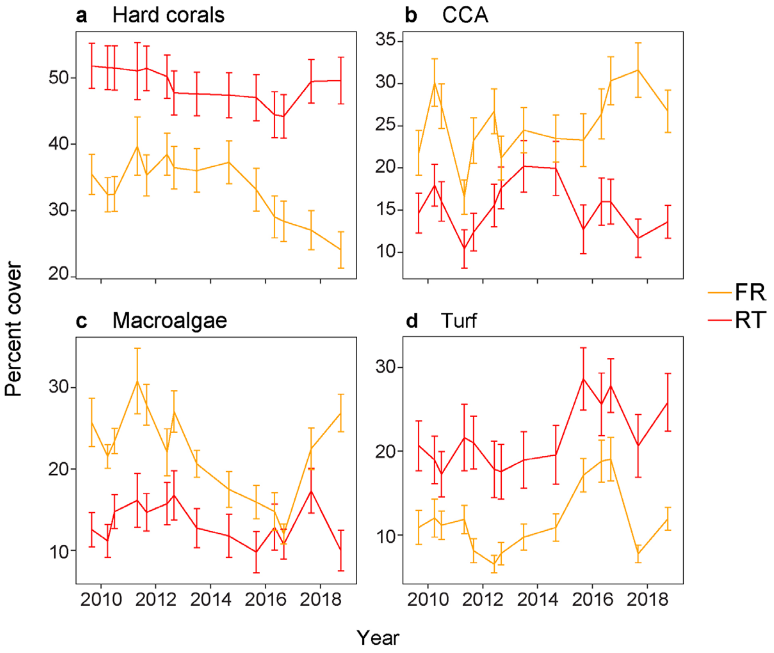
SUPPLEMENTARY MATERIALS



Supp. Figure 2.1: **(a)** SCUBA diver with photoquadrat frame (actual quadrat dimensions specified) and an example of a photoquadrat **(b)** prior to and **(c)** after the image digitization process, along with a sample legend identifying dominant taxa



Supp. Figure 2.2: *In situ* sea surface temperature data by site over time on Palmyra. Measurements were taken by sensors where possible every 30 min; the points connected by lines represent monthly means for each site



Supp. Figure 2.3: Interaction plots for percent cover (mean ± SE) at each habitat and time point by benthic functional group

Supp. Table 2.1: Comparison of 35 studies on coral reef community composition through time, incorporating benthic categories other than just hard corals. The time spans do not include historical data, only data collected by the authors themselves; note also that this is not an exhaustive list, rather contains examples of long-term spatial and/or temporal trends

Authors	Year published	Study site/ Region	Habitat; Depth	Bleaching event(s)	Method	Benthic categories	Time span	Sampling frequency	Summary of findings
Adjeroud et al.	2009	Moorea, French Polynesia	outer reef slope; 10-12 m	1991, 1994, 2002, 2003	point-intercept method	algal turf, macroalgae, and hard corals	15 years	yearly	between 1991 and 1994, coral cover declined whereas turf algae rapidly colonized; by 2006, this "phase shift" seemed to have reversed, with corals and turf returning to pre-disturbance levels
Aronson et al.	2002	Channel Cay, Belize	fore reef, offshore platforms & central shelf lagoon; 3-15 m	1998	linear point-intercept	hard corals, "CTB" (crustose/turf/bare), macroalgae, and sponges	~5 years	variable (9 time points)	no signs of coral recovery by 2001; macroalgal cover also remained consistently low; "CTB" increased significantly directly after the bleaching event and then returned to pre-bleaching levels after 2000
Arthur et al.	2006	Lakshadweep Islands in the Indian Ocean	reef slope; 5-12 m	1998	estimating areal cover for quadrats along transect lines; quadrats were each subdivided into 25 squares	live hard corals, algal turf, fleshy macroalgae, CCA, filamentous and calcareous algae, other sessile invertebrates including soft coral, coral rubble, and sand	3-4 years	~yearly	coral cover in 2000 was less than 6% on average for all sites whereas 25-48% of the reef substrate was occupied by algal turfs; fleshy macroalgae cover never exceeded 5% while CCA were more common (up to ~45% at one site)
Burt et al.	2013	Bahrain, in the southern Arabian Gulf	all major reef areas including offshore; <10-20 m or >40 m	1996, 1998	point-count for images taken along transects	live hard corals, fleshy algae, turf algae, coralline algae, "other," dead, rubble, and sand/rock	N/A	1 time point	compared to historical data, fleshy and turf algae now dominate the reefs (mean: 72% cover), and live coral cover, formerly dominated by *Acropora*, is now very low (mean: 5.1%)
Cruz-García et al.	2020	Nayarit, Mexico	patch reefs; 3-12 m	2011 and 2015	visual estimation *in situ* of quadrats along permanent transects	hard corals, macroalgae, turf, CCA, and sponges	5 years	every 2 months	temperature anomalies caused a short-term decrease in coral cover and a concomitant increase in CCA, but communities returned to coral-dominated states by 2015
De Bakker et al.	2017	Curaçao and Bonaire	fore reef slope; 10-40 m	1998, 2005, 2010	point-analysis for permanent quadrats	hard corals, algal turfs, benthic cyanobacterial mats, macroalgae, sponges, and CCA	40 years	3 to 6-year intervals	general decrease in the cover of calcifying organisms (corals and CCA) over time, which was initially replaced by algal turfs or fleshy macroalgae; after 2002, cyanobacterial mats became the most dominant benthic component across all sites and depths
Done	1992	Great Barrier Reef, Australia	inner-shelf, mid-shelf, or outer-shelf reefs; 2-8 m, 1-18 m, 0-18 m, respectively	1982	photo-transects and visual surveys	hard corals, "EAC" (epilithic algal community, which includes bare space, turf, small macroalgae and CCA), and other organisms (zoanthids, soft corals and macroalgae)	10 years	~yearly	from 1980-1985, most transects had lost coral cover and/or moved to an "EAC" or other state; in the next 5 years, however, some of these trajectories seemed to reverse largely as a result of coral recruitment and growth of survivor colonies

Supp. Table 2.1: Comparison of 35 studies on coral reef community composition through time, incorporating benthic categories other than just hard corals. The time spans do not include historical data, only data collected by the authors themselves; note also that this is not an exhaustive list, rather contains examples of long-term spatial and/or temporal trends

Authors	**Year published**	**Study site/ Region**	**Habitat; Depth**	**Bleaching event(s)**	**Method**	**Benthic categories**	**Time span**	**Sampling frequency**	**Summary of findings**
Done et al.	2007	Pandora Reef, nearshore Great Barrier Reef	fore reef and back reef; 3-11 m	1998, 2002	photo-transects (visual estimates) and video-transects (point-count)	hard corals, soft corals, and macroalgae	24 years	variable (<10 time points)	reef-wide, there was a catastrophic loss of coral cover in 1998 and then a gradual rise until 2005 at up to ~20%; meanwhile, there was a post-1998 increase in average macroalgal cover, with considerable variability among sites
Emslie et al.	2008	Great Barrier Reef, Australia	reef slope; 6-9 m or up to 30 m	1998	video footage along a transect; point-count	total hard corals, tabulate Acropora, branching Acropora, coralline algae, and turf algae	15 years	yearly	coralline algae either showed no overall trends or decreased through the study period; turf algae decreased each year until 1998, then stabilized; branching Acropora cover increased linearly
Fox et al.	2021	Phoenix Islands	fore reefs; 10-15 m	2002, 2009, 2015-2016	point-count for images taken along transects	hard corals only	18 years	every 2-3 years	proportional cover of the most common coral genera remained consistent across multiple heatwaves; Acropora and Pocillopora spp. experienced near-complete mortality from 2002 to 2005 yet a relative increase since 2009 and high survivorship in 2015
Gleason	1993	Moorea, French Polynesia	outer fore reef slope and back reef; 10 m or 1-2 m, respectively	1991	replicated chain transects	hard corals, crustose algae, filamentous algae, and other algae	1 year	2 time points	coral cover did not decline significantly (only ~3%), though cover of filamentous algae increased by 16% while crustose algae decreased by 11% on average
Graham et al.	2015	Seychelles	fringing reefs, rocky reefs, and patch reefs; 3-10 m	1998	point-count during field surveys	hard corals, macroalgae, sand, rubble, and rock	17 years	4 time points	after the bleaching event, coral cover was reduced by >90% yet between 2005 and 2011, coral and macroalgal cover steadily increased; 12 out of 21 reefs had recovered to pre-disturbance levels (in terms of live coral) by 2011 while 9 reefs underwent regime shifts to fleshy macroalgae
Guest et al.	2016	Singapore	reef crest and reef slope; 3-4 m or 6-7 m, respectively	1998, 2010	line-intercept transect method, estimating cover visually	hard corals, macroalgae, epilithic algal turfs, CCA, sponges, soft corals, zoanthids, other biota, and other substrata	27 years	~yearly	between 1998 and 2010, there was an overall ~12% decline in mean hard coral cover at the shallow sites, whereas at deep sites there was a decline of almost 30%; in contrast, mean cover of macroalgae only increased by ~4% at shallow sites and ~1% at deep sites
Hardman et al.	2004	Mauritius and Rodrigues, Indian Ocean	reef flat, reef front, and patch reefs within a lagoon; up to 6-8 m	2002	rapid assessment surveys to visually estimate percent benthic cover	hard substrate, live hard coral, dead coral, soft coral, turf algae, macroalgae, coralline algae, sponges, or other	N/A	1 time point	no significant difference in median % hard coral cover nor % dead coral cover; however, turf and macroalgal cover increased

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Authors	Year published	Study site/ Region	Habitat; Depth	Bleaching event(s)	Method	Benthic categories	Time span	Sampling frequency	Summary of findings
Jones et al.	2020	Southeast Florida Reef Tract	nearshore barrier reefs; 5-17 m	2009, 2015	point-count for images taken along permanent belt transects	hard corals, octocorals, sponges, macroalgae, CCA, turf algae/substrate, and cyanobacteria	10 years	yearly	declines in the cover of reef-building corals by 63% from 2007 to 2016 and a concomitant 92% increase in macroalgae; cover of weedy corals was unaffected or positively related to heat stress duration; sponge cover increased
Karisa et al.	2020	Kenya	patch, fringing, lagoon, and channel reefs; 6.5-18 m or 0-6 m	2016	point-count for photoquadrats taken along belt-transects	hard corals, coralline algae, macroalgae, turf algae, soft corals, Halimeda, bare substrate, dead coral, other invertebrates, rubble, sand, seagrass, and silt	2 years	1 time point	differences in benthic community composition across geographic zones, habitats, and management status; shallow reefs most proximal to land were dominated by macroalgae and turf whereas deep wave-exposed reefs were generally dominated by coralline algae and hard corals
Khalil et al.	2017	Central Saudi Arabian Red Sea	reef wall and reef crest; 10 m and 1-3 m, respectively	2010	line-intercept method along transects	hard corals, soft corals and zoanthids, sponges, CCA, turf algae, and other algae	N/A	1 time point	coral cover differed significantly between inshore and offshore reefs; inshore reefs had higher cover of corals and turf
Koester et al.	2020	Aldabra Atoll, Seychelles	lagoon and seaward reefs; 2 m or 5-15 m, respectively	2015-2016	point-count for photoquadrats taken along permanent transects	hard corals, soft corals, turf algae, CCA, and Halimeda	5 years	yearly	hard coral reductions of up to 62% at deeper seaward reefs, while lagoonal coral loss was lower at 34%; between 2016 and 2019, deeper reefs remained dominated by turf algae and Halimeda, whereas hard coral cover was mostly restored at shallow reefs
Krishnan et al.	2018	Gulf of Mannar and Palk Bay, India	unspecified; 6-10 m or 2-3 m	2016	visually estimating benthic cover along transects	live hard coral, dead coral, dead coral with algae, macroalgae, and “other” (sand, rock, rubble)	N/A	1 time point	benthic communities were dominated by live hard coral (up to 40% on average), macroalgae (also up to 40%) and “other”
McClanahan	2000	Maldives	windward, leeward and lagoonal reef sites from 1-30 m	1998	point-intercept method along line transects	coralline and turf algae (combined into one category), erect algae, hard coral, sand, and other invertebrates	N/A	1 time point	coralline and turf algae dominated the benthos at 63% of the total cover, followed by erect algae (9%), hard coral (8%), sand (7%), and other invertebrate groups (<3.5%), though there was variation between sites and depth
McClanahan et al.	2001	Kenya	back reef; <3 m	1998	line transects	hard coral or soft coral; fleshy, turf, red coralline, and green calcareous algae; sponge, seagrass, or sand	2 years	3-5 time points	increase (up to 220%) in fleshy algal cover and a decrease (by >85% and ~75%) in hard and soft coral cover, respectively, following bleaching; no clear relationship between the change in coral cover and fleshy algae

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Authors	Year published	Study site/ Region	Habitat; Depth	Bleaching event(s)	Method	Benthic categories	Time span	Sampling frequency	Summary of findings
Monroe et al.	2018	Saudi Arabian Red Sea	offshore, inshore, and midshelf reefs; 5, 10, and 15 m	2015-2016 vs. 2010	line-intercept transects	mainly hard corals, but also soft corals, sponges, turf, CCA, rubble, sand, and "other"	N/A	1 time point	coral cover was higher on midshelf and offshore reefs; bleaching was most prevalent on inshore reefs and shallower transects; turf algae and CCA each took up as much as 20% of the benthos
Muhando and Mohammed	2002	Tanzania	offshore and inshore reefs; unspecified depths	1998	line-intercept point method for random and permanent quadrats	mainly hard corals, but also fleshy and coralline algae, sponges, and soft corals; rubble, rock, or sand	N/A	1 time point	differential responses among sites and species: on one reef, live coral cover declined after the bleaching event and non-living substrate increased more than two-fold while the relative cover of fleshy and coralline algae stayed the same; on other reefs, fleshy algal cover increased
Ostrander et al.	2000	San Salvador, Bahamas	offshore reefs; 15-18 m	1995	"chain-link method" along permanent transects	hard corals, algae	~4 years	every 3-9 months	after the bleaching event, corals of all growth forms declined while algal cover increased significantly
Raj et al.	2021	Gulf of Mannar, India	unspecified; <5 m	2010, 2016	line-intercept transects	hard corals, soft corals, algae (macroalgae and turf), CCA, abiotic, and other invertebrates	12 years	yearly	simultaneous decrease in relative coral cover (36% on average) and increase in algae cover (45%); responses varied by coral morphotype and island, associated with environmental co-factors
Reverter et al.	2020	Gulf of Aqaba, Red Sea	fringing fore reefs and reef slopes; 5 and 10 m	none	point-intercept method along line transects	hard corals, soft corals, sponges, coralline algae, turf algae, fleshy macroalgae, cyanobacterial mats, abiotic, and other organisms	11 years	twice yearly	significant increases in fleshy macroalgae (by ~6 to 15%) and cyanobacterial mats (~6 to 12%) at all site clusters, related to a decline in grazer urchins; increase in diseased corals but no significant reduction in hard coral cover
Ridgway et al.	2016	Barrow Island, Western Australia	offshore reefs; ~3-6 m	2013	photoquadrats taken along a transect and analyzed with CPCe software (random points)	soft corals, sessile invertebrates, macroalgae, turf/coralline algae, abiotic, and hard corals	4 years	~yearly	significant decline in hard coral cover in 2013 and a subsequent shift to increased turf/coralline algal cover
Roelfsema et al.	2021	Southern Great Barrier Reef, Australia	reef flat (0.5-2 m) and reef slope (4-7 m) zones	2002, 2016, 2017	photoquadrats analyzed via machine learning	hard corals, algae, sand, soft corals, and rock	17 years	~yearly	overall, hard coral cover increased from 2009 to 2016 and decreased thereafter; reef flat sites had lower average coral cover than reef slopes

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Authors	Year published	Study site/ Region	Habitat; Depth	Bleaching event(s)	Method	Benthic categories	Time span	Sampling frequency	Summary of findings
Ruzicka et al.	2013	Florida Keys	patch reefs and fore reefs; “shallow” or “deep”	1998	video footage along a transect; point-count	macroalgae, octocorals, sponges, hard corals, and zoanthids	10 years	yearly	hard coral cover remained relatively consistent, not recovering; there were no significant changes in macroalgal cover overall
Sheppard et al.	2017	Chagos Archipelago, Indian Ocean	lagoons and ocean-facing reef slopes; 5-25 m	1998, 2015	by-eye measurements of percent cover within quadrats, or point-count of images from video surveys	hard corals, soft corals	20 years	variable (<10 time points)	reduction in coral cover in 1998, after which recovery lasted until 2015; between 2015 and 2017, hard coral cover decreased from 40-50% to about 5%; prolonged warming almost eliminated soft corals
Shulman and Robertson	1996	San Blas, Panama	lagoonal patch reefs; 1-5 m	1983	point-intercept transect	hard corals, hydrocorals, macroalgae, microalgae, and coralline algae	7 years	initially every 6 months; then ~yearly	macroalgal cover increased through 1998; there were no consistent changes in encrusting coralline algae cover, while coral cover drastically decreased
Smith et al.	2008	Scott Reef system, Australia	reef slopes; 9 m	1998	video footage along a transect; point-count	hard and soft corals, algae (but not macroalgae)	~10 years	yearly from 1994-2000, and again in 2001 and 2004	majority of corals bleached and died shortly after the bleaching event, yet returned to ~40% of their pre-bleaching level by 2004; following the bleaching, turf and coralline algal cover both increased significantly while fleshy macroalgae cover remained at <1% throughout the study period
Stuart-Smith et al.	2018	Great Barrier Reef and western Coral Sea	unspecified; 4-10 m or >10 m	2016	photoquadrats taken along a transect, analyzed via point-count	hard corals, algae	N/A	2 time points ('before' and 'after')	the extent of coral loss varied by site, though many of the reefs experienced absolute declines in live coral cover which was generally replaced by algae
Wilson et al.	2012	Inner Seychelles, Indian Ocean	reef slopes; 4-9 m	1998	visual estimates within circular areas (7 m radius) by a diver hovering over the reef	hard corals, macroalgae	17 years	variable (4 times total)	in 1994 the average coral cover was 7%; since 2005, mean coral cover across all sites increased by approximately 1% per year, reaching about 14% in 2011; the rate of increase in macroalgal cover was strongly associated with coral recovery
Witman	1992	St. John, U.S. Virgin Islands	reef slopes; 4 and 12 m	1987	tracing color enlargements of photoquadrats with an “electronic digitizer”	hard corals, hydrocorals, gorgonians, sponges, and algal turf	6 years	9 time points between 1985-1991	after the disturbances (including hurricanes which dislodged many coral colonies), cover of filamentous algal turf increased by two to three-fold

Supp. Table 2.2: Statistical output from a three-way PERMANOVA (9999 permutations) based on Bray-Curtis dissimilarity for benthic community responses over time (i.e., yearly from 2009 to 2018) by year, habitat, site (nested within habitat), and their interactions. Bold indicates statistical significance (α = 0.05)

Source	Df	SumSqs	MeanSqs	F.Model	R^2	Pr(>F)
Year	9	2.524	0.2804	4.550	0.02838	**<0.001**
Habitat	1	10.222	10.2222	165.862	0.11494	**<0.001**
Year * Habitat	9	1.176	0.1307	2.121	0.01323	**<0.001**
Site(Habitat)	6	28.499	4.7499	77.071	0.32045	**<0.001**
Year * Site(Habitat)	54	2.880	0.0533	0.866	0.03239	0.8852
Residuals	708	43.634	0.0616		0.49062	
Total	787	88.937			1.00000	

Supp. Table 2.3: Results from two-tailed t-tests for the mean difference in cover one year after each bleaching event, as compared to zero, by site and benthic group. Significant p-values (< 0.05) are bolded

			1st bleaching event				**2nd bleaching event**			
Benthic group	Site	Df	t	Significance (two-tailed)	Mean difference	SE	t	Significance (two-tailed)	Mean difference	SE
Hard corals	**FR3**	9	-4.783	**0.001**	-9.136	1.910	-1.514	0.164	-6.572	4.341
	FR5	9	-0.320	0.756	-0.448	1.398	-0.546	0.599	-1.511	2.768
	FR7	9	-0.720	0.490	-2.969	4.121	-0.872	0.406	-1.478	1.695
	FR9	9	-3.838	**0.004**	-5.814	1.515	-5.480	**0.000**	-5.742	1.048
	RT1	9	0.367	0.722	0.474	1.291	0.634	0.542	0.949	1.498
	RT4	9	0.481	0.642	0.791	1.643	-1.997	0.077	-7.696	3.853
	RT10	9	0.567	0.585	0.922	1.625	1.790	0.107	2.677	1.496
	RT13	9	-2.567	**0.030**	-3.437	1.339	-3.760	**0.004**	-7.242	1.926
CCA	**FR3**	9	1.409	0.192	1.376	0.976	3.857	**0.004**	7.554	1.959
	FR5	9	3.828	**0.004**	9.853	2.574	3.583	**0.006**	6.870	1.917
	FR7	9	2.801	**0.021**	7.037	2.513	3.546	**0.006**	14.489	4.087
	FR9	9	0.519	0.616	1.215	2.339	0.434	0.674	0.893	2.057
	RT1	9	-0.052	0.960	-0.144	2.759	-1.579	0.149	-3.774	2.391
	RT4	9	1.682	0.127	4.310	2.563	0.547	0.597	2.700	4.932
	RT10	9	1.034	0.328	1.737	1.679	3.462	**0.007**	14.155	4.089
	RT13	9	-0.648	0.533	-0.392	0.605	0.779	0.456	0.059	0.076
Macro-algae	**FR3**	9	5.962	**0.000**	8.807	1.477	-0.959	0.363	-2.963	3.090
	FR5	9	-2.074	0.068	-15.477	7.461	-1.313	0.222	-9.242	7.040
	FR7	9	-2.060	0.069	-9.037	4.386	-0.152	0.883	-0.333	2.195
	FR9	9	2.064	0.069	4.246	2.057	-0.828	0.429	-1.202	1.451
	RT1	9	-0.060	0.954	-0.103	1.719	-2.558	**0.031**	-8.161	3.190
	RT4	9	1.625	0.139	2.392	1.472	2.752	**0.022**	5.871	2.133
	RT10	9	2.205	0.055	2.135	0.968	1.732	0.117	2.115	1.221
	RT13	9	1.930	0.086	4.401	2.280	3.806	**0.004**	4.017	1.056
Turf	**FR3**	9	-0.657	0.527	-1.241	1.888	0.476	0.646	2.045	4.299
	FR5	9	0.691	0.507	4.172	6.035	1.935	0.085	10.033	5.186
	FR7	9	-2.967	**0.016**	-3.366	1.134	-4.379	**0.002**	-9.473	2.163
	FR9	9	0.307	0.766	0.317	1.034	2.286	**0.048**	6.562	2.871
	RT1	9	-0.373	0.717	-0.586	1.568	4.978	**0.001**	10.564	2.122
	RT4	9	-2.625	**0.028**	-7.899	3.009	-0.074	0.943	-0.472	6.394
	RT10	9	-1.800	0.105	-4.794	2.663	-4.534	**0.001**	-18.032	3.977
	RT13	9	-0.121	0.906	-0.325	2.686	1.850	0.097	4.652	2.515

Supp. Table 2.4: Statistical output from two-way ANOVAs for net changes in percent cover (i.e., between 2009 and 2018) for each group by habitat and site (nested within habitat). Bold indicates statistical significance ($\alpha = 0.05$)

Benthic group	Source	Df	SumSqs	MeanSqs	F value	Pr(>F)
Hard corals	Habitat	1	1465.4	1465.36	7.9403	**<0.001**
	Site(Habitat)	6	1972.9	328.82	1.7818	0.1154
	Residuals	70	12918.4	184.55		
CCA	Habitat	1	555	554.9	3.750	0.0568
	Site(Habitat)	6	2072	345.4	2.334	**0.0411**
	Residuals	70	10358	148.0		
Macroalgae	Habitat	1	264.6	264.55	2.1782	0.1445
	Site(Habitat)	6	3829.7	638.28	5.2554	**<0.001**
	Residuals	70	8501.7	121.45		
Turf	Habitat	1	257.5	257.51	1.2167	0.2738
	Site(Habitat)	6	1577.1	262.85	1.2419	0.2958
	Residuals	70	14815.8	211.66		
Reef builders	Habitat	1	458.6	458.56	2.2440	0.1386
	Site(Habitat)	6	724.1	120.69	0.5906	0.7367
	Residuals	70	14304.0	204.34		
Fleshy algae	Habitat	1	61	60.95	0.2352	0.6292
	Site(Habitat)	6	2069	344.83	1.3303	0.2554
	Residuals	70	18144	259.20		

Supp. Table 2.5: Results from two-tailed t-tests for the mean net change in cover between 2009 and 2018, by group for each site, as compared to zero. Significant p-values (< 0.05) are bolded

Benthic group	Site	t	Df	Significance (two-tailed)	Mean difference	SE	95% Confidence Interval	
							Lower	Upper
Hard corals	**FR3**	-5.557	9	**0.000**	-19.361	3.484	-27.243	-11.480
	FR5	-3.139	8	**0.014**	-10.826	3.450	-18.780	-2.873
	FR7	-3.593	8	**0.007**	-12.903	3.591	-21.185	-4.621
	FR9	-0.994	9	0.346	-3.286	3.307	-10.768	4.195
	RT1	-2.016	9	0.075	-8.876	4.402	-18.834	1.083
	RT4	0.357	9	0.729	2.460	6.886	-13.116	18.037
	RT10	-0.590	9	0.570	-1.814	3.074	-8.769	5.141
	RT13	-0.690	9	0.508	-3.405	4.938	-14.574	7.765
CCA	**FR3**	4.179	9	**0.002**	11.460	2.742	5.257	17.663
	FR5	1.598	8	0.149	6.923	4.333	-3.069	16.914
	FR7	0.866	8	0.412	2.926	3.379	-4.865	10.717
	FR9	-1.532	9	0.160	-4.875	3.182	-12.072	2.323
	RT1	-0.254	9	0.805	-1.163	4.576	-11.516	9.189
	RT4	-1.496	9	0.169	-7.842	5.241	-19.698	4.014
	RT10	0.391	9	0.705	1.872	4.784	-8.950	12.694
	RT13	1.452	9	0.180	2.051	1.412	-1.144	5.246
Macroalgae	**FR3**	2.850	9	**0.019**	11.058	3.881	2.279	19.837
	FR5	-2.068	8	0.072	-12.419	6.005	-26.266	1.428
	FR7	0.299	8	0.773	1.132	3.789	-7.606	9.870
	FR9	1.129	9	0.288	2.463	2.182	-2.473	7.398
	RT1	1.585	9	0.147	4.236	2.672	-1.808	10.280
	RT4	-2.232	9	0.053	-3.188	1.428	-6.420	0.043
	RT10	-1.080	9	0.308	-1.333	1.235	-4.127	1.460
	RT13	-2.246	9	0.051	-10.913	4.859	-21.905	0.078
Turf	**FR3**	-1.366	9	0.205	-2.455	1.796	-6.518	1.609
	FR5	-0.317	8	0.760	-3.078	9.720	-25.491	19.335
	FR7	2.218	8	0.057	3.398	1.532	-0.135	6.931
	FR9	6.032	9	**0.0002**	6.109	1.013	3.818	8.400
	RT1	0.448	9	0.665	0.762	1.700	-3.085	4.609
	RT4	1.339	9	0.213	6.931	5.176	-4.779	18.641
	RT10	-0.173	9	0.866	-0.737	4.254	-10.361	8.887
	RT13	1.980	9	0.079	11.735	5.927	-1.673	25.143
Reef builders	**FR3**	-2.980	9	**0.015**	-8.828	2.963	-15.530	-2.126
	FR5	-0.659	8	0.529	-3.950	5.996	-17.778	9.878
	FR7	-2.313	8	**0.049**	-10.800	4.669	21.567	-0.032
	FR9	-3.167	9	**0.011**	-8.688	2.743	-14.894	-2.483
	RT1	-1.816	9	0.103	-7.603	4.186	-17.073	1.867
	RT4	-1.108	9	0.297	-5.577	5.034	-16.965	5.811
	RT10	0.283	9	0.784	1.280	4.523	-8.950	11.511
	RT13	-0.193	9	0.852	-1.108	5.754	-14.124	11.908
Fleshy algae	**FR3**	0.035	9	0.973	0.091	2.610	-5.814	5.996
	FR5	0.012	8	0.991	0.122	9.997	-22.932	23.175
	FR7	3.557	8	**0.007**	8.903	2.503	3.131	14.675
	FR9	6.122	9	**0.000**	7.482	1.222	4.717	10.246
	RT1	2.951	9	**0.016**	15.031	5.094	3.508	26.555
	RT4	1.321	9	0.219	7.264	5.497	-5.171	19.699
	RT10	-0.176	9	0.864	-0.768	4.352	-10.614	9.078
	RT13	0.359	9	0.728	2.067	5.763	-10.970	15.105

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CHAPTER 3: Species-Specific Responses of Individual Coral Colonies to Two Thermal Anomalies on Palmyra Atoll, Central Pacific

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ABSTRACT

Thermal anomalies, large-scale warming, and coral bleaching events have become more frequent and intense across the world's oceans over the last several decades. Here, we use an 11-year time series of permanent benthic photoquadrats taken on Palmyra Atoll, central Pacific from 2009 to 2019 to track the growth, discoloration (i.e., lack of pigmentation), partial or whole-colony mortality, survival, and/or regrowth of 314 individual coral colonies of nine dominant reef-building species from two habitats. During this period, thermal anomalies occurred on Palmyra in conjunction with El Niño-Southern Oscillation in both 2009 and 2015, of which the latter was more thermally-severe. We found that coral community responses varied by habitat, over time, within and among species, and/or according to the degree of thermal stress. Nearly all species, particularly *Stylophora pistillata* and *Pocillopora damicornis*, responded more negatively to the 2015 anomaly compared to 2009 in terms of the amount of discoloration by colony and loss in live planar area. Colony fate was associated with discoloration severity at the time of warming: one year following the first anomaly, colonies with more discoloration were more likely to grow but following the second anomaly, colonies with more discoloration were less likely to grow; instead, shrinkage or mortality were more common. However, colonies that were more discolored in 2015 were not necessarily those that were more discolored in 2009. While colonies of *Pavona duerdeni* and *Astreopora myriophthalma* had the highest survivorship,

new individuals of all species were established throughout the time series. Overall, this contributes to our understanding of species-specific responses to thermal disturbance at the individual colony level over time, which could better inform conservation efforts in an era of widespread coral decline.

INTRODUCTION

Coral bleaching and mortality are becoming more prevalent due to climate change (Hoegh-Guldberg et al. 2007; Hughes et al. 2017), which is transforming coral assemblages on a regional scale (Hughes et al. 2018a; Gardner et al. 2003; Bruno and Selig 2007). Bleaching is the breakdown of corals' symbiotic relationship with zooxanthellae (i.e., microalgae) that provide corals with much of their energy through photosynthesis (Wooldridge 2013) as well as their coloration. While recovery from bleaching is possible, a bleached coral colony is more vulnerable to disease, mortality, or reduced growth and reproduction (Baird and Marshall 2002) as coral energy reserves are depleted (Anthony et al. 2009). Despite evidence that some coral communities can adapt to rising seawater temperatures (Palumbi et al. 2014; Romero-Torres et al. 2020; Fox et al. 2021), under projected climate scenarios the majority of reefs will likely continue to face repeated bleaching, extensive reductions in community-wide live area, and a shift in community structure toward more stress-tolerant species (Logan et al. 2014; Pandolfi et al. 2011), fundamentally changing not only these ecosystems themselves (Hughes et al. 2018b) but also their capacity to provide key ecosystem services (Eddy et al. 2021).

When mass coral bleaching was first documented in 1983, it was believed to have been associated with ocean warming; however, the mechanism of zooxanthellae loss was unclear (Glynn 1984). By 1996, it was collectively hypothesized that either (i) the zooxanthellae enzyme systems responsible for detoxifying reactive forms of oxygen are disrupted under high temperature and irradiance (Lesser et al. 1990), (ii) the photosynthetic pathways of zooxanthellae are impaired under thermal stress, which activates their dissociation from corals (Iglesias-Prieto et al. 1992) or (iii) coral host cells are detached along with their endosymbionts due to temperature shock (Gates et al. 1992). Through experiments, it was later determined that coral bleaching generally results from accumulated oxidative stress (Lesser 1997; Downs et al. 2002), which involves damage to Photosystem II (Warner et al. 1999; Tchernov et al. 2004). However, the exact cellular processes were mostly unknown (Douglas 2003; Baker et al. 2008; Dove and Hoegh-Guldberg 2006). In fact, even today the underlying mechanisms of photosynthesis and calcification are not well-described in corals (Tresguerres et al. 2013), let alone during bleaching (Gómez-Campo et al. 2022). Moreover, mechanisms might be context-dependent (Barott et al. 2015), which limits our ability to predict coral responses on a cellular, organismal, or community level. Coral species and morphologies are also known to differ in their susceptibility to thermal stress (Loya et al. 2001; Marshall and Baird 2000; van Woesik et al. 2011), which can be linked to their specific microalgal symbionts (Berkelmans and van Oppen 2006) or microbial communities (Peixoto et al. 2020), heterotrophic plasticity (Fox et al. 2019b), prior history of thermal exposure (Grottoli et al. 2014; Maynard et al. 2008), life history strategies (Darling et al. 2013), and even their gene expression or other mechanisms of local adaptation (Kenkel and Matz 2016; Seneca and Palumbi 2015).

Nevertheless, progress has been made in developing indicators for coral bleaching. For example, we can now use the Degree Heating Week (DHW) index (Liu et al. 2006) as a measure of accumulated heat stress, which was preceded by other thermal anomaly indices (see Goreau and Hayes 1994; Podestá and Glynn 1997; Berkelmans et al. 2004). DHW is based on the number of weeks over a 12-week period in which temperatures exceeded the mean monthly maximum temperature by at least one degree Celsius (Liu et al. 2006). This index was developed by the National Oceanic and Atmospheric Administration's (NOAA) Coral Reef Watch program to predict bleaching events around the world based on satellite sea surface temperatures (SST). DHW values above 4 are thought to cause significant bleaching whereas DHW values above 8 correspond to severe widespread bleaching and mortality (Liu et al. 2014). Although this index is certainly useful for predicting large-scale bleaching, it is not always accurate at detecting milder bleaching events (McClanahan et al. 2007), highlighting the importance of maintaining *in situ* observations and measurements.

While it is known that there are several environmental triggers for coral bleaching, including reduced salinity, decreased seawater temperature, solar and ultraviolet radiation, or bacterial infection (Brown 1997), "bleaching" in the classic sense is caused by exposure to anomalous or persistent warm water temperatures. It should be noted, however, that corals can experience natural variation in color and pigmentation resulting in paling, patchy coloration or "discoloration" (i.e., not necessarily due to thermal stress; see Supp. Fig. 3.1) within and between coral colonies. Discoloration can be seen as a result of predation (e.g., by *Drupella* snails or crown-of-thorns sea stars, *Acanthaster*) or coral disease (such as White Syndrome or White Band Disease) leading to necrosis or death, revealing the white coral skeleton beneath the damaged tissue. Additionally, the active growth tips or margins of some fast-growing coral taxa (e.g., branching *Acropora* or foliose *Montipora*) commonly appear white prior to acquiring zooxanthellae (Work and Aeby 2006). Since coloration, or lack thereof, can be a proxy for coral condition (Bahr et al. 2020; Siebeck et al. 2006), it would be beneficial to take into account a colony's naturally-occurring discoloration in order to know how much of the total "bleaching" or whiteness is actually temperature-induced. Santavy et al. (2005) introduced the term “causal bleaching” to distinguish mass bleaching from paling caused by other factors, while others have suggested differentiating between non- or sublethal bleaching and “lethal bleaching” (Suggett and Smith 2011), but this approach has not been adopted by the scientific community. Quantifying a given coral colony’s bleaching, paling, or “discoloration” at multiple points in time and monitoring how this changes in the context of thermal stress would be more informative than single-snapshot surveys, but few such data sets are available. Further, coral responses are often genus or species-specific (Ritson-Williams and Gates 2020; McClanahan 2004; Obura 2001, Marshall and Baird 2000) and each taxon likely has a unique natural baseline of coloration which may vary across habitats, depth, and fluctuate seasonally and/or with temperature or other environmental stressors.

In this study, we aimed to quantify species-specific, colony-level variability in discoloration and live planar area of hard corals on Palmyra Atoll from 2009 to 2019. Palmyra’s reefs have been monitored at least yearly for over the past decade, during which they have experienced thermal anomalies associated with El Niño-Southern Oscillation (ENSO) in both 2009 and 2015-16 (Williams et al. 2010; Fox et al. 2019a). This presents a unique opportunity to study long-term patterns of discoloration, growth, partial or whole-colony mortality, and survival. Since we are quantifying the lack of coloration (either naturally-occurring or caused by thermal stress) at every time point, not all of which were thermally anomalous, we are referring to this metric as “discoloration” rather than bleaching. The goals of this study were to explore if and how reef-building coral communities on Palmyra varied by habitat, over time, and/or across two thermal anomalies, and whether some species were more susceptible or tolerant than others in terms of changes in live area or discoloration. We also assessed whether discoloration severity at the time of warming corresponded to colony fate (with respect to growth and partial or whole-colony mortality) one year post-anomaly, and whether colonies that were more discolored during the first anomaly were more or less discolored during the second anomaly. We expected to see differential responses within and among species across successive anomalies, possibly tied to the degree of thermal stress.

METHODS

Study Site

Palmyra (5.89 ºN, 162.08 ºW) is a remote atoll in the Northern Line Islands, located approximately 1,300 km south of Hawaiʻi in the central Pacific. Palmyra is federally-protected as a National Wildlife Refuge part of the Pacific Remote Island Areas National Marine Monument. Aside from a brief period of military occupation during WWII, Palmyra is uninhabited and experiences minimal human impact. As such, its coral reefs are considered quasi-pristine (Sandin et al. 2008), making this an ideal location to study global change in the absence of confounding local stressors such as fishing and pollution (Braun et al. 2009). Palmyra's reefs are characterized by an abundance of corals and other reef builders such as crustose coralline algae (Williams et al. 2013), as well as high herbivore biomass and density (Williams et al. 2011; Hamilton et al. 2014).

Data Collection

Photoquadrats (90 cm x 60 cm) were taken on Palmyra by SCUBA divers along a transect for a total of eight sites visited between one and three times per year from 2009 to 2019. Four of the sites were at the slightly deeper, wave-exposed Fore Reef (FR at 10 m depth), and four sites were at the shallower, wave-sheltered Reef Terrace (RT at 5 m depth). We used image analysis tools in Adobe Photoshop (Creative Cloud) to determine planar areas of live hard corals in each image, as well as the proportion of discoloration for individual coral colonies at every time point (see Supp. materials for detailed methods and justification). Coral colonies were manually assigned identification labels to match the same colonies through time. We also calculated the total percent cover of hard corals in each quadrat and site, by species over time. To find SST anomalies on Palmyra at the times when imagery was collected (Supp. Fig. 3.5), we used NOAA's Coral Reef Watch twice-weekly 50-km product (https://coralreefwatch.noaa.gov/data3/50km/vs/timeseries/vs_ts_PalmyraAtoll.txt).

Statistical Analyses

All analyses were conducted in R software version 3.6.3 (R Core Team 2018). First, to visualize coral community composition at the beginning of the study, we constructed a non-metric multidimensional scaling (nMDS, via *metaMDS* in *vegan* for R; Oksanen et al. 2019) ordination plot for the initial time point in September 2009. This nMDS was based on Bray-Curtis dissimilarity measures for coral species percent cover data by quadrat and site, applying a square-root transformation to balance the effect of disproportionately-abundant species. Next, to describe coral community composition on Palmyra throughout the entire study period, we plotted the mean percent coral cover by habitat and species for each time point. To explore if coral community structure varied across space (habitat and site nested within habitat) and/or time (year), we conducted a three-way permutational multivariate analysis of variance (PERMANOVA with 9999 permutations via *adonis* in *vegan*; Anderson 2001, Oksanen et al. 2019) on square-root-transformed coral species percent cover data over time. When differences were detected, we identified the species that contributed most to these differences through SIMPER or "similarity percentages" analysis (via *simper* in *vegan*; Clarke 1993, Oksanen et al. 2019) using the same distance matrix.

Next, for a subset of nine dominant species whose colonies were entirely present within the photoquadrat frame (*Astrea curta*, *Astreopora myriophthalma*, *Goniastrea stelligera*, *Hydnophora microconos*, *Pavona chiriquiensis*, *Pavona duerdeni*, *Pocillopora damicornis*, *Pocillopora meandrina*, and *Stylophora pistillata*; see Supp. Table 3.1), we examined changes in area of individual coral colonies through time. Linear mixed-effects models were used for each species separately to test whether live planar area or percent discoloration varied over time, by habitat, and/or with temperature. The models were fitted by restricted maximum likelihood using the '*lmer*' function from the *lme4* package (Bates et al. 2014) and assumptions of normality of residuals were met. We chose a mixed-effects model instead of a standard repeated measures analysis of variance (ANOVA) because of our unbalanced design, since we did not have observations of all colonies at every time point. Further, the mixed-effects model allowed us to treat time as a continuous variable, given that our time points were not always evenly spaced. Time (months since initial observation) and habitat were treated as fixed effects (where possible; not all species had representatives from both habitats) and temperature (in terms of SST anomaly at the time of observation) was treated as a covariate. Colony was treated as a random effect to account for repeated measures on each individual colony. To identify significant fixed effects, we ran a Type-II ANOVA with Satterthwaite's approximation method on each model. We also investigated whether there was a relationship between SST anomaly and percent discoloration using Pearson's correlation. To quantify short-term responses, we calculated the percent change in live area for individual colonies, averaged by species, one year after each of the thermal anomalies in 2009 and 2015 (i.e., 2010 and 2016, respectively). We also plotted the cumulative proportion of colonies surviving from 2009 until the final time point in 2019 to track long-term survivorship by species.

Additionally, to explore whether a colony's level of discoloration during warming corresponds to their fate (i.e., colony growth, shrinkage, or whole-colony mortality) one year later, we constructed transition matrices in a format adapted from Williams et al. (2017) showing the likelihood of different fates following each thermal anomaly. Colonies were grouped into discoloration categories based on severity: 0%, <25%, 25-50%, 50-75%, and >75% (none, low, moderate, high, or severe discoloration, respectively) and the number of colonies within a category experiencing each fate was tallied to calculate frequencies and represented through histograms. Given limited sample sizes, for the purpose of these transition matrices we combined colonies of all nine species. To determine whether colony fate was dependent on discoloration severity, we used Fisher's exact test on count data from both anomalies to compare whether colonies of each discoloration category grew, shrank, or died differently than would be expected by chance (Fisher 1922).

RESULTS

Coral Community Composition by Habitat Over Time

Species richness of reef-building hard corals was greater on the fore reef, with at least 30 species found in photoquadrats taken at this habitat compared to 22 on the reef terrace (Fig. 3.1). Of all hard coral taxa, encrusting *Lobophyllia corymbosa* and branching *Acropora acuminata* contributed most to total benthic cover on the fore reef (Fig. 3.1a), whereas common coral taxa on the reef terrace (Fig. 3.1b) include table *Acropora (A. cytherea* and *A. hyacinthus)* and encrusting *Montipora (M. flabellata* and *M. patula)*. Coral community composition at the reef terrace was relatively consistent through time while the fore reef was more dynamic. For example, the cover of *A. acuminata* on the fore reef fluctuated significantly; it was particularly abundant in September 2015 at the time of the second anomaly, after which it sharply declined within one year. Overall, coral cover was higher on the reef terrace at 49.0 ± 0.6% (mean ± SE) and remained stable over time. Coral cover on the fore reef was lower at 32.2 ± 1.6% and experienced a gradual decline by 2019.

Coral community structure was more similar within habitats than among habitats based on Bray-Curtis similarity measures calculated from percent cover at the initial time point in 2009 (Fig. 3.2). Across the entire time series, coral community composition varied significantly by habitat and site within habitat (PERMANOVA, $p < 0.001$; Table 3.1), but not over time, and there were no interactions found. Further, habitat was a better predictor of coral community composition than time, explaining 24% of the variation ($R^2 = 0.240$) with site explaining about 10% ($R^2 = 0.099$; Table 3.1). A SIMPER analysis revealed that the taxa contributing most to habitat dissimilarity included *Montipora* and *Acropora* spp., *Pocillopora meandrina*, *Goniastrea stelligera*, and *Porites arnaudi* (Table 3.2).

Live Area and Discoloration Trajectories in Relation to Temperature

Change in live planar area and colony-level discoloration varied by habitat and/or over time, which in some cases was related to SST anomalies. Colonies of *Astrea curta* ($n = 19$, all but one from FR) were small compared to other taxa (mean size in 2009 at 32.5 ± 5.9 cm^2) and *A. curta* live planar area declined significantly through time ($p < 0.001$; Table 3.3) to 5.7 ± 1.5 cm^2 per colony in 2019 (Fig. 3.3a). Percent discoloration did not vary significantly over time or with SST anomaly (Table 3.4) in *A. curta*. For *Astreopora myriophthalma*, colonies (n = 7, exclusively from RT) were larger on average at 149.1 ± 67.5 cm^2 in 2009, increasing steadily to 562.0 ± 264.4 cm^2 per colony by 2019 (Fig. 3.3b). In general, there was a significant increase in live planar area (p = 0.017; Table 3.3) over time. While percent discoloration varied over time in *A. myriophthalma* (p = 0.008; Table 3.4), this was not associated with SST anomaly.

Goniastrea stelligera colonies (n = 49, the majority from FR) gradually increased in live area from about 102.7 ± 23.3 cm^2 per colony in 2009 to 221.2 ± 67.3 cm^2 in May 2016, after which they decreased to 44.1 ± 13.4 cm^2 in 2019 (Fig. 3.3c). Overall, there was a significant interaction between time and habitat (p <0.001; Table 3.3) where colonies at RT maintained their live area through time while colonies on the FR sites lost much of their live area by 2019 (data not shown). Overall, *G. stelligera* planar area peaked in 2016 and has subsequently shown a marked decline through 2019. Percent discoloration in *G. stelligera* did not change significantly over time but was consistently higher at RT (p = 0.003; Table 3.4). Live planar area of *Hydnophora microconos* colonies (n = 9, exclusively from FR) varied significantly over time (p <0.001; Table 3.3) and exhibited highly variable, yet non-significant, discoloration over time but neither were associated with SST anomalies (Fig. 3.4d). Average colony size in *H. microconos* was similar in 2009 (231.2 ± 96.3 cm^2) and 2019 (220.2 ± 138.9 cm^2). *Pavona chiriquiensis* (n = 37, all but one from FR) had 64.7 ± 10.2 cm^2 live planar area per colony in 2009, which remained consistent until a sharp drop to 21.1 ± 10.1 cm^2 in 2018; this was partially restored by 2019 (Fig. 3.3e). Changes in *P. chiriquiensis* live area were significant over time and with SST anomaly (p <0.001 and p = 0.005, respectively; Table 3.3). There was little discoloration in *P. chiriquiensis* but this varied over time (p <0.001; Table 3.4) with no clear relationship to SST anomaly. In contrast, *P. duerdeni* colonies (n = 8, only from FR) gradually increased in live planar area from 225.0 ± 86.2 cm^2 per colony in 2009 to 379.3 ± 145.9 cm^2 in 2019 (Fig. 3.3f) however there was no significant variation in live area nor discoloration throughout the time series (Fig. 3.4f).

Pocillopora damicornis colonies (n = 38, exclusively from RT) increased in live area from 42.9 ± 5.9 cm^2 per colony in 2009 to 67.4 ± 34.1 cm^2 in 2015, followed by a decline in May 2016 and an increase through 2019 (Fig. 3.3g). This corresponded to a peak in percent discoloration in *P. damicornis* to 19.3 ± 7.5% in 2015 (Fig. 3.3g). In general, live planar area varied over time and by SST anomaly ($p <0.001$ and $p = 0.016$, respectively; Table 3.3). Colonies of *P. meandrina* (n = 140, largely from FR) increased in live area from 82.2 ± 6.6 cm^2 per colony in 2009 to 169.2 ± 28.2 cm^2 in 2019 (Fig. 3.3h). There were differences in planar area between habitats, with colonies at RT significantly smaller than those at FR (data not shown). Additionally, colonies were generally more discolored at RT than FR (6.9 ± 1.0% vs. 16.2 ± 3.2%, respectively; Fig. 3.4h; $p <0.001$) but there were no significant effects of SST anomaly on percent discoloration. Colonies of *Stylophora pistillata* (n = 7, only from FR) were about 40.1 ± 8.7% discolored during the warming in 2015 (Fig. 3.4i), the highest among all other taxa at that time point. Live planar area in *S. pistillata* colonies increased from 83.2 ± 45.6 cm^2 per colony in 2009 to 308.5 ± 128.8 cm^2 in 2014 (Fig. 3.3i) but dropped to 222.9 ± 118.9 cm^2 at the time of the 2015 thermal anomaly, and this was not restored by 2019.

For all species, much of the variation not explained by fixed effects was explained by differences in individual coral colonies. Although the highest discoloration values were observed when SST anomaly was at its highest (19.6 ± 1.9% and 23.3 ± 5.0% discoloration at FR and RT, respectively, corresponding to +1.18 ºC in 2015; Fig. 3.5), there was no significant correlation between SST anomaly and percent discoloration (Pearson's $r = 0.29$, $p = 0.19$), suggesting that for this data set, SST anomalies alone cannot be used to predict discoloration. While discoloration was consistently higher at RT than FR for this subset of colonies (Fig. 3.5), this was not necessarily representative of habitat trends overall.

Coral Colony Fate Following Thermal Anomalies

Survivorship curves tracking the cumulative proportion of colonies alive from 2009 through 2019 (not including individuals established after 2009) showed that colonies of certain species dropped off more gradually (e.g., *Pocillopora meandrina* and *P. damicornis, Goniastrea stelligera,* and *Astrea curta*) while mortality was more staggered for other taxa (*Stylophora pistillata* and *Hydnophora microconos;* Fig. 3.6a). Ultimately by 2019, *Pavona duerdeni* had the highest colony survival rate (50%), followed by *Astreopora myriophthalma* (42.9%). While original colonies of *Pocillopora damicornis*, *Pavona chiriquiensis*, and *Pocillopora meandrina* had the lowest survival rates (7.9%, 8.1%, and 11.4%, respectively), new individuals of these species emerged in subsequent years at both FR (Fig. 3.6b) and RT (Fig. 3.6c).

Percent change in live planar area of the same individual colonies also varied by species and anomaly. Species which, on average, lost live area one year following the first anomaly in 2009 (*P. damicornis* and *S. pistillata*) lost around the same or more live area one year following the second anomaly in 2015 (Table 3.5). Species that gained live area one year following the first anomaly (*A. curta*, *A. myriophthalma*, *G. stelligera*, and *H. microconos*) lost live area following the second anomaly. Colonies of *S. pistillata* were the most severely affected by the 2015 anomaly in terms of their partial mortality one year later, while *P. duerdeni* colonies maintained their live area following both anomalies. Although colonies of *P. meandrina* gained live area following both anomalies, there were many cases of whole-colony mortality (e.g., only about

21.6% of colonies remained by 2015). Overall, colonies that were more discolored in 2009 were not necessarily those that experienced whole-colony mortality or higher discoloration in 2015. In fact, most colonies experiencing whole-colony mortality by 2015 were only between 0 to 25% discolored in 2009 (Fig. 3.7). For *A. curta*, *H. microconos*, *P. damicornis*, *P. meandrina*, and *S. pistillata*, discoloration was generally greater in 2015 compared to 2009. Averaging across all species, the first anomaly led to a 23.4 ± 5.7% gain in colony live area one year later whereas the second anomaly led to a 7.4 ± 5.7% loss in colony live area (Table 3.5).

As for colony fates by discoloration severity, of the colonies that were not at all discolored in 2009, the majority (73.0%) grew by 2010 (Table 3.6a, Supp. Fig. 3.7a). In contrast, 57.1% of colonies lacking any discoloration in 2015 increased in size in 2016 (Table 3.6b, Supp. Fig. 3.7b). None of the colonies that were highly or severely discolored in 2009 died one year later, whereas colonies that were severely discolored in 2015 experienced either shrinkage or whole-colony mortality by 2016 (although the sample size was low). In 2010, shrinkage was most common when colonies had low to moderate discoloration the previous year (Table 3.6a) whereas in 2016, shrinkage was a relatively common fate for colonies of any amount of discoloration (Table 3.6b). Colonies with increasingly more discoloration in 2009 were less likely to die and more likely to grow in 2010, yet colonies with increasingly more discoloration in 2015 were less likely to grow in 2016. Statistically, the association between discoloration severity and colony fate after one year was found to be significant ($p = 0.03$, two-sided Fisher's exact test at the 0.05 significance level). The 2015 anomaly led to more variable responses within and between discoloration categories, although sample sizes were limited for highly or severely-discolored colonies.

DISCUSSION

Given the unprecedented decline of coral communities worldwide (Hughes et al. 2017; Souter et al. 2020; Eddy et al. 2021), understanding species-specific thermal tolerance may provide insight into which corals can withstand or recover from anthropogenic warming. While most *in situ* observational studies tend to categorize corals by their bleaching response (e.g., Hédouin et al. 2020; Raymundo et al. 2019; Caroll et al. 2017; Vargas-Ángel et al. 2011) or bleaching susceptibility index (following McClanahan 2004), bleaching based upon a definition of paling or discoloration is not a categorical process but rather continuous. Similarly, in response to a thermal anomaly, there are multiple possible outcomes for corals beyond whole-colony survival or complete mortality, since partial mortality also falls along a spectrum and coral tissue can regenerate or regrow (Glynn and Fong 2006; Loch et al. 2002). However, current analyses rarely consider the growth trajectories and bleaching proportions of individual coral colonies (but see: Ritson-Williams and Gates 2020; Matsuda et al. 2020), whether at the time of thermal anomalies (which in themselves can range in severity) or otherwise. Thus, when evaluating coral condition over time, it is important to quantify responses at the species and colony level while also taking into account thermal variability.

Palmyra experienced two thermal anomalies during this study, which differed in magnitude and duration. The first anomaly in 2009 was relatively mild (Williams et al. 2010) while the second was more thermally-severe and longer-lasting (Fox et al. 2019a). Here we explored species-specific responses to each of these anomalies by quantifying colony-level discoloration using a new photographic approach (Supp. materials). In addition to discoloration, we also measured changes in colony live area over time across the two reef habitats on Palmyra. We found that colonies generally responded more negatively to the second anomaly in terms of loss in live planar area and percent discoloration. For these 314 focal colonies, discoloration was higher at RT than FR throughout the time series; however, by 2019, community-wide coral cover declined on FR whereas it was maintained at RT. While the strength of SST anomaly was not directly predictive of discoloration, a colony's fate one year post-anomaly was associated with its level of discoloration at the time of warming.

Among the most-discolored species on Palmyra in 2015 was the branching *Stylophora pistillata*, whose colonies also showed the highest bleaching prevalence and severity in 2009 (Williams et al. 2010) and lost more live area than other species one year following each of the thermal anomalies (up to 35% on average in 2016). *S. pistillata* is relatively fast-growing and short-lived (i.e., "weedy"), as are *Pocillopora* spp. (Darling et al. 2013). Although we saw more whole-colony mortality and lower survivorship rates in *Pocillopora* across the 11-year time span, new individuals were established yearly throughout the time series. Live planar area in both *P. meandrina* and *P. damicornis* colonies varied over time and by SST anomaly, yet there was no significant effect of either time or anomalous temperature on their discoloration. Williams et al. (2010) similarly found that *Pocillopora* spp. had among the lowest bleaching prevalence on Palmyra in 2009. Meanwhile, *Goniastrea stelligera* and *Astrea curta*, both massive species which are generally thought to be more resistant to bleaching (Loya et al. 2001), showed higher bleaching prevalence in 2009 (Williams et al. 2010) and no significant variation in discoloration throughout the time series, yet lost much of their live area by 2019. Colonies of another massive species, *Pavona duerdeni,* were more stable in terms of both their live area trajectories and discoloration proportions and had the highest overall survivorship. However, it is worth noting the variability in responses within species, also seen in other studies (Matsuda et al. 2020), which may be attributed to individual differences such as colony size (Brandt 2009; Shenkar et al.

2005), initial bleaching extent (Neal et al. 2017), or the particular symbiont community structure (Cunning et al. 2016).

One limitation of our study is that we could not measure the responses of all common coral species on Palmyra at the colony level, nor look more closely at site-specific patterns. When using imagery to measure the growth and pigmentation of the same individual coral colonies through time, ideally the entire colony is in view; however, in our small-scale images (0.54 m^2 quadrats), colonies were often cut off by the photoquadrat frame and excluded from colony-level analyses, which constrained our sample sizes. Large-scale imagery (e.g., 100 m^2 photomosaics as in Edwards et al. 2017) might be better-suited for comprehensive analyses, although methods for quantifying precise bleaching proportions in individual colonies using this technology have not yet been developed. For our subset of species with sufficient colony sample sizes, we did not always have representatives from both habitat types. Bleaching responses on Palmyra have been found to vary by habitat, with more subsequent mortality on the fore reef yet limited mortality on the reef terrace (Fox et al. 2019a). Coral cover on Palmyra's fore reef has been gradually declining since 2015 whereas the reef terrace has generally remained stable (Khen et al. 2022). Aside from depth and wave exposure, Palmyra's reef habitats differ in their sedimentation and turbidity (Williams et al. 2010), hydrodynamic connectivity (Williams et al. 2018), pH and dissolved oxygen fluxes (Cyronak et al. 2020; Takeshita et al. 2016), and heterotrophic resource availability (Rogers et al. 2017). Given that abiotic and biotic factors likely influence local bleaching prevalence (Yee and Barron 2010; Fitt et al. 2001), it would be informative to consider additional environmental variables at the habitats or sites from which each coral colony was sampled.

Trajectories of colony live area and discoloration were in some cases significantly affected by the degree of thermal stress, which aligns with findings from previous studies (Knipp et al. 2020, Rodgers et al. 2017). We did not incorporate accumulated heat stress in the form of DHWs into our analyses because DHW on Palmyra is typically zero (other than at the time of mass bleaching events, where they reached 9.1 ºC-weeks by late November 2009 and 11.9 ºC-weeks by early October 2015; NOAA Coral Reef Watch), which would limit our predictive power. Instead, we used SST anomaly at the time of sampling, which was 0.81 ºC and 1.26 ºC, respectively, in September 2009 and 2015, and as low as -0.93 ºC in June 2012 (Supp. Fig. 3.5). This allowed us to examine natural variations in discoloration and how this may deviate from "normal" during anomalously high temperatures. In our study, heat-stress associated bleaching and natural paling were combined into one metric termed discoloration, but future studies could try to distinguish between them, using each metric separately where relevant. For example, quantifying only the heat-stress-related bleaching (as opposed to total discoloration) may have helped to clarify our results, in which percent discoloration was not significantly correlated to SST anomaly.

Nevertheless, there was a discernible yet nuanced relationship between the severity of discoloration of a particular colony at the time of warming and its fate one year post-anomaly. Previous studies have similarly found a significant positive association between bleaching severity and subsequent colony mortality (Williams et al. 2017; Matsuda et al. 2020), but our results further indicate how these responses may differ across successive thermal anomalies. Following the first, less thermally-severe anomaly in 2009, growth was the most common outcome in 2010 for all colonies regardless of their discoloration severity, and colonies with more discoloration had lower mortality rates and were more likely to grow. However, following the more thermally-severe anomaly in 2015, colony fates were more variable. Colonies with more discoloration in 2015 were less likely to grow in 2016, with many colonies experiencing shrinkage or whole-colony mortality. This suggests that perhaps under more stressful conditions, a colony's fate depends more so on other colony-specific characteristics (e.g., more thermally-tolerant coral and/or symbiont species or larger colony size) than its amount of discoloration. With coral reefs repeatedly facing large-scale disturbances due to climate change, these inter- and intraspecific factors may become more critical in governing bleaching tolerance or susceptibility.

Overall, this study demonstrates variability in coral responses by habitat and taxa in the context of thermal anomalies, emphasizing the need for more precise long-term monitoring at the species and individual colony level. Tracking parameters such as growth, bleaching or discoloration, recovery, and partial or whole-colony mortality in the same colonies at multiple points in time will improve our understanding of the effects of thermal stress on coral communities and their constituent taxa. Further, documenting the natural history of quasi-pristine, intact ecosystems such as Palmyra Atoll allows us to establish baseline information on coral reefs under global stressors, which is becoming increasingly relevant for the management and restoration of more-degraded reefs at higher risk of collapse.

ACKNOWLEDGMENTS

We thank the staff of The Nature Conservancy, U.S. Fish and Wildlife Service, and the Palmyra Atoll Research Consortium (PARC) for their logistical support and access to the refuge. We thank Gareth Williams, Brian Zgliczynski, Clinton Edwards, Amanda Carter, Samantha Clements, and Stuart Sandin for their assistance with fieldwork. We thank Karina Arzuyan, Marie Diaz, Sarah Romero, Kyle Conner, Shelley Hazen, and Kailey Ramsing for their help with image digitization. Adi Khen was supported by the National Science Foundation Graduate Research Fellowship and the Beyster Family Fellowship in Conservation and Biodiversity. Funding for this work was generously provided by the Scripps Family Foundation, the Bohn Family, and the Gordon and Betty Moore Foundation.

Chapter 3, in part, is currently being prepared for submission for publication of the material. Khen, Adi; Fox, Michael D; Johnson, Maggie D; Smith, Jennifer E. The dissertation author was the primary investigator and author of this material.

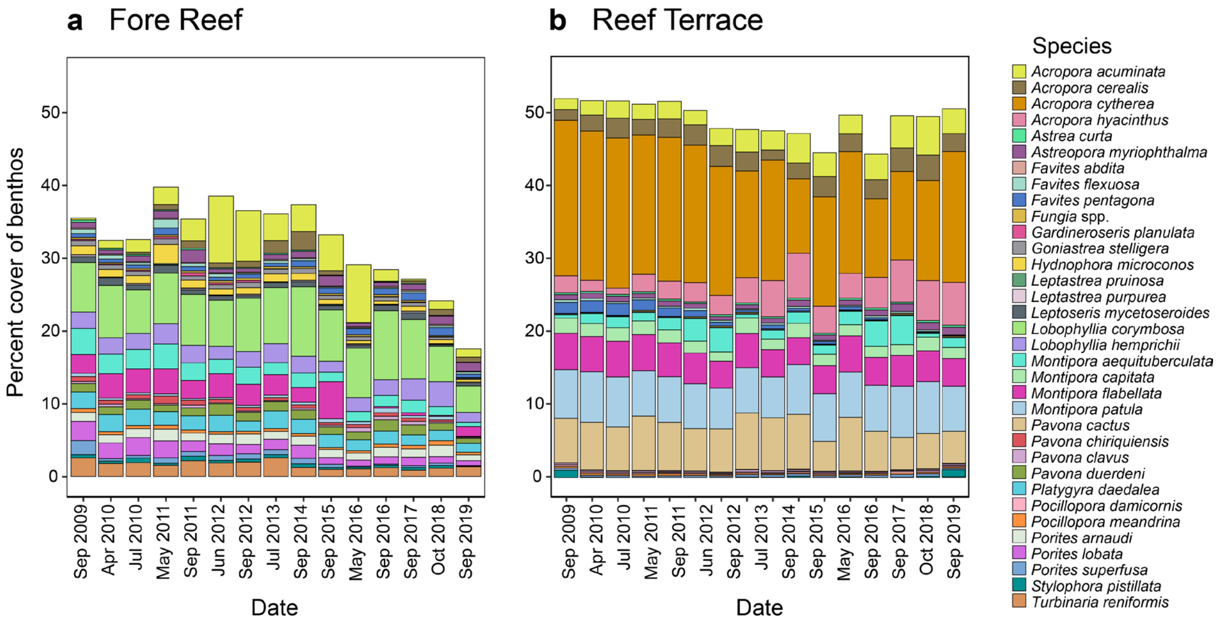


Figure 3.1: Mean percent benthic cover of hard corals (averaged across sites) at the **(a)** Fore Reef and **(b)** Reef Terrace habitats on Palmyra, by species, over time

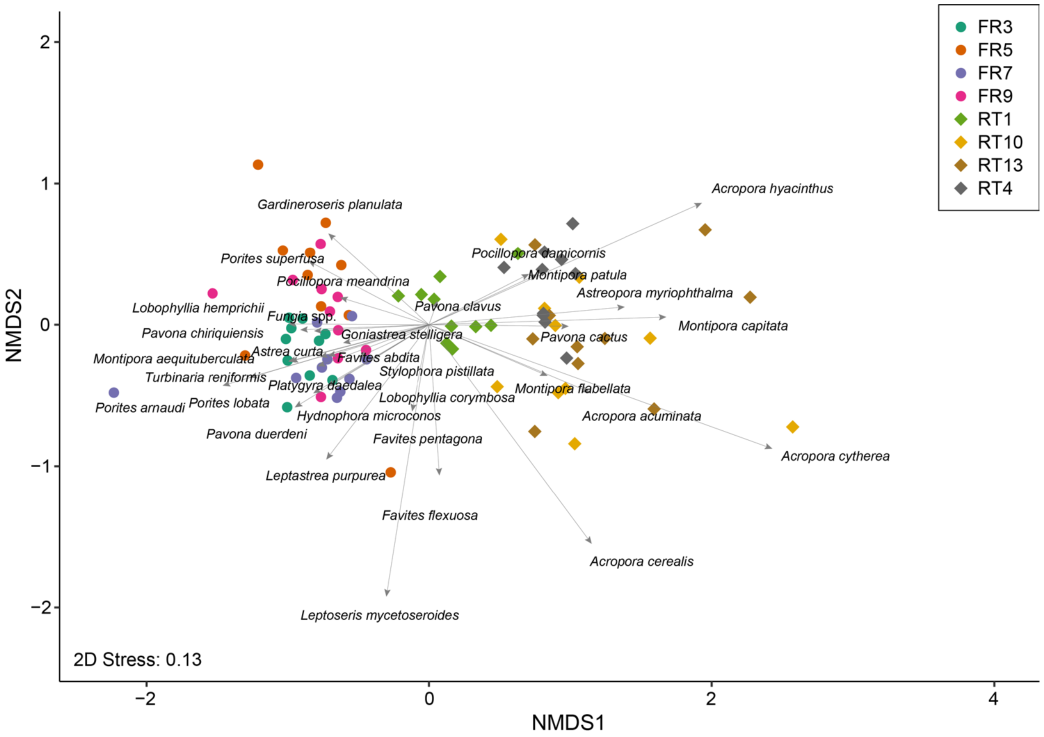


Figure 3.2: Non-metric multidimensional scaling (nMDS) based on Bray-Curtis dissimilarity measures of coral community composition by species (in terms of square-root-transformed percent cover data) at each site in 2009. Circles or diamonds represent replicate quadrats (n = 10) at sites from the Fore Reef (FR) or Reef Terrace (RT) habitats, respectively

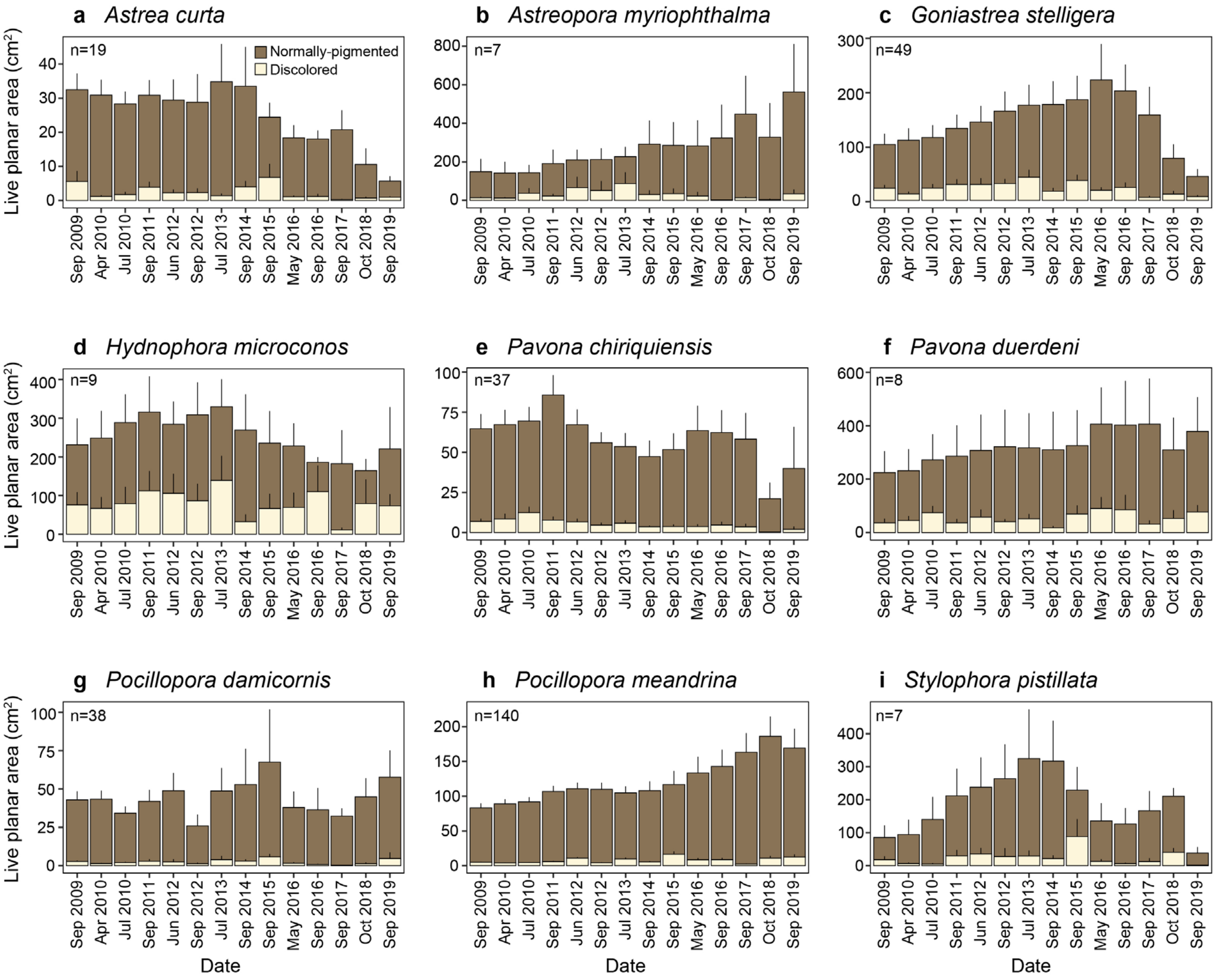


Figure 3.3: Discolored and normally-pigmented live planar areas (mean ± SE) for individual coral colonies over time by species. Colony sample sizes are shown on the top left

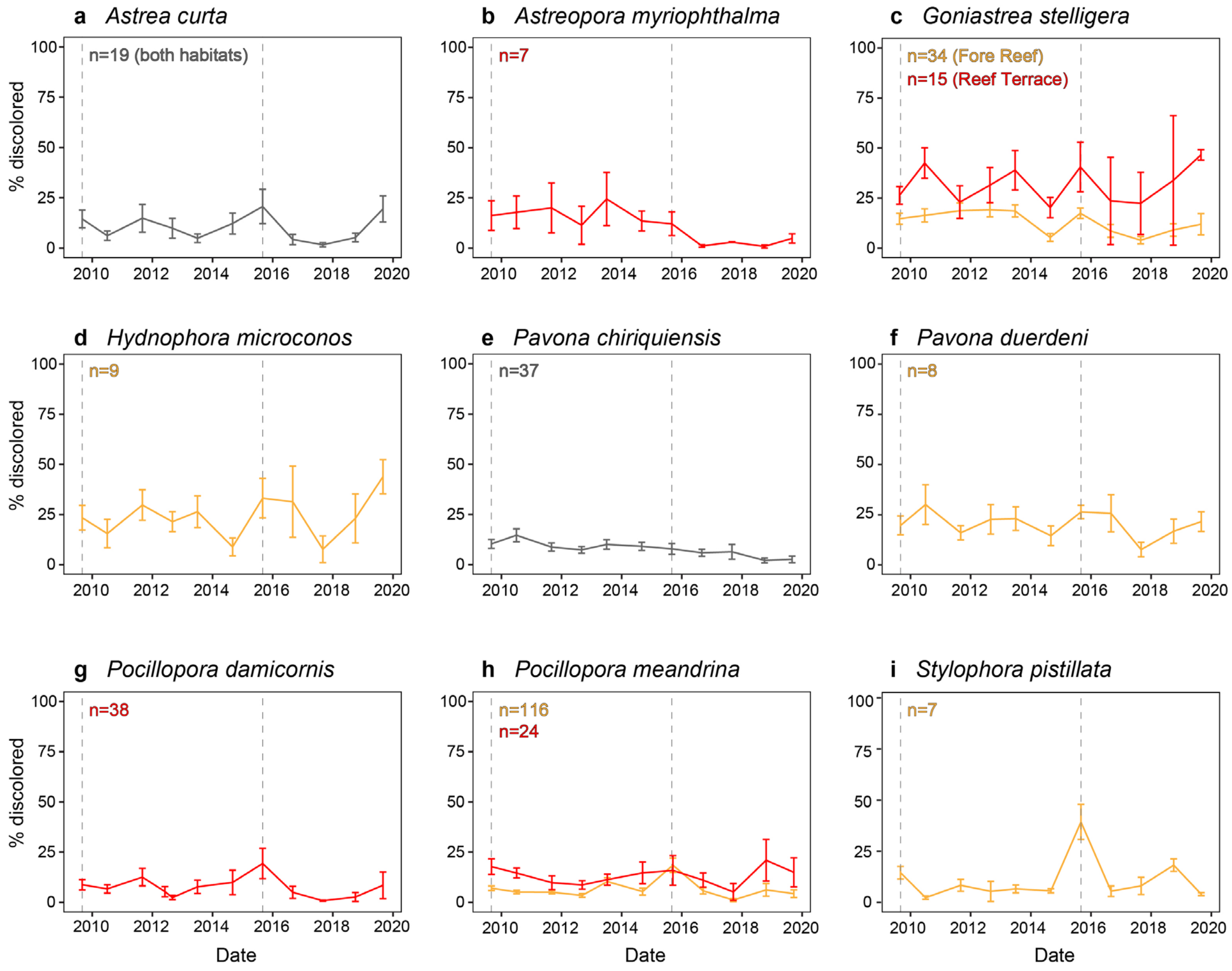


Figure 3.4: Percent discoloration (mean ± SE) for individual coral colonies over time by species and, where possible, habitat (Fore Reef in orange, Reef Terrace in red, and both in gray). Colony sample sizes are shown on the top left. Dashed vertical lines indicate thermal anomalies in 2009 and 2015

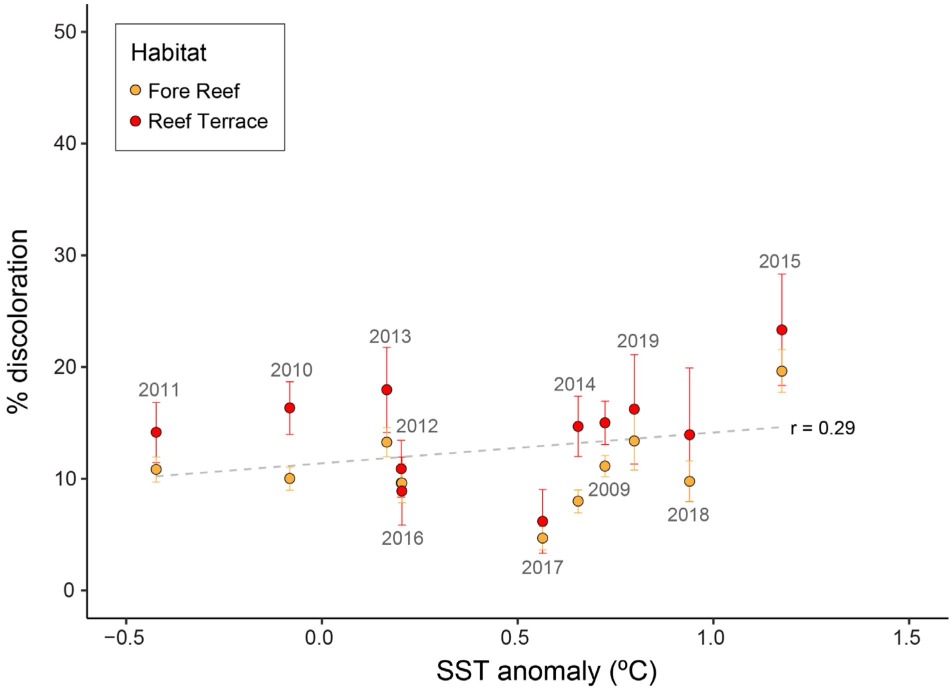


Figure 3.5: Scatterplot for percent discoloration (mean ± SE) by habitat (Fore Reef in orange, Reef Terrace in red) corresponding to the sea surface temperature anomaly at each observation time point, labeled by year. Pearson's correlation coefficient is shown on the right of the trendline

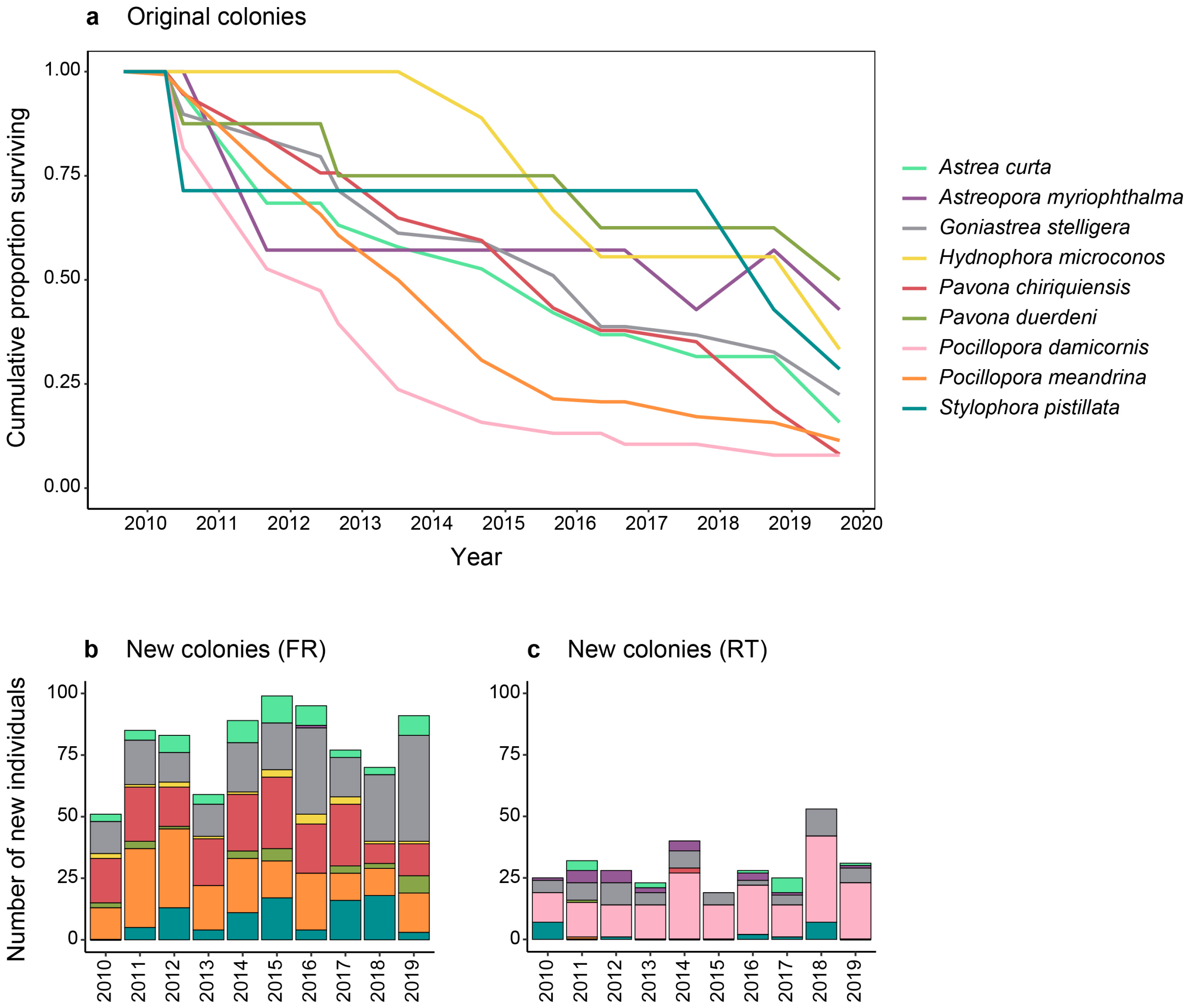


Figure 3.6: (a) Survivorship curves (for a subset of species) tracking the cumulative proportion of original colonies (i.e., since 2009) from both habitats surviving through 2019. The number of new individual colonies of these species per year are shown below for the **(b)** Fore Reef and **(c)** Reef Terrace habitats

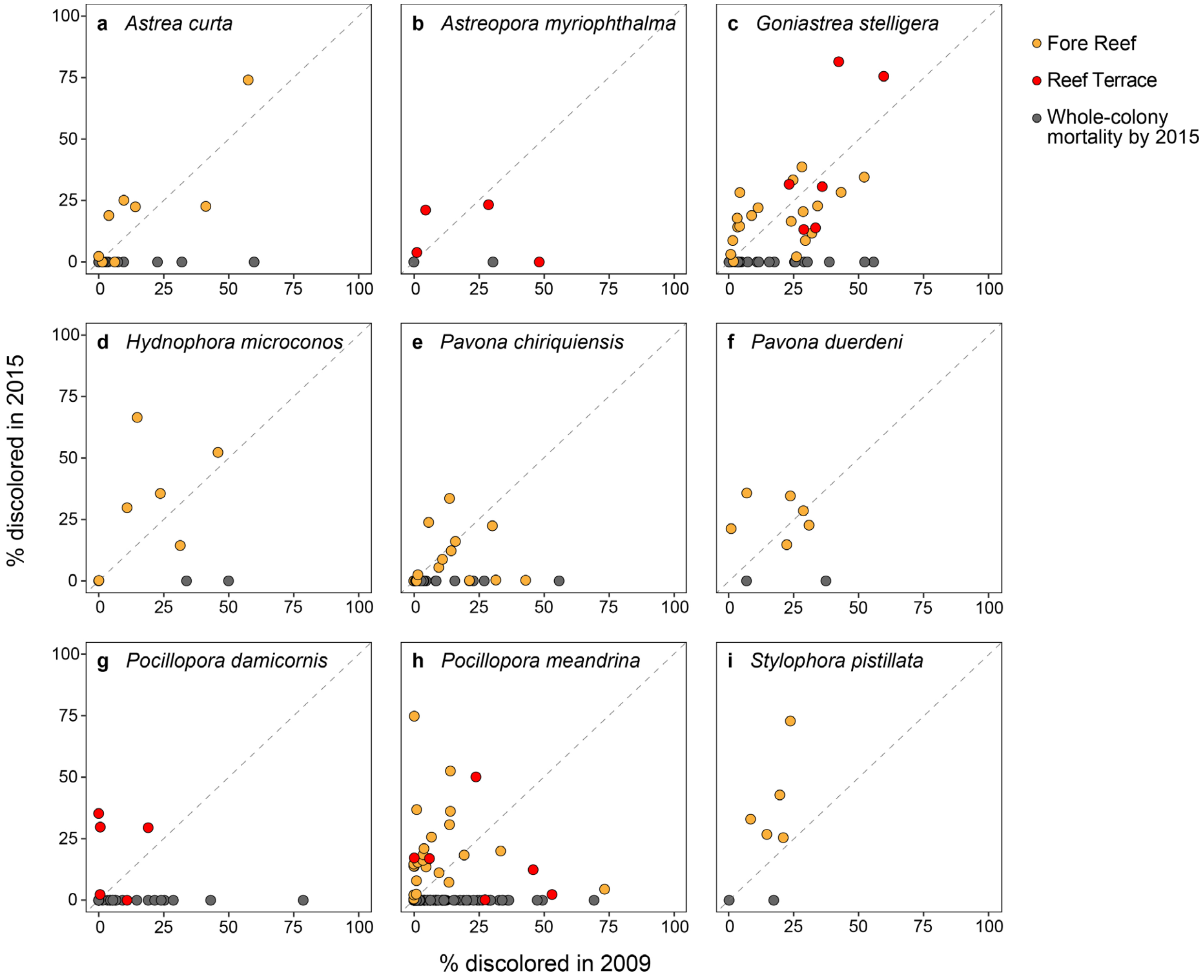


Figure 3.7: Scatterplots comparing percent discoloration in 2009 and 2015 for individual coral colonies by species. The diagonal dashed line indicates the 1:1 slope in which colonies were discolored by the same amount in both years. Each point represents a coral colony, color-coded by habitat with orange for Fore Reef and red for Reef Terrace; gray points represent whole-colony mortality by 2015

Table 3.1: Statistical output from a three-way PERMANOVA (9999 permutations) on Bray-Curtis similarities for square root-transformed coral species cover data by habitat, time, site (nested within habitat), and their interactions. Bold indicates statistical significance ($\alpha = 0.05$)

Source	Df	SumSqs	MeanSqs	F.Model	R^2	Pr(>F)
Habitat	1	110.52	110.523	417.63	0.240	**<0.001**
Time	16	5.07	0.317	1.20	0.011	0.066
Site(Habitat)	6	45.67	7.611	28.76	0.099	**<0.001**
Habitat * Time	15	4.43	0.296	1.12	0.010	0.168
Site(Habitat) * Time	84	7.86	0.094	0.35	0.017	1.000
Residuals	1084	286.88	0.265		0.623	
Total	1206	460.43			1.000	

Table 3.2: SIMPER output identifying the species contributing most to community composition differences between habitats

Species	Avg abundance at FR	Avg abundance at RT	Avg contribution to overall dissimilarity (± SD)	Cumulative contribution (%)
Montipora patula	0.155	22.293	0.288 (± 0.249)	29.63
Montipora flabellata	0.491	10.667	0.147 (± 0.183)	44.787
Pocillopora meandrina	4.357	0.298	0.059 (± 0.063)	50.866
Goniastrea stelligera	4.174	0.214	0.054 (± 0.066)	56.42
Porites arnaudi	3.431	0	0.042 (± 0.083)	60.782
Acropora cytherea	0	4.012	0.037 (± 0.156)	64.572
Acropora acuminata	0.449	2.461	0.037 (± 0.113)	68.335
Montipora capitata	0	2.378	0.036 (± 0.097)	72.087

Table 3.3: Statistical output from a Type-II ANOVA for the effects of month, habitat, and/or SST anomaly on live planar area of individual coral colonies, by species. Bold indicates statistical significance ($\alpha = 0.05$)

Species	Source	SumSqs	Df (num, den)	F value	Pr(>F)
Astrea curta	**Months**	19321.1	1, 260.78	83.630	**<0.001**
	SSTa	111.2	1, 260.88	0.481	0.489
Astreopora myriophthalma	**Months**	40275	1, 100	5.908	**0.017**
	SSTa	6813	1, 100	0.999	0.320
Goniastrea stelligera	**Months**	314303	1, 668.06	69.937	**<0.001**
	Habitat	40911	1, 49.33	9.103	**0.004**
	SSTa	8926	1, 668.14	1.986	0.159
	Months * Habitat	134741	1, 668.07	29.982	**<0.001**
Hydnophora microconos	**Months**	381920	1, 118.05	11.655	**<0.001**
	SSTa	40257	1, 118.14	1.229	0.270
Pavona chiriquiensis	**Months**	173182	1, 523.35	174.728	**<0.001**
	SSTa	7808	1, 523.19	7.878	**0.005**
Pavona duerdeni	Months	348.6	1, 112	0.043	0.835
	SSTa	15174.9	1, 112.01	1.889	0.172
Pocillopora damicornis	**Months**	68546	1, 542.68	124.021	**<0.001**
	SSTa	3225	1, 542.85	5.835	**0.016**
Pocillopora meandrina	**Months**	705149	1, 1934.47	200.166	**<0.001**
	Habitat	46693	1, 182.07	13.254	**<0.001**
	SSTa	29339	1, 1931.68	8.328	**0.004**
	Months * Habitat	58568	1, 1931.89	16.625	**<0.001**
Stylophora pistillata	Months	12811.6	1, 96.999	1.016	0.316
	SSTa	7.7	1, 97.001	0.001	0.980

Table 3.4: Statistical output from a Type-II ANOVA for the effects of month, habitat, and/or SST anomaly on percent discoloration of individual coral colonies, by species. Bold indicates statistical significance (α = 0.05)

Species	Source	SumSqs	Df (num, den)	F value	Pr(>F)
Astrea curta	Months	4.215	1, 160.06	0.030	0.863
	SSTa	101.142	1, 149.83	0.719	0.398
Astreopora myriophthalma	**Months**	1429.14	1, 65.985	7.398	**0.008**
	SSTa	7.93	1, 62.082	0.041	0.840
Goniastrea stelligera	Months	644.65	1, 439.09	2.889	0.090
	Habitat	2069.77	1, 67.74	9.274	**0.003**
	SSTa	104.15	1, 413.52	0.467	0.495
	Months * Habitat	666.39	1, 446.92	2.986	0.085
Hydnophora microconos	Months	622.90	1, 93.868	2.239	0.138
	SSTa	0.23	1, 91.82	0.001	0.977
Pavona chiriquiensis	**Months**	2059.58	1, 347.18	18.170	**<0.001**
	SSTa	3.01	1, 327.77	0.027	0.871
Pavona duerdeni	Months	13.578	1, 89.978	0.072	0.789
	SSTa	163.716	1, 87.872	0.872	0.353
Pocillopora damicornis	Months	4.487	1, 206.82	0.053	0.818
	SSTa	38.305	1, 196.52	0.455	0.501
Pocillopora meandrina	Months	139.68	1, 1073.67	1.242	0.265
	Habitat	2653.29	1, 206.41	23.587	**<0.001**
	SSTa	23.46	1, 965.03	0.209	0.648
	Months * Habitat	17.64	1, 1072.79	0.157	0.692
Stylophora pistillata	Months	9.45	1, 71.553	0.077	0.782
	SSTa	805.88	1, 69.872	6.583	**0.012**

Table 3.5: Percent change (mean ± SE) in live planar area for individual colonies by species, one year following the thermal anomalies in 2009 and 2015. Positive change (i.e., growth) is shaded in green, negligible change (defined as <5%) in gray, and negative change (i.e., partial mortality) in red. Sample sizes are inconsistent across anomalies because of some cases of whole-colony mortality by 2015

	1st thermal anomaly		**2nd thermal anomaly**	
Species	Colony sample size	% change in colony live area one year later (mean ± SE)	Colony sample size	% change in colony live area one year later (mean ± SE)
Astrea curta	18	13.5 ± 11.9	8	-8.6 ± 23.7
Astreopora myriophthalma	7	18.1 ± 17.6	4	-9.5 ± 16.3
Goniastrea stelligera	46	37.3 ± 23.9	25	-28.6 ± 10.1
Hydnophora microconos	6	7.6 ± 7.1	6	-13.2 ± 32.2
Pavona chiriquiensis	36	11.4 ± 11.5	16	2.3 ± 16.7
Pavona duerdeni	8	2.8 ± 20.1	6	-1.6 ± 22.8
Pocillopora damicornis	38	-13.2 ± 16.2	5	-17.6 ± 22.8
Pocillopora meandrina	139	36.8 ± 7.5	30	11.9 ± 10.9
Stylophora pistillata	7	-6.6 ± 25.1	5	-34.8 ± 15.6
Average (all species)	305	23.4 ± 5.7	105	-7.4 ± 5.7

Table 3.6: Transition matrices showing the likelihood of different fates for individual coral colonies one year after the **(a)** 2009 and **(b)** 2015 thermal anomalies, based on their discoloration at the time of warming. Colony sample sizes within each discoloration category are indicated in the first column and boxes are shaded according to greater likelihood of outcome. For example, of the 37 colonies that were not at all discolored in 2009, 73.0% of colonies grew the following year while 16.2% of colonies shrank and 10.8% were completely dead by 2010

a

		Colony fate in 2010		
		Growth	Shrinkage	Mortality
Discoloration in 2009	**0%** (n=37)	73.0%	16.2%	10.8%
	<25% (n=209)	63.2%	32.1%	4.8%
	25-50% (n=48)	56.3%	35.4%	8.3%
	50-75% (n=10)	90%	10%	0%
	>75% (n=1)	100%	0%	0%

b

		Colony fate in 2016		
		Growth	Shrinkage	Mortality
Discoloration in 2015	**0%** (n=7)	57.1%	14.3%	28.6%
	<25% (n=60)	50%	43.3%	6.7%
	25-50% (n=24)	41.7%	41.7%	16.7%
	50-75% (n=6)	33.3%	50%	16.7%
	>75% (n=2)	0%	50%	50%

SUPPLEMENTARY MATERIALS

Image Digitization Methods

Images were analyzed in Adobe Photoshop (Creative Cloud). First, the raw images were white-balanced using the whitest point on the photoquadrat frame. The borders of all live coral areas were traced manually with the pencil tool (2-pixel width) on a duplicate image layer. The paint bucket was then used to fill in each coral colony with the corresponding genus/species swatch color to the finest possible taxonomic resolution. Coral colonies of all species were each assigned an identification number and digitally labeled; this was useful for tracking the same individual colonies' changes in planar areas throughout the rest of the time series. Next, while having coral areas selected via the magic wand, the color range command in Photoshop was used to detect "highlights," otherwise known as the discolored surface coral tissue. Essentially, this tool is converting the entire image (or selected regions) to grayscale to isolate only certain pixels based on a pre-determined brightness threshold (Supp. Fig. 3.2). Fuzziness was set to 0% and range was set to 190; the Fuzziness setting increases or decreases the number of partially-selected pixels and range (i.e., of brightness) is measured on a scale from 0 (black) to 255 (white). If range is set to 255, it will select pure white (i.e., totally bleached) pixels; if range is set to ~190, it will also select partially-bleached or discolored pixels. We chose 190 because this range of values (190-255) has been proven to be most comparable to a human's by-eye bleaching designations (see further justification below).

Discoloration was filled in with solid white on another image layer using the paint bucket; however, if for some reason the computer was not accurate in its designations, we manually corrected them. Discrepancies were largely caused by unfavorable lighting conditions at the time the pictures were taken; for example, in the case of overexposure, the computer may have detected more artificial "whiteness," which the human would erase accordingly. Alternatively, if corals were under a shadow at the time when the picture was taken and thus discoloration was not picked up by the computer, the human would consult their judgment and add in those areas by hand. Thus, although discoloration detection is carried out semi-automatically using Photoshop-based tools, it ultimately relies on human expertise, allowing for efficiency, objectivity, and accuracy.

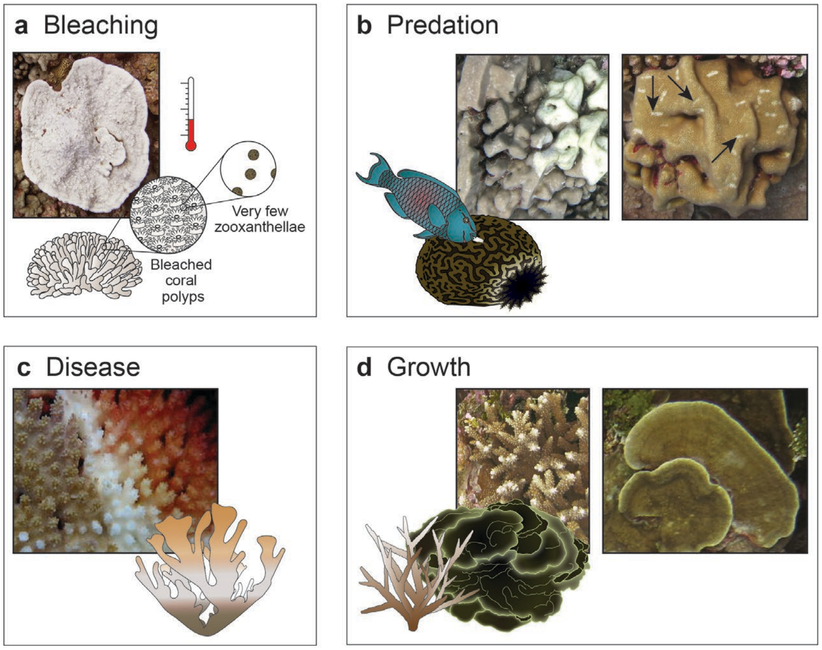
Data were extracted directly in Photoshop by first using the magic wand tool to select the color that corresponded to the corals being measured, one species or colony at a time. The 'contiguous' setting was turned on (this will select only pixels that are touching one another). Tolerance was set to 0 (only selecting pixels of the same exact color value). Next, the image analysis tool was used to find total planar area measurements of each live coral colony as well as discoloration within that colony. The measurement scale was set to custom and the ruler was placed along the distance between the inner corners of either the long or short edge of the photoquadrat frame, whichever was completely in the image. The logical length was either 90 or 60 (for the long or short edge, respectively), and the logical units were centimeters. When generating measurements, Photoshop converts the pixel counts to planar areas in cm^2. This process was repeated for each coral colony, recording both the total (live) and discolored planar areas; the difference between them is the normally-pigmented coral planar area.

Discoloration Detection: Justification for Choosing a Grayscale Range

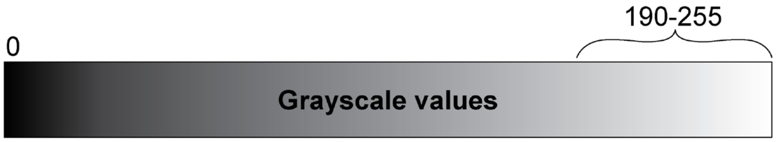
Although the grayscale range 190-255 for detecting coral discoloration may seem arbitrary, the lower limit of 190 has been tested against every other possible value between 165 and 215, in increments of 5, for discolored pixel counts within all coral colonies from a random subset of images (n = 58 images total from multiple sites and time points) that were analyzed both “by-eye” (i.e., derived from a human expert’s hand-tracings, assuming these are the most trustworthy) and semi-automatically using Photoshop. Results showed that having 190 as the lower limit of the range leads to a nearly negligible difference on average from what would be selected “by-eye” (Supp. Fig. 3.3). Any value below or above 190 would, respectively, over- or underestimate discoloration.

Discoloration Detection: Justification for Choosing a Photo-Editing Method

Similarly, we must also recognize that the photo-editing method on a raw image (e.g., unedited, color-corrected, or white-balanced) will affect the brightness of the image, which in turn could yield slightly different discoloration amounts detected by Photoshop. As such, we have compared the “by-eye” (human-designated) discolored pixel counts to those obtained semi-automatically in Photoshop for the same subset of images. Results showed that either color-corrected or white-balanced images are the most similar to “by-eye” on average (Supp. Fig. 3.4). However, considering that we are measuring discoloration for the same colonies over time, we want to avoid the outliers (likely due to overexposure) associated with color-correcting the image. Thus, white-balancing the images was chosen as the appropriate photo-editing method because it most closely matches “by-eye” designations with relatively fewer outliers.

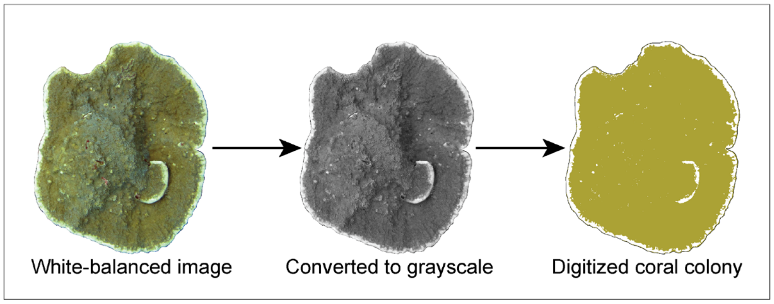


Supp. Figure 3.1: Examples of coral discoloration from Palmyra and their respective causes, resulting from **(a)** thermal stress (otherwise known as bleaching) or naturally through **(b)** predation, **(c)** disease, or **(d)** growth

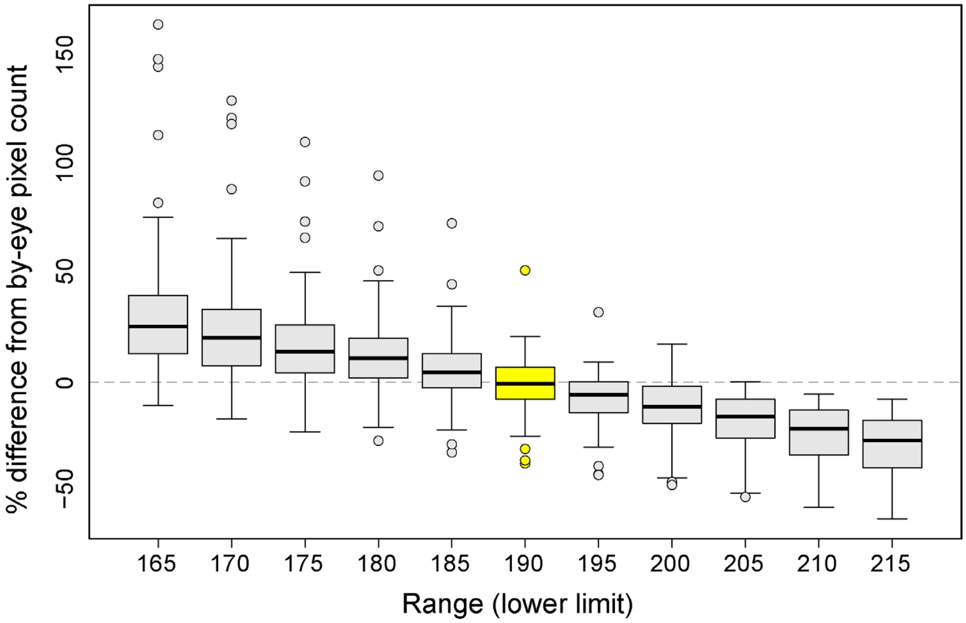


Steps:

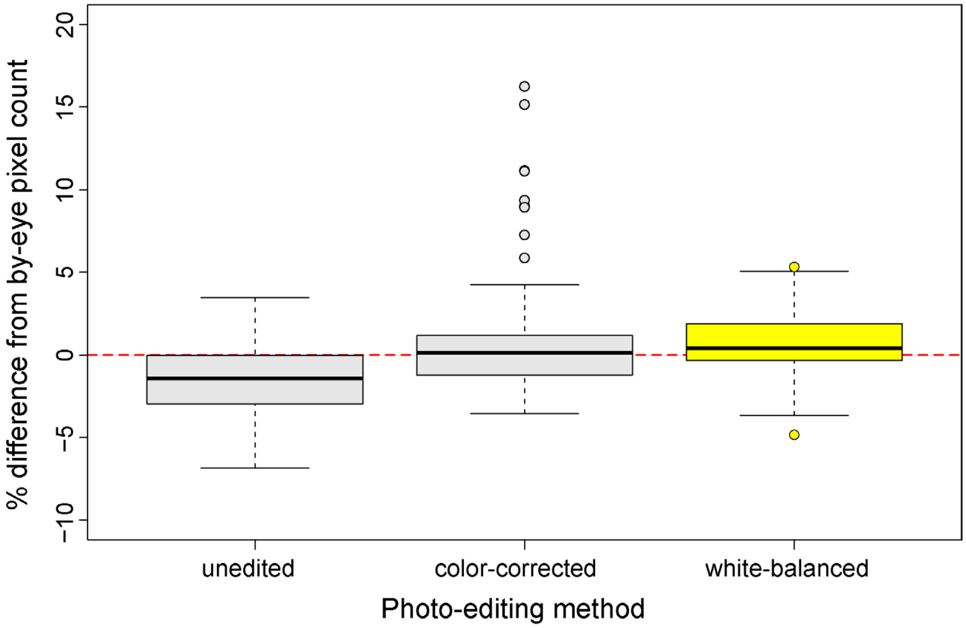
1) Trace the borders of the coral colony
2) Convert the image to grayscale
3) Select pixels within the range 190-255
4) Fill in discoloration with white
5) Quantify total and discolored planar areas



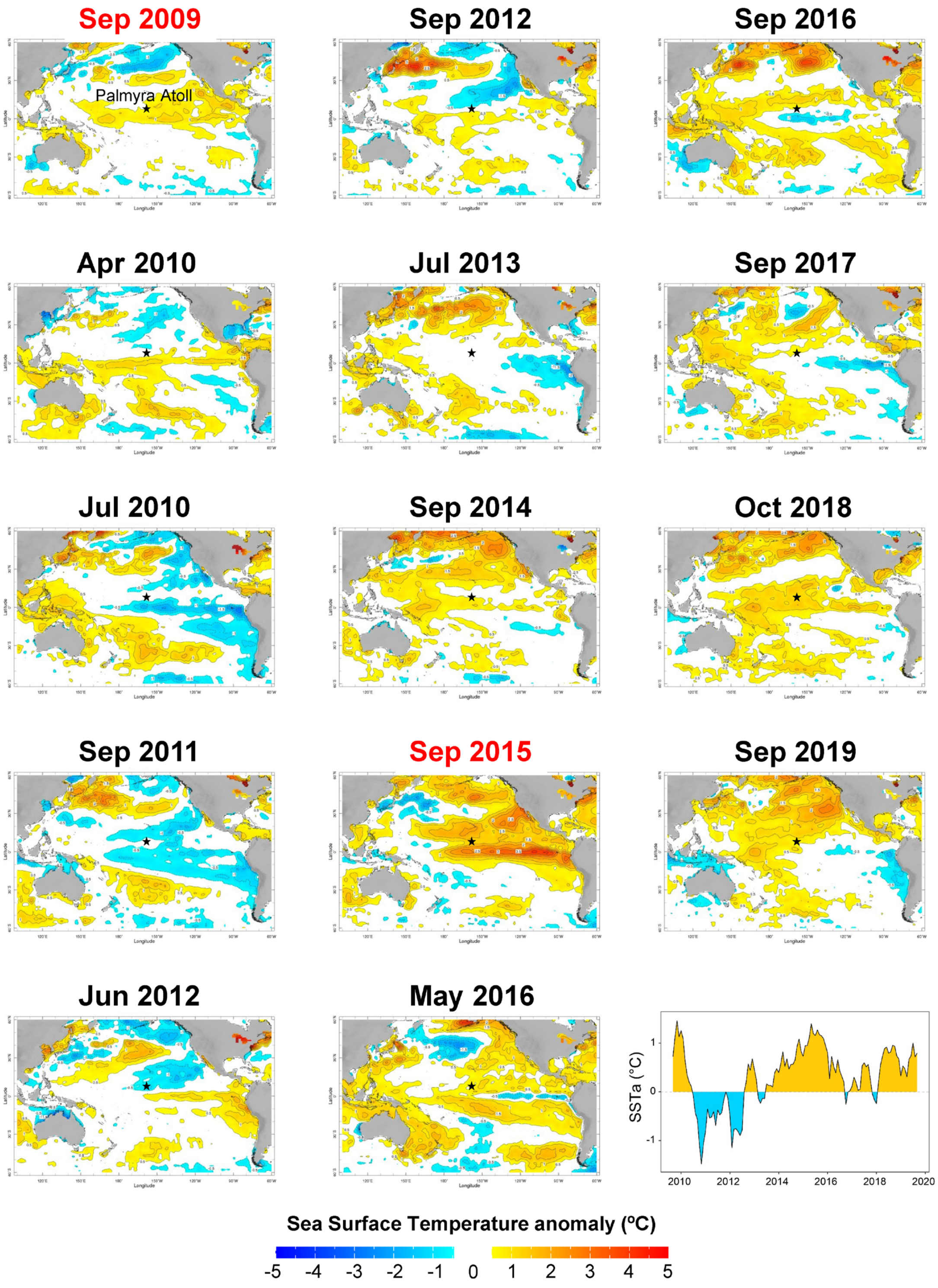
Supp. Figure 3.2: Image digitization process for detecting coral discoloration using grayscale



Supp. Figure 3.3: Boxplots comparing the discoloration detected semi-automatically using various grayscale ranges to "by-eye" (i.e., human-designated) discoloration

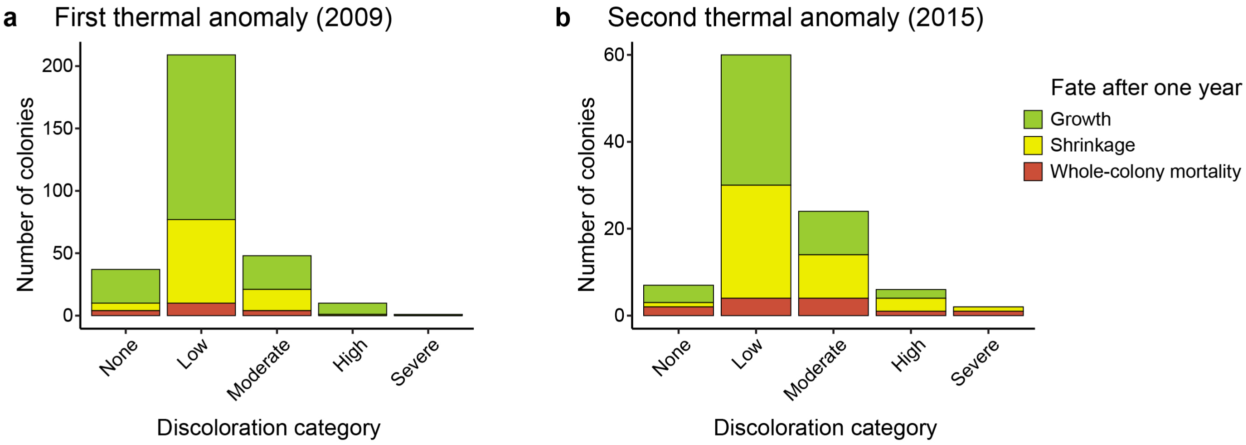


Supp. Figure 3.4: Boxplots comparing the discoloration detected semi-automatically using various photo-editing methods to "by-eye" (i.e., human-designated) discoloration



Data sources: Reynolds and Smith OISST
Version 2 & NOAA's Coral Reef Watch 50-km

Supp. Figure 3.5: Maps showing sea surface temperature anomalies (SSTa) on Palmyra Atoll (denoted by a black star) at each observation time point; red labels indicate mass coral bleaching events in 2009 and 2015. Palmyra's thermal history from 2009 to 2019 in terms of SSTa is plotted on the bottom right



Supp. Figure 3.6: Histograms showing the number of colonies from each discoloration category experiencing growth (in green), shrinkage (yellow), or whole-colony mortality (red) one year following the **(a)** 2009 and **(b)** 2015 thermal anomalies

Supp. Table 3.1: Sample sizes for colony-specific analyses, by species at each habitat. Overall, 314 individual colonies from nine different species were tracked in total. Only colonies that were fully within the photoquadrat frame were included in colony-specific analyses

Species	Fore Reef (FR)	Reef Terrace (RT)	Total
Astrea curta	18	1	19
Astreopora myriophthalma	0	7	7
Goniastrea stelligera	34	15	49
Hydnophora microconos	9	0	9
Pavona chiriquiensis	36	1	37
Pavona duerdeni	8	0	8
Pocillopora damicornis	0	38	38
Pocillopora meandrina	116	24	140
Stylophora pistillata	7	0	7
Grand total	228	86	314

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CHAPTER 4: Coral Reef Algal Community Dynamics on Palmyra Atoll Across a Decade and Two Large-Scale Thermal Anomalies

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ABSTRACT

Coral reef algae provide various ecological functions, from primary productivity to nutrient uptake and reef stabilization, and their growth is known to be influenced by environmental conditions. While effects of increased seawater temperature on tropical algae are commonly studied in short-term laboratory manipulations, information on longer-term dynamics of *in situ* algal communities is lacking. It is generally thought that following a warm-water period and subsequent coral mortality, algal cover should increase, potentially driving a phase shift to a macroalgal-dominated state. However, given their vast morphological and taxonomic diversity, algal responses are variable and may be specific to species, genus, or functional group (i.e., turf, crustose coralline algae, and macroalgae). We used a long-term monitoring time series data set to investigate the temporal dynamics of benthic algae on Palmyra Atoll, central Pacific, in the context of temperature. We quantified the percent cover of each algal taxon via image analysis of permanent benthic photoquadrats taken at two habitats on Palmyra: the fore reef (10 m depth) and reef terrace (5 m depth), yearly from 2009 to 2019. We found that habitats were characterized by distinct algal communities which fluctuated over time and/or in response to thermal anomalies that occurred in 2009 and 2015. Further, the abundance of fleshy and calcareous macroalgae was associated with monthly mean sea surface temperatures and in particular, the macroalgal genus, *Halimeda* spp., showed evidence of temperature sensitivity.

Given that some algal taxa contribute significantly to reef building as well as sand, sediment, and carbonate production, understanding their responses to thermal stress will be critical as climate change continues to jeopardize the future health of coral reefs.

INTRODUCTION

Benthic algae are key components of coral reefs and the abundance (or lack thereof) of one functional group or taxon over another can have implications for the type of ecosystem services provided (Woodhead et al. 2019). Although many coral reefs are shifting from coral to algal dominance (Hughes et al. 2017; Pandolfi et al. 2003; McManus and Polsenberg 2004), algae themselves have often been overlooked and understudied despite their functional, morphological, and taxonomic diversity (Fong and Paul 2011). While marine heatwaves are thought to lead to the proliferation of algae (Anton et al. 2020; Graham et al. 2015), less is known about how individual algal taxa or groups will respond to a combination of stressors (Wernberg et al. 2012). Laboratory-based experiments have assessed the short-term effects of elevated temperature and acidification on algal growth, calcification, and/or photosynthesis, finding contrasting responses between fleshy and calcareous algae (Johnson et al. 2014), but *in situ* studies can reveal longer-term dynamics of benthic algal communities.

Crustose coralline algae (CCA) are encrusting, calcifying red algae that serve as active reef builders along with hard corals. CCA secrete calcium carbonate, solidifying the reef framework and protecting against wave or storm damage (Littler 1972), thus increasing a given reef's capacity to build structurally-complex features (Setchell 1930). They promote reef growth by releasing chemical cues for larval corals and other invertebrates to settle (Harrington et al. 2004). Under prolonged periods of elevated seawater temperature, high mortality rates have been observed in CCA in both experimental and field settings (Anthony et al. 2008; Martin and Gattuso 2009; Short et al. 2015). Turf algae are a diverse multi-species assemblage of largely fleshy filamentous algae, juvenile macroalgae, and/or cyanobacteria that are typically less than 2 cm tall (Adey and Steneck 1985). They tend to be competitive, opportunistic, and are rapid colonizers of open space, especially after disturbances such as coral bleaching and disease outbreaks (Diaz-Pulido and McCook 2002). They can inhibit coral recruitment (Birrell et al. 2008) and have also been found to harbor pathogenic microbes that alter the coral microbiome and compromise coral health (Pratte et al. 2018). Though often considered "bare space," ecologically, they are important primary producers and a main food source for grazers (Carpenter 1986). Not only are they already occupying much of the benthos on today's reefs (Wismer et al. 2009), since they are known to thrive under conditions that threaten corals, including nutrient pollution (Smith et al. 2010), ocean acidification (Falkenberg et al. 2013), and sedimentation (Birrell et al. 2005), they will likely become more abundant with warming (Tebbett and Bellwood 2019; Harris et al. 2015).

Fleshy macroalgae typically grow faster than calcareous macroalgae and are a preferred (i.e., more palatable) food source to herbivores such as fish or urchins. However, fleshy macroalgae are potentially harmful to corals via abrasion or releasing chemical compounds, including toxic allelochemicals, through direct physical contact (McCook et al. 2001; Rasher et al. 2012). Fleshy algae can also cause hypoxia along competitive borders with corals, leading to physiological stress (Barott et al. 2012) by limiting photosynthetic activity and depleting the corals of energy (Titlyanov et al. 2007). However, shading by macroalgae may also protect some corals from bleaching (Jompa and McCook 2003). Calcareous algae are generally considered more benign competitors than fleshy algae when interacting with corals (Barott et al. 2012; but see: Longo and Hay 2015, where corals frequently experienced damage when contacted by calcareous algae), although their competitive ability may be influenced by seasonality (Brown et al. 2020). The relative balance of fleshy (turf and fleshy macroalgae) to reef-building taxa (corals and CCA) may be indicative of degraded vs. healthier reefs (Smith et al. 2016). Therefore, to holistically evaluate the ecological implications of stressors such as warming, it may be informative to look not only at variability across individual algal taxa or functional groups but also between fleshy and calcareous algal cover.

The macroalgal genus *Halimeda* is a siphonous, calcareous group of green algae that contribute principally to productivity and calcification on coral reefs worldwide (Hillis-Colinvaux 1980). In fact, *Halimeda* spp. may contribute more to tropical carbonate budgets than corals (Rees et al. 2007) due to their fast growth and high turnover rates (Vroom et al. 2003; Smith et al. 2004). They provide nutrition for parrotfish (Hamilton et al 2014), although they can also contain chemical defenses to deter grazing (Hay et al. 1988). Most species of *Halimeda* are holocarpic and as such, they die after reproducing and their calcified segments break down into sand, producing a large percentage of local sediment (Harney and Fletcher 2003). *Halimeda* spp. are synchronous spawners that release all of their gametes simultaneously, leading to complete adult mortality (Hay 1997), although the exact mechanisms that trigger their reproduction are unknown (Clifton 2013; Clifton and Clifton 1999). Considering the high abundance, cosmopolitan distribution, and ecological significance of *Halimeda* spp., it is important to monitor their cover on a consistent basis as well as before, during, and after thermal anomalies. Few studies have examined the long-term changes in cover of *Halimeda* spp. *in situ* (but see: Lambo and Ormond 2006, where *Halimeda* cover decreased in Kenya at the time of the 1998 coral bleaching event but increased drastically by 2004).

Here, we measured benthic algal cover within an 11-year time series of permanent photoquadrats from two reef habitats on the remote, uninhabited Palmyra Atoll, which experienced thermal anomalies in 2009 and 2015 (Williams et al. 2010; Fox et al. 2019). A comprehensive analysis of Palmyra's algal communities has not been conducted since 2008 (Braun et al. 2009). Our goals were to describe algal community composition on the fore reef and reef terrace habitats, track the abundance of individual algal taxa or functional groups, compare fleshy (turf and fleshy macroalgae) vs. calcareous (CCA and calcareous macroalgae) cover, and determine whether this varied over time and/or co-varied with temperature. Additionally, for the major calcareous macroalgal genus, *Halimeda*, we quantified yearly changes in cover by habitat and site to explore our hypothesis that *Halimeda* spp. may be temperature-sensitive and negatively affected by warm-water periods.

METHODS

Study Site

Palmyra Atoll (5.89 ºN, 162.08 ºW) is situated within the Northern Line Islands, central Pacific, in the low-pressure area of the intertropical convergence zone. Palmyra was designated as a National Wildlife Refuge in 2001 and this protection was further expanded in 2009 as part of the Pacific Remote Islands Marine National Monument. The Atoll was temporarily occupied by the U.S. military during WWII but is currently uninhabited aside from a field research station. Thus, its reefs are considered quasi-pristine (Sandin et al. 2008) and relatively undisturbed from human impact. Palmyra's benthic communities are dominated by reef builders such as hard corals and CCA, with remaining surfaces covered by turf algae, macroalgae, soft corals, and other invertebrates (Williams et al. 2013; Braun et al. 2009).

Data Collection

In September 2009, permanent monitoring plots (90 cm x 60 cm) were established in the two primary reef habitats on Palmyra: the wave-exposed fore reef (FR) at 10 m depth and the wave-sheltered reef terrace (RT) at 5 m depth, with four sites at each habitat and ten plots per site. Plots were marked using stainless steel eye bolts in opposing corners and secured with marine epoxy; replicate plots were 5 m apart along a 50 m transect perpendicular to shore. At least once a year from 2009 to 2019, typically in the late summer or early fall, plots were photographed by SCUBA divers using a digital camera on a PVC frame. All images were digitized (i.e., manually traced) in Adobe Photoshop (Creative Cloud) to quantify abundance of algal taxa in terms of planar areas and percent cover, at the functional group level for CCA and turf, and genus or species-level for macroalgae. Palmyra's sea surface temperature record was obtained from the National Oceanic and Atmospheric Administration's Coral Reef Watch twice-weekly 50-km product (https://coralreefwatch.noaa.gov/data3/50km/vs/timeseries/vs_ts_PalmyraAtoll.txt).

Statistical Analyses

All analyses were conducted in R software version 3.6.3 (R Core Team 2018). First, using only yearly time points taken during the late summer or fall (excluding irregular time points to avoid seasonal variation), we constructed a non-metric multidimensional scaling (nMDS, via *metaMDS* in *vegan* for R; Oksanen et al. 2019) ordination plot visualizing the trajectory of algal community composition through time at each habitat. This nMDS was based on Bray-Curtis dissimilarity measures for square-root-transformed algal percent cover data. We applied a square-root transformation to balance the effect of disproportionately-abundant taxa.

We tested the effects of habitat, year, and/or their interaction by conducting a three-way permutational multivariate analysis of variance (PERMANOVA with 9999 permutations via *adonis* in *vegan*; Anderson 2001, Oksanen et al. 2019) on the same Bray-Curtis distance matrix. We did not include site as a nested factor because not all algal taxa were present at each site within a habitat. To identify which algal taxa were the main contributors to differences among habitats, we ran a SIMPER or "similarity percentages" analysis (via *simper* in *vegan*; Clarke 1993, Oksanen et al. 2019).

Algal taxa were grouped as either calcareous (CCA, *Halimeda* spp., *Galaxaura rugosa*, and *Peyssonnelia* spp.) or fleshy (*Avrainvillea amadelpha*, *Lobophora variegata*, *Dictyosphaeria cavernosa*, *Caulerpa serrulata*, and turf). Then, to explore possible effects of monthly mean sea surface temperature (SST) on calcareous vs. fleshy algae over time, we ran three-way analyses of covariance (ANCOVAs) separately by algal group, testing whether percent cover varied by habitat, year, and/or co-varied with temperature. Assumptions of normality of residuals and homogeneity of variance were met. Habitat and year were both considered fixed factors whereas temperature was continuous; only monthly mean SST values at the time of yearly sampling were included in the analysis. We did not incorporate repeated measures and instead treated years independently because different algal populations were sampled each year rather than the same individuals. Post-hoc letter groupings were assigned via Tukey multiple comparisons.

The ANCOVA and multiple comparisons across years were repeated on a single taxon of interest, *Halimeda*, using square-root-transformed percent cover data to normalize the distribution of residuals and correct for zero-inflation (since *Halimeda* spp. were not present in all quadrats). To investigate patterns in abundance for this particular genus, we also plotted its percent cover within each quadrat, by site, over time. Lines were smoothed by local regression (i.e., LOESS in *ggplot2*; Wickham 2016). Finally, we calculated the difference in mean percent cover of *Halimeda* by site (with quadrats as replicates) between consecutive years. Two-tailed t-tests were used to determine which sites experienced significant changes not overlapping zero (e.g., an increase or decrease in percent cover one year later).

RESULTS

Algal Community Composition at Each Habitat Over Time

The algal community on Palmyra's fore reef consisted of relatively more CCA, *Peyssonnelia*, and *Halimeda* whereas the reef terrace consisted of a greater abundance of turf algae, *Lobophora*, and *Dictyosphaeria* (Fig. 4.1). Certain taxa were only present in either habitat: *Galaxaura rugosa* on the reef terrace and *Avrainvillea amadelpha* on the fore reef. Overall, the most abundant algal taxa or groups on Palmyra included CCA (exhibiting a percent cover range of 0 to 87.6% within a single quadrat, average = 20.3%), turf (percent cover = 0 to 88.3%, average = 16.7%), and *Halimeda* (percent cover = 0 to 92.3%, average = 8.4%). The least abundant algal taxa were *Avrainvillea* (percent cover = 0 to 1.7%, average = 0%), *Dictyosphaeria* (percent cover = 0 to 27.1%, average = 0.4%), and *Caulerpa* (percent cover = 0 to 46.6%, average = 0.6%). In an nMDS for the yearly trajectories of algal community composition by habitat over time (Fig. 4.2), habitats were situated on opposite sides of the plot. The fore reef had a greater abundance of calcareous algae while the reef terrace had more fleshy algal taxa. There was more year-to-year variation in algal community composition at the fore reef compared to the reef terrace, particularly after the second thermal anomaly in 2015. Algal community composition on Palmyra varied significantly by habitat, year, and their interaction, indicating that algal community structure in each habitat changed differently across years

(PERMANOVA, p <0.001; Table 4.1). Habitat was a better predictor for algal community response than year, explaining 11.6% of the variation ($R^2 = 0.116$; Table 4.1). A SIMPER analysis revealed that the taxa contributing most to habitat differences were CCA, turf algae, and *Halimeda* (Table 4.2).

Cover of Individual Algal Taxa by Habitat and Year

Overall, CCA were more abundant on the fore reef than the reef terrace at 25.3 ± 0.8% (mean ± SE) and 15.4 ± 0.8%, respectively (Fig. 4.2b). In contrast, turf algae were more abundant on the reef terrace than the fore reef at 21.3 ± 1.0% and 11.5 ± 0.5%, respectively (Fig. 4.2g). Between 2014 and 2015 on the reef terrace, there was a decline in CCA cover from 20.0 ± 3.2% to 12.7 ± 2.9% and a concomitant rise in turf algae from 19.6 ± 3.5% to 28.6 ± 3.7%; the increase in turf at the time of the second thermal anomaly was seen to a lesser extent on the fore reef. However, by 2017, turf and CCA cover were restored to pre-disturbance levels in both habitats. Benthic cover of *Caulerpa serrulata*, found almost exclusively at the reef terrace, was highest in the fall of 2010 and 2019 at 3.6 ± 1.5% but dropped to undetectable levels in fall 2012, 2014, and 2018 (Fig. 4.2a). Similarly, also on the reef terrace, *Dictyosphaeria cavernosa* comprised up to 1.5% total cover but was nearly negligible in the fall of 2014, 2015, 2018, and 2019 (Fig. 4.2c). The reef terrace had 4.3 ± 0.6% cover of *Galaxaura rugosa* in fall 2019 but was typically around 2.5% (Fig. 4.2d). There was consistently higher cover of *Lobophora variegata* on the reef terrace (5.0 ± 0.5%) compared to the fore reef (1.9 ± 0.2%; Fig. 4.2e). Cover of *Peyssonnelia* spp., found mainly at the fore reef, was lowest in the fall of 2017 at 1.2 ± 0.3% yet reached up to 10-15% of the benthos every fall between 2011 and 2014 (Fig. 4.2f). *Avrainvillea amadelpha* was not plotted because it occupied less than 0.01% of the benthos.

Calcareous vs. Fleshy Algal Cover with Respect to Temperature

Throughout the entire time series, the fore reef had higher cover of calcareous algae than fleshy algae, at 46.5 ± 0.8% and 13.4 ± 0.5% respectively (Fig. 4.4a), whereas the reef terrace had similar cover of calcareous and fleshy algae, at 22.1 ± 0.8% and 28.0 ± 0.9% respectively (Fig. 4.4b). Percent cover of fleshy algae varied by habitat and year with no significant interaction, and co-varied with SST (Table 4.3). While percent cover of calcareous algae did not co-vary significantly with SST, habitat and year were found to be significant along with their interaction, indicating that habitats were changing differently across years. Notably, at the reef terrace, the cover of fleshy and calcareous algae generally remained consistent through time. At both habitats in 2015, when monthly mean SST was highest at 29.8 ºC, calcareous algal cover was at its lowest on average (37.3 ± 3.4% at the fore reef and 16.4 ± 3.1% on the reef terrace) whereas fleshy algal cover was among its highest (19.1 ± 2.0% at the fore reef and 34.8 ± 3.4% on the reef terrace; Fig. 4.4).

Abundance of Halimeda spp. with Respect to Temperature

Halimeda spp. (primarily *H. opuntia* with minor coverage by *H. taenicola* and *H. fragilis*) were more abundant on the fore reef, at 14.2 ± 0.8% throughout the time series compared to 4.4 ± 0.3% on the reef terrace (Fig. 4.5). Following the first thermal anomaly, when monthly mean SST was 29.4 ºC, *Halimeda* cover dropped from 18.8 ± 3.2% in 2009 to 10.3 ± 1.6% in 2010 at the fore reef but remained mostly unchanged on the reef terrace. Following the second thermal anomaly, benthic cover of *Halimeda* was at its lowest, dropping from 10.7 ± 1.9% in 2014 to 4.5 ± 0.9% in 2015 on the fore reef and 3.7 ± 0.9% in 2014 to 0.7 ± 0.2% in 2015 on the reef terrace. There were significant effects of habitat, year, and their interaction on

Halimeda cover ($p < 0.05$, Table 4.4) but not SST. Regardless of the amount of *Halimeda* within each quadrat or site, its abundance throughout the time series generally followed a similar trajectory with sharp declines in 2015 and growth or no change thereafter (Fig. 4.6). Between 2009 and 2010, *Halimeda* cover decreased significantly at four out of eight sites; this was also observed between 2014 and 2015 in both habitats (Table 4.5). Between 2016 and 2017, *Halimeda* cover increased significantly at six out of eight sites by up to 20% (Table 4.5). Thus, in all cases where significant differences were detected through two-tailed t-tests, the sites that changed did so in the same direction (i.e., either all increasing or decreasing).

DISCUSSION

Algae are expected to become more abundant on reefs worldwide as corals suffer widespread declines with the progression of climate change (Reverter et al. 2021, Hughes et al. 2017, Pandolfi et al. 2003). However, "algae" encompass a heterogenous group functionally, morphologically, and taxonomically (Fong and Paul 2011). While short-term changes in macroalgae abundance, including seasonality, have been well-documented (Águila-Ramírez et al. 2003; Ateweberhan et al. 2006; Lefèvre and Bellwood 2010), longer-term dynamics of all benthic algae at the community level are poorly understood. A decade-long time series from a disturbed reef ecosystem in Panama in the Caribbean showed that spatial variability in macroalgal abundance was linked to local and regional stressors (Sanguil and Guzman 2016). Here, we present results of an 11-year time series from Palmyra Atoll in the central Pacific which, given its remote location and highly protected status, can provide baseline information on algal communities in the context of global stressors such as temperature.

The latest comprehensive analysis of Palmyra's benthic algal communities included summary data from surveys conducted sporadically in certain years between 2004 to 2008 (Braun et al. 2009). These were preceded by early explorers' species lists (Rock 1916; Dawson et al. 1955; Dawson 1959). The most common macroalgal genera on Palmyra as of 2008 were *Halimeda*, *Lobophora*, *Galaxaura*, and *Dictyosphaeria* (Braun et al. 2009). This remained consistent as of 2019, although we also identified *Caulerpa serrulata* as a common macroalgal taxon on the reef terrace (Table 4.2). Additionally, Braun et al. (2009) mentioned high cover of the red alga *Dichotomaria marginata* near a shipwrecked longliner vessel which was removed in 2013. *Dichotomaria* was entirely absent from our analyses, although not all of the same reef sites were represented here and our study involved small-scale photoquadrats as opposed to large spatial scale surveys. Notably, the prior study found algal communities to be relatively similar across sites from both habitats throughout the atoll, whereas in the present study algal communities showed distinct differences by habitat and over time. Calcareous algal cover was consistently higher at the fore reef than the reef terrace. The abundance of fleshy algae fluctuated significantly with temperature yet remained stable overall throughout the decade, more so at the reef terrace than the fore reef. At the time of the second thermal anomaly in 2015, there was a general decrease in calcareous algae at both habitats accompanied by an increase in fleshy algae, but this was restored within two years.

For algae and other primary producers, it can be expected that temperature will increase metabolic and photosynthetic rates until a thermal tolerance limit is exceeded (Davison 1991). Perhaps this was the case for calcareous algae, whose calcification may have initially benefited from the warmer temperatures until prolonged exposure led to mortality or reduction in productivity, as seen in experimental studies (Anthony et al. 2008; Martin and Gattuso 2009). In contrast, fleshy algae have been found to respond positively to thermal stress in field studies (Graham et al. 2015; Burt et al. 2013; McClanahan et al. 2001). Although our study only evaluated the effects of temperature, the combined effects of multiple stressors can otherwise be synergistic (Ellis et al. 2019) or antagonistic (Darling et al. 2010). For example, ocean acidification has been found to cause net negative or species-specific effects on tropical calcareous algae while stimulating growth in some fleshy algae (Johnson et al. 2014), but when combined with warming, effects can be interactive (Diaz-Pulido et al. 2012; Kram et al. 2016).

It has long been known that ecological succession and community structure can also be driven by physical forces such as light and sediment transport (Glynn 1976), irradiance and water motion (Done 1982), and wave energy (Dollar 1982). On Palmyra, environmental factors likely contributed to the spatial variability in algal communities. The shallower reef terrace, which receives more light and solar irradiance (Hamilton et al. 2014) as well as an influx of nutrients and sediments from the nearby lagoon (Rogers et al. 2017), had a higher cover of turf and other fleshy algae throughout the study (Fig. 4.3). Filamentous algal turfs benefit from nutrient availability (Williams and Carpenter 1988), can deposit sediments (Birell et al. 2005), and are tolerant of high light intensity, which increases their productivity (Carpenter 1985; Klumpp and McKinnon 1989). Overall, fleshy algal abundance on Palmyra (average percent cover = 20.9%) was low in comparison to reefs with local human populations (average percent cover = 59.3% on inhabited islands according to Smith et al. 2016). The fore reef was characterized by CCA and other calcareous algae (Fig. 4.2) and is subject to more wave action and water motion (Williams et al. 2013; Hamilton et al. 2014; Gove et al. 2015). Encrusting algae such as CCA and *Peyssonnelia* are less vulnerable to dislodgement by waves than upright algal growth forms (Steneck and Dethier 1994), which may explain their relative dominance in this habitat (Fig. 4.1). *Halimeda* spp., also more abundant on the fore reef, contain specialized photosynthetic accessory pigments that allow them to efficiently harvest light at deeper depths (Drew 2011). Nutrients supplied from upwelling and internal tides (Williams et al. 2018) may have promoted the growth of *Halimeda* (Smith et al. 2004) and other macroalgae on the fore reef.

While we did not quantify herbivore abundance in this study, given that Palmyra has extremely high fish biomass (Williams et al. 2011; Edwards et al. 2014) and that grazing pressure is also known to drive algal succession (Hixon and Brostoff 1996; Carpenter 1986), biological factors such as grazing may have further contributed to differences in algal community structure. Herbivores can help control fleshy algal cover (Burkepile and Hay 2009; Littler et al. 2006) and their presence is associated with higher cover of corals and CCA (Smith et al. 2010). With herbivores now being used as a restoration tool to reverse coral-algal phase shifts on degraded reefs (Ladd and Shantz 2020; Mumby 2014), Palmyra exemplifies the role of herbivory in maintaining a "healthy" calcifier-dominated reef. Palmyra's reef system is dominated by top predators and larger-bodied grazers (e.g., parrotfish and surgeonfish) as opposed to small planktivores or echinoids (Sandin et al. 2008). Hamilton et al. (2014) found that Palmyra's reef terrace had a higher density of herbivorous fish and higher grazing intensity (in terms of bite rates) than the fore reef. Most herbivorous fish on Palmyra feed preferentially on algal turfs (Hamilton et al. 2014), which are more abundant on the reef terrace, suggesting that habitat-specific differences in algal and herbivore assemblages are interrelated.

Further, our study provides observational evidence that species in the calcareous macroalgal genus, *Halimeda*, may be sensitive to warming. Although *Halimeda* cover did not co-vary significantly with SST (Table 4.4), during both thermal anomalies on Palmyra, when monthly mean SST reached 29.4 ºC and 29.8 ºC in 2009 and 2015, respectively, there were declines in *Halimeda* at most sites (Table 4.5). It has previously been proposed that *Halimeda* growth and calcification could benefit from seawater temperatures ranging from 24 to 32 ºC, but that extreme temperatures above 34 ºC will have negative impacts that may become lethal at 36 ºC (Wei et al. 2020). Perhaps if SSTs on Palmyra had reached a more extreme upper limit, this would have had a measurable effect on *Halimeda* cover. In the future, to strengthen these findings, we could complement our image-based data set of planar cover with laboratory-based physiological response data from temperature-controlled tank experiments representing a wider thermal range. Other experimental studies have shown that exposure to elevated temperatures can either inhibit (Sinutok et al. 2011) or enhance (Campbell et al. 2016) photosynthetic efficiency, calcification, and growth in *Halimeda* spp., indicating that results may be context-dependent or species-specific. Given their role in both primary and calcium carbonate production on reefs (Rees et al. 2007) and as a preferred food source to many reef fishes (Mantyka and Bellewood 2004; Hamilton et al. 2014), refining the thermal sensitivity limits of *Halimeda* by species and identifying the mechanisms behind this observed phenomenon will be ecologically relevant.

In conclusion, in order to better understand algal community dynamics, it is important to monitor long-term spatial and temporal patterns on reefs such as Palmyra Atoll with intact ecosystem structure and functioning. Characterizing taxon-specific or functional group responses of benthic algae to environmental variables will help in anticipating possible population and community-level changes. Although Palmyra's reefs have remained calcifier-dominated, trajectories from Palmyra could inform mitigation strategies at more degraded reefs shifting toward fleshy algal dominance.

ACKNOWLEDGMENTS

We thank the staff of The Nature Conservancy, U.S. Fish and Wildlife Service, and the Palmyra Atoll Research Consortium (PARC) for their logistical support and access to the refuge. We thank Gareth Williams, Brian Zgliczynski, Clinton Edwards, Amanda Carter, Samantha Clements, and Stuart Sandin for their assistance with fieldwork. We thank Karina Arzuyan, Marie Diaz, Sarah Romero, Kyle Conner, Shelley Hazen, and Kailey Ramsing for their help with image digitization. Adi Khen was supported by the National Science Foundation Graduate Research Fellowship and the Beyster Family Fellowship in Conservation and Biodiversity. Funding for this work was generously provided by the Scripps Family Foundation, the Bohn Family, and the Gordon and Betty Moore Foundation.

Chapter 4, in part, is currently being prepared for submission for publication of the material. Khen, Adi; Johnson, Maggie D; Fox, Michael D; Smith, Jennifer E. The dissertation author was the primary investigator and author of this material.

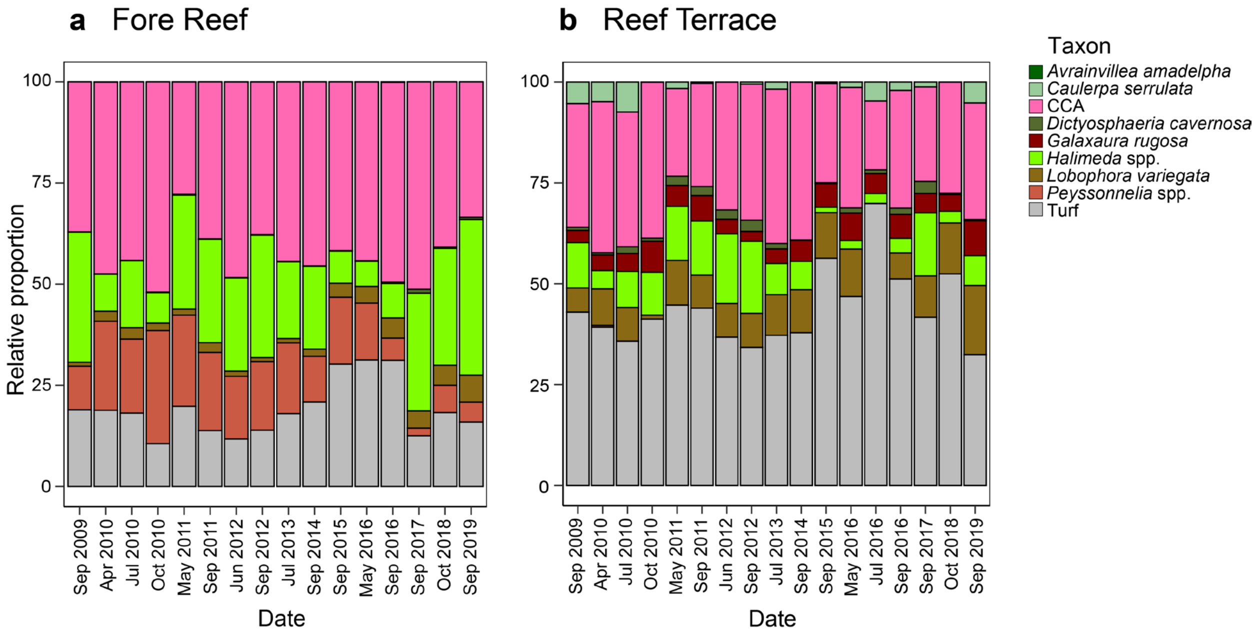

Figure 4.1: Algal community composition over time on Palmyra at the **(a)** Fore Reef and **(b)** Reef Terrace habitats in terms of relative proportions of each taxon

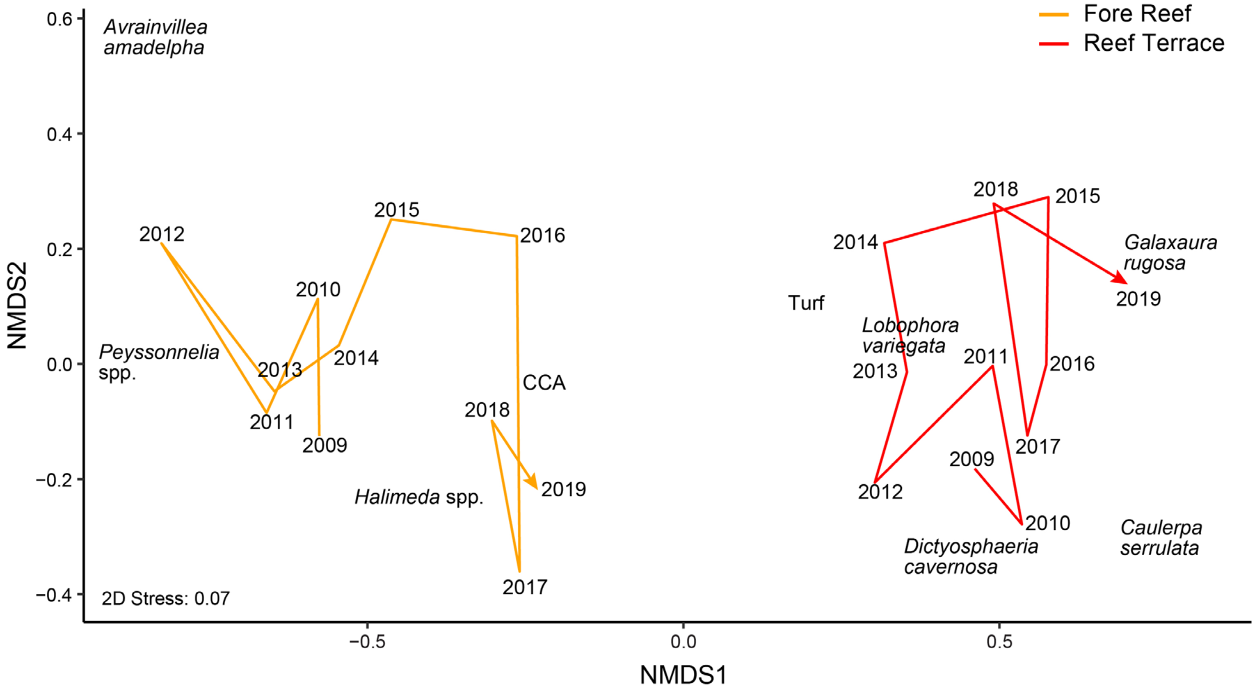

Figure 4.2: Non-metric multidimensional scaling (nMDS) based on Bray-Curtis dissimilarity measures of algal community composition by taxon (in terms of square-root-transformed percent cover data). Lines terminating in an arrowhead represent the yearly trajectory of each habitat from 2009 to 2019

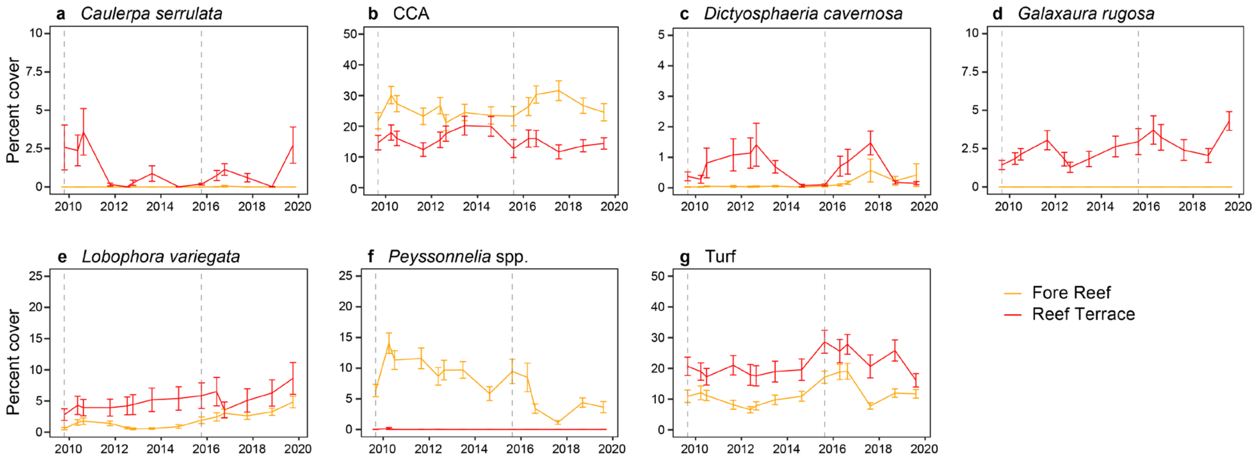

Figure 4.3: Percent cover (mean ± SE) of each algal taxon through time, by habitat. Orange lines represent the Fore Reef and red lines represent the Reef Terrace. Dashed vertical lines indicate the warm-water events in 2009 and 2015. Note the different y-axis scales

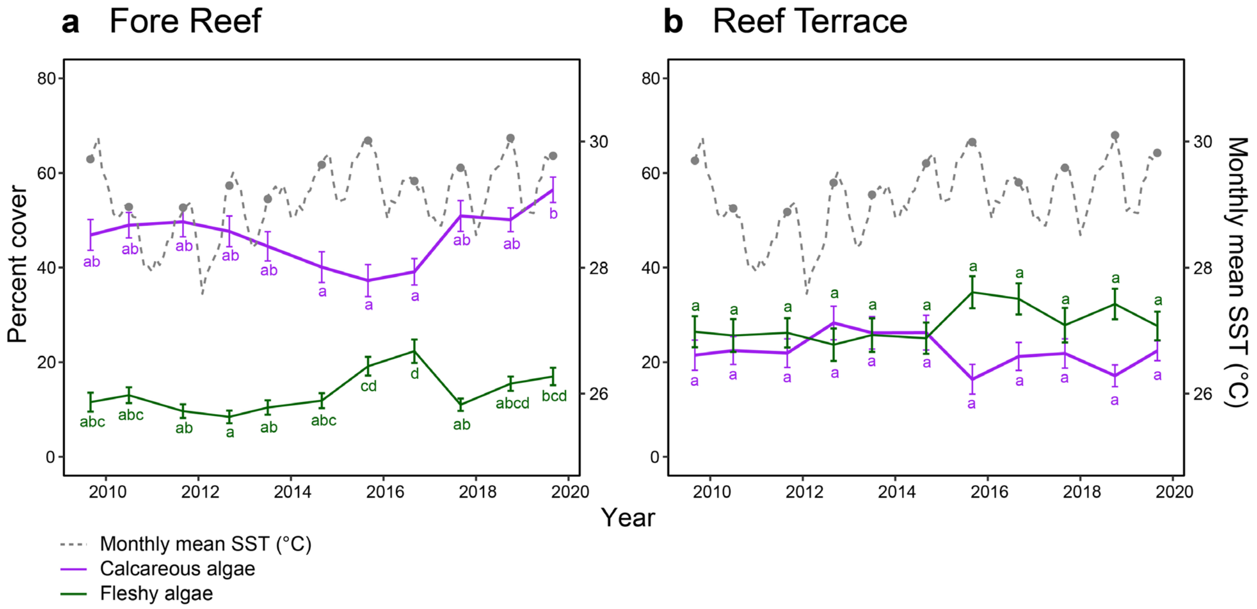

Figure 4.4: Percent cover (mean ± SE, on the primary y-axis) of calcareous and fleshy algae on Palmyra at the **(a)** Fore Reef and **(b)** Reef Terrace habitats, along with post-hoc letter groupings for differences among years. The dashed gray lines, plotted on the secondary y-axis, represent monthly mean sea surface temperatures, with points indicating values at the time of yearly sampling

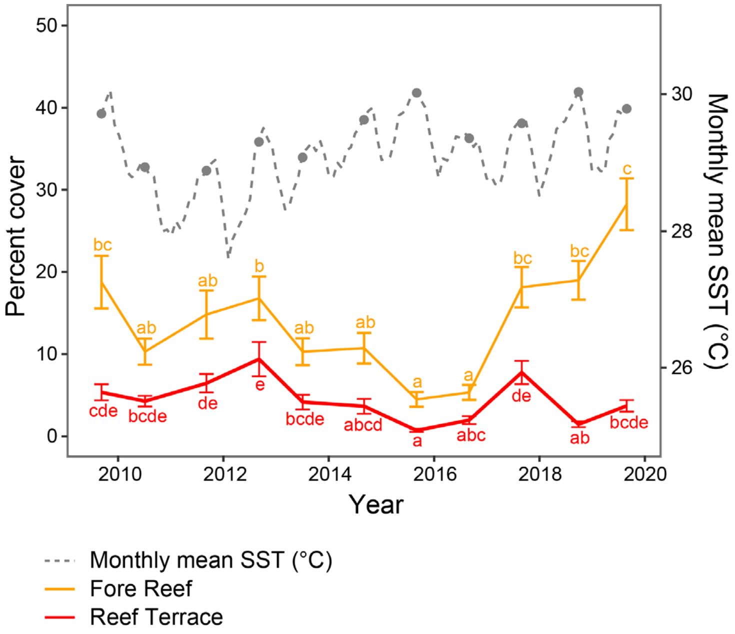

Figure 4.5: Percent cover (mean ± SE, on the primary y-axis) of *Halimeda* spp. on Palmyra by habitat, with post-hoc letter groupings for differences among years. The dashed gray lines, plotted on the secondary y-axis, represent monthly mean sea surface temperatures, with points indicating values at the time of yearly sampling

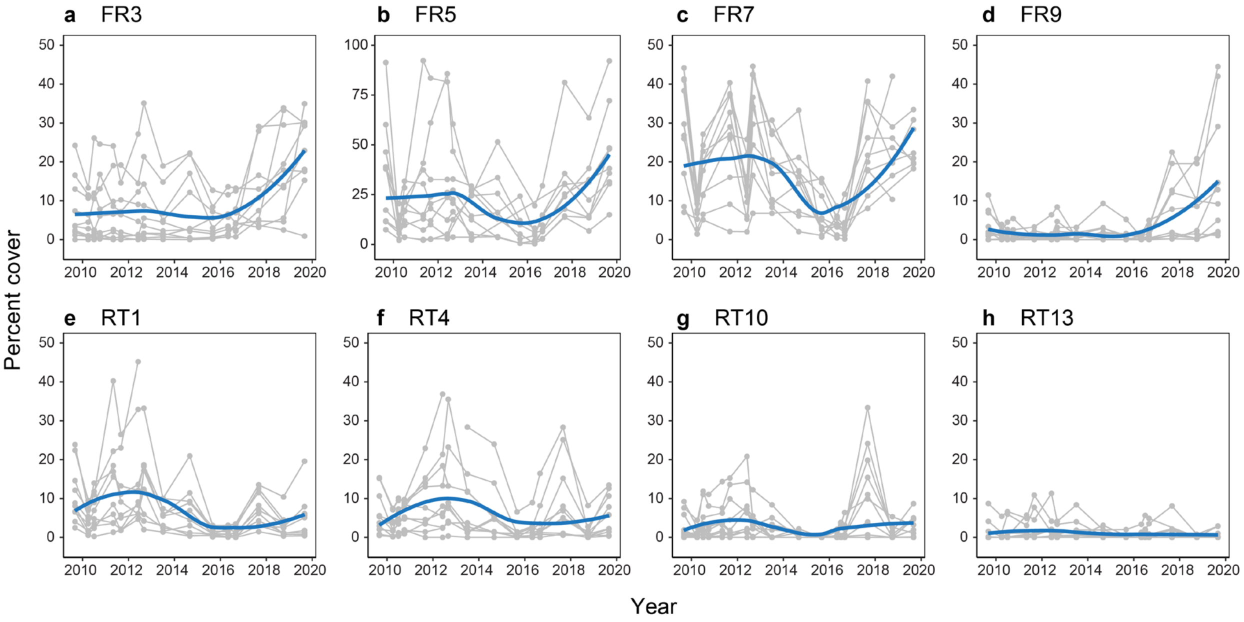

Figure 4.6: Percent cover of *Halimeda* spp. at each site over time. Gray lines represent individual quadrats within each site. Site-specific trajectories, smoothed via LOESS regression, are overlaid in blue. Note the different y-axis scales

Table 4.1: Statistical output from a three-way PERMANOVA (9999 permutations) for algal community response (square-root-transformed percent cover) by habitat, year, and their interaction. Bold indicates statistical significance ($\alpha = 0.05$)

Source	Df	SumSqs	MeanSqs	F.Model	R^2	Pr(>F)
Habitat	1	19.445	19.445	119.401	0.116	**<0.001**
Year	10	7.310	0.731	4.489	0.0434	**<0.001**
Habitat * Year	10	4.048	0.405	2.486	0.0241	**<0.001**
Residuals	844	137.451	0.163		0.817	
Total	865	168.254			1.000	

Table 4.2: SIMPER output identifying the taxa contributing most to algal community composition differences between habitats

Taxon	Avg abundance at FR	Avg abundance at RT	Avg contribution to overall dissimilarity (± SD)	Cumulative contribution (%)
CCA	25.266	15.393	0.186 (± 0.144)	29.64
Turf	11.468	21.292	0.168 (± 0.145)	56.36
Halimeda spp.	14.247	4.432	0.122 (± 0.125)	75.78
Peyssonnelia spp.	6.983	0.004	0.066 (± 0.080)	86.26
Lobophora variegata	1.937	5.0152	0.049 (± 0.079)	94.04
Galaxaura rugosa	0	2.482	0.021 (± 0.032)	97.42
Caulerpa serrulata	0.005	1.107	0.009 (± 0.038)	98.92
Dictyosphaeria cavernosa	0.151	0.651	0.007 (± 0.021)	100

Table 4.3: Statistical output from three-way ANCOVAs on percent cover of fleshy or calcareous algae by year and/or habitat, with monthly mean SST as a covariate. Bold indicates statistical significance (α = 0.05)

Type	Source	Df	SumSqs	MeanSqs	F value	Pr(>F)
Fleshy algae	**SST**	1	3247	3247	11.497	**<0.001**
	Habitat	1	45402	45402	160.772	**<0.001**
	Year	9	8724	969	3.433	**<0.001**
	Habitat * Year	10	969	97	0.343	0.969
	Residuals	844	238343	282		
Calcareous algae	SST	1	1361	1361	3.699	0.055
	Habitat	1	126519	126519	343.816	**<0.001**
	Year	9	8358	929	2.524	**0.007**
	Habitat * Year	10	8488	849	2.307	**0.011**
	Residuals	844	310580	368		

Table 4.4: Statistical output from three-way ANCOVAs on square-root-transformed percent cover of *Halimeda* spp. by year and/or habitat, with monthly mean SST as a covariate. Bold indicates statistical significance (α = 0.05)

Source	Df	SumSqs	MeanSqs	F value	Pr(>F)
SST	1	2.2	2.2	0.817	0.366
Habitat	1	549.0	549.0	207.029	**<0.001**
Year	9	314.9	35.0	13.196	**<0.001**
Habitat * Year	10	148.7	14.9	5.608	**<0.001**
Residuals	844	2237.9	2.7		

Table 4.5: Difference in mean percent cover (± SE) of *Halimeda* spp. from the previous year, by site (with quadrats as replicates). Matrix cells are color-coded according to the average magnitude of loss (in red), gain (green), or lack thereof (yellow). Significant differences from zero (p <0.05) according to two-tailed t-tests are bolded

	2009-2010	2010-2011	2011-2012	2012-2013	2013-2014	2014-2015	2015-2016	2016-2017	2017-2018	2018-2019
FR3	-0.64 (±1.13)	-0.54 (±1.62)	3.05 (±2.13)	-3.67 (±1.71)	2.63 (±1.34)	-4.04 (±1.96)	**1.70** **(±0.55)**	6.31 (±3.03)	5.24 (±2.81)	**7.63** **(±3.31)**
FR5	**-19.46** **(±7.64)**	9.97 (±6.87)	0.32 (±3.82)	**-9.99** **(±4.56)**	1.51 (±4.10)	-11.53 (±3.29)	3.50 (±2.22)	**19.81** **(±4.78)**	-4.06 (±3.59)	**19.47** **(±3.69)**
FR7	**-10.76** **(±2.56)**	**8.42** **(±2.32)**	4.24 (±2.69)	**-12.22** **(±2.97)**	-2.67 (±2.21)	**-8.73** **(±3.19)**	-2.20 (±1.95)	**19.36** **(±3.29)**	2.97 (±3.61)	1.37 (±3.99)
FR9	**-2.31** **(±0.81)**	-0.44 (±0.55)	1.27 (±0.64)	-1.13 (±0.85)	1.05 (±0.64)	-0.94 (±0.46)	0.41 (±0.49)	**6.44** **(±2.31)**	-0.51 (±1.60)	**8.81** **(±3.44)**
RT1	**-4.29** **(±1.63)**	3.28 (±1.89)	**7.47** **(±2.34)**	**-12.11** **(±4.21)**	1.39 (±1.35)	**-5.35** **(±1.76)**	0.22 (±0.18)	**5.96** **(±1.04)**	**-4.45** **(±0.84)**	**2.37** **(±0.92)**
RT10	1.38 (±0.71)	0.64 (±0.73)	-1.46 (±1.34)	-1.50 (±0.91)	-1.22 (±1.02)	**-0.64** **(±0.27)**	**1.62** **(±0.65)**	**10.21** **(±3.36)**	**-10.81** **(±3.57)**	1.93 (±0.98)
RT13	-0.03 (±0.34)	1.02 (±0.58)	-1.51 (±1.02)	0.62 (±0.43)	-0.79 (±0.80)	-0.49 (±0.31)	0.72 (±0.42)	0.46 (±0.49)	-1.32 (±0.80)	0.58 (±0.33)
RT4	-1.40 (±0.94)	**3.79** **(±1.41)**	7.24 (±3.29)	**-7.92** **(±2.89)**	-1.70 (±1.14)	**-5.01** **(±1.81)**	**2.49** **(±1.04)**	**5.90** **(±1.93)**	**-8.00** **(±2.68)**	**4.11** **(±1.19)**

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