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Shading from Topographical Complexity Mitigates Bleaching Severity of Pocillopora spp. During Thermal Stress

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Shading from Topographical Complexity Mitigates Bleaching Severity of *Pocillopora* spp. During Thermal Stress

A Thesis submitted in partial satisfaction of the requirements for the degree Master of Science

in

Marine Biology

by

Mary B. Liesegang

Committee in charge:

Professor Stuart Sandin, Chair
Professor Brice Semmens
Professor Jennifer Smith

2022

The Thesis of Mary B. Liesegang is approved, and it is acceptable in quality and form for publication on microfilm and electronically.

University of California San Diego

2022

DEDICATION

For Grammie. Thank you for the days we sat by the ocean listening to the waves and smelling the breeze, the afternoons at the Birch Aquarium, the trips to Hawaii where mom and dad had to drag me out of the water at sunset, the dinners full of conversations about my scientific curiosities, and the support to make my dreams a reality. I see you in the sunsets and I hope are you looking down from heaven proud.

EPIGRAPH

The ocean stirs the heart,
inspires the imagination,
and brings eternal joy to the soul.
-Robert Wyland

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ABSTRACT OF THE THESIS

Shading from Topographical Complexity Mitigates Bleaching
Severity of *Pocillopora* spp. During Thermal Stress

by

Mary B. Liesegang

Master of Science in Marine Biology

University of California San Diego, 2022

Professor Stuart Sandin, Chair

Bleaching susceptibility of coral varies among species, environmental conditions, and spatial patterns on a reef. As bleaching events become more frequent and severe, understanding the factors that increase resiliency against thermal stress is critical. Here, we used large scale imagery collected at the remote atoll of Palmyra in the central Pacific during the 2015 thermal stress event to investigate the role of topographically produced

shade in mitigating bleaching severity. Change in planar area over two years, bleaching severity, and estimated amount of shade provided by neighboring reef structures was measured for the common coral genus *Pocillopora*. Colonies that bleached more severely had higher rates of mortality than colonies with less severe bleaching. Further, those colonies with less severe bleaching had a higher proportion of colonies experiencing growth. Bleaching severity was correlated with the estimated irradiance, as more daily sunlight resulted in more severe bleaching than corals experiencing less daily sunlight. Structural complexity and variability in reef topography provide regions of shade where the compound impact of temperature and irradiance is alleviated, resulting in less-severe bleaching outcomes for an abundant and cosmopolitan coral genus. While some studies have considered artificially shading reefs during warm water events, we highlight the importance of existing structural complexity in providing shade, ultimately leading to increased reef resilience in the face of a changing climate.

Introduction

Corals reefs are the world's most biodiverse ecosystems, responsible for providing habitat to one third of marine species (Knowlton et al. 2010). Coral reefs are also a vulnerable ecosystem in the face of a changing climate and the increase in frequency and severity of global bleaching events threatens their survival (Hoegh-Guldberg 1999, Hughes et al. 2018). Coral bleaching occurs when there is a breakdown in the fragile relationship between coral hosts and the pigmented symbiotic algae which live inside coral tissue (Iglesias Prieto et al. 1992, Hoegh-Guldberg & Smith 1989). Bleaching is often induced by thermal stress caused by sea surface temperature anomalies as little as 1°C above the monthly mean summer temperature tolerance (Glynn 1984, Brown 1997, Berkelmans & Willis 1999, Hoegh-Guldberg 1999). Bleaching events can also be induced by increased irradiance (Lesser et al. 1990), sedimentation (Bak 1978, Philipp & Fabricius 2003), decreased salinity (Coles & Jokiel 1978, Coles & Jokiel 1992), or a combination of factors associated with photo-physiological stress (Fitt et al. 2001).

Photosynthesizing *Symbiodinium*, the single celled symbiotic algae that live within the coral, transform sunlight into the energy required for growth, reproduction, and maintenance of the coral host (Goreau 1959; Muscatine 1990). Under stressful conditions, such as increased sea surface temperature, corals bleach through either eviction of their *Symbiodinium* or loss of the pigment within their *Symbiodinium*, resulting in a white coral colony (Glynn 1984, Brown 1997). Extended periods without the energy provided by their symbionts results in tissue loss and ultimately coral mortality. Bleached corals may take up their formerly evicted *Symbiodinium* and recover depending on the severity and length of the warm water event (Glynn 1984, Hughes et al. 2018). Corals are colonial, with each polyp being an individual organism, and can lose single polyps without death of the entire colony (Hughes & Jackson 1980). This can result in partial survival and regrowth following bleaching induced tissue loss (Hughes & Jackson 1980). Since global bleaching events are increasing in frequency, shorter recovery windows between thermal stress may negatively impact the likelihood of survival and regrowth after subsequent events (Hughes et al. 2018).

Colonies with a history of surviving bleaching may have increased acclimation to future bleaching events, resulting in increased thermal tolerance and stress resistance (Donner 2011, Thomas et al. 2018). Coral in regions that experience high daily fluctuations in temperature have better resilience to withstand thermal stress by adapting to regularly changing temperatures (van Woesik et al. 2012, Thomas et al. 2018). Further, different species of corals have displayed varied responses to thermal stress, with branched corals being the most susceptible morphology to bleaching compared to encrusting or massive corals (Loya et al. 2001, Darling et al. 2012). When bleaching events occur, not all corals bleach equally. Some corals pale, other bleach partially, others bleach completely, while still others show no signs of bleaching. Understanding the mechanisms and adaptations that increase resilience is important as reef are increasingly threatened.

As autotrophic organisms, reef building corals require light for *Symbiodinium* to complete photosynthesis and provide the coral host with nutrients (Yonge 1963). Irradiance is composed of both ultraviolet radiation (UV, 280-400nm), which can be harmful to photosynthesizing organisms like algae, and photosynthetically active radiation

(PAR, 400-700nm), which is required for conversion of sunlight to energy (Jokiel 1980, Lesser et al. 1990, Roth 2014). Growth rates are dependent on light intensity (Barnes & Taylor 1973) and decreased irradiance has been shown to inhibit the growth of some coral species by reducing light available for photosynthesis (Stimson 1985). Because of the necessity of light for symbionts to photosynthesize, corals are typically found in clear tropical waters and are limited in habitat by decreased irradiance with depth (Huston 1985).

Symbiodinium in corals have different light tolerances and thus different photosynthesis responses to changing light regimes (Wethey & Porter 1976). Both coral hosts and algal symbionts can have light adaptations and preferences, with shade loving and sun loving species (Jokiel 1980). Symbionts photo-acclimate to lower light levels at depth by increasing the number and size of their photosynthetic units to maximize light uptake, effectively becoming more shade tolerant (Iglesias Prieto & Trench 1994). Transplantation of corals from low light to high light locations can lead to bleaching-like responses and death in the absence of thermal stress (Vareschi & Fricke 1986, Hoegh-Guldberg & Smith 1989, Gleason & Wellington 1993).

Corals found in shallow waters can adapt to higher light levels by becoming photo inhibited. Under intense irradiance, the primary protein complex in the photosynthetic reaction, photosystem II (PSII), can decrease photosynthetic efficiency, or become photo inhibited, to protect from cellular damage. In shallow water with high light, 10-20% of symbionts PSII are chronically inhibited (Gorbunov et al. 2001). Exposure to high irradiance under increased temperature compounds the impacts of thermal stress, leading to more severe bleaching. Reducing irradiance during thermal stress events can relieve PSII and mitigate bleaching severity (Coles & Jokiel 1978, Fitt & Warner 1995, Warner et al. 1999, Lesser & Farrell 2004).

Decreased light, as a tool to mitigate bleaching, has been studied before in relation to cloud cover (Mumby et al. 2001), turbidity (Glynn 1993, van Woesik et al. 2012, Cacciapaglia & van Woesik 2016), depth (Dustan 1982), and in laboratory experiments (Brown 1997, Hoegh-Guldberg & Smith 1989). Artificial shading studies have also been conducted and shown that shading provides refuge during warm water events (Coelho et al. 2017). These findings have encouraged further studies investigating the potential of shade in coral resilience (West & Salm 2003).

The three-dimensional structures of the reef, referred to as structural complexity, has become a focus of research as reef are degrading due to bleaching. Increases in structural complexity creates microhabitats and has been associated with increased diversity and abundance of reef dwelling organisms such as fish, urchins, and invertebrates (Risk 1972, Luckhurst & Luckhurst 1978, Vytopil & Willis 2001, Lee 2006). Structural complexity also impacts variance in light across the reef, with massive and tabular corals, as well as large thickets of branching corals such as *Acropora*, creating shade for neighboring corals (Hoogenboom et al. 2017). As mentioned previously, branching species of corals, which often produce high levels of structurally complex, are more susceptible to bleaching than massive and encrusting species because they devote their energy to growth rather than stress tolerance (Loya et al. 2001, Darling et al. 2012). As a result, with increased global bleaching followed by macroalgal overgrowth, the selective shift in morphology from fast growing corals to stress resistant corals has led to declines in complexity, negatively impacting these reef communities.

Here, we focus on the impact of varying shade from structural complexity on reef resilience. Using 3D models of a remote reef in the central Pacific during a warm water event, this study investigates the relationship between changes in estimated irradiance from shade provided by reef structures and bleaching severity. We hypothesize that reduced irradiance from shade produced by neighboring taller or larger corals and other rugose reef structures decreased bleaching severity of coral colonies during the 2015 bleaching event on Palmyra Atoll. We propose that colonies receiving less daily sunlight bleached less severely relative to colonies in high sun areas and investigate existing structural complexity of the reef as a form of resilience against bleaching. We highlight the importance of maintaining varied reef topography under changing climate conditions.

Methods

Study Organism

The focal taxon of this study were two monophyletic species in the genus *Pocillopora*: *Pocillopora meandrina* and *Pocillopora verrucosa*. Because they are morphologically indistinguishable and functionally similar, they were grouped as "*Pocillopora"* for the purposes of this study (Pinzón & LaJeunesse 2011, Pinzón et al. 2013). *Pocillopora* are highly abundant and widely distributed across the tropical central Pacific, comprising 15% of the total coral cover and 12% coral colony abundance at the study site, Palmyra Atoll (Edwards et al. 2017). *P. meandrina* and *P. verrucosa* exhibit a corymbose morphology and display low resistance to disturbance events such as bleaching, but early colonization and fast growth, often allowing rapid recovery (Loya et al. 2001, Darling et al. 2012, Kayal et al. 2015).

Study Site

This study was conducted using large scale imagery collected from Palmyra Atoll (5°88′N, 162°08′W), an unpopulated atoll in the central Pacific which has limited exposure to local stressors such as nutrient pollution and overfishing (Sandin et al. 2008). Palmyra is protected as part of the Pacific Remote Islands Marine National Monument (Kenyon et al. 2012). The isolation of this atoll provides an opportunity to determine the impacts of natural fluctuations without local anthropogenic influence.

Palmyra experienced a severe bleaching event with measured Degree Heating Weeks (DHW) of 11.9DHW in 2015 (Fox et al. 2019). Previous studies have shown that 4DHW results in bleaching, with mortality common above 8DHW (Eakin et al. 2009). The global event, which was attributed to increased sea surface temperatures during the 2014-2016 El Niño Southern Oscillation, resulted in four times the amount of bleaching on the Great Barrier Reef than was seen in the 1998 and 2002 warm water events. It is considered to be the worst global bleaching event on record (Hughes et al. 2017). During this bleaching event, 90% of the corals on Palmyra bleached, with 32% of bleaching classified as severe. Despite the severity, there was only 9% coral mortality (Fox et al. 2019).

Model Collection

Methods were adapted from Edwards et al. (2017). We used imagery collected from four established $100m^2$ fore reef plots along the 10m isobath (Figure 1). The plot boundaries were marked with six steel pins and the pins along the 10m isobath were georeferenced with GPS coordinates for annual sampling and model alignment. Models were created through large area image reconstruction, by which a diver operating a camera system with two DSLR cameras, one with a 55mm focal lens and another with 18mm focal lens, swam a gridded pattern one meter above the reef, capturing one image per second. The result was approximately 2500 images per camera per plot with significant image overlap.

The raw imagery was used to create 3D point cloud reconstructions in the Structure-from-Motion software *Agisoft (*Agisoft LLC., St. Petersburg, Russia)*.* These point clouds were converted into 2D top down orthoprojections in custom software *Viscore*. *Viscore* uses a 2D-to-3D approach, which produces orthoprojections directly from the point cloud to minimize distortion and avoid geometric inaccuracies that may be caused by sloping and structural complexity (Petrovic et al. 2014). Scale bars on established reef plots were used to ensure accurate scale in *Viscore*. Using depth of the steel pins marking the plot boundaries, the plane of reference was defined as parallel to the sea surface (Figure 2). Models in *Viscore* were rotated using the associated GPS coordinates from the center steel pins so that the up vector represented north within +/-10-degree margin of error, allowing for accurate directional analysis. This study used a two-year time series of 2015 and 2016, with 2015 capturing the bleaching event and 2016 used to determine survivorship and recovery.

Model Processing

Within the four sites, 573 individual colonies of *Pocillopora* were segmented by hand tracing colony boundaries and annotating class label on the orthoprojection in the program *TagLab,* a software designed to support large scale orthographic analysis (Pavoni et al. 2022). Colonies were defined as a patch of continuous live tissue (Highsmith 1982) and spatially linked raw imagery of both 55mm and 18mm lenses were used for higher resolution tracing of colony borders. Between years, colonies were manually matched in *TagLab*. Change in planar area between the matched colonies was used to determine survivorship of the colony, classified as experiencing growth, no change (less than 5% change in area), shrinkage, or death (which included death and algal overgrowth, upheaval to different unidentifiable location, or complete coverage by other reef structures). 2D planar area has been shown to scale linearly with 3D surface area and volume (House et al. 2018). Colonies with an initial size of less than 5cm diameter were considered juvenile (Pedersen et al. 2019) and removed for the purposes of this study due to inaccuracy in using color to determine bleaching. Additionally, colonies that split or fused between years were removed from analysis.

Spatially linked raw imagery was then used to examine the entire colony from multiple perspectives. Colonies were assigned one of five bleaching severity categories based on the percent of the whole colony affected. Bleaching severity was adapted from Gleason (1993) and classified as follows: *not bleached* (0% of colony bleached), *less than 10% bleached* (1-9% of colony bleached), *somewhat bleached* (10-50% of colony bleached), *mostly bleached* (51-99% of colony bleached), and *completely bleached* (100% of colony bleached) (Figure 3). Colonies with macroalgal overgrowth were considered dead and not included in the study.

The point cloud in *Viscore* was used to determine the impact of light through shading from neighboring reef structures. A grid with measurement units of 4cm was placed on the model. A profile gauge which included the x, y, and z coordinates of the corresponding point in the point cloud was placed at the centroid of the colony and the associated colony ID from *Taglab* was identified. A profile gauge was snapped to the model at every grid vertex (4cm apart) to the west direction. The change in z coordinate and change in x-y coordinate was used determine the arc of shade between the two points through trigonometry. Arcs of shade at each grid vertex were measured up to 1 meter away from the centroid of the colony. The largest angle within that meter was recorded as the main provider of shade for the colony, with 0° representing no topographically elevated structures nearby, and thus no shading, and 90° representing full coverage by a topographical feature (Figure 4). Negative arcs of shade were noted as 0°, as there were no shading structures nearby. The process was repeated to the east.

The amount of sunlight the colony experienced based off neighboring structures was converted to a single arc of sunlight measurement. This measurement represents the amount of daily sunlight from west to east and was determined by subtracting the east and west angles from 90° and adding those inverse angles together (Figure 4). A small arc of sunlight approaching 0° represents significant shading and a larger arc of 180° represents no shading.

Statistical Analyses

All data analysis was performed in R Statistical Software (R Development Core Team). Difference in severity of bleaching between sites was tested using a χ^2 analysis. The relationship between bleaching severity and the survivorship of the colony the following year (grow, shrank, no change, dead) was plotted. Bleaching severity was grouped as severe (*completely bleached* and *mostly bleached*) and mild (*somewhat bleached* and *less than 10% bleached*) to meet test criteria and a χ^2 test was completed. Due to low sample size in the *completely bleached* (8) and *not bleached* (0) categories, these categories were removed from the remainder of the analyses. Fate was designated as live (grow, no change, or shrank) and die (dead). The mean initial individual colony area (cm^2) for each bleaching category was log transformed and a one-way ANOVA and Tukey's Honest Significant Difference were completed to determine the relationship between initial colony size and bleaching severity categories.

A bootstrapping approach analogous to an ANOVA was used to analyze the relationship between shading and colony bleaching severity. Across all levels, bootstrapped replicates were randomly redistributed among the bleaching categories. The mean arc of sunlight and deviation was calculated for each category, then the process was repeated 1000 times to determine the null distribution. This approach was then repeated for the arc of shade in the east and west direction. The means and deviations of the data were compared to the null distribution in order to determine whether distributions were different among bleaching categories. Using a Bonferroni alpha adjustment to correct for multiple comparisons, percentiles greater than 0.966 and less than 0.034 were considered significant.

Results

We measured planar area, bleaching severity, and degree of shading for 573 *Pocillopora* colonies across four sites at Palmyra Atoll during the bleaching event in 2015 and the following year. Of the colonies studied, 1.4% were *completely bleached*, 24.1% *mostly bleached*, 65.7% *somewhat bleached*, 7% *less than 10% bleached*, and 0% *not bleached*.

Bleaching severity varied between sites ($p<0.001$, $\chi^2=68.331$). Site FR8 had the least severe colony bleaching (*completely bleached*: 0%, *mostly bleached*: 12%, *somewhat bleached*: 71%, *less than 10% bleached*: 17%, *not bleached*: 0%) (Figure 5). Site FR38 had the most severe colony bleaching (*completely bleached*: 2.5%, *mostly bleached* 33.5%, *somewhat bleached*: 64%, *less than 10% bleached*: 0%, *not bleached* 0%) (Figure 5). The sites on the south side of the atoll had more severe bleaching, with both sites having colonies that were completely bleached, than the sites on the north side (Figure 5).

Bleaching severity also varied based on size of the colony ($p<0.001$) (Figure 6). Colonies that were *mostly bleached* had the smallest mean planar area of 99.3 ± 9.7 cm^2 (± SE). *Somewhat bleached* colonies had a mean planar area of 174.3 ± 5.5 cm^2 (± SE) and *less than 10% bleached colonies* were largest with a mean planar area of 192.3 ± 19.7 cm^2 (± SE). Tukey's post-hoc test revealed that means of initial colony area between *somewhat bleached* and *less than 10% bleached* colonies differed significantly from *mostly bleached* colonies ($p<0.001$; $p<0.001$). There was no significant difference in initial area between *somewhat bleached* colonies and *less than 10% bleached* colonies ($p=0.76$).

Of the 573 colonies observed, 103 died, 87 shrank, 25 had no more than a 5% change in area, and 358 grew. Of the 8 colonies that were *completely bleached*, 62.5% died, 25% had no change, and 12.5% grew. Of the 138 colonies that were *mostly bleached*, 30.4% died, 23.9% shrank, 2.2% had no change in area, and 43.5% grew. The majority of the *somewhat bleached* and *less than 10% bleached* colonies grew, 68.2% and 82.5% respectively. For the remainder of *somewhat bleached* colonies, 13.4% died, 13.1% shrank, and 5.2% had no change. The remaining seven *less than 10% bleached* colonies were split between death and shrinkage with 10% and 7.5% respectively. For statistical purposes, the bleaching severity categories were grouped as severe bleaching (*mostly bleached* and *completely bleached*) and mild bleaching (*somewhat bleached* and *less than 10% bleached*). There was a significant relationship between mild bleaching and severe bleaching and fate the following year ($p<0.001$, $\chi^2=42.959$). Colonies experiencing less severe bleaching resulting in a higher likelihood of growth (70%) and a lower likelihood of death (13%) when compared to more severely bleached colonies which exhibited 42% growth and 32% death (Figure 7).

The arc of sunlight was defined as the arc of sunlight between 0-180° that the coral received based on neighboring structures in the east and west direction, with a larger arc representing more sunlight and a smaller arc representing less sunlight (Figure 4). *Less than 10% bleached* corals had the smallest mean arc of sunlight of 148.97 ± 3.96° (± SE). *Somewhat bleached* colonies had a moderate arc of sunlight of 157.85 ± 1.10° (± SE) and *mostly bleached* colonies had the largest arc of sunlight of 164.45 ± 1.19° (± SE) (Figure 8). The arc of sunlight was significantly different based bleaching categories (quantile<0.001). All pairwise comparisons between bleaching categories were significant under percentiles determined by the Bonferroni alpha adjustment (0.966 quantile and 0.033 quantile): *mostly bleached* and *less than 10% bleached* (quantile=1), *mostly bleached* and *somewhat bleached* (quantile = 0), and *somewhat bleached* and *less than 10% bleached* (quantile = 0.991).

The arc of shade was measured as the angle between the centroid of the colony and the object with the most significant change in z, which was considered the object providing the greatest shading, within 1 meter. An arc of shade of 0° represented no shading and an arc of shade of 90° represented full shade (Figure 4). In the west direction, *mostly bleached* colonies had the smallest arc of shade of 8.48 ± 0.84° (± SE), *somewhat bleached* colonies had a moderate arc of shade of 11.31 ± 0.72° (± SE), and *less than 10% bleached* colonies has the largest arc of shade 16.05 ± 2.63° (± SE) (Figure 9). Arc of shade in the east direction followed the same pattern with *mostly bleached* colonies having an angle of elevation of 7.07 ± 0.83° (± SE), *somewhat bleached* colonies angle of 10.84 ± 0.76° (± SE), and *less than 10% bleached* colonies having an angle of 14.98 ± 2.91° (± SE) (Figure 9).

The west arc of shade varied with bleaching categories (quantile < 0.05). All pairwise comparisons in the west direction were greater than 0.966 quantile or less than 0.033 quantile as defined by Bonferroni alpha adjustment: *less than 10% bleached* and *mostly bleached* (quantile = 0.001), *less than 10% bleached* and *somewhat bleached* (quantile = 0.025), *somewhat bleached* and *mostly bleached* (percentile = 0.989). The east arc of shade also varied with bleaching categories (quantile = 0.01). However, pairwise comparisons only varied significantly between *less than 10% bleached* and *mostly bleached* (quantile = 0), and *mostly bleached* and *somewhat bleached* (quantile = .996). *Somewhat bleached* and *less than 10% bleached* had a percentile of 0.055, greater than the Bonferroni alpha adjustment interval of less than 0.033. The magnitude of the arcs in the east and west direction were similar, meaning there was no directional bias in the impact of shade on bleaching severity.

Discussion

Here, we explored the role that shade from structural complexity of reef topography plays in mitigating bleaching severity colonies of *Pocillopora* during the global warm water event of 2015. Colonies were categorized by the percentage of the whole colony bleached then examined over a two-year time series to track survivorship. The impact of shade was quantified by measuring the angle between the centroid of the colony and the object within 1 meter providing the largest change in z coordinate in the east and west direction. This was converted to a single arc of sunlight measurement, with more sun represented by a larger arc and less sun represented by a smaller arc.

Bleaching severity showed site specific differences, with more severe bleaching on the south side of the atoll than the north. Williams et al. 2018 found no significant difference in inorganic nutrient concentration or mean irradiance between northwest, northeast, southwest, or southeast sites on Palmyra atoll. Further, they found that there was no difference in deep pulses (upwelling) across sites, but surface pulses were strongest in the northeast and the mean duration of a surface pulse was the longest the northwest (Williams et al. 2018). Surface pulses move surface waters that cool overnight from shallow to deep. Stronger surface pulses of cold water on the north side of the atoll may provide thermal mitigation during the bleaching event. Wave energy on the south side of the atoll is typically lower than on the north side, partially because the central lagoon blocks incoming waves from reaching the south side (Gove et al. 2015). This may provide more water flow to the north side of the atoll, which has been shown to reduce bleaching. However, during the bleaching event there was a strong southern swell (Clinton Edwards, personal communication). Therefore, future studies are suggested to investigate the relationship between intra-atoll site specific bleaching severity and the associated environmental conditions.

Bleaching severity varied with initial size of the colony. *Mostly bleached* colonies were significantly smaller than *somewhat bleached* and *less than 10% bleached* colonies. In the absence of thermal stress, *Pocillopora* demographic studies have concluded that larger coral colonies experience lower mortality than smaller colonies (Kodera et al. 2020). Because rates of passive diffusion are more rapid in smaller corals, it has been hypothesized that smaller corals should have higher survivorship than large corals during thermal and light stress (Nakamura & van Woesik 2001). However, the impact of colony size on bleaching severity has been highly variable, with some studies concluding that smaller corals bleach more severely than larger colonies (Johnston et al. 2020) and others demonstrating larger colonies experiencing more severe bleaching than small colonies (Shenkar et al. 2005, Brandt 2009). Additional studies have found that relationship between colony size and bleaching severity is dependent on the genus (Pratchett et al. 2013) and this relationship may be shifting under a changing climate.

The survivorship of the colonies was related to bleaching severity. As bleaching became less severe, the percent of colonies that grew increased from 42% to 70%. The opposite pattern was seen with the proportion of colonies dying decreasing by over half with less severe bleaching. Colonies with severe bleaching typically die or experience a large amount of tissue loss (Gleason 1993). Because of the colonial nature of corals, partial mortality of less severely bleached corals may allow for recovery following a bleaching event (Hughes & Jackson 1980). It is expected that corals that experience less severe bleaching have a higher chance of partial mortality, and therefore recovery, which is supported by the evidence of this study. Less severely bleached colonies had a higher proportion of colonies that had recovered and grown the following year than severely bleached colonies.

The amount of sunlight coral colonies received, measured as both the arc of sunlight and the arc of shade in east and west direction, was related to the severity of bleaching. Colonies receiving more sunlight (larger arc of sunlight and smaller arc of shade) were more likely to have severe bleaching and colonies receiving less sunlight (smaller arc of sunlight and larger arc of shade) were more likely to have less severe bleaching. *Mostly bleached* colonies had the largest mean arc of sunlight, and *less than 10% bleached* colonies had the smallest mean arc of sunlight. Further, the influence of light from the east and the west direction were of equal importance in providing shade, as seen by the arcs of shade in the east and west direction having similar magnitudes for each bleaching category. We conclude that colonies that bleach more severely are more likely to die and that shading from neighboring topographical structures mitigates bleaching severity during thermal stress events.

It is well understood that shading may provide refuge to corals during warm water events through both experimental and observational studies in the field and laboratory environment (Coles & Jokiel 1978, Warner et al. 1999). Structural complexity providing microhabitats with varied shade regimes and its impact on bleaching severity has been studied and concluded that corals in crevices or under overhangs bleached less severely than corals in open, elevated, or sandy substrate (Hoogenboom et al. 2017). Our study furthers this hypothesis by estimated the amount of light corals are receiving based on the shade produced by structural complexity and comparing it to bleaching severity in situ.

Cloud cover was attributed with alleviating bleaching that was expected due to increased sea surface temperatures during the 1997/1998 global bleaching event (Mumby et al. 2001). Contrastingly, an unexpected increase in severe coral bleaching during a mild thermal stress event was observed under conditions of calm seas and cloudless skies and was attributed to a combination of temperature and less mixed water column increasing irradiance (Glynn 1993). Additionally, near shore turbid environments have been named a refuge during thermal stress due to increased particles in the water column absorbing light before it reaches the corals on the benthos (van Woesik et al. 2012). However, turbidity is often proximal to human population or a result from anthropogenic run-off, both of which can be harmful to corals. Decreased irradiance with depth has also been shown to serve as a refuge during warm water events, with shallow water corals often bleaching more severely than deeper water corals (Huston 1985, Muir et al. 2017).

Experimental studies have investigated the idea of artificial shade as a mechanism to decrease bleaching severity during thermal stress events. Under thermal stress, *Acropora, Pocillopora,* and *Porites* have displayed decreased severity of bleaching with shading in tank experiments with temperature stress up to 8DHW (Coelho et al. 2017). Corals under low light take longer, and require a higher temperature threshold, to experience the same level of bleaching than corals in brighter light (Fitt & Warner 1995).

Further, high light combined with thermal stress resulted in mortality, while 70% light at the same temperature resulted in growth (Coles & Jokeil 1978).

Decreased light may serve as a refuge, however, changes in light intensity of high or low-light acclimated corals can impact bleaching severity and growth. Light acclimated corals do not do well under transplant conditions. Corals found in deeper water transplanted to shallow water with higher light showed visible bleaching and paling after 21 days and mortality in 30 days (Vareschi & Fricke 1986, Gleason & Wellington 1993). If structures providing shade such as massive and tabular corals or *Acropora* thickets bleach and subsequently die and are overgrown with algae, shaded corals may experience rapid changes in irradiance which will alter the light environment corals are acclimated to, potentially leading to bleaching or death in the absence of thermal stress (Stimson 1985, Gleason & Wellington 1993). Therefore, understanding the importance of shade for species susceptible to bleaching, such as *Pocillopora*, is increasingly important as reef structural complexity continues to change.

An alternative explanation for the changes in bleaching severity between corals is the impact of structural complexity on water flow. When considering coral reef structure, increased structural complexity results in higher water flow (Reidenbach et al. 2006). Coral colonies that grow upwards away from the reef decrease the thickness of the benthic boundary layer which increases water flow of surface corals but reduces the water flow and of the colonies lower within the reef (Shashar et al 1996). As a result, colonies that have elevated neighboring structures are likely to experience less active water flow. Survivorship of corals during periods of increased sea surface temperature has been attributed with increase water flow preventing buildup of toxins associated with bleaching (Nakamura & van Woesik 2001). Additionally, increased water flow has been shown to alleviate bleaching severity during high temperature and irradiance (Nakamura & van Woesik 2001, West & Salm 2003). As a result, it would be expected that corals in more protected portions of the reef, such as corals with larger arcs of shade to neighboring structures, would have decreased waterflow, which would increase the impact of sea surface temperature anomaly. Contrastingly, we found that protected corals had decreased bleaching severity, which we attribute to decreased irradiance rather than water flow.

This study focused on light directionally from the east and the west, as Palmyra is near the equator so that is the primary path of sun travel. Nevertheless, light does not move through the water in uniform and directional waves like it does through air. When light hits the sea surface, it is both reflected towards the atmosphere and refracted, or bent, as it enters the water. Within the water column, light is scattered and absorbed by suspended particles. As a result, capturing arcs of shade from only the east and west directions does not fully encompass the ambient light coral colonies are receiving. However, when examining colony-specific bleaching patterns, bleaching was found to be dependent upon the location which the colony receives the greatest direct irradiance. Coral bleaching has been seen on the top surfaces of colonies or branch tips, where they are receiving direct light, but not on sides, deeper tissue, or in fissures or crevices that are receiving less direct sunlight (Glynn 1984, Glynn & D'Croz 1990, Fenner & Heron 2008). Because the temperature is the same in the water surrounding the colony, it has been hypothesized that these patterns are related to light. Self-shading by colony morphology may result in less severe whole colony bleaching, and therefore less likelihood of full mortality. As a result, our study only looking at directional shade does capture the light that is most associated with impacting bleaching severity. Still, future studies should investigate the impact of ambient or diffuse light, rather than directional light, to enhance the understanding of the impact of lower levels of irradiance on resilience during bleaching events.

Our observational study was limited in scope of the inquiry and statistical power. Future work is recommended in order to understand how, within each bleaching level, fate is impacted by degree of shading. Experimental studies which track fate by the combination of bleaching severity and shading are suggested. Shaded corals have slower growth rates (Coelho et al. 2017) which implies there may be a tradeoff between alleviation from thermal stress during bleaching events while sacrificing with slower growth that could impact survivorship and competition for space on the reef during normal conditions.

Conservation and restoration efforts have begun to look at light as a factor in considering recovery efforts. Increased depth has been proposed to decrease both temperature and light for regrown reefs (Muir et al. 2017). There have also been proposals of Marine Brightened Clouds (MBC) (Latham et al. 2014) and introducing artificial shading apparatuses during bleaching events to decrease irradiance stress. This study concludes that an increase in angle between the colony and a neighboring colony as little as a 10-20° provides enough shade significantly decreases the likelihood of severe bleaching. This reinforces the importance of maintaining existing structural and morphological complexity and considering its importance in quantifying reef health.

Restoration efforts that fragment and plant corals often rebuild reefs primarily made of one easy-to-grow species. These reefs lack the structural complexity that comes with variance in sizes and morphology, therefore lacking diverse microhabitats with different amounts of sunlight. The importance of creating these microhabitats must be considered when making decisions on locations for reef rebuilding, the rugosity of the benthos the fragments are being attached to, and the morphological variability of the species within the reefs.

Our study also stresses the importance of looking at bleaching on a spectrum, not simply as binary categories of bleached or not bleached. To understand coral bleaching patterns, studies should consider both how and where on the colony corals are bleaching in order to determine factors that impact that bleaching severity. Rather than thinking of a colony as an individual, we propose a shift to thinking about the colonial nature of corals, with each polyp being an individual, in analyzing bleaching responses.

As the frequency, severity, and length of thermal stress events increases, it is important to consider the factors impacting bleaching susceptibility of corals. Like other studies, we conclude that corals that experience more severe bleaching are more likely to face mortality, while corals with less severe bleaching are more likely to experience recovery and growth. We also confirm hypotheses about factors known to impact bleaching severity, such as site and size-based differences.

Our study tested, in situ, the hypothesis that shade resulting from structural complexity may mitigate thermal stress and lead to less severe bleaching. We found that corals with neighboring structures providing shade were less likely to experience severe bleaching than corals that are receiving full direct sunlight. We conclude that increased shade, as little as 20° of elevation, may alleviate the compounded impact of high temperature and high irradiance during thermal stress events. The neighborhood that a coral lives in is important in addition to the demography of the coral. Shade that results from existing structural complexity should be considered in measuring reef health. Further, when implementing restoration efforts, the neighborhood of restored reefs should be considered, taking into account structural and morphological complexity as a means of increasing resilience. While mitigating the impact of increasing sea surface temperature is not likely in the short term, mitigation of the impact of light, which we know provides refuge to corals during thermal stress, is an actionable step to protect coral reefs under changing climate conditions.

Material from this thesis is currently being prepared for submission for publication. Liesegang, Mary B.; Edwards, Clinton B.; Pedersen, Nicole E.; Petrovic, Vid; Sandin, Stuart A. The thesis author was the primary author of this material.

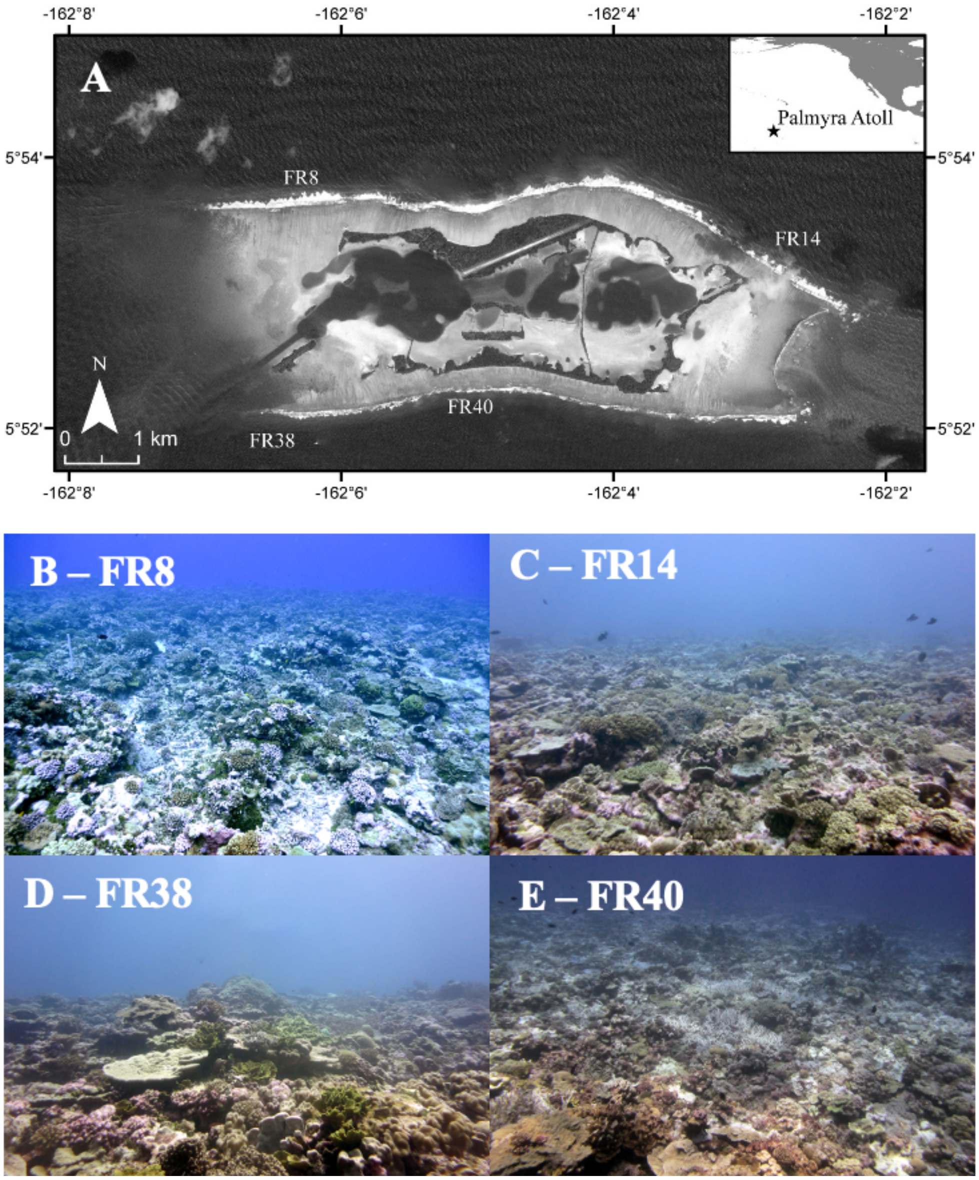

Figure 1: Study Location. A) Map of Palmyra Atoll including four fore reef study sites. FR8 is on the north-west side of the atoll, FR14 on the north-east side, FR38 on the south-west and FR40 in the south-central part of the atoll. B-E) Images of reef study sites. Adapted from Edwards et al. 2017.

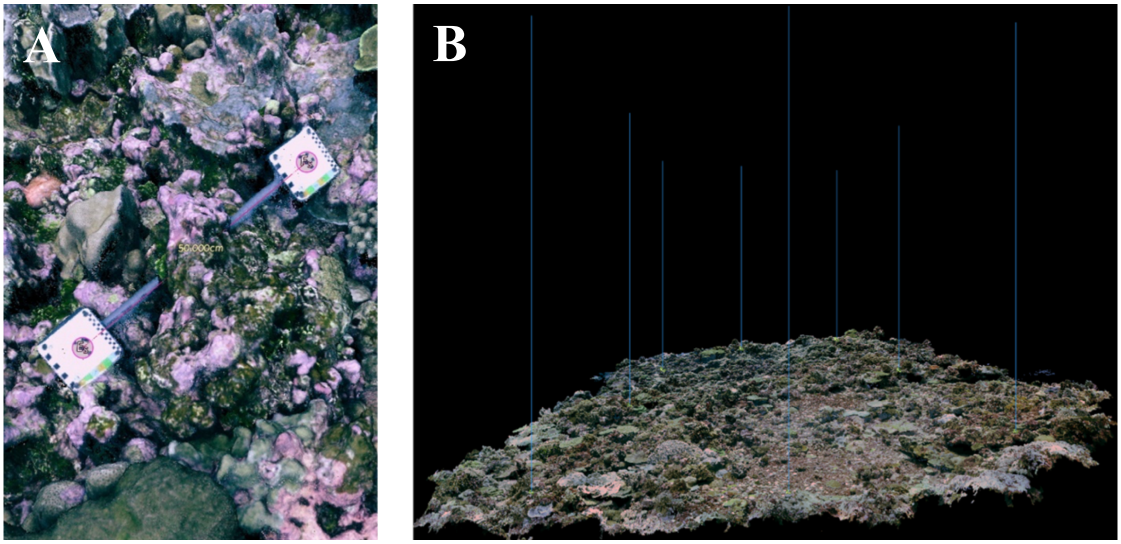

Figure 2: Scale, depth, and orientation of the 3D model. A) 50cm scale bars deployed on plot and visible in 3D model used to assign scale. B) Depth vectors extended from measured depth of plot boundaries to surface which orient the model relative to the plane of the sea surface.

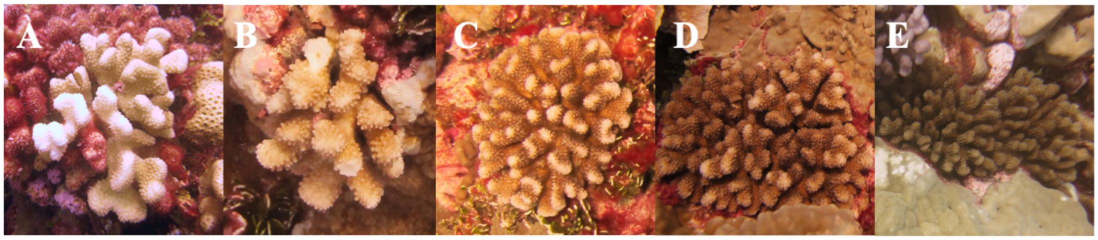

Figure 3: Bleaching severity classifications assigned based on percentage of the whole colony experiencing bleaching. A) *Completely Bleached.* B) *Mostly Bleached* (51-99%). C) *Somewhat Bleached* (10-50%). D) *Less than 10% Bleached* (1-9%). E) *Not Bleached* (0%). Bleaching categories were adapted from Gleason 1993.

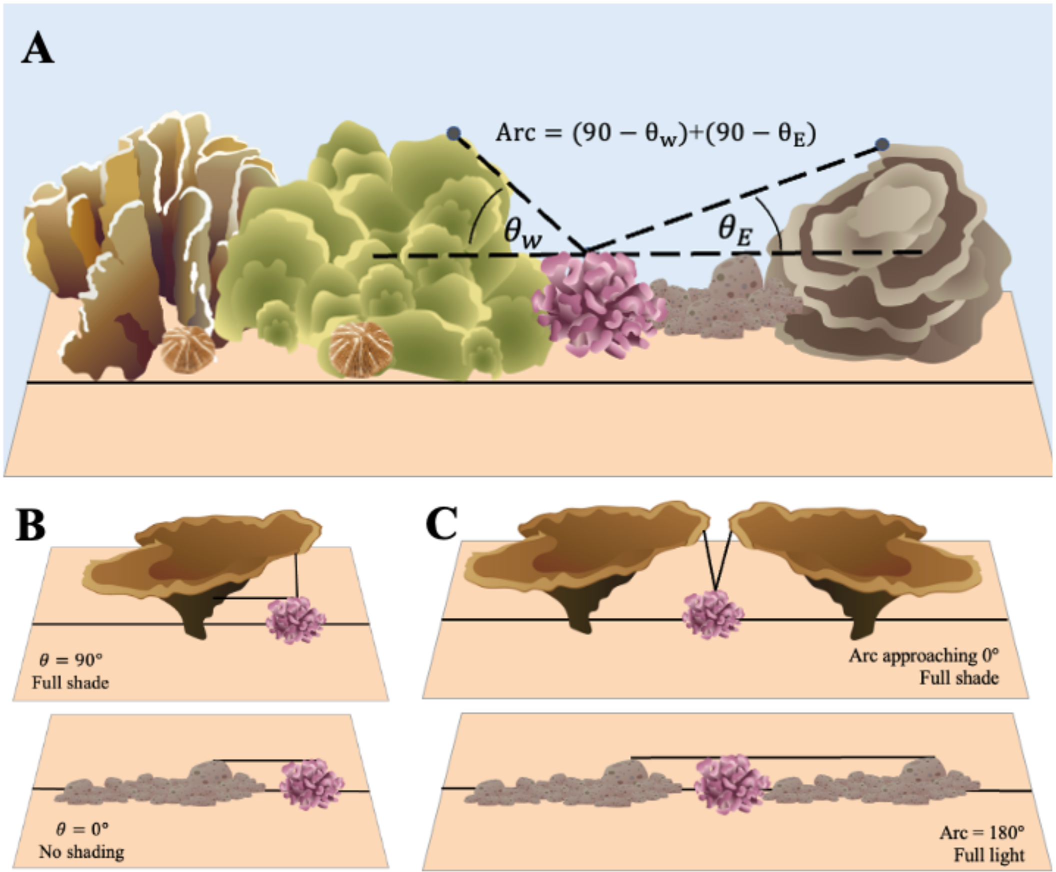

Figure 4: Measurement of shading. A) Arc of shade towards the east and west direction were measured by placing a profile gauge in the centroid of the colony and measuring the greatest change in elevation (z coordinate) between that point and the profile gauge of the tallest structure within 1m. The arc of sunlight was calculated using the sum of the inverse angles in the east and west direction. B) An arc of shade of 90° represents full shade and an arc of 0° represents no shade. Larger arc depicts more shade C) Arc of sunlight approaching 0° represents full shade and arc of sunlight equal to 180° represents full sun.

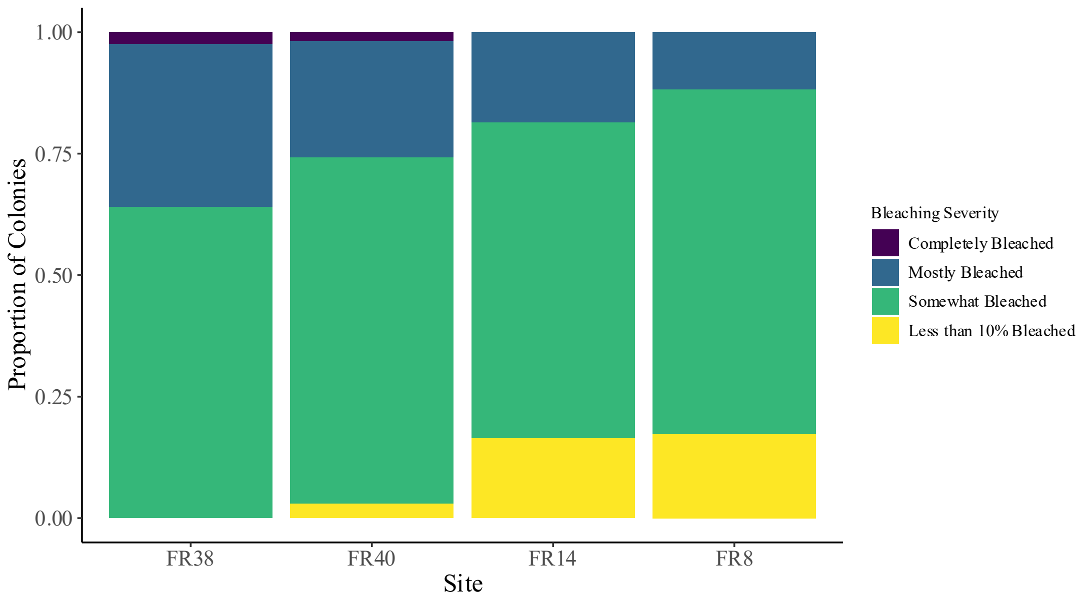

Figure 5: Proportion of colonies with each bleaching severity category across sites from most severe bleaching at FR38 to least severe bleaching at FR8.

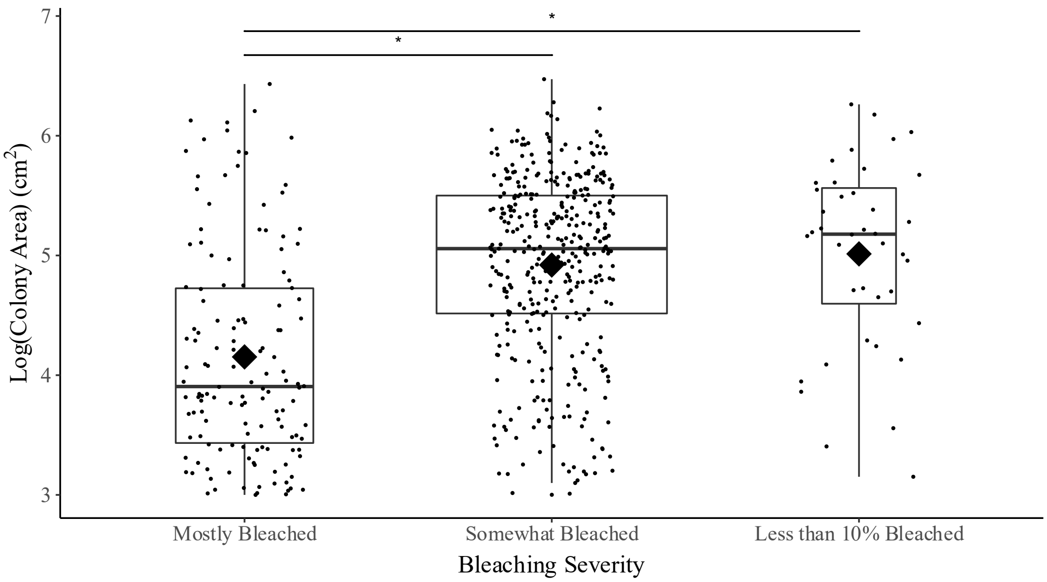

Figure 6: Boxplot comparing initial colony planar area in cm^2 by bleaching severity. Colony area has been log transformed. Diamond point represents group mean, median is represented by horizontal bar within box, box length describes interquartile range, and minimum and maximum values are shown by whiskers. Raw data points are included. Width of boxes represents number of datapoints within that category. Asterisks represent significance between categories.

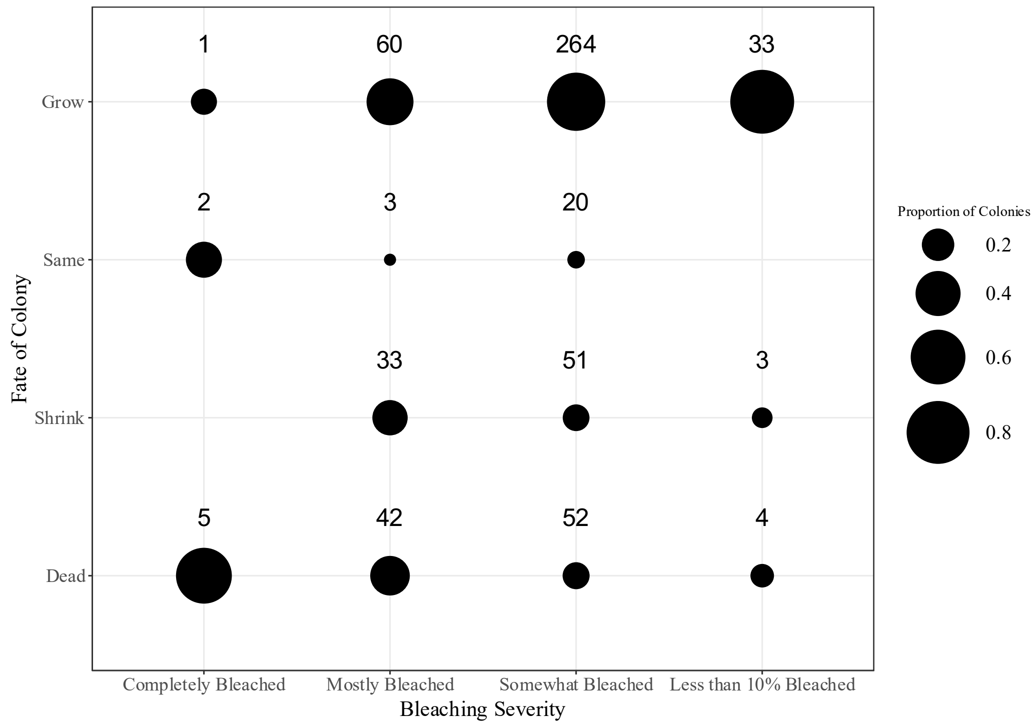

Figure 7: Fate of colony based on bleaching severity. Size of point represents proportion of colonies with that fate from the associated bleaching category. Number of colonies represented are displayed above each point.

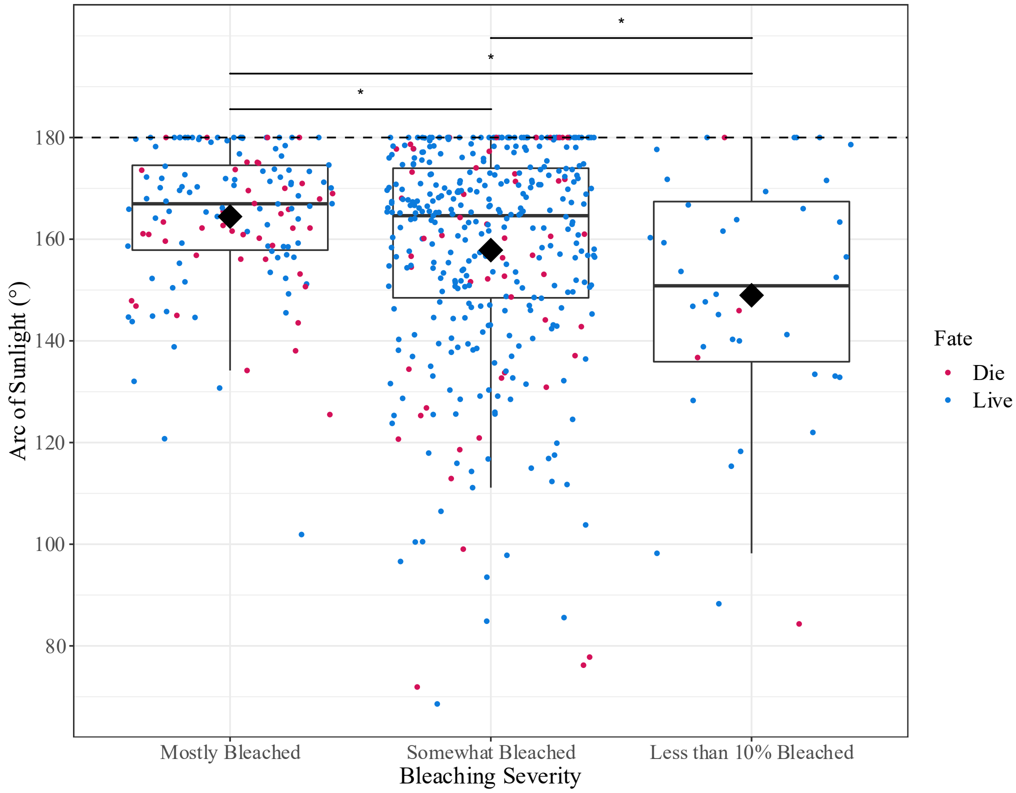

Figure 8: Boxplot comparing arc of sunlight by bleaching severity. A 180° arc of sunlight represents full sun. A small arc of sunlight approaching 0° represents full shade. Diamond points display group mean, median is represented by horizontal bar within box, box length describes interquartile range, and minimum and maximum values are shown by whiskers. Raw data points are included and coded by survivorship of that colony the following year. Asterisks represent significance between categories.

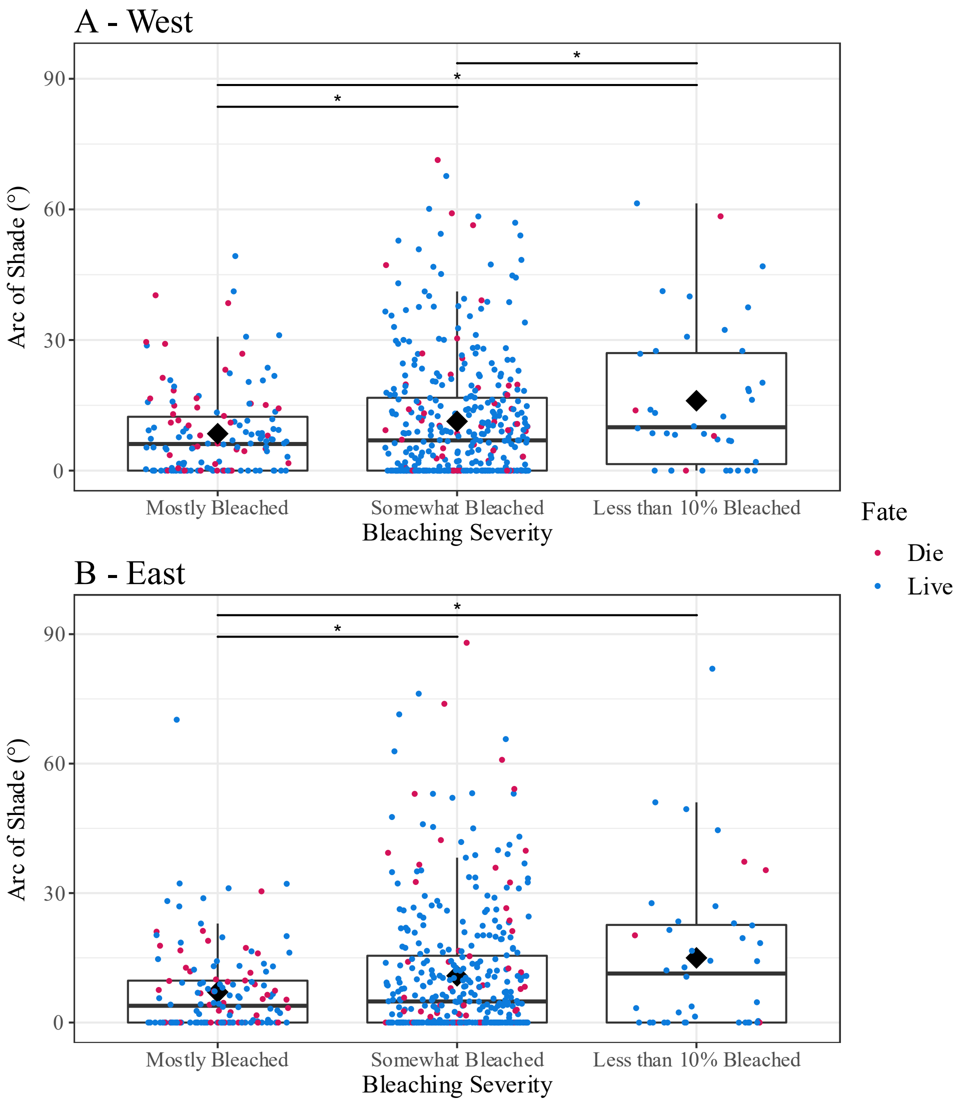

Figure 9: Boxplot comparing arc of shade in the east and west direction by bleaching severity. The arc of shade is measured as the angle between the centroid of the colony and the object within 1m of that colony in the east or west direction providing shade. A 90° arc represents full shade and a 0° arc represents no shade. Diamond points display group mean, median is represented by horizontal bar within box, box length describes interquartile range, and minimum and maximum values are shown by whiskers. Raw data points are included and coded by survivorship of that colony the following year. Asterisks represent significance between categories.

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