



Shading from topographical complexity mitigates bleaching severity of *Pocillopora* spp. during thermal stress

M. B. Liesegang*, C. B. Edwards, N. E. Pedersen, V. Petrovic, S. A. Sandin

Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA 92037, USA

ABSTRACT: Thermally induced bleaching susceptibility of coral varies among species, regional environmental conditions, and local 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 mapping products from large-area imagery collected at the remote atoll of Palmyra in the central Pacific during the 2015 marine heatwave to investigate the role of topographically produced shade in modifying bleaching severity. Change in planar area over 2 yr, bleaching severity, and estimated amount of shade provided by neighboring reef structures were measured for the common coral genus *Pocillopora*. Bleaching severity was correlated with the estimated irradiance, as colonies in more exposed areas (and thus receiving more daily sunlight) experienced more severe bleaching than corals in more shaded areas. 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 populations of this cosmopolitan coral taxon. While some studies have considered artificially shading reefs during warm water events, we highlight the importance of existing structural complexity in providing shade, ultimately contributing to the mitigation of thermal impacts in the face of a changing climate.

KEY WORDS: Coral · Bleaching · Irradiance · Shading · Structural complexity

Resale or republication not permitted without written consent of the publisher

1. INTRODUCTION

Bleaching of reef-building corals can be induced by many environmental forcings, including thermal stress (Glynn 1984, Brown 1997, Berkelmans & Willis 1999, Hoegh-Guldberg 1999), increased irradiance (Lesser et al. 1990), sedimentation (Bak 1978, Philipp & Fabricius 2003), and decreased salinity (Coles & Jokiel 1978, 1992). Notably, the effects of these forcings can be interactive, with combinations of factors leading to higher probabilities of bleaching than predicted based on the levels of each forcing individually (Fitt et al. 2001).

Concurrent episodes of thermal stress and increased irradiance (due to shifting wave or wind pat-

terns calming the sea surface) may result in particularly acute coral bleaching events, and shading has been shown to reduce coral mortality during mass bleaching events (Mumby et al. 2001, Tagliarico et al. 2022). For example, unexpectedly severe coral bleaching was observed during a mild thermal stress event under conditions of anomalously high irradiance, the latter linked to calm seas and cloudless skies (Glynn 1993). Contrastingly, cloud cover was credited with alleviating bleaching that was expected due to increased sea surface temperatures during the 1997/1998 global bleaching event (Mumby et al. 2001). In a global study of over 35 000 corals spanning 32 yr, higher levels of cloudiness reduced bleaching response of corals exposed to severe

*Corresponding author: maryhope.liesegang@gmail.com

bleaching-level heat stress (Gonzalez-Espinosa & Donner 2021).

Similarly, nearshore turbid environments have been considered refuges during thermal stress due to increased particles in the water column absorbing light and lessening realized irradiance experienced by corals (van Woesik et al. 2012, Cacciapaglia & van Woesik 2016, Sully & van Woesik 2020). Additionally, recent research on corals growing on mangrove roots suggests that the shade provided by mangrove canopies offers a vital refuge from light stress and contributes to improved coral survival during thermal stress, compared to nearby shallow reefs (Yates et al. 2014, Stewart et al. 2021). Macroalgae cover, though often harmful in outcompeting corals during favorable conditions, has been shown to provide refuge by reducing solar irradiance, particularly for branching corals (Smith et al. 2022).

High light combined with thermal stress can result in coral mortality. In an experimental study manipulating both light and thermal stress, high levels of both resulted in coral mortality, while 70% light at the same temperature resulted in limited mortality and coral growth (Coles & Jokiel 1978). Relatedly, artificial shade during thermal stress decreased bleaching of 3 common coral species, with heavier shading decreasing growth rate but increasing survival rate of the colonies (Coelho et al. 2017). These findings have encouraged further studies investigating the potential of shade in coral resilience (West & Salm 2003, Ban et al. 2014). Environmental features can also contribute to shading in natural settings. For example, the topography of a reef due to structural complexity of massive and tabular corals, as well as large thickets of branching corals such as *Acropora*, naturally enhances reef topography. Variety in the physical structure influences environmental factors such as light intensity and water flow, which both impact bleaching severity (Hoogenboom et al. 2017, Lenihan et al. 2008).

Here, we explored the interaction of local shading produced from reef structural complexity on the incidence of coral bleaching in a natural setting during a thermal stress event. Using 3D models of coral reefs on a remote reef in the central Pacific during a marine heatwave, we investigated how local shading (at the scale of the colony) is associated with bleaching severity. We hypothesized that reduced irradiance from shade produced by neighboring topographical features will reduce bleaching severity of coral colonies. We consider existing structural complexity of the reef as a form of protection against bleaching and highlight the importance of maintaining varied reef topography under changing climate conditions.

2. MATERIALS AND METHODS

2.1. Study site

Data were collected in 2015 and 2016 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 over-fishing (Sandin et al. 2008). 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 a maximum of 11.9 degree heating weeks (DHWs) measured between July and September 2015 and peak *in situ* nighttime temperature on the fore reef measured in September 2015 (Fox et al. 2019). Previous studies have shown that 4 DHWs result in bleaching, with mortality common above 8 DHWs (Eakin et al. 2009). During this bleaching event, 90% of the corals on Palmyra bleached, with 32% of bleaching classified as severe. Despite the severity, most corals survived, with only 9% coral mortality (Fox et al. 2019). Four fore-reef sites, 2 on the north side of the atoll and 2 on the south side of the atoll, were identified for use in this study (FR8 and FR14, FR38 and FR40, respectively; Fig. 1A).

2.2. Study organism

The focal taxon of this study was the genus *Pocillopora*, represented by 2 species: *P. meandrina* and *P. verrucosa*. Because the species are morphologically 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 and comprise 15% of the total coral cover and 12% coral colony abundance at Palmyra, making it the third most abundant coral taxonomic group (Edwards et al. 2017). Given their corymbose morphology, identifying colony borders for accurate size measurement is straightforward. *P. meandrina* and *P. verrucosa* exhibit a competitive life history strategy with low resistance to disturbance events and fast colonization and growth, often allowing rapid recovery (Loya et al. 2001, Darling et al. 2012, Kayal et al. 2015).

2.3. Model construction

Methods of large-area imaging and exploration of resulting 3D models were adapted from Edwards et al.

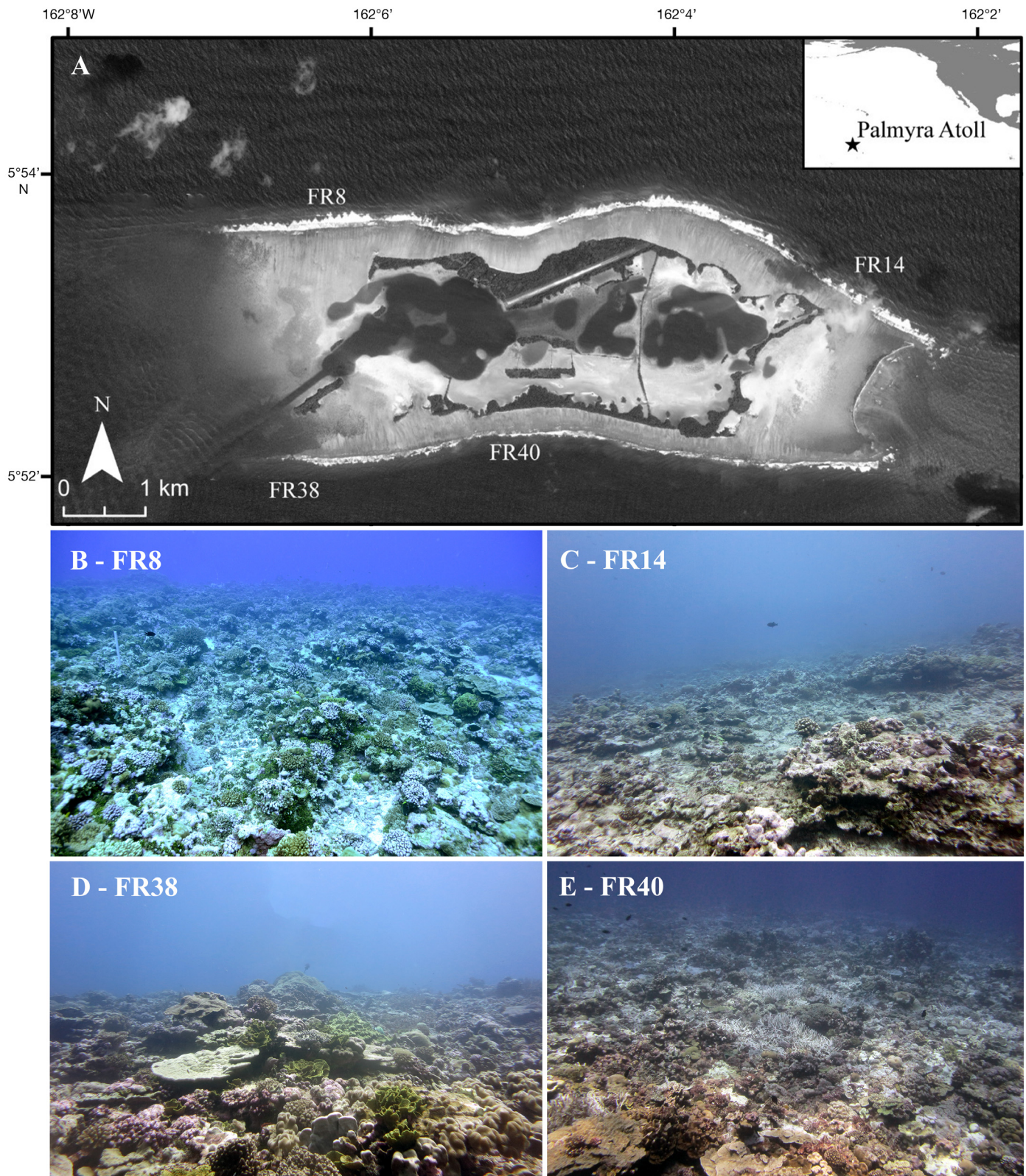


Fig. 1. Study location. (A) Palmyra Atoll, central Pacific, showing the 4 fore-reef study sites. (B–E) Images of reef study sites. Adapted from Edwards et al. (2017)

(2017). In September and October 2015, during the peak of the thermal stress event, and September 2016, imagery was collected from 100 m² fore-reef plots ($n = 4$) along the 10 m isobath (Fig. 1B). The central axis of the plot was marked with 2 steel pins along the 10 m isobath. The lefthand pin (with relative position assessed while facing onshore) was georeferenced with GPS coordinates for annual sampling and the compass bearing from the lefthand to righthand pin (approximately parallel to shore) was recorded. Models of each site were collected through large-area imaging techniques, with a diver operating a camera system with 2 Nikon D7000 DSLR cameras, one with a 55 mm focal lens and another with 18 mm focal lens, with the cameras mounted one above the other. The diver swam a gridded pattern approximately 1.5 m above the reef, capturing 1 image per second, resulting in approximately 2500 images per camera per plot with significant image overlap across the seascape (targeting >20 images per point on the benthos).

The raw imagery was used to create 3D point cloud reconstructions in the Structure-from-Motion software Metashape (Agisoft Metashape 2016). These point clouds were coregistered across time and converted into temporally aligned 2D top-down orthoprojections using the custom software Viscore (Petrovic et al. 2014). Scale bars on established reef plots were used to ensure accurate scale and the plane of reference for orthorectification was defined as that parallel to the sea surface, estimated based on the depths of the markers identifying the plot boundaries. Models in Viscore were oriented according to cardinal directions using the alongshore compass bearing, allowing for directional analysis. This study used a 2 yr time series of 2015 and 2016, with 2015 capturing the bleaching event and 2016 used to determine survivorship and recovery.

2.4. Data extraction

Within the 4 sites, 618 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 from both cameras (with the 55 and 18 mm lenses) were used to increase precision in mapping colony borders. Colonies whose boundaries could not be confidently defined based on the details of the 3D models (those near plot borders, those com-

pletely under overhangs that were occluded in the model) were excluded.

Between years, colonies were manually matched in TagLab, thus providing the ability to evaluate colony-specific shifts in condition or size through time. Change in planar area between the matched colonies was used to determine fate of the colony, classified as experiencing growth, no change (less than 5% change in area), shrinkage, or death (which included death with skeleton still visible, upheaval to different unidentifiable location, or complete coverage by other reef structures). Size estimates were constrained to 2D orthoprojections to increase measurement precision; notably, 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 5 cm 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 to avoid complications of calculating area under partial mortality. A total of 45 colonies (~7%) were removed for this reason, leaving 573 colonies for analysis.

Colonies were assigned 1 of 5 bleaching severity categories (for the 2015 time point) based on the percent of the whole colony affected. Bleaching severity was adapted from Gleason (1993) and Burgess et al. (2021) and classified as follows: not bleached (no loss of pigmentation), less than 10% bleached (some loss of pigmentation in branch tips), somewhat bleached (many pale branch tips), mostly bleached (white branch tips with bleaching extending down branches), and completely bleached (full colony white) (Fig. 2).

The point cloud in Viscore was used to determine the impact of light through shading from neighboring reef structures. A 4 cm grid, oriented east/west, was placed over the model representing a 2D grid (x, y). At the coordinate of each vertex of the grid, a point was defined on the 3D point cloud, with the z dimension defined by the depth of the model at each (x, y) coordinate defined. For each coral colony, an additional point was placed at the centroid of the planar projection of the colony and positioned at the depth of the colony at this point (z); the associated colony ID from Taglab was linked to this point for identification.

For each colony, relative shading was defined as the size of the arc of unobstructed view from the colony to the ocean surface along the east–west axis (Fig. 3A). The change in z coordinate and change in x, y coordinate was used to determine angle of elevation, θ , between the 2 points through trigonometry

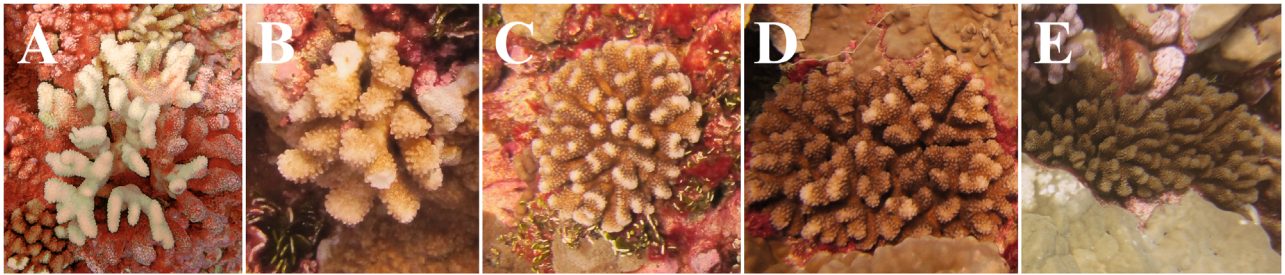


Fig. 2. Bleaching severity classifications assigned based on percentage of the whole colony experiencing bleaching. (A) Completely bleached (whole colony is white). (B) Mostly bleached (white branch tips with bleaching extending down branches). (C) Somewhat bleached (many pale branch tips). (D) Less than 10% bleached (some loss of pigmentation in the branch tips). (E) Not bleached (no loss of pigmentation). Bleaching categories were adapted from Gleason (1993) and Burgess et al. (2021)

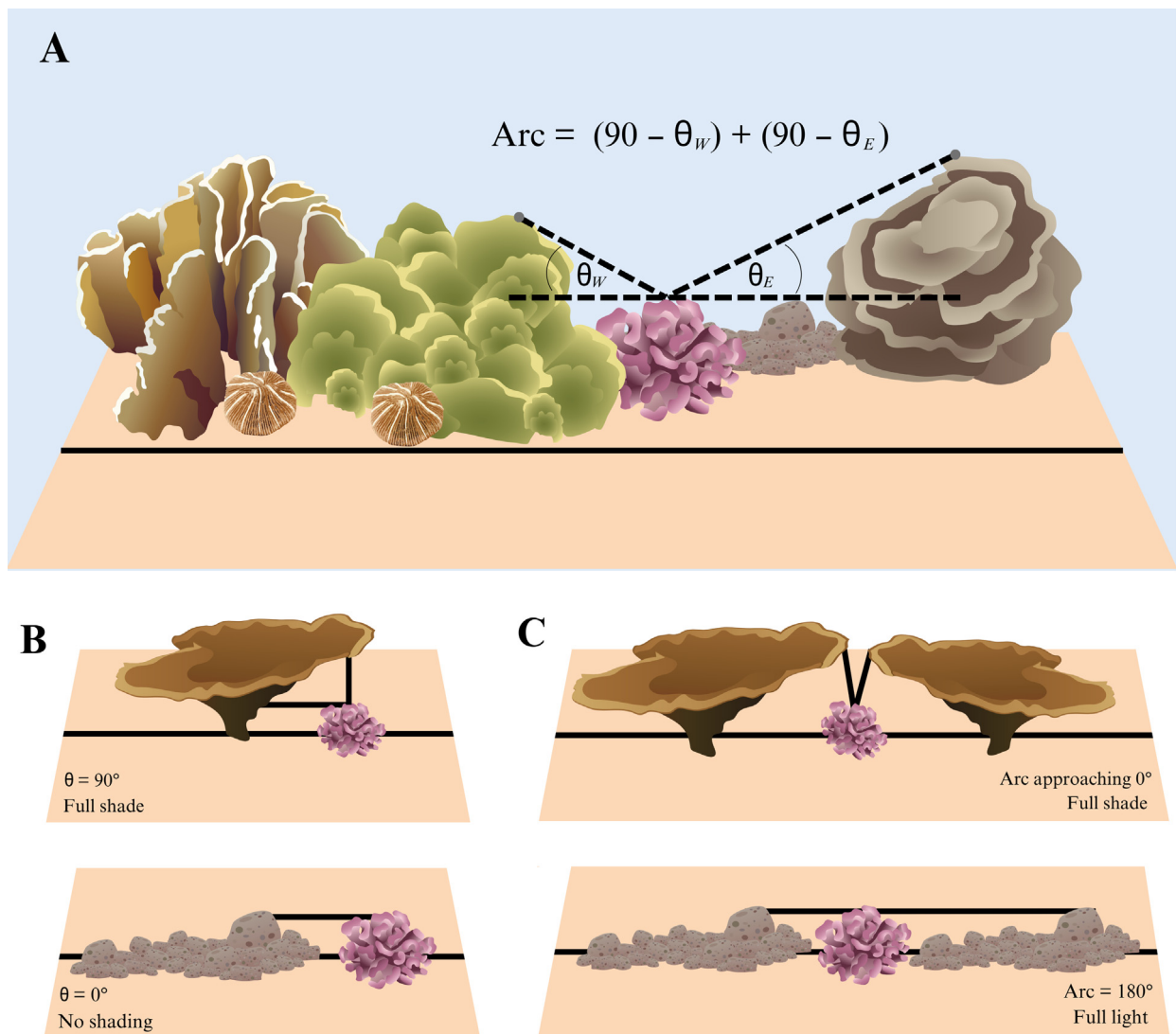


Fig. 3. Measurement of shading. (A) Relative shading: θ_W and θ_E represent the angles between the colony and the nearest obstructing objects along the east and west axes. (B) Arc of shade: the largest angle of elevation within 1 m from the colony's centroid. (C) Arc of sunlight: the sum of the inverse angles in the east and west directions

$$\theta = \tan^{-1} \frac{\Delta z}{\Delta xy}$$

Change in elevation between the colony and neighboring structure at each grid vertex was measured up to 1 m away from the centroid of the colony. The largest angle within that meter was recorded as the arc 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 (Fig. 3B). Negative arcs of shade were noted as 0°, as there were no shading structures nearby. The process was done in both the east and west direction. Because Palmyra is located at 5.89° N latitude, the path of daily sun travels directionally from east to west with less significant light coming from north or south directions, which were not included in this study.

The amount of sunlight the colony experienced based on neighboring structures was converted to a single arc of sunlight measurement by subtracting the east and west angles from 90° and adding those in-

verse angles together (Fig. 3C). A small arc of sunlight approaching 0° represents significant shading, and a larger arc of 180° represents no shading.

2.5. Statistical analyses

All data analysis was performed in R Statistical Software Version 1.4.1103 (R Core Team 2022). Difference in severity of bleaching between sites was tested using a χ^2 analysis. Pairwise comparisons were performed using Fisher's exact test.

Bleaching severity was grouped as severe (completely bleached and mostly bleached) and mild (somewhat bleached and less than 10% bleached) for the remainder of the analyses. The relationship between bleaching severity and fate the following year was tested using a χ^2 analysis.

Logistic regression was used to analyze the relationship between arc of sunlight and colony bleaching severity. The model considers whether the probability of a colony experiencing mild vs. severe bleaching is a function of level of exposure to sunlight. This approach was then repeated for the arc of sunlight in both the east and west directions. The relationship between arc of sunlight and bleaching was similar across sites (data presented in Fig. A1 in the Appendix), so all data are aggregated across sites in the analyses presented.

3. RESULTS

We measured planar area, bleaching severity, and estimated irradiance for 573 *Pocillopora* colonies across 4 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, 67.5% somewhat bleached, 7% less than 10% bleached, and 0% not bleached.

Bleaching severity varied between sites, with FR8 having the least severe colony bleaching and FR38 having the most severe colony bleaching ($p < 0.001$, $\chi^2 = 68.3$) (Fig. 4). Pairwise comparisons showed significantly different bleaching between all sites except between FR38 and FR40.

Of the 573 colonies observed, 103 died, 87 shrank, 25 had no more than a 5% change in area, and 358 grew. Due to sample size, bleaching severity categories were grouped as severe bleaching (mostly bleached and completely bleached) and mild bleaching (somewhat bleached and less than 10% bleached). Of the 146 severely bleached colonies, 42% grew, 3% had no

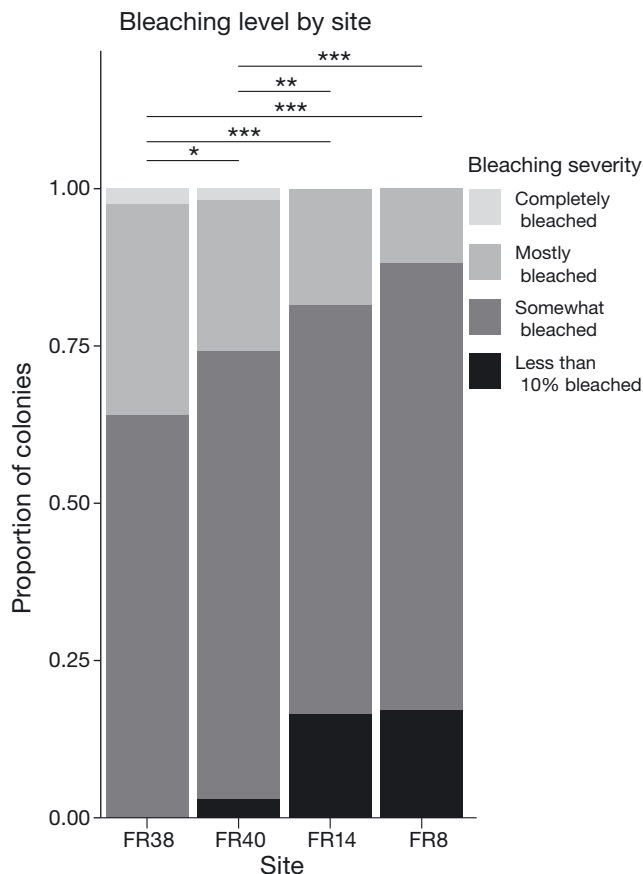


Fig. 4. Proportion of colonies with each bleaching severity category across sites, from most severe bleaching at FR38 to least severe bleaching at FR8. Asterisks indicate the level of statistical significance between categories (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$)

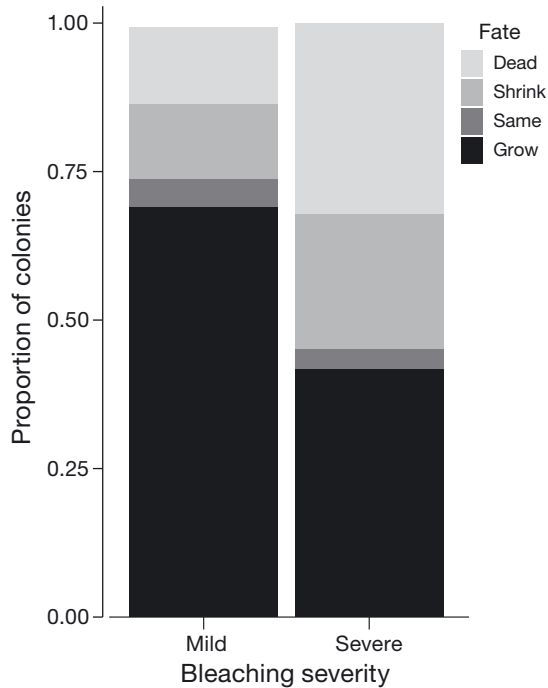


Fig. 5. Proportion of colonies based on fate the year following bleaching by bleaching severity

change, 23% shrank, and 32% died. Of the 427 mildly bleached colonies, 69% grew, 5% had no change, 13% shrank, and 13% died (Fig. 5). There was a significant relationship between mild bleaching and severe bleaching and fate the following year ($p < 0.001$, $\chi^2 = 43.0$). Colonies experiencing less severe bleaching resulted in a higher likelihood of growth (69%) and a lower likelihood of death (13%) when compared to more severely bleached colonies which exhibited 42% growth and 32% death (Fig. 5).

Mildly bleached colonies had a smaller arc of sunlight, defined as the angle produced by neighboring structures in the combined east and west direction, of $156.6 \pm 1.0^\circ$ (\pm SE). Severely bleached colonies had a larger arc of sunlight of $165.6 \pm 1.0^\circ$ (Fig. 6). The probability of a colony suffering severe vs. mild bleaching was positively related to the arc of sunlight (logistic regression: arc of sunlight effect 0.030 ± 0.007 ; $p < 0.001$; Fig. 6).

In the west direction, mildly bleached colonies had a larger mean arc of shade of $11.9 \pm 0.7^\circ$, and severely bleached

colonies had a smaller mean arc of shade of $7.9 \pm 0.8^\circ$ (Fig. 7A). In the east direction, mildly bleached colonies had a larger mean arc of shade of $11.4 \pm 0.7^\circ$ and severely bleached colonies had a smaller mean arc of shade of $6.5 \pm 0.7^\circ$ (Fig. 7B). 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. Results of logistic regression revealed similar positive effects of arc of sunlight on probability of a colony suffering severe bleaching (west: 0.028 ± 0.009 , $p < 0.05$; east: 0.034 ± 0.010 , $p < 0.05$).

4. DISCUSSION

Here, we explored the role that shade from structural complexity of reef topography played in mitigating bleaching severity of *Pocillopora* during the marine heat wave of 2015 at Palmyra Atoll. Our findings suggest that the amount of sunlight coral colonies received, measured as both the arc of sunlight and the arc of shade in the east and west direction, was related

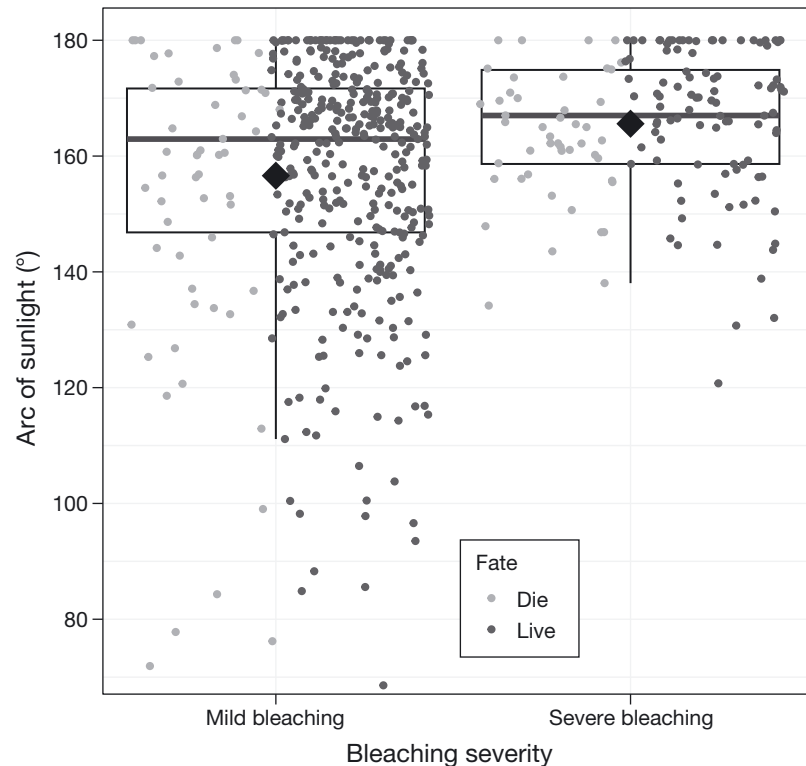


Fig. 6. Arc of sunlight by bleaching severity. A 180° arc of sunlight represents full sun. A small arc of sunlight approaching 0° represents full shade. Large diamond displays group mean, median is represented by horizontal bar within the box, box length describes interquartile range, and minimum and maximum values are shown by whiskers. Raw data points are included and coded by survivorship of that colony the following year

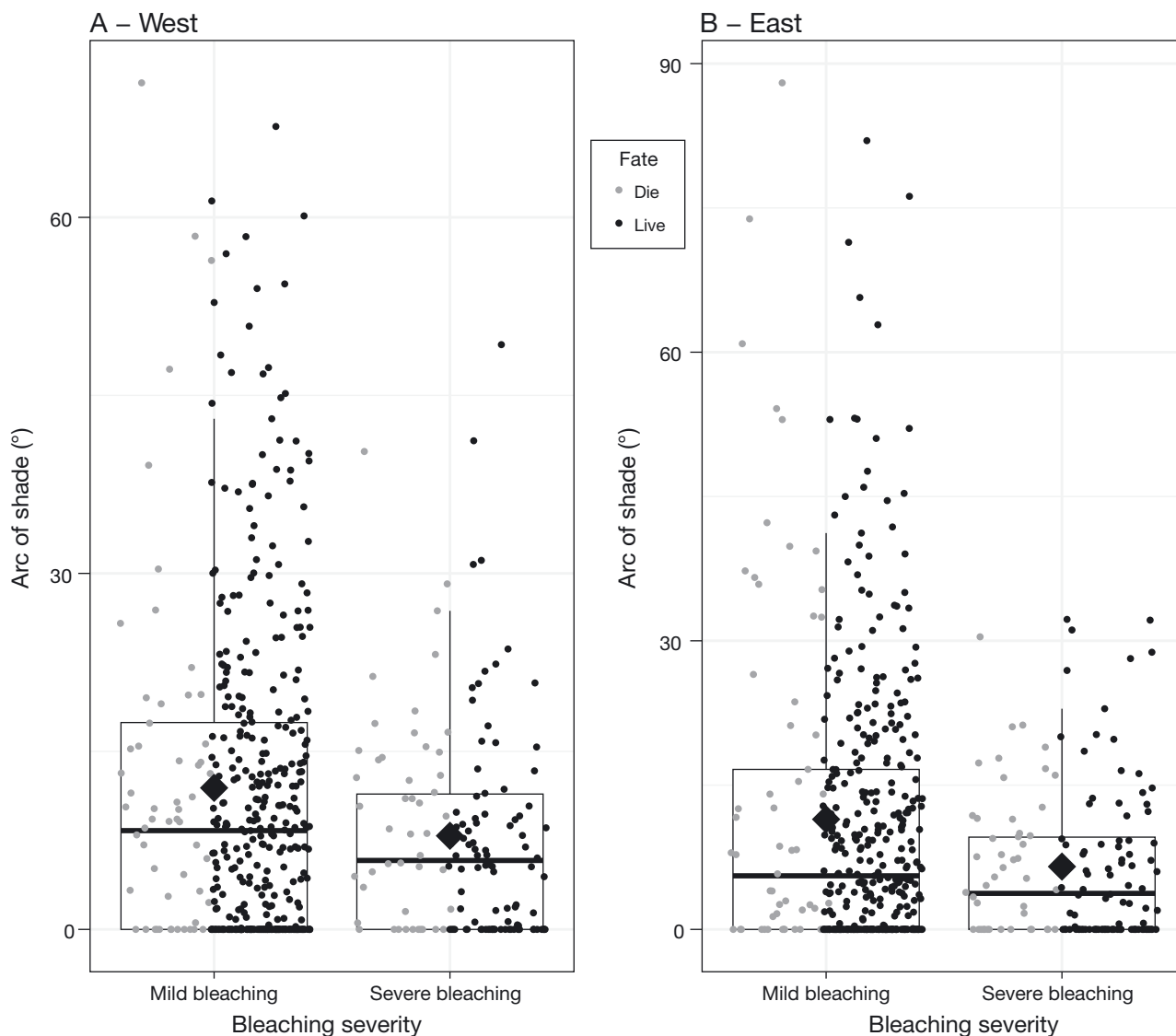


Fig. 7. Arc of shade in the (A) west and (B) east direction by bleaching severity. The arc of shade is measured as the angle between the centroid of the colony and the object within 1 m of that colony in the east or west direction providing shade. A 90° arc represents full shade and a 0° arc represents no shade. Boxplot parameters as in Fig. 6

to the severity of bleaching. Colonies exposed to more sunlight experienced more severe bleaching, while colonies in shaded areas exhibited milder bleaching. Colonies with mild bleaching had a higher likelihood of growth, and colonies with more severe bleaching were more likely to die.

Similarly, while shading consistently influenced bleaching patterns within sites, we observed site-specific differences in the overall magnitude of bleaching severity, which has been demonstrated previously (McClanahan et al. 2020). Site-specific differences in bleaching severity within the same species has been attributed to local upwelling bringing

cool, nutrient-rich water to the surface (Goreau et al. 2000, Spring & Williams 2023), thermal history and acclimation to past bleaching events (Coles & Jokiel 1978), water flow and currents (Nakamura & van Woesik 2001), and depth, which decreases the combined thermal and light stress (Huston 1985, Muir et al. 2017). At Palmyra Atoll, despite the lack of site-specific differences in nutrient concentration and irradiance, wave energy on the north side of the atoll is typically higher than on the south side (Gove et al. 2015, Williams et al. 2018). This could explain why corals on the north side experienced less severe bleaching, as increased wave energy provides more

water flow to help flush toxins and increased passive diffusion during warm water events (Nakamura & van Woesik 2001).

In line with previous research, our results confirm that colonies experiencing severe bleaching typically die or suffer significant tissue loss, while less severely bleached colonies are more likely to survive and grow (Gleason 1993). In our study, mildly bleached colonies exhibited more growth compared to those that were severely bleached. 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). Our study confirms that corals with less bleaching have limited mortality and are more likely to survive the following year.

In addition to supporting observations largely derived from experimental studies, we focused on the role of structural complexity and varied light regimes in mitigating the compounded impact of thermal stress and irradiance during a marine heatwave. We used reef topography and the 'neighborhood' in which the coral lives as predictors of the amount of shade corals received and considered how varied light regimes, resulting from reef structural complexity, mitigated the compounded impacts of thermal stress and irradiance during a marine heatwave. Shaded colonies of *Pocillopora*, with smaller arcs of sunlight, bleached less severely than colonies with larger arcs of sunlight that were receiving more direct irradiance. Experimentally, 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).

Our results underscore the importance of structural complexity in creating microhabitats that mitigate bleaching severity. Consistent with earlier studies showing that coral in crevices or under overhangs experience less severe bleaching compared to those in open, elevated, or sandy substrate (Hoogenboom et al. 2017, van Woesik & McCaffrey 2017), we add quantitative data of the complementary importance of local shading on estimated irradiance levels and associated bleaching.

The microhabitats created by structural complexity affect more than shading, likely influencing patterns of water flow and other environmental specifics that can affect coral bleaching (Lenihan et al. 2008). While water flow is difficult to assess through photographic analysis, reduced flow is often expected in complex environments like shaded crevices, which theoretically should increase susceptibility to bleaching. However, our study found that these crevices, despite potentially decreased water flow, still offered significant protec-

tion. This suggests that the decreased thermal stress in protected areas may be more significant than the contribution of water flow to bleaching resilience.

Structural complexity on reefs is in many cases formed by the coral assemblage itself, suggesting that coral mortality might contribute toward reductions in complexity. Magel et al. (2019) investigated the role of thermal stress and human activity on reef topographical complexity and found that both bleaching-associated coral mortality and human disturbance decreased the density of branching and massive corals. The associated flattening of the reef would minimize the microhabitats that provide local shade which can mitigate bleaching. Similarly, cyclones, which are increasing in intensity and frequency under a changing climate, result in mechanical disturbance which can reduce structural complexity on reefs by dislodging shade-producing structures such as massive corals and the branches of branching corals (Massel & Done 1993, Fabricius et al. 2008). As climate change progresses, we expect reefs globally to become less complex, which has profound implications when considering the importance of shade.

As thermal stress events increase in frequency, severity, and duration, understanding the factors that influence bleaching susceptibility of corals is increasingly important. Consistent with previous 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 (Gleason 1993). We also confirm the importance of site-specific differences in bleaching severity (McClanahan et al. 2020).

Our study tested, *in situ*, the hypothesis that shade resulting from structural complexity can mitigate thermal stress and reduce bleaching severity. We found that corals with neighboring structures providing shade were less likely to experience severe bleaching than corals that received full direct sunlight. We conclude that increased shade, as little as 10° of elevation, may alleviate some of the compounded impact of high temperature and high irradiance during thermal stress events. In addition to the demography of the coral, the neighborhood in which it lives is important.

Acknowledgements. The present work was part of M.B.L.'s Master's thesis (available at <https://escholarship.org/uc/item/15h4j48q>). This research was made possible by the Nature Conservancy, the US Fish and Wildlife Service, and the Palmyra Atoll Research Consortium under special US Fish and Wildlife Special Use Permits #12533-15017 and #12533-16023. Funding was provided by National Fish and Wildlife Foundation #0302.16.053589 and a generous donation from the Scripps Family Foundation.

LITERATURE CITED

- Agisoft Metashape (2016) Agisoft PhotoScan Professional (version 1.4.5). www.agisoft.com/downloads/installer/
- ✦ Bak R (1978) Lethal and sublethal effects of dredging on reef corals. *Mar Pollut Bull* 9:14–16
- ✦ Ban SS, Graham NA, Connolly SR (2014) Evidence for multiple stressor interactions and effects on coral reefs. *Glob Change Biol* 20:681–697
- ✦ Berkelmans R, Willis BL (1999) Seasonal and local spatial patterns in the upper thermal limits of corals on the inshore Central Great Barrier Reef. *Coral Reefs* 18:219–228
- ✦ Brown BE (1997) Coral bleaching: causes and consequences. *Coral Reefs* 16:S129–S183
- ✦ Burgess SC, Johnston EC, Wyatt ASJ, Leichter JJ, Edmunds PJ (2021) Response diversity in corals: hidden differences in bleaching mortality among cryptic *Pocillopora* species. *Ecology* 102:e03324
- ✦ Cacciapaglia C, van Woesik R (2016) Climate-change refugia: shading reef corals by turbidity. *Glob Change Biol* 22:1145–1154
- ✦ Coelho VR, Fenner D, Caruso C, Bayles BR, Huang Y, Berkeley C (2017) Shading as a mitigation tool for coral bleaching in three common Indo-Pacific species. *J Exp Mar Biol Ecol* 497:152–163
- ✦ Coles SL, Jokiel PL (1978) Synergistic effects of temperature, salinity and light on the hermatypic coral *Montipora verrucosa*. *Mar Biol* 49:187–195
- Coles SL, Jokiel PL (1992) Effects of salinity on coral reefs. In: Connell DW, Hawker DW (eds) *Pollution in tropical aquatic systems*. CRC Press, Boca Raton, FL, p 147–163
- ✦ Darling ES, Alvarez-Filip L, Oliver TA, McClanahan TR, Côté IM (2012) Evaluating life-history strategies of reef corals from species traits. *Ecol Lett* 15:1378–1386
- ✦ Eakin CM, Lough JM, Heron SF (2009) Climate variability and change: monitoring data and evidence for increased coral bleaching stress. *Ecol Stud* 205:41–67
- ✦ Edwards CB, Eynaud Y, Williams GJ, Pedersen NE and others (2017) Large-area imaging reveals biologically driven non-random spatial patterns of corals at a remote reef. *Coral Reefs* 36:1291–1305
- ✦ Fabricius KE, De'ath G, Puotinen ML, Done T, Cooper TF, Burgess SC (2008) Disturbance gradients on inshore and offshore coral reefs caused by a severe tropical cyclone. *Limnol Oceanogr* 53:690–704
- ✦ Fitt WK, Warner ME (1995) Bleaching patterns of four species of Caribbean reef corals. *Biol Bull* 189:298–307
- ✦ Fitt WK, Brown B, Warner M, Dunne R (2001) Coral bleaching: interpretation of thermal tolerance limits and thermal thresholds in tropical corals. *Coral Reefs* 20:51–65
- ✦ Fox MD, Carter AL, Edwards CB, Takeshita Y and others (2019) Limited coral mortality following acute thermal stress and widespread bleaching on Palmyra Atoll, central Pacific. *Coral Reefs* 38:701–712
- ✦ Gleason MG (1993) Effect of disturbance on coral communities: bleaching in Moorea, French Polynesia. *Coral Reefs* 12:193–201
- ✦ Glynn PW (1984) Widespread coral mortality and the 1982–83 El Niño warming event. *Environ Conserv* 11: 133–146
- ✦ Glynn PW (1993) Coral reef bleaching: ecological perspectives. *Coral Reefs* 12:1–17
- ✦ Gonzalez-Espinosa PC, Donner SD (2021) Cloudiness reduces the bleaching response of coral reefs exposed to heat stress. *Glob Change Biol* 27:3474–3486
- ✦ Goreau T, McClanahan T, Hayes R, Strong AL (2000) Conservation of coral reefs after the 1998 global bleaching event. *Conserv Biol* 14:5–15
- ✦ Gove JM, Williams GJ, McManus MA, Clark SJ, Ehse JS, Wedding LM (2015) Coral reef benthic regimes exhibit non-linear threshold responses to natural physical drivers. *Mar Ecol Prog Ser* 522:33–48
- ✦ Highsmith RC (1982) Reproduction by fragmentation in corals. *Mar Ecol Prog Ser* 7:207–226
- ✦ Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Mar Freshw Res* 50:839–866
- ✦ Hoogenboom MO, Frank GE, Chase TJ, Jurriaans S and others (2017) Environmental drivers of variation in bleaching severity of *Acropora* species during an extreme thermal anomaly. *Front Mar Sci* 4:376
- ✦ House JE, Brambilla V, Bidaut LM, Christie AP, Pizarro O, Madin JS, Dornelas M (2018) Moving to 3D: relationships between coral planar area, surface area and volume. *PeerJ* 6:e4280
- ✦ Hughes TP, Jackson JB (1980) Do corals lie about their age? Some demographic consequences of partial mortality, fission, and fusion. *Science* 209:713–715
- ✦ Huston MA (1985) Patterns of species diversity on coral reefs. *Annu Rev Ecol Syst* 16:149–177
- ✦ Kayal M, Vercelloni J, Wand MP, Adjeroud M (2015) Searching for the best bet in life-strategy: a quantitative approach to individual performance and population dynamics in reef-building corals. *Ecol Complex* 23:73–84
- ✦ Lenihan HS, Adjeroud M, Kotchen MJ, Hench JL, Nakamura T (2008) Reef structure regulates small-scale spatial variation in coral bleaching. *Mar Ecol Prog Ser* 370:127–141
- ✦ Lesser MP, Stochaj WR, Tapley DW, Shick JM (1990) Bleaching in coral reef anthozoans: effects of irradiance, ultraviolet radiation, and temperature on the activities of protective enzymes against active oxygen. *Coral Reefs* 8: 225–232
- ✦ Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, van Woesik R (2001) Coral bleaching: the winners and the losers. *Ecol Lett* 4:122–131
- ✦ Magel JMT, Burns JHR, Gates RD, Baum JK (2019) Effects of bleaching-associated mass coral mortality on reef structural complexity across a gradient of local disturbance. *Sci Rep* 9:2512
- ✦ Massel SR, Done TJ (1993) Effects of cyclone waves on massive coral assemblages on the Great Barrier Reef: meteorology, hydrodynamics and demography. *Coral Reefs* 12: 153–166
- ✦ McClanahan TR, Maina JM, Darling ES, Guillaume MM and others (2020) Large geographic variability in the resistance of corals to thermal stress. *Glob Ecol Biogeogr* 29: 2229–2247
- ✦ Muir PR, Marshall PA, Abdulla A, Aguirre JD (2017) Species identity and depth predict bleaching severity in reef-building corals: Shall the deep inherit the reef? *Proc R Soc B* 284:20171551
- ✦ Mumby PJ, Chisholm JRM, Edwards AJ, Andrefouet S, Jauibert J (2001) Cloudy weather may have saved Society Island reef corals during the 1998 ENSO event. *Mar Ecol Prog Ser* 222:209–216
- ✦ Nakamura T, van Woesik R (2001) Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. *Mar Ecol Prog Ser* 212:301–304
- ✦ Pavoni G, Corsini M, Ponchio F, Muntoni A and others (2022)

- Taglab: AI-assisted annotation for the fast and accurate semantic segmentation of coral reef orthoimages. *J Field Robot* 39:246–262
- Pedersen NE, Edwards CB, Eynaud Y, Gleason A, Smith JE, Sandin SA (2019) The influence of habitat and adults on the spatial distribution of juvenile corals. *Ecography* 42: 1703–1713
- Petrovic V, Vanoni DJ, Richter AM, Levy TE, Kuester F (2014) Visualizing high resolution three-dimensional and two-dimensional data of cultural heritage sites. *Mediterr Archaeol Archaeom Int J* 14:93–100
- Philipp E, Fabricius K (2003) Photophysiological stress in scleractinian corals in response to short-term sedimentation. *J Exp Mar Biol Ecol* 287:57–78
- Pinzón JH, LaJeunesse TC (2011) Species delimitation of common reef corals in the genus *Pocillopora* using nucleotide sequence phylogenies, population genetics and symbiosis ecology. *Mol Ecol* 20:311–325
- Pinzón JH, Sampayo E, Cox E, Chauka LJ, Chen CA, Voolstra CR, LaJeunesse TC (2013) Blind to morphology: genetics identifies several widespread ecologically common species and few endemics among Indo-Pacific cauliflower corals (*Pocillopora*, Scleractinia). *J Biogeogr* 40: 1595–1608
- R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Sandin SA, Smith JE, DeMartini EE, Dinsdale EA and others (2008) Baselines and degradation of coral reefs in the Northern Line Islands. *PLOS ONE* 3:e1548
- Smith HA, Prenzlau T, Whitman T, Fulton SE and others (2022) Macroalgal canopies provide corals limited protection from bleaching and impede post-bleaching recovery. *J Exp Mar Biol Ecol* 553:151762
- Spring DL, Williams GJ (2023) Influence of upwelling on coral reef benthic communities: a systematic review and meta-analysis. *Proc R Soc B* 290:20230023
- Stewart HA, Kline DI, Chapman LJ, Altieri AH (2021) Caribbean mangrove forests act as coral refugia by reducing light stress and increasing coral richness. *Ecosphere* 12: e03413
- Sully S, van Woesik R (2020) Turbid reefs moderate coral bleaching under climate-related temperature stress. *Glob Change Biol* 26:1367–1373
- Tagliafico A, Baker P, Kelaher B, Ellis S, Harrison D (2022) The effects of shade and light on corals in the context of coral bleaching and shading technologies. *Front Mar Sci* 9:919382
- van Woesik R, McCaffrey KR (2017) Repeated thermal stress, shading, and directional selection in the Florida Reef Tract. *Front Mar Sci* 4:182
- van Woesik R, Houk P, Isechal AL, Idechong JW, Victor S, Golbuu Y (2012) Climate-change refugia in the sheltered bays of Palau: analogs of future reefs. *Ecol Evol* 2:2474–2484
- West JM, Salm RV (2003) Resistance and resilience to coral bleaching: implications for coral reef conservation and management. *Conserv Biol* 17:956–967
- Williams GJ, Sandin SA, Zgliczynski BJ, Fox MD and others (2018) Biophysical drivers of coral trophic depth zonation. *Mar Biol* 165:60
- Yates KK, Rogers CS, Herlan JJ, Brooks GR, Smiley NA, Larson RA (2014) Diverse coral communities in mangrove habitats suggest a novel refuge from climate change. *Biogeosciences* 11:4321–4337

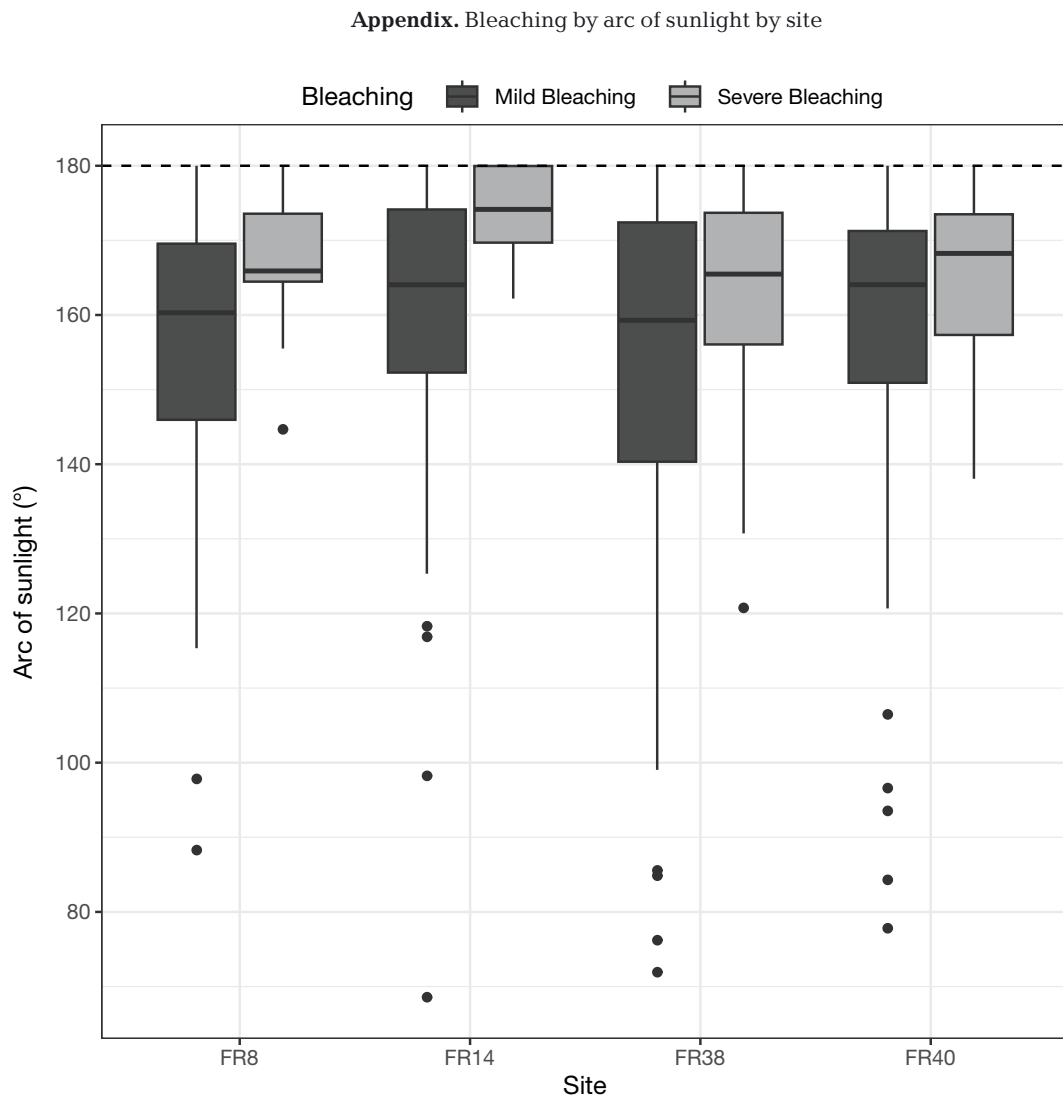


Fig. A1. Arc of sunlight by bleaching severity at each fore-reef site on the north (FR8, FR14) and south (FR38, FR40) side of the atoll. Arc of sunlight approaching 0° represents full shade and arc of sunlight equal to 180° represents full sun. The central line of the box plot represents the median, the box encompasses the interquartile range (IQR), spanning from the 25th to the 75th percentile.

Whiskers extend to the minimum and maximum values within 1.5 times the IQR. Data points outside this range are outliers

*Editorial responsibility: Peter Edmunds,
Northridge, California, USA
Reviewed by: 3 anonymous referees*

*Submitted: May 29, 2024
Accepted: November 14, 2024
Proofs received from author(s): December 28, 2024*