



Environmental Drivers of Variation in Bleaching Severity of *Acropora* Species during an Extreme Thermal Anomaly

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High sea surface temperatures caused global coral bleaching during 2015–2016. During this thermal stress event, we quantified within- and among-species variability in bleaching severity for critical habitat-forming *Acropora* corals. The objective of this study was to understand the drivers of spatial and species-specific variation in the bleaching susceptibility of these corals, and to evaluate whether bleaching susceptibility under extreme thermal stress was consistent with that observed during less severe bleaching events. We surveyed and mapped *Acropora* corals at 10 sites ($N = 596$) around the Lizard Island group on the northern Great Barrier Reef. For each colony, bleaching severity was quantified using a new image analysis technique, and we assessed whether small-scale environmental variables (depth, microhabitat, competition intensity) and species traits (colony morphology, colony size, known symbiont clade association) explained variation in bleaching. Results showed that during severe thermal stress, bleaching of branching corals was linked to microhabitat features, and was more severe at reef edge compared with lagoonal sites. Bleaching severity worsened over a very short time-frame (~1 week), but did not differ systematically with water depth, competition intensity, or colony size. At our study location, within- and among-species variation in bleaching severity was relatively low compared to the level of variation reported in the literature. More broadly, our results indicate that variability in bleaching susceptibility during extreme thermal stress is not consistent with that observed during previous bleaching events that have ranged in severity among globally dispersed sites, with fewer species escaping bleaching during severe thermal stress. In addition, shaded microhabitats can provide a refuge from bleaching which provides further evidence of the importance of topographic complexity for maintaining the biodiversity and ecosystem functioning of coral reefs.

Keywords: spatial refugia, environmental gradients, *Symbiodinium*, niche construction, thermal performance

INTRODUCTION

Mass coral bleaching in response to increased sea surface temperature is a major threat to the persistence of coral reefs. Analyses of sea surface temperature data indicate that ocean warming has accelerated in recent decades, and that coral reefs are increasingly being exposed to thermal stress (Heron et al., 2016). Since the 1980s, global mass bleaching events have caused large-scale and significant coral loss. For example, in 1998, increased seawater temperatures caused widespread bleaching and coral mortality in most of the world's coral reef regions, with mortality in excess of 90% on some reefs in the central and western Indian Ocean (Spalding and Brown, 2015). Moreover, between June 2014 and April 2016, bleaching was observed throughout the global oceans during what is now considered to be the longest bleaching event on record (Eakin et al., 2016). In the context of bleaching, temperature stress is often measured in “degree heating weeks” (DHW, °C-weeks), a metric which summarizes the duration of time over which temperatures have been above the average temperature of the warmest summer month at each location (e.g., Eakin et al., 2010). The recent thermal stress event caused severe bleaching on the northern section of the Great Barrier Reef in 2016, where approximately one third of reefs experienced levels of heat stress that were up to two-fold higher than those experienced in the 1998 bleaching event in the same region (Hughes et al., 2017). We here investigate whether species susceptibility to bleaching under extreme heat stress is consistent with species susceptibility reported during previous bleaching events.

Different coral species respond differently to environmental stressors, leading to substantial among-species variability in bleaching susceptibility. In general, the literature documents relatively high bleaching severity for branching corals from the genera *Stylophora*, *Acropora*, and *Pocillopora*, and lower bleaching severity for mound-shaped *Porites* and *Diploastrea* (e.g., Marshall and Baird, 2000; Loya et al., 2001; van Woesik et al., 2011; Swain et al., 2016). However, bleaching severity is spatially patchy (e.g., Wooldridge and Done, 2004; Penin et al., 2007). For instance, bleaching severity varies between habitats with some studies reporting bleaching to be less severe in shallow compared with deep lagoons (Grimsdich et al., 2010), while others report the opposite trend (Fisk and Done, 1985; Muhando, 1999). Bleaching severity can also vary with depth (e.g., Penin et al., 2007), although some studies have reported no significant variation in bleaching with depth when values were pooled across genera (Bruno et al., 2001). While temperature stress is recognized to be the primary driver of mass-bleaching (Berkelmans et al., 2004; Hughes et al., 2017), there is no strong consensus about additional environmental drivers of spatial variation in bleaching severity. It is likely that a combination of environmental factors (e.g., local light intensity and water flow) and biological factors (including species-specific responses, and local abundances of susceptible vs. tolerant species) influence spatial patterns of bleaching severity.

In addition to among-species variation in bleaching susceptibility, there is often high variation in the bleaching responses of individuals of the same species. For instance,

during the 1998 bleaching event, massive *Porites* were more susceptible to bleaching in the Palm Islands on the central GBR than they were at nearby Magnetic Island (Marshall and Baird, 2000). Similarly, during a bleaching event in the central Pacific, bleaching was observed at some sites but not others for each of several monitored species (Fagerstrom and Rougerie, 1994). Indeed, numerous studies report within-species variation in bleaching severity across different habitats (e.g., Bruno et al., 2001; Aronson et al., 2002; Hardman et al., 2004). There are numerous potential biotic drivers of this within-species variability. First, different types of *Symbiodium* are more resistant to increased ocean temperature than others (e.g., Thornhill et al., 2006; Jones et al., 2008; Lesser et al., 2010; Howells et al., 2013), and many coral species can associate with more than one type of *Symbiodinium* (Baker, 2003; Sampayo et al., 2008). Therefore, we assessed whether species that have the capacity to associate with more than one symbiont type show lower bleaching severity, on average, than other species. Second, bleaching severity is influenced by coral colony size. For example, larger colonies experienced more extensive bleaching than smaller colonies of several species during a major Caribbean bleaching event in 2005 (Brandt, 2009). However, other studies have found contrary results with higher bleaching for smaller colonies for some species (Pratchett et al., 2013), or that colony size only influences bleaching prevalence for certain colony morphologies in certain locations (Wagner et al., 2010). Finally, other benthic organisms that compete for space with corals, such as soft corals and macroalgae, contain secondary metabolites that can lead to the expulsion of *Symbiodinium* (i.e., bleaching, Aceret et al., 1995). Moreover, competition can influence coral fitness more generally (e.g., by growth suppression, see Horwitz et al., 2017), and such effects might act as an additional stressor that increases bleaching severity. To the best of our knowledge, effects of competition on bleaching severity have not previously been investigated *in situ*.

The topographic complexity of reefs results in high variability in environmental conditions over small spatial scales. For instance, stable and biologically significant temperature variation occurs at small scales (1–2 m, e.g., Gorospe and Karl, 2011), and also at larger between-habitat scales (hundreds of meters, e.g., Lundgren and Hillis-Starr, 2008). Water flow also varies within- and among-habitats (e.g., Fulton and Bellwood, 2005; Hoogenboom and Connolly, 2009). Therefore, spatial variation in abiotic drivers, such as light intensity, water flow, temperature, and turbidity, influences which corals bleach and where (e.g., West and Salm, 2003). Previous studies report different effects of water flow on bleaching severity, with evidence of increased bleaching severity at exposed sites with high wave activity (McClanahan et al., 2007), as well as evidence of reduced bleaching, along with higher survival of bleached corals, under high water flow conditions (Nakamura and van Woesik, 2001; Nakamura and Yamasaki, 2005). Variability in bleaching among different reef habitats is also associated with site-specific turbidity levels (e.g., Williams et al., 2010). However, observed responses range from a negative effect of turbidity whereby suspended particulates are thought to act as an additional stressor that lowers temperature tolerance (Williams et al., 2010; Hongo and Yamano, 2013), to predictions that turbidity may lessen the

severity of bleaching in some shallow habitats by reducing light penetration (West and Salm, 2003; Cacciapaglia and van Woesik, 2016).

Methodological issues associated with quantifying bleaching severity in the field might also lead to variation between studies. While observer differences are unlikely to explain variation in bleaching severity between habitats reported in a single study, observers can differ in color sensitivity or in training (e.g., Siebeck et al., 2006). Many observer methods measure bleaching in simple categories (e.g., “pale,” “partially bleached,” and “bleached”), and this categorization can obscure color gradation. To overcome issues associated with categorization of bleaching, some studies estimate the proportion of each coral colony that is healthy vs. bleached (e.g., Obura, 2001), providing a finer resolution of bleaching severity. Despite these advances, however, a recent review highlighted the relatively high measurement uncertainty for bleaching severity, and noted that standardizing measuring protocols would help to increase the precision of bleaching estimates (Swain et al., 2016). To help standardize bleaching measurements, we developed a new quantification of bleaching severity by measuring coral “whiteness” in individually white-balanced images of healthy, pale and bleached corals.

The objective of this study was to understand the drivers of small-scale variation in the bleaching susceptibility of branching corals, and to evaluate whether bleaching susceptibility under extreme thermal stress is consistent with that observed during previous (less severe) bleaching events. We focused on corals from the genus *Acropora* due to their high abundance on Indo-Pacific reefs, their importance for the structural complexity of reefs, and their variable bleaching severity within- and among-species (e.g., Marshall and Baird, 2000; Loya et al., 2001; Swain et al., 2016). Specifically, we aimed to understand whether and how variation in bleaching severity was associated with depth, spatial location of colonies relative to the reef edge (a measure of exposure to wave energy and general reef habitat), microhabitat, colony size, colony morphology, and the level of competition and the identity of competitors. We also evaluated whether association with multiple symbiont types could explain among-species variation in bleaching severity using data from the Geosymbio database (Franklin et al., 2012). Finally, we compiled literature data on the response of *Acropora* species during previous thermal stress events, and assessed whether those species that have been consistently reported to be severely bleached in previous studies were also the most severely bleached during the extreme thermal anomaly which occurred on the Great Barrier Reef during the austral summer of 2016.

MATERIALS AND METHODS

Field Data Collection

Surveys of coral bleaching were conducted at predominantly shallow, lagoonal sites, and at one additional mid-shelf location, within and around the Lizard Island group (northern Great Barrier Reef, 14°40.140S, 145°27.649E) during early March 2016 ~2 weeks after bleaching was first reported at the location. Thermal stress at this location reached ~10 DHW during this bleaching event (Hughes et al., 2017) and *in situ* temperature

loggers (Onset Hobo) measured an average temperature of 30.3°C (range 27.7–33.2°C) at two reef crest sites during February and March 2016. At the time of the surveys, significant bleaching of susceptible coral species had been observed, but mortality was still negligible (widespread bleaching-related mortality was observed on reefs in the region 1 month later, Hoogenboom unpubl. data). Over a period of 8 days, divers conducted in-water surveys at 10 sites where the bleaching status of ~60 *Acropora* colonies was monitored per site. Colonies were selected haphazardly as divers swam along a depth contour from a randomly selected starting place, making a conscious effort to observe colonies from different reef microhabitats as far as practicable given the topography of each site. The spatial position of each colony was taken using a towed GPS (Garmin eTRex) that was time-synchronized with a dive watch, and the depth of each colony was recorded using a dive computer (Suunto, D4 and Zoop). Each colony was photographed from directly above (as described below), and additional photographs of colony morphology, local reef topography and colony microhabitat, neighboring competitors, and corallite shape were taken to enable measurement of colony size and competition intensity, and to assist species-level identification. We also kept track of the time and date of observations because ongoing heat stress suggested that bleaching severity would continue to increase during and after the observation period. The full dataset, including coral images and spatial positions, is available in Critchell and Hoogenboom (2017).

Measurement of Bleaching Severity (Response Variable)

Individual coral colonies were photographed from directly overhead, without flash, and from as close as practicable, with a Canon G16 digital camera in an underwater housing. Each photograph contained a color reference chart and scale bar. As differing light conditions of each colony did not allow for identical camera settings to be used in each photograph, individual settings based on the highest image quality (pixel count) and lowest sensitivity (ISO) settings were used. Post-processing was conducted using Adobe Photoshop Creative Cloud (2015) software with images transformed into the device-independent CIEL*a*b* color space which measures color based on lightness (L), along a green-red gradient (a), and along a blue-yellow gradient (b). All images were individually white balanced by identifying true black, true white, and 50% gray thresholds in each photograph. Subsequently, four regions of the colony were selected haphazardly from across the surface area of each coral colony, using the color sample tool. Each sampled region was a constant distance from the branch tip (1–2 cm), and avoided the outer margins of the colonies where branches are often oriented in slightly different directions, and can be shaded by upper branches. The color sample tool in the software was set to capture an 11 × 11 pixel sample for each region of the coral surface, and calculated the average color across each 121 pixels region. The four L*a*b* color samples were averaged for each colony, in order to gain a single numerical measurement of color, the divergence of each L*a*b* average value from black was calculated as ΔE

(after Riggs, 1997). This method generated a value for each colony within a range of 0–100, with increasing values representing increasingly bleached (nearest to white) colonies. To determine a reference point for the color of healthy (unbleached) corals, the same technique was used to calculate “whiteness” values for *Acropora* colonies ($n = 12$) that showed normal coloration, and that were surveyed and photographed during March 2016 at sites around Orpheus Island. These additional colonies included the same species and colony morphologies as observed at Lizard Island.

Drivers of Bleaching Severity (Explanatory Variables)

Image Analysis

Images of each coral colony ($N = 596$) were analyzed to determine coral colony morphology after Wallace (1999) as either digitate, corymbose, arborescent, tabular, arborescent table, or hispidose/caespitose. Each coral colony was identified to species level based on Wallace et al. (2012) and Wallace (1999) except for 7 colonies for which species identification could not be reliably determined from the photographs (referred to in our dataset as *Acropora* spp.). We note that many coral species display morphological plasticity and certain pairs of species have overlapping variation in morphology which poses a challenge for species identification. In our study, some colonies within the following species pairs were difficult to distinguish from each other from photos alone and, therefore, species-level differences between these pairs should be interpreted with caution: *A. loripes* and *A. longicyathus*, *A. nasuta* and *A. valida*, *A. humilis* and *A. gemmifera*.

Colony planar surface area was measured for each colony using image analysis in Image J (version 1.51 h, US National Institute for Health). For each colony we measured the longest diameter and the diameter perpendicular to that and calculated planar area based on the geometric formula for the area of an ellipse. The microhabitat of each colony was also assessed from images of the localized reef topography, and was categorized as: “elevated” (where the topography of the reef meant the coral was > 40 cm above the surrounding corals) “open” (where the colony was on flat reef substratum without any obvious shading by competitors), “crevice” (where the colony grew within a crack in the reef matrix), “overhang” (where the colony was shaded by the reef matrix or other colonies), or “sand” (where the colony grew above a sand patch). Competition intensity was measured by dividing each coral into 8 equal segments centered over the mid-point of the colony, and counting the number of these “octants” in which a benthic competitor was within ~ 5 cm of the focal colony, after Hoogenboom et al. (2011). These data were subsequently categorized as either: “no competitors,” “low” (competitors present in 1–2 of octants), “medium” (competitors present in 3–4 octants), and “high” (competitors present in > 4 octants). In addition, we noted whether competitors included soft corals (categorical variable with soft corals present or absent) and macroalgae (categorical variable with macroalgae present or absent). Only 8 of 596 colonies were in competition with macroalgae so this variable was excluded from subsequent analysis.

Spatial Data

For each colony, depth data measured in the field were converted to depth below lowest astronomical tide based on the known tidal height at the time of sampling. The spatial position data for each colony was used to calculate the position of each colony relative to the open ocean. To do this, the position of the reef edge was defined from reef polygons extracted from Google Earth images (Lizard Island, $-14.666777S$ $145.462971E$, image date 10/10/2011 accessed 06/02/2017 with eye altitude of 6.9 km; No Name Reef, $-14.641968S$ $145.653061E$, image date 15/09/2016 accessed 07/02/2017 with eye altitude of 4.36 km), and were imported into ArcGIS (ESRI, version 10.2). The spatial position of each coral colony and the reef polygons were transformed to GDA 1994 MGA Zone 55 projection to enable measurement of distances in meters with conversion from decimal degrees. The “near” function was used in ArcGIS to calculate the distance (m) of each point (i.e., each coral colony) from the nearest reef edge.

Coral-Symbiodinium Associations

Given the influence of different *Symbiodinium* on the thermal tolerance of *Acropora* corals (e.g., Howells et al., 2013), we determined the total number of *Symbiodinium* clades reported in the GeoSymbio database for the surveyed *Acropora* species (Franklin et al., 2012). Only records that identified *Symbiodinium* using denaturing gradient gel electrophoresis profiles of the internal transcribed spacer 2 region of rDNA were included to avoid confounding effects due to the use of different methods of identifying *Symbiodinium*. Furthermore, only *Acropora* species for which there were more than three records in the database were included in this analysis.

Reported Bleaching Severity of *Acropora* during Previous Bleaching Events

To compare the results from our in-water surveys with observations of *Acropora* bleaching in previous events, we conducted a comprehensive literature search using Web of Science to conduct cited reference searches for Marshall and Baird (2000) and Loya et al. (2001), and an additional keywords search for “*Acropora*” and “bleaching.” To capture the gray literature we also scanned all papers listed in the online bleaching database ReefBase (1631 records, as of March 2016, ReefBase, 2017) and extracted data from publications that were publically available. Among this set of publications, data were only used if the study reported field observations during a thermal bleaching event (not laboratory experiments), if corals were identified to species level, and if bleaching was quantified in a way that captured gradation in bleaching severity. We excluded papers where bleaching effects were measured as a change in coral cover between different observation periods due to difficulty ascribing changes in abundances solely to bleaching. In total, 57 publications matched our criteria, yielding 527 records of bleaching for 86 *Acropora* species. We retained species names as reported in the original publications despite some subsequent synonymization of names (e.g., *A. wallaceae* was synonymized with *A. samoensis* by Wallace, 1999), and we recorded colony morphologies of species based on Wallace (1999) and Veron (2000).

To standardize bleaching metrics between studies, data extracted from each publication were re-categorized as follows: “none” means no bleaching of that species was reported in that study; “low” means that the study recorded the species to be partially bleached or with <25% of colonies affected; “moderate” means that 26–50% of colonies were bleached or there was partial bleaching with low levels of recorded mortality; “high” means 50–80% of colonies were bleached and/or mortality was observed; “severe” means that more than 80% of colonies of that species were bleached and/or high levels of bleaching-related mortality were recorded. Data are presented as the percentages of records for each species that fell within each of these categories. In both the data from Lizard Island, and the literature data, the measurement of bleaching severity reflects the short- and long-term thermal history of each colony because measurements were made under natural field conditions. The database we have compiled is accessible in the Supplementary Material.

Data Analysis

To identify the strongest predictors of bleaching severity during the extreme thermal anomaly, we used a linear mixed-effects model that included all main effects (day of observation, colony morphology, depth, microhabitat, competition intensity, presence of soft corals, colony size, and distance to open ocean, where the latter captures variation in environmental conditions between reef-edge and lagoon habitats), and a set of specific interaction terms that were established *a-priori* based on evidence in the literature. Water flow potentially modulates bleaching severity through effects on gas exchange which are, in turn, affected by both colony morphology and colony size (Hoogenboom and Connolly, 2009). Consequently, we included interaction terms between distance from ocean (a proxy for wave exposure and general reef habitat) and colony morphology, and between distance from ocean and colony size. Colony morphology determines how much light impinges on the coral tissue surface, and light intensity also changes with depth (Hoogenboom et al., 2008). Therefore, we considered that different morphologies might bleach differently at different depths and included a depth by morphology interaction. Different coral morphologies use different competition strategies and the outcome of competition can depend on colony size (Jackson, 1979). Therefore, we included competition by colony size and competition by morphology interaction terms. Finally, we considered that different coral morphologies might bleach at different rates and included the interaction between day of observation and morphology. We had no *a priori* reason to expect that effects on bleaching severity from the day of observation (duration of exposure to thermal stress), or that effects of the presence of soft corals, should depend on any other environmental factor and therefore omitted those interactions. The dataset includes two random effects; “site” (because corals were observed at a random selection of sites at the location) and “species” (because we observed a random subset of the pool of species based on which species were present at each site rather than observing species selected *a priori*). We used model selection based on a likelihood ratio test to assess whether the mixed-effects model should include random effects for both “site”

and “species within site.” All statistical analyses were performed using the R statistical software (R Development Core Team, 2017).

Our assessment of the *Acropora* community naturally present at each site meant that we were likely to have different numbers of observations of bleaching severity for different species, and a different composition of species at different sites. To determine whether differences in species composition between sites contributed to among-site variation in bleaching severity we categorized sites as either “exposed” (<420 m from reef edge, 4 sites) or “lagoon” (>510 m from reef edge, 6 sites), and calculated community similarity between pairs of sites using the Bray–Curtis index of dissimilarity. The categorization of “exposed” vs. “lagoon” was based on a natural distance division in our data which yielded approximately equal numbers of sites in each category. This community similarity approach was chosen in place of a multivariate species-by-site ordination because the latter technique is not recommended when there are many more variables (species) than samples (sites). A similar approach was used to assess whether the relative frequency of microhabitats differed between exposed and lagoon sites using a χ^2 goodness of fit test.

Data describing *Symbiodinium* association of *Acropora* were only available for a subset of the species we observed. These sparse data did not permit quantitative analysis and, therefore, we used graphical analysis to assess whether the capacity to host different symbiont types was related to bleaching severity. Finally, hierarchical cluster analysis was used to group coral species based on their bleaching severity during previous bleaching events as reported in the literature. Subsequently, we applied the same species groupings to the species observed at Lizard Island, and assessed whether mean bleaching severity observed at our study site differed systematically among these predetermined species groups.

RESULTS

Bleaching severity values measured using our new method ranged from 42 (least “white”) to 99 (very close to pure white) across the 10 Lizard Island study sites. In contrast, “whiteness” values for unbleached corals at Orpheus Island (photographed at the same time of year, and including the same coral species and morphologies as at Lizard Island) averaged 43 (\pm s.e. 3.2, range 21–61). Overall, 97% of coral colonies observed at Lizard Island ($N = 596$) showed whiteness values outside of the range observed for unbleached corals at Orpheus Island, and 71% of colonies had whiteness values >80 (Figure 1).

Among the set of hypothesized correlates of bleaching severity, only day of observation, microhabitat, distance of colonies from the open ocean, and colony morphology explained a significant amount of the variation in bleaching severity. We observed a clear signal of increased bleaching severity over time, despite the relatively short observation period (8 days, Table 1). This temporal variation was equivalent in magnitude to the variation in bleaching severity among microhabitats (average bleaching values were \sim 79 on day 1 and \sim 88 on day 8, Figures 2A,C). In addition, hispidose, digitate, and

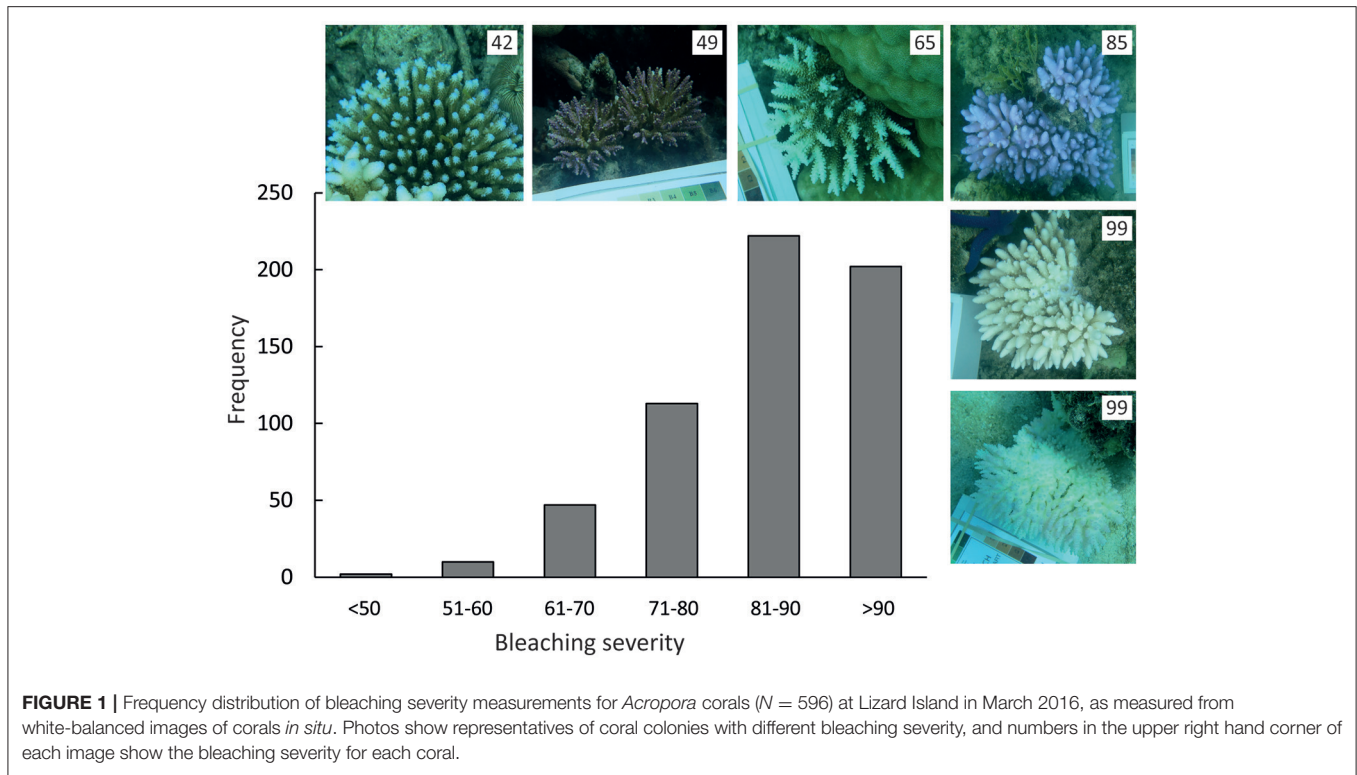


TABLE 1 | Results of general linear mixed effects model of bleaching severity, with site and species included as random effects in the model.

Factor	Df	F	p
Day of observation	1, 8	13.3	<0.01
Colony morphology	5, 381	3.5	<0.01
Microhabitat	4, 381	20.6	<0.001
Distance from open ocean	1, 381	5.5	<0.02

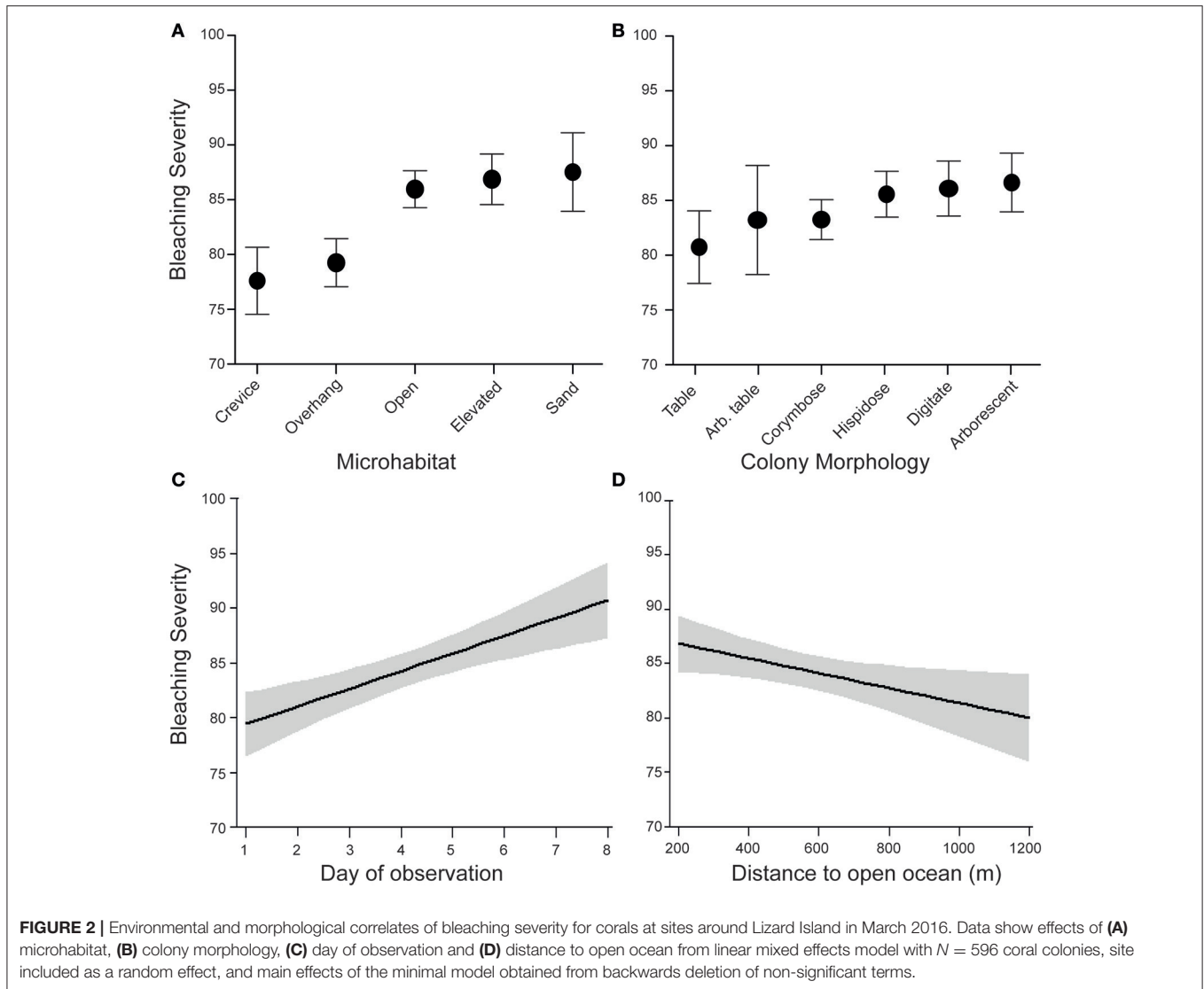
All other main effects and interaction terms were not significant ($p > 0.08$) and were excluded from the final model based on a backwards-deletion approach.

arborescent morphologies were the most severely bleached, whereas tabular morphologies were the least severely bleached (Table 1, Figure 2B). Finally, bleaching severity decreased with distance away from the open ocean, with corals at sites in the lagoon generally showing lower bleaching severity than those at sites close to the reef edge (Table 1, Figure 2D).

Corals growing in crevice and overhang environments showed significantly less severe bleaching than corals in open, elevated, and sand microhabitats (Figure 2, Table 1), supporting the general consensus that bleaching is more severe under conditions of high irradiance. In contrast, depth (range -0.5 to 5 m below LAT) was not significantly associated with bleaching [GLMM, “depth” effect, $F_{(1, 570)} = 0.08$, $p = 0.78$]. The relative frequency of different microhabitats occupied by the coral colonies we observed differed between sites that were close to the reef edge and sites that were close to the center of the lagoon (Figure 3). Overall, *Acropora* colonies were more frequently found in open

microhabitats at reef edge sites compared with a higher frequency of elevated and crevice microhabitats at lagoonal sites (Goodness of fit test, $\chi^2 = 19.3$, $df = 4$, $p < 0.001$). Despite these differences in microhabitat availability, Bray–Curtis similarity of species composition between pairs of sites was approximately equal when reef edge sites were compared with each other (mean dissimilarity 0.54 between 6 pairs of sites), to when lagoonal sites were compared with each other (mean dissimilarity 0.53 between 15 pairs of sites), and to when lagoonal sites were compared with reef edge sites (mean dissimilarity 0.51 between 24 pairs of sites).

Corymbose coral species, including *A. secale*, *A. selago*, and *A. nasuta* were among the least severely bleached whereas arborescent species, including *A. listeri*, *A. grandis* and *A. aspera*, were among the most severely bleached (Figures 2B, 4A). Species’ mean bleaching severity values ranged from 74 (for *A. aculeus*) to 95 (for *A. carduus*) and we observed relatively small within-species variation in bleaching severity with the coefficient of variation of bleaching severity for each species ranging from 1 to 21% (average 10%). However, clear interpretation of among-species variation is hindered by differences in sample sizes; our assessment of the *in situ* *Acropora* community meant that we observed only single colonies of some species but >40 colonies of other species (Figure 4A). In addition, formal model selection did not support the inclusion of “species within site” as a random effect in the GLME (likelihood ratio test, model with “species within site” was not superior to a model with only “site” as a random effect, likelihood ratio 0.49, $p = 0.48$). This result indicates that differences in bleaching intensity among species were generally consistent among sites. Finally, although data

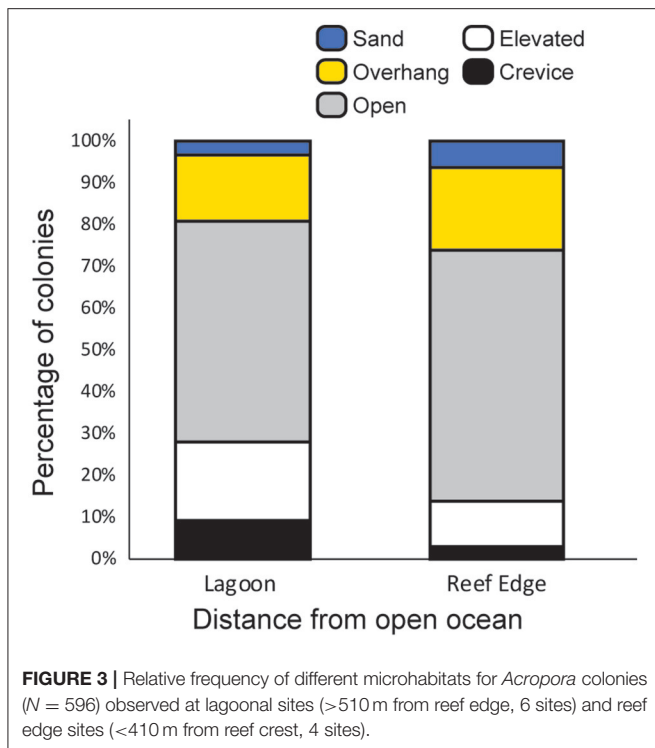


documenting symbiont clade diversity for the coral species we observed were too sparse to permit formal analysis, we found no clear indication that species which associated with more than one symbiont clade bleached less severely (**Figure 4B**).

Competition intensity had no effect on bleaching severity [GLME, “competition” effect, $F_{(3, 570)} = 2.2$, $p = 0.09$], nor did the presence of soft corals [GLME, “soft corals” effect, $F_{(1, 570)} = 0.31$, $p = 0.58$], or the size of the coral colony [GLME, “colony area” effect, $F_{(1, 570)} = 0.02$, $p = 0.90$]. We found no evidence that distance from the open ocean, depth, or competition intensity affected bleaching severity differently for different colony morphologies [GLME, “morphology by distance,” $F_{(5, 535)} = 1.8$, $p = 0.12$; “morphology by depth,” $F_{(5, 535)} = 1.0$, $p = 0.39$; “morphology by competition,” $F_{(15, 535)} = 0.9$, $p = 0.57$]. Similarly, the effect of competition intensity on bleaching severity did not depend on colony size [GLME, “competition by colony area,” $F_{(3, 535)} = 0.57$, $p = 0.63$], nor did the effect of distance from the open ocean depend on

colony size [GLME, “colony area by distance,” $F_{(1, 535)} = 1.9$, $p = 0.16$]. Finally, our analysis did not support the hypothesis that different morphologies bleached at different rates [GLME, “day by morphology,” $F_{(5, 535)} = 0.63$, $p = 0.68$].

Published records of bleaching severity of *Acropora* species from previous bleaching events indicate high variability between morphologies (**Figure 5**), as well as high variability within and among species (**Figure 6**). Consistent with our observations of *Acropora* at Lizard Island, the literature demonstrates that arborescent and hispidose *Acropora* are more frequently observed to be severely bleached, while arborescent tables are among the least severely bleached in both datasets (**Figures 2B, 5**). However, digitate and tabular morphologies showed contrasting bleaching severity at Lizard Island compared with the literature. When the responses of different coral species are considered, the literature indicates a greater degree of within- and among-species variability in bleaching severity than we observed at Lizard Island, despite having similar number of



observations in both cases ($N = 596$ colonies measured at Lizard Island, $N = 532$ literature records), and data for a large number of species in both cases (40 species at Lizard Island, 87 species in the literature). In the literature, for the 48 species with at least 5 records of bleaching severity, 27% (13 species) showed high fidelity to a single bleaching category despite inevitable variation in the intensity of thermal stress among locations and bleaching events. In addition, 63% of species had records of bleaching within at least 3 categories, and 23% of species showed the full range of bleaching severity scores (from none to severe, **Figure 6**). Only one species (*A. desalwii*) was never recorded to show above “moderate” bleaching, likely due to its restricted geographic distribution and occurrence below 15 m depth (Wallace, 1999). Cluster analysis of the literature data for the subset of *Acropora* species we observed at Lizard Island revealed 7 clusters based on the bleaching severity categories most often recorded for those species during previous bleaching events (**Figure 7**). However, we found no evidence of systematic variation in average bleaching scores measured at Lizard Island for these clusters of species (**Figure 8**).

DISCUSSION

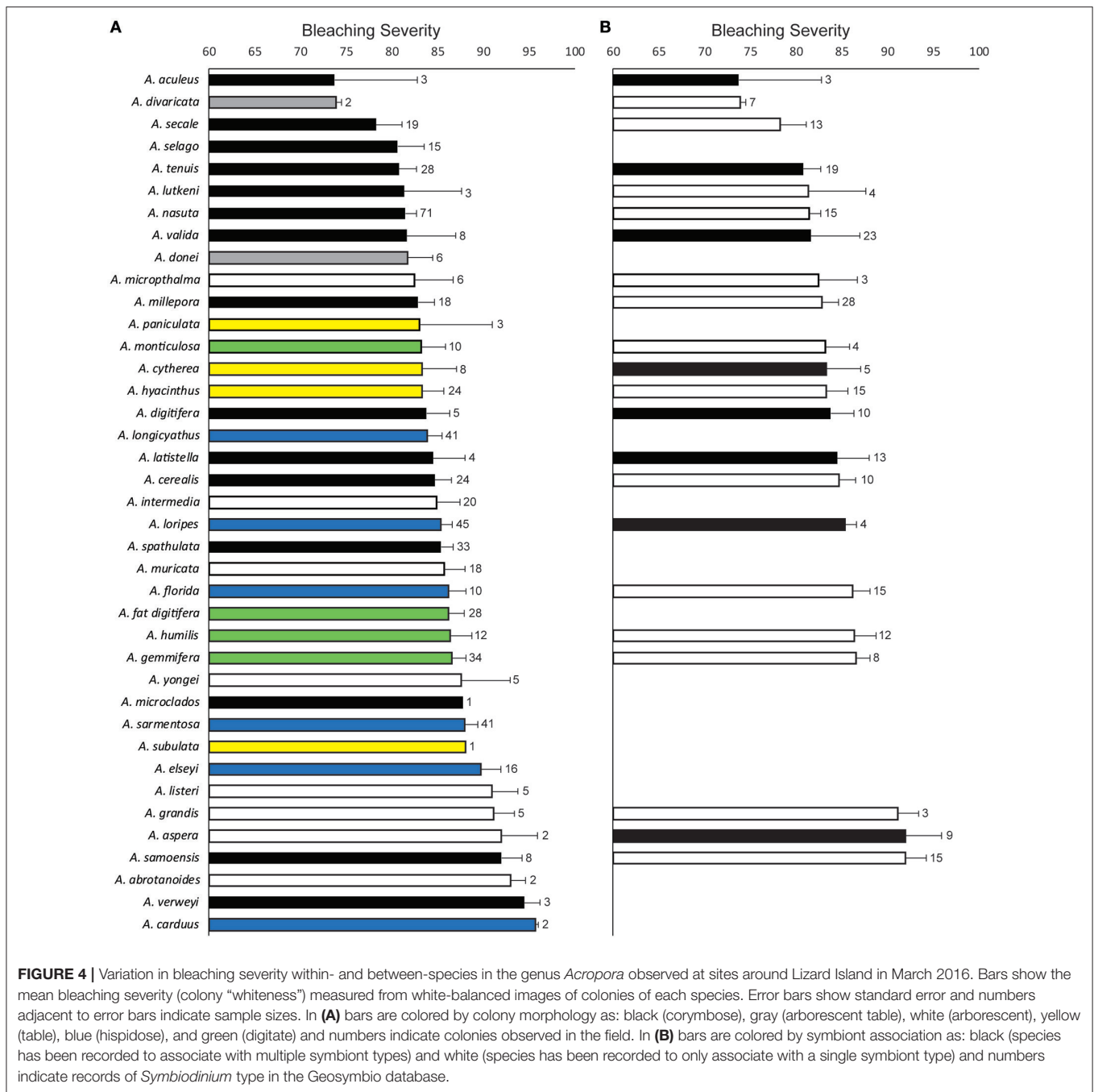
The results of this study show that during severe thermal stress, small-scale spatial variation in the bleaching susceptibility of branching corals is linked to microhabitat availability, and the proximity of sites to the open ocean, and that bleaching severity worsens over a very short time-frame (~ 1 week). We found no evidence that water depth (range -0.5 to 5 m below LAT), competition intensity (range no competition to competitors

surrounding entire colony circumference), or colony size (range 5–90 cm diameter) systematically influenced bleaching severity. At our study location, different colony morphologies differed in their bleaching severity under temperature stress, but within- and among-species variation in bleaching severity was low compared with the variation reported in the literature.

Environmental Drivers of Bleaching Severity

Our results generally support the hypothesis that coral bleaching is caused by a combination of high water temperature and high solar radiation (Jokiel and Coles, 1990; Lesser et al., 1990; Brown et al., 1994). Colonies in shaded microhabitats (crevices and overhangs) were less severely bleached than those in microhabitats with higher light exposure (open, elevated, and sand). The structural complexity of reefs causes high variation in irradiance among microhabitats (Brakel, 1979), whereby overhangs and crevices receive $\leq 40\%$ of the irradiance that reaches open habitats at a similar depth (3–5 m, Anthony and Hoegh-Guldberg, 2003). Consistent with previous studies (e.g., Williams et al., 2010), colonies in sandy patches were the most severely bleached, likely because carbonate sand is highly reflective and amplifies light intensity (Ortiz et al., 2009). While colonies in microhabitats with low irradiance can have low survival (Baird and Hughes, 2000) and growth (Anthony and Hoegh-Guldberg, 2003) under normal conditions, our results support that crevice and overhang habitats may serve as refuges from thermal stress (see also West and Salm, 2003). Consequently, reefs’ structural complexity supports ecosystem functioning and biodiversity not only by providing habitat and shelter for mobile reef organisms (Syms and Jones, 2000; Pratchett et al., 2008), but also by providing microhabitats that can increase coral survival during periods of thermal stress. In contrast to the strong effect of microhabitat, competition intensity had no effect on bleaching severity. One explanation for this is that some corals retract their polyps when exposed to high water temperatures (Jones et al., 2000) which might lower the incidence of contact between competitors and/or prevent the release of secondary metabolites. However, other species increase their feeding rates in response to bleaching (Grottoli et al., 2006), which is likely to increase the incidence of tissue contact between adjacent colonies. Further research into species-specific tissue retraction behaviors during thermal stress is required to explain this result.

In our study, water depth did not influence bleaching severity for corals that occur within the upper ~ 6 m depths of the reef. A likely explanation for this finding is that water temperatures are often similar across this depth range, as the thermocline occurs at depths that are usually well below 20 m on coral reefs (e.g., Grigg, 2006). Moreover, the generally high water clarity at the study sites means there would have been limited attenuation of light over this depth range. Both still water conditions and water clarity increase the penetration depth of solar radiation into seawater, consequently increasing radiant heating throughout the water column and reducing variability in temperature with depth (Glynn, 1993; Brown, 1997). In our dataset, 90% of the surveyed



colonies were located at a depth of <2.5 m below LAT (~3–4 m water depth given the tidal range at the location). Based on estimates of light attenuation from other offshore reefs with high water clarity (Cooper et al., 2007), light intensity at this depth would be ~70% of subsurface light intensity. Collectively these results indicate that crevice and overhang microhabitats provide a greater shading effect than light attenuation with depth in clear waters across the surveyed depth range. The absence of a depth effect also demonstrates that abnormally low sea levels were not the cause of coral bleaching at our study location. Although low sea levels due to El Niño Southern Oscillation have been

associated with a local coral mortality event in Indonesia (Ampou et al., 2017), a strong depth-dependent pattern of bleaching severity, with higher severity in the shallowest depths (i.e., <1 m depth), would be expected in areas where coral bleaching was caused by tidal emersion.

We used distance from the open ocean as a metric to capture potential spatial variation in wave energy and other environmental conditions between reef-edge and lagoonal sites. Previous studies reveal contrasting effects of water flow on bleaching severity. Thermal bleaching is linked to photoinhibition of photosynthesis (e.g., Jones et al., 2000) and

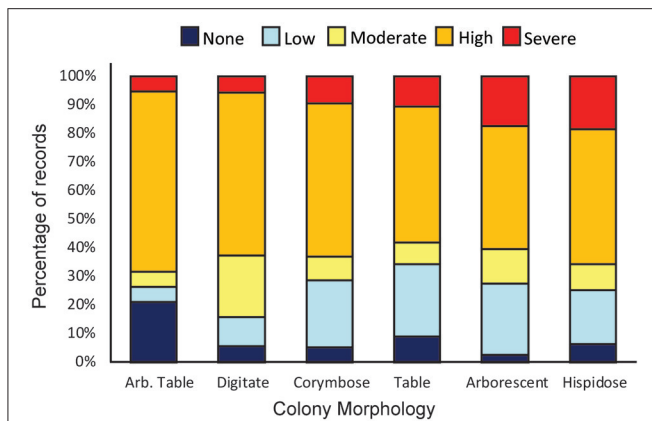


FIGURE 5 | Records of bleaching severity for different *Acropora* colony morphologies compiled from the literature. Bars show the percentage of records in the literature for each colony morphology in each bleaching severity category ($N = 429$). Data for elkhorn and encrusting colony morphologies have been excluded to facilitate comparison with data from Lizard Island plotted in **Figure 2B**. Numbers of records for each morphology are 19 (Arb. Table), 70 (digitate), 95 (corymbose), 64 (table), 149 (Arborescent) and 32 (hispidose/caespitose).

this inhibition can be mitigated by higher water flow (Nakamura et al., 2005). However, contrary to such effects, we found lower bleaching severity in lagoon sites which generally have low wave energy and low flow compared with reef edge locations (Fulton and Bellwood, 2005). This result is consistent with a field study in the Indian Ocean which also found a positive correlation between bleaching intensity and water flow speed (McClanahan et al., 2007). Coral reef lagoons are characterized by shallow water with limited mixing, which facilitates heating until surface waves force cooler waters over the reef crest (Monismith, 2007). Consequently, corals in lagoon environments experience greater variability in their local temperature. Heat stress experiments indicate that corals from habitats with high variability in temperature have lower mortality rates than corals from habitats with moderate thermal variability (Oliver and Palumbi, 2011). While we do not have site-specific temperature data at our survey sites, temperature loggers deployed at the study location indicate that the lagoon had slightly higher and more variable temperatures than the reef edge during December through to March 2016 (reef edge site: average 29.7°C range 27.9–31.7°C; lagoon site: average 30.0°C range 25.6–33.2°C). Overall, our results support the hypothesis that prior exposure to variable temperature regimes can promote thermal tolerance of coral colonies. Nevertheless, the declining bleaching severity with distance from the open ocean might also be related to differences in microhabitat availability across this gradient as we observed a higher frequency of crevice microhabitats, and a lower frequency of open microhabitats, at lagoonal sites.

Among-Species Variation in Bleaching Severity

Bleaching severity differed among the various branching morphologies of *Acropora* observed at Lizard Island. Previous

studies have reported disparate results regarding the effect of colony morphology on bleaching, including: no clear effect of morphology (Williams et al., 2010); higher bleaching susceptibility for branching and tabular corals compared with massive and encrusting colonies (Marshall and Baird, 2000; Loya et al., 2001); and higher bleaching severity of massive corals compared with branching corals (Ortiz et al., 2009). These disparate results might be partially explained by variation in growth rates, both among-species and among-locations due to changes in environmental conditions. Fast-growing branching morphologies are more susceptible to bleaching than morphologies with slower growth rates (e.g., massive corals, Hoegh-Guldberg and Salvat, 1995; Marshall and Baird, 2000; Brandt, 2009). This pattern is thought to be related to metabolic rates: fast-growing colonies have higher metabolic rates and, thus, accumulate more harmful oxygen free radicals which result in oxidative stress that is linked to bleaching susceptibility (e.g., Jokiel and Coles, 1974; Hoegh-Guldberg and Salvat, 1995; Baird and Marshall, 2002). Among *Acropora* corals specifically, a recent study by Dornelas et al. (2017) showed that digitate and corymbose growth forms have slower growth rates than arborescent and tabular growth forms. These results are broadly consistent with the bleaching severity of these species reported in the literature. However, in our surveys, tabular corals were the least severely bleached despite having rapid growth rates (Dornelas et al., 2017). At present, we do not have a clear explanation for these contrasting results and further studies are required to disentangle the influence of growth rate compared with other environmental variables on coral bleaching susceptibility.

The type of *Symbiodinium* present within coral tissues can have a significant influence on the bleaching susceptibility of corals (e.g., Glynn, 1993; Baker, 2003; Berkelmans and Van Oppen, 2006; Abrego et al., 2008). In particular, some corals can increase their thermal tolerance if they can change the dominant symbiont clade in their tissues to a more thermally tolerant one (Berkelmans and Van Oppen, 2006). This implies that corals harboring multiple symbiont types potentially have an ecological advantage if they can shuffle their symbionts to “match” their ambient environmental conditions. However, under times of stress, this advantage can only manifest if the symbiont community includes symbionts that are tolerant to a given stressor. Our data showed no clear relation between bleaching severity and the capacity of *Acropora* species to harbor multiple *Symbiodinium* types. This result suggests that it is the presence of a specific heat-tolerant symbiont, rather than the ability to host multiple symbiont types, that confers thermal tolerance. We note, however, that while there is an increasing research emphasis on the functional differences between *Symbiodinium* clades (e.g., Suggett et al., 2015, 2017), the coral species coverage of these data remains relatively sparse and this constrained our analyses. We limited our analysis to the level of *Symbiodinium* clades, but differences in thermal tolerance exist among *Symbiodinium* belonging to the same clade (Tchernov et al., 2004; Sampayo et al., 2008; Correa and Baker, 2009; LaJeunesse et al., 2014). Thus, while our results suggest that *Acropora* species known to associate with one or multiple *Symbiodinium* clades did not

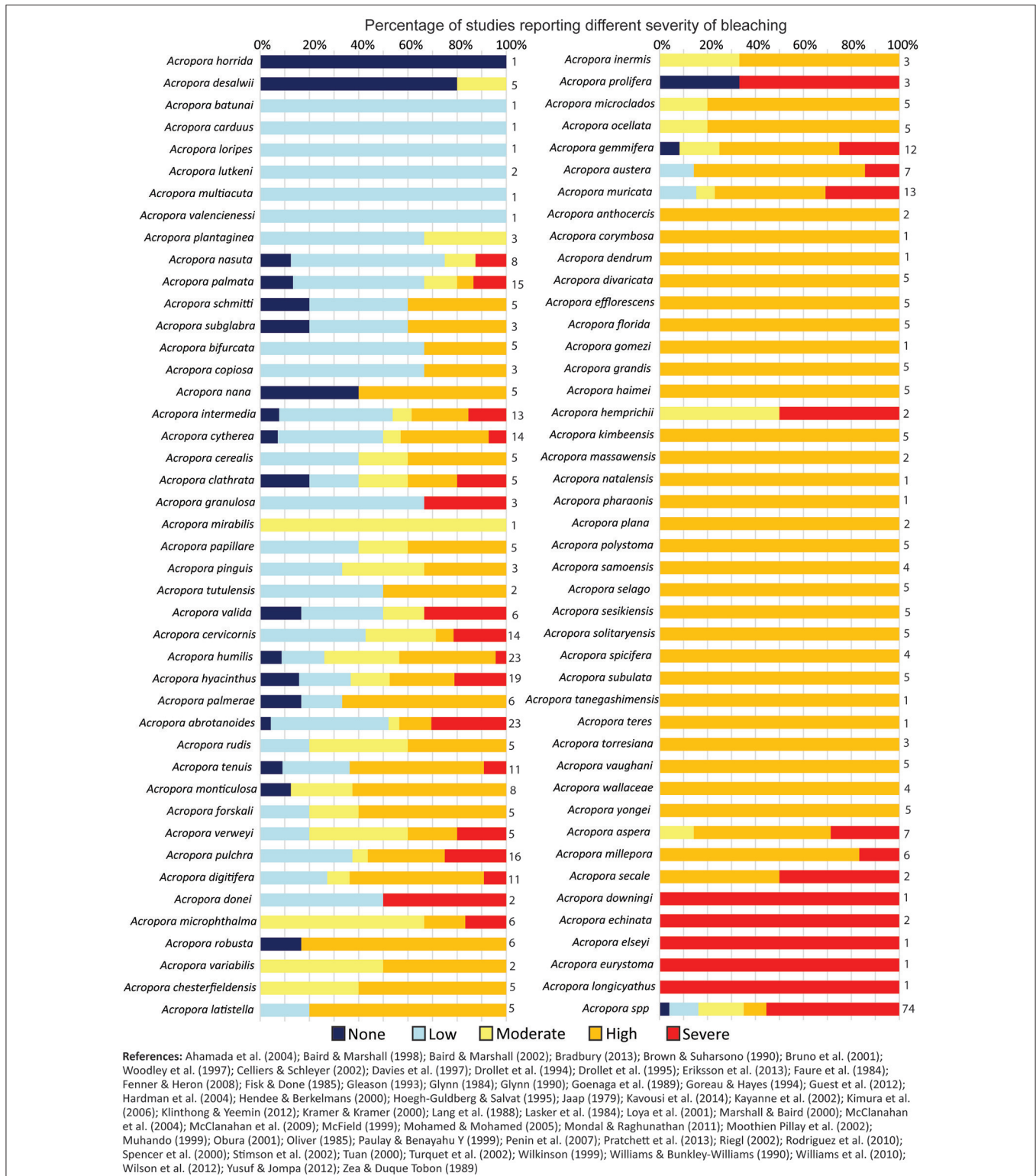


FIGURE 6 | Records of bleaching severity for different *Acropora* species compiled from the literature. Bars show the percentage of records in the literature for each species in each bleaching severity category ($N = 527$) and numbers adjacent to bars indicate number of records per species.

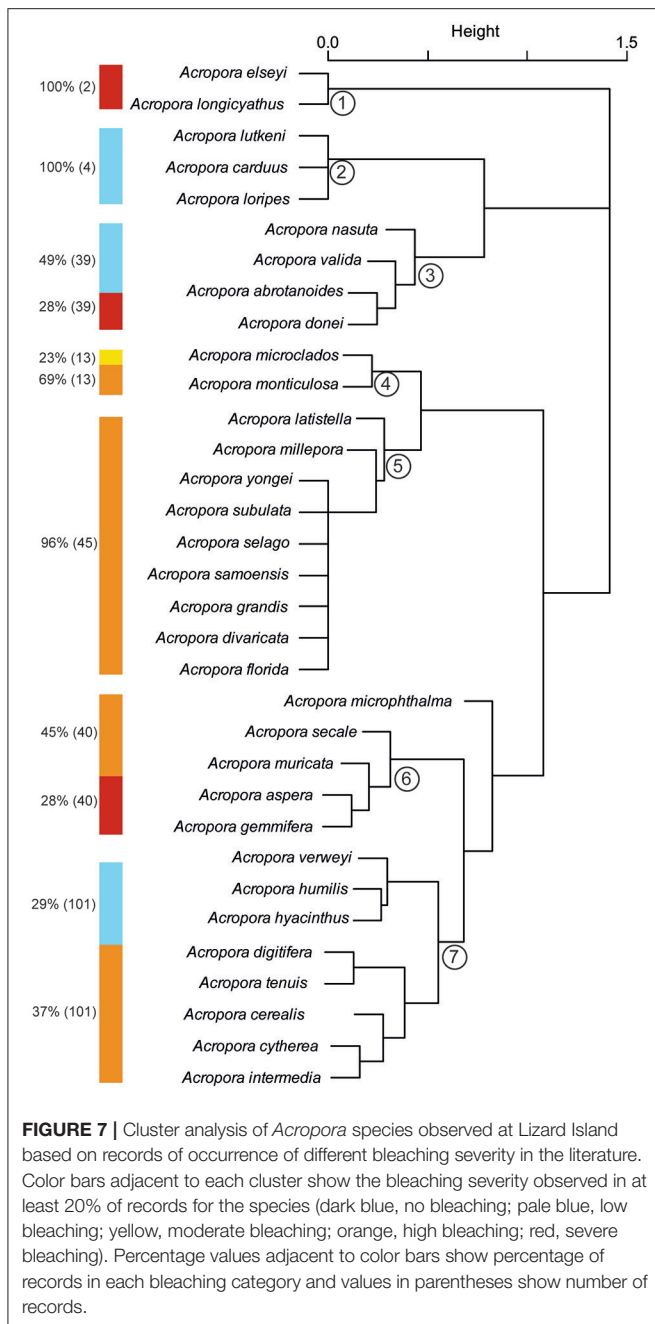
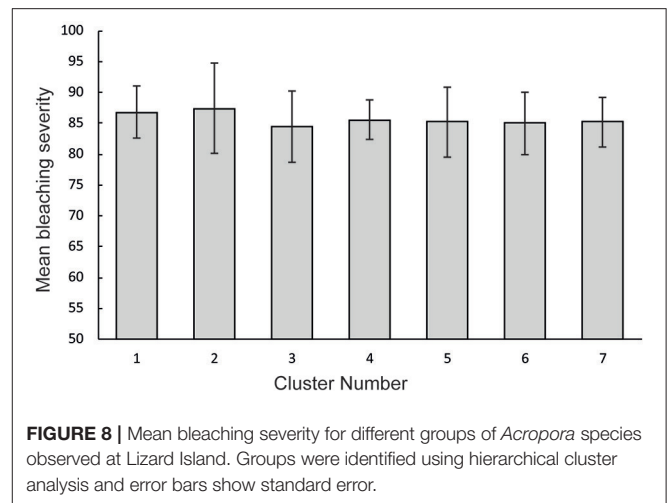


exhibit differences in bleaching resistance, finer-scale resolution of symbiont identities may have explained additional variation in bleaching intensity (Sampayo et al., 2008).

A Standardized Method for Measuring Bleaching Severity

The image analysis technique developed here provides a sensitive measure of bleaching severity that captures gradation within and between species, and that overcomes some of the limitations of survey observation methods (e.g., Siebeck et al., 2006). First, our technique eliminates *in situ* observer bias and corrects for color variation due to differences in the *in situ* light environment.



Second, the data are continuous which allows a more precise measure of bleaching severity by avoiding the loss of information that occurs with categorical data. Third, photographs provide a permanent photographic record of the state of each individual colony which may be useful for future comparisons. Finally, this technique can be developed further, and extended to other coral groups, by quantifying the “whiteness” of healthy corals to provide a species-specific baseline for coral colony health in the absence of environmental stressors. Despite these advantages, this new technique is more time consuming than *in situ* observer based techniques. White-balancing and color analysis took ~3–5 min per image, with approximately half of this time spent on white-balancing. In addition, many corals contain fluorescent proteins in their tissues which give colonies a blue or pink colouration that overlays the golden brown color of the *Symbiodinium* within the coral cells (e.g., Alieva et al., 2008). Our technique likely underestimates bleaching severity of heavily pigmented colonies because these host-pigments make them appear to be less white than a non-pigmented colony with the same level of bleaching (i.e., symbiont loss). However, this issue makes our results conservative as to the differences between morphologies, microhabitats and sampling days because it introduces additional variability in the dataset. We also note that, when colonies are only partially bleached (e.g., where the upper surface of the colony is whiter than the lower surfaces, Harriott, 1985), more than four measurement points may be needed to accurately represent the color distribution of each colony.

CONCLUSIONS

During the extreme heat stress that affected the northern GBR in 2016, 97% of *Acropora* colonies observed at our study location were pale or bleached, and ~70% of colonies had whiteness values consistent with a categorization of “severe” bleaching. In contrast, in previous bleaching events nearly a quarter of *Acropora* species were reported to show high within-species variability in bleaching severity, with scores ranging from

“none” to “severe.” Overall, we consistently observed severe bleaching during the extreme thermal anomaly experienced at our study location, in comparison to more variable bleaching severity reported during a broad range of bleaching events described in the literature. These comparisons highlight the importance of measuring and reporting the magnitude of thermal stress experienced at different sites during bleaching so that species- and/or location-specific temperature thresholds for different levels of bleaching can be quantified. Our results also highlight the importance of monitoring and reporting the timing of bleaching surveys relative to the onset of thermal stress, as our new image analysis technique detected a 10% increase in bleaching severity over a period of 1 week. Microhabitat structure, but not competition intensity, water depth or colony size, also contributed to variation in bleaching severity of *Acropora* corals. Crevices and overhang microhabitats, which can mitigate bleaching severity, are more prevalent in structurally complex reefs. Such complexity is a product of the successful recruitment and growth of morphologically complex species, such as *Acropora* species that are important contributors to spatial complexity in Indo-Pacific reefs (Pratchett et al., 2008). Collectively, these results suggest a negative feedback loop whereby bleaching reduces the abundance of branching species, which lowers the occurrence of shaded microhabitats, which then leads to more severe bleaching.

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AUTHOR CONTRIBUTIONS

All authors contributed to the initial conceptualization of this project. Field data were collected by GF, TC, and SJ (at Lizard Island) and by KP, BR, KB, and MH (at Orpheus Island). Color analyses were conducted by GF and AP, and colony size measurements were conducted by MÁ-N and SJ. Coral identification, microhabitat and competition data were compiled by MH, KN, AP, TC, and GF. Spatial analyses were conducted by KC. MH analyzed the data and wrote the first draft of the paper with all authors making a substantial contribution to subsequent drafts (particularly SJ, KP, and MÁ-N).

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2017.00376/full#supplementary-material>

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