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Anomalous temperatures and extreme tides: Guam staghorn *Acropora* succumb to a double threat

L. J. Raymundo[1,*], D. Burdick[2], V. A. Lapacek[1], R. Miller[2], V. Brown[3]

[1]University of Guam Marine Laboratory, UOG Station, Mangilao, Guam 96923, USA
[2]NOAA Guam Coral Reef Monitoring Program, University of Guam Marine Laboratory, UOG Station, Mangilao, Guam 96923, USA
[3]NOAA Fisheries Habitat Conservation Division, Pacific Island Region, Guam Field Office, Tiyan, Guam 96913, USA

ABSTRACT: Anomalously warm sea surface temperature events are increasing in frequency, generating global concern regarding the adaptive and acclimatizing capacities of corals. Staghorn *Acropora* corals, important ecologically as habitat structurers, are particularly vulnerable to temperature-related bleaching. Here, we report a catastrophic mass mortality event that affected shallow staghorn communities in Guam, Micronesia. Mortality began in conjunction with a mass bleaching event in late 2013, initiated by anomalous warm sea surface temperatures and doldrum winds over a 4 mo period. A second warming event followed less than 8 mo later, concurrent with a period of extreme low tides resulting in repeated periods of subaerial exposure of shallow corals. This combination of stressors acted synergistically to trigger an extended mass mortality event. In 2015, we conducted rapid assessment surveys of 7 species in 21 previously mapped populations to determine mortality extent and pattern. Mortality from these combined environmental stressors resulted in a 53 ± 10% reduction in Guam's staghorn population, covering an estimated 17.5 ha of coral communities. Greater water circulation appeared to be associated with higher survival during both warm temperature periods and extreme low tides; populations in slightly deeper water, closer to well-flushed reef margins, showed lower mortality. A better understanding of the environmental drivers of the mortality patterns we observed is currently being applied to developing strategies to restore and manage remaining populations.

KEY WORDS: Staghorn · *Acropora* · Bleaching · Guam · Mortality · ENSO

INTRODUCTION

Mass coral bleaching episodes resulting from anomalously warm seawater are predicted to become more frequent and severe over the coming decades (Donner et al. 2005, McWilliams et al. 2005, Maynard et al. 2015). However, whether coral communities can acclimate or adapt to changing environments in ecological time scales remains uncertain (van Hooidonk et al. 2014). While resilience capacity differs significantly between coral taxa, it can also be influenced by local environment and recent exposure history (Golbuu et al. 2007, Maynard et al. 2008, Fabricius et al. 2013). A more thorough understanding of the relationship between species-specific resilience capacity and environmental influences is required to develop more accurate predictions of the future state of coral reef ecosystems at local scales and inform management aimed at restoring ecosystem function lost as a result of thermal stress-associated mass mortality events.

Arborescent branching *Acropora*, referred to here as staghorn *Acropora*, are notable inhabitants of shallow tropical and subtropical coral reefs. These

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*Corresponding author: ljraymundo@gmail.com species can form extensive, complex thickets, offering refuge for a diverse assemblage of fishes and invertebrates (Johnson et al. 2011, Kuffner & Toth 2016). Paradoxically, while these fast-growing, asexually fragmenting species have dominated shallow reefs for at least 1.8 million years (Renema et al. 2016), extant populations are currently considered to be particularly vulnerable to anthropogenic stress. At present, populations worldwide suffer accelerating rates of mortality from bleaching, predator outbreaks, and disease and are generally considered to be particularly vulnerable to stress (Sano et al. 1984, Bythell & Shepphard 1993, van Woesik et al. 2004, Macintyre et al. 2007, Houk & van Woesik 2008, Muller et al. 2008). The decline of 2 key Caribbean species, *Acropora cervicornis* and *A. palmata*, is well documented, and in 2005 they gained the dubious distinction of being the first hermatypic corals to be listed as Threatened under the US Endangered Species Act of 1973 (Vollmer & Palumbi 2006, IUCN 2015). In Guam, staghorn *Acropora* are generally found on the island's shallow reef flats and lagoonal patch reefs, where they provide critical habitat for ecologically, commercially, and culturally important fish and invertebrate species. In previous decades, Guam's staghorn populations were impacted by typhoons, *Acanthaster planci* outbreaks, extreme low tide events, and sedimentation from coastal development, but remaining populations appeared relatively stable over the last decade (D. Burdick pers. obs.) until 2 consecutive severe bleaching episodes in 2013 and 2014.

Over the past 2 decades, temperature anomalies have coincided with mild to moderate bleaching resulting in little mortality in the Marianas archipelago (Paulay & Benayahu 1999, Burdick et al. 2008), despite the high levels of mortality observed at other locations during the El Niño Southern Oscillation (ENSO)-driven global bleaching event in 1997 and 1998 (Wilkinson 2002). In 2013, an unprecedented region-wide bleaching event occurred within the archipelago, beginning in August and tapering off by December (Reynolds et al. 2014). The 2013 event was triggered by a prolonged period of high sea surface temperatures and doldrum wind conditions. A second bleaching event occurred the following June triggered by a second warming event and coinciding with extreme low tides, resulting in many shallow coral populations being subaerially exposed for prolonged periods. Many staghorn communities that survived the first episode succumbed to the second, resulting in extensive mortality (Fig. 1). Here, we report the combined impacts of these 2 bleaching events on the staghorn *Acropora* communities of Guam.

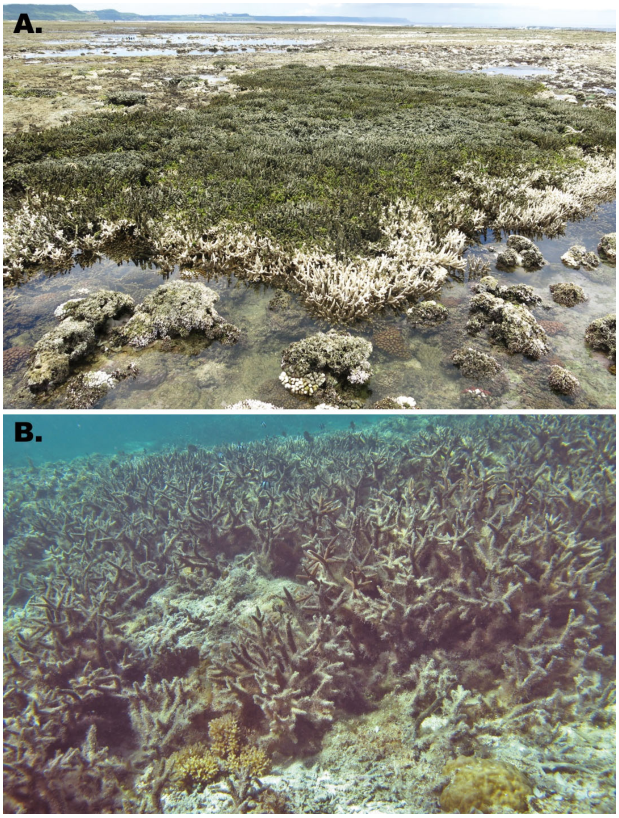

Fig. 1. Bleaching mortality in *Acropora* cf. *pulchra*, a common staghorn coral on Guam reef flats. (A) Extreme low tide event, causing coral exposure during mid-afternoon at Site 20; (B) post-bleaching mortality of a nearshore thicket at Site 7

MATERIALS AND METHODS

Temperature data were obtained from 2 sources. The NOAA Coral Reef Watch website (https://coralreefwatch.noaa.gov/satellite/hdf/index.php) provided data on degree heating weeks and sea surface temperature for Guam during the 2 bleaching periods, and Onset® Hobo tidbit data loggers deployed continuously at 4 reef flats along Guam's northwestern coast provided shallow water temperature readings that were recorded hourly (L. J. Raymundo unpubl. data). Prior to deployment, loggers were calibrated against mercury thermometers. On the reef flats, loggers were placed in shaded crevices on reef flat existing structure, to avoid erroneously high readings due to direct exposure to solar heating. Sea level and tidal height data were provided for the Apra Harbor station by NOAA NOS (2016a).

To quantify the extent of mortality in staghorn communities from the 2013 and 2014 back-to-back events, previous records of the location, areal extent, and species composition of known staghorn *Acro-*

pora populations along the Guam coastline were first compiled by D. Burdick (unpubl. data). The pre-bleaching areal extent and species composition of major staghorn communities around Guam had been opportunistically documented between 2009 and 2013 and combined into a single spatial data layer. The majority of polygons representing staghorn thickets were delineated within ArcGIS through the heads-up digitization of a 2011 Worldview-2 satellite image mosaic. The boundaries of some moderately sized, discrete thickets were delineated *in situ* using a Garmin 76S hand-held global positioning system (GPS) unit, while coordinates were obtained at the center of numerous small thickets and their size visually estimated *in situ*. Underwater images georeferenced using the GPS-Photo Link application and personal observations obtained during swims across the extent of major staghorn coral locations around Guam were used to inform the delineation and attribution of the staghorn polygons during the heads-up digitization process. The polygons were logically grouped into separate sites based on proximity to each other and their shared association with distinct geomorphological features, such as coastal embayments, reef flats, patch reefs, and lagoons.

A total of 21 sites at which staghorn *Acropora* were previously documented were surveyed between January and March 2015. The survey sites included all major staghorn coral communities around Guam as well as some areas with relatively small, isolated stands. At each site, systematic search swims were undertaken to locate all or most thickets or individual colonies. The location of colonies and extensive thickets was verified using a hand-held GPS; colonies were identified to species, and bleaching and mortality status were recorded (unbleached, % bleached, % mortality, notes and photo-documentation of pattern, and location of mortality per colony or thicket). Estimations of percent of colony affected and within-colony mortality patterns were obtained by a single observer (L. J. Raymundo) trained in visual estimation based on quantitative calibration practice using quadrats placed over colonies to assess the amount of colony surface area impacted or partially dead. Percent mortality per site was also categorized as low (1–30% mortality), medium (31–75% mortality), or high (75–100% mortality). Signs of recovery were also noted as presence or absence and defined as evidence of tissue regrowth over dead skeleton. To account for the uncertainty inherent in visual estimates, we defined the range in percent mortality to extend 10% either side of site observations when summarizing the area of coral impacted.

The spatial data layer developed prior to the bleaching event was then further developed using observations and georeferenced images obtained during the bleaching and mortality status surveys. Specifically, living and recently dead staghorn corals that had not been previously represented in the spatial data layer were added, thus increasing the accuracy of the pre-bleaching extent and species composition spatial data. The post-bleaching areal extent of staghorn coral communities was calculated by multiplying the percent mortality estimates obtained for each site with the total pre-bleaching area for the sites, and the estimated area of staghorn coral lost was calculated as the difference between the pre- and post-bleaching area values.

In September 2013, site-scale patterns in bleaching prevalence and bleaching-associated mortality were assessed at one of Guam's largest (~64 000 m^2) staghorn thickets (West Agaña Bay reef flat). Using ArcGIS 10.x, the locations of twelve 25 m transects were generated randomly and constrained to the boundary of the thicket as delineated using the heads-up digitization of a 2011 Worldview-2 satellite image mosaic. Each transect began at the coordinates generated by ArcGIS and extended 25 m due east. Depth was generally consistent across all transects, varying no more than 0.5 m. The surveys involved placing 0.25 m^2 quadrats every meter along the transect and identifying benthic features directly below 16 evenly spaced points within each quadrat. For points that fell on coral, the species and condition of the coral at that exact point were recorded. Coral condition was scored as normal, pale, bleached, recently dead–bleaching, recently dead–other, and old–dead. The relationship between bleaching severity (including bleaching-associated mortality) and the relative distance from the reef margin was tested using a simple linear regression analysis. Distance values were obtained using the 2011 Worldview-2 satellite imagery in ArcGIS and were measured as the perpendicular distance between each site and a line running parallel to the reef margin and through the site located closest to the margin.

RESULTS

In Guam, sea surface temperature exceeded the maximum monthly mean during 8 consecutive months (May through mid-December) in 2013 and again for the same months (May through mid-December) in 2014 (NOAA Coral Reef Watch 2014) (Fig. 2A). Anomalous warming and doldrums were

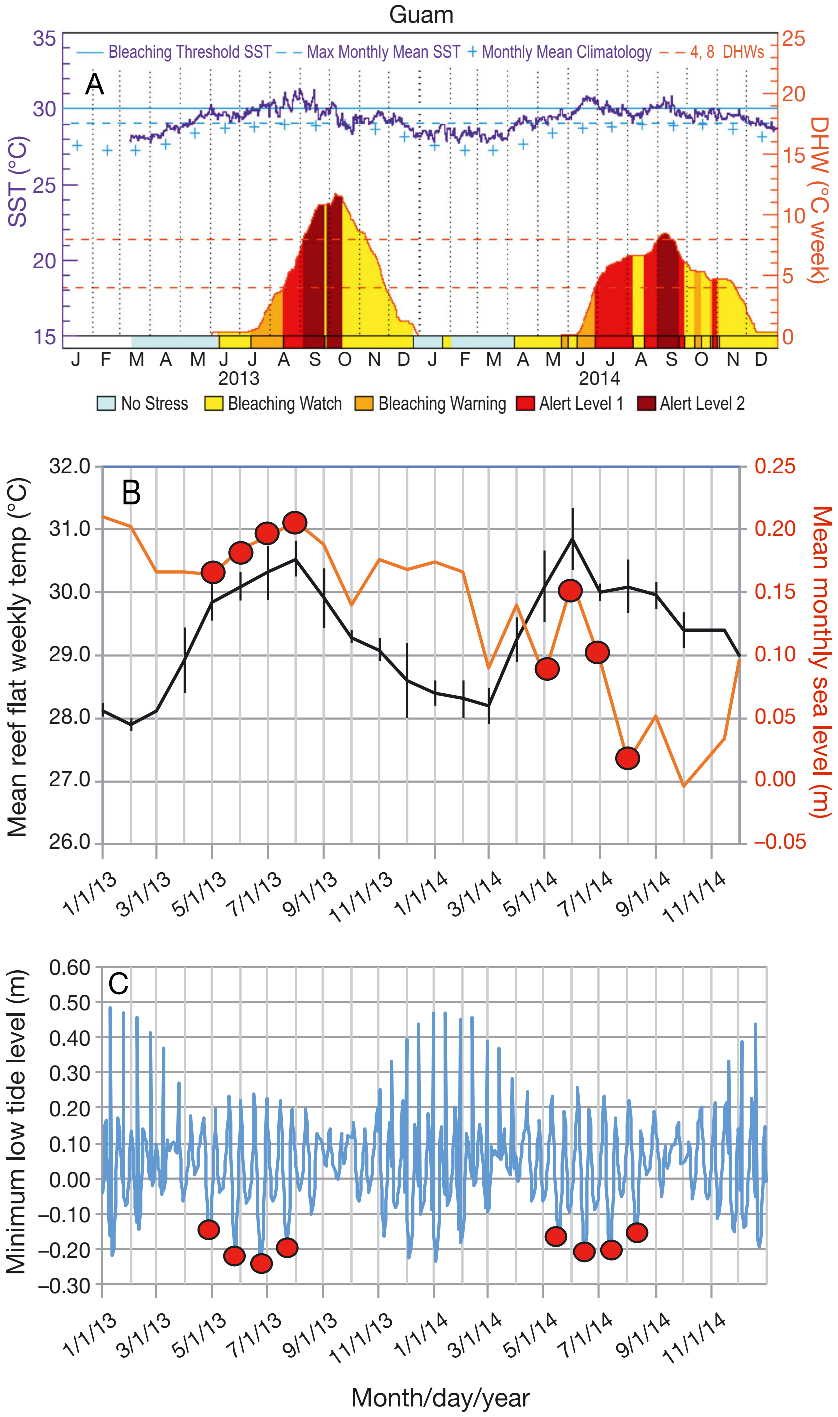

Fig. 2. Extreme environmental conditions coinciding with staghorn mass bleaching and low tide exposure events on Guam. (A) NOAA Coral Reef Watch bleaching stress levels showing sea surface temperatures (SST) and degree heating weeks (DHW) in 2013 and 2014; (B) mean weekly temperature (black line) for 4 monitored reef flats along Guam's western coast (L. J. Raymundo unpubl. data) and tidal height recorded at Apra Harbor (red line); (C) daily minimum sea levels recorded from Apra Harbor, 2013 to 2014 (Apra Harbor data from http://tidesandcurrents.noaa.gov/sltrends/sltrends_station.shtml?stnid=1630000). Red circles on (B) and (C) denote weeks when extreme low tides occurred between 13:00 and 15:00 h

temporarily disrupted by Typhoon Francisco in October 2013 but then quickly reestablished. Records from NOAA NOS (2016b) of monthly mean sea level indicated a steady rise at a mean rate of 4.55 mm yr^{-1} since 1993, reaching a high of 0.21 m above mean sea level by 2014. However, values began to plunge in early 2014, reaching a low of 0 m mean sea level by August 2014 (NOAA NOS 2016b; Fig. 2B). The drop in sea level, which resulted in exceptionally low spring tides, continued through 2014 and into 2015. Extreme low spring tides occurred every afternoon for 1 wk out of each month during bleaching events in both 2013 and 2014 (Fig. 2C), resulting in air exposure of reef flat corals for 3 to 4 h d^{-1}.

Pre-bleaching staghorn *Acropora* stands varied in size from 12 m^2 (0.0012 ha) to 77 883 m^2 (7.8 ha), covering a total of 33.3 ha on Guam's reef flats across 21 sites (Table 1, Fig. 3). All sites but one were located along the western coast. Extensive thickets (≥20 000 m^2) were found at 8 sites and dominated by *Acropora* cf. *pulchra*, *A. muricata*, *A.* cf. *acuminata*, and *A. aspera* (D. Randall & D. Burdick pers. comm.). *A.* cf. *pulchra* was the most common, found on 15 of the 21 sites surveyed. Other species, including *A. vaughani*, *A. virgata*, *A. austera*, and *A. teres*, were uncommon to rare and often located at slightly greater depths, either along margins of shoals in Apra Harbor (3–4 m) or in small, isolated clusters.

Applying our visual estimates of the percent mortality per colony, stand, or thicket to pre-bleaching values of areal extent of *Acropora* per site, we calculated that the mean whole-island post-bleaching areal cover of *Acropora* populations was 15.79 ha (Table 1). This constitutes a 53% decline in staghorn *Acropora* on Guam from pre-bleaching populations. By applying 10% variability from the mean values we calculated, this gives a whole-island post-bleaching areal cover

Table 1. Summary of areal coverage of staghorn *Acropora* populations pre- and post-bleaching and estimated percent mortality as a result of the 2014 bleaching event. High and low estimates are based on 10% deviation from the mean calculated values

Site	Area pre-bleaching (m^2)	Estimated mortality (%) mortality (%)			Estimated area post-bleaching (m^2)		
		Mean	Low	High	Mean	Low	High
1. Double Reef	234	30	20	40	164	140	187
2. Tanguisson/Sharks Hole	6523	30	10	20	4566	5218	5871
3. Tumon–Ypao	77 883	75	65	85	19 471	11 682	27 259
4. Tumon–Central	53 601	40	30	50	32 161	26 801	37 521
5. Tumon–Outrigger	19 939	40	30	50	11 963	9970	13 957
6. East Agaña	27 952	20	10	30	22 362	19 566	25 157
7. West Agaña	64 372	55	65	75	28 967	16 093	22 530
8. Piti Bomb Holes	485	90	80	95	49	24	97
9. Asan-Adelup	3221	30	10	20	2255	2577	2899
10. Luminao	890	80	70	90	178	89	267
11. Apra–Big Blue Shoals	809	80	70	90	162	81	243
12. Apra–Western Shoals	435	80	70	90	87	44	131
13. Apra–Dogleg	13	30	20	40	9	8	10
14. Apra–Gabgab	391	90	80	100	39	0	78
15. Agat–Cemetery	24 488	25	15	35	18 366	15 917	20 815
16. Agat Bay	12	25	15	35	9	8	10
17. Agat–Alutom	24 652	100	90	100	247	0	2465
18. Cocos Lagoon	853	85	75	95	128	43	213
19. Achang	21 338	30	20	40	14 937	12 803	17 070
20. Togcha	5035	65	75	85	1762	755	1259
21. Calvo Beach	75	70	60	80	22.5	30	15
Total	333 201		157 905	121 849	178 054		
Percent decline			53	63	47		

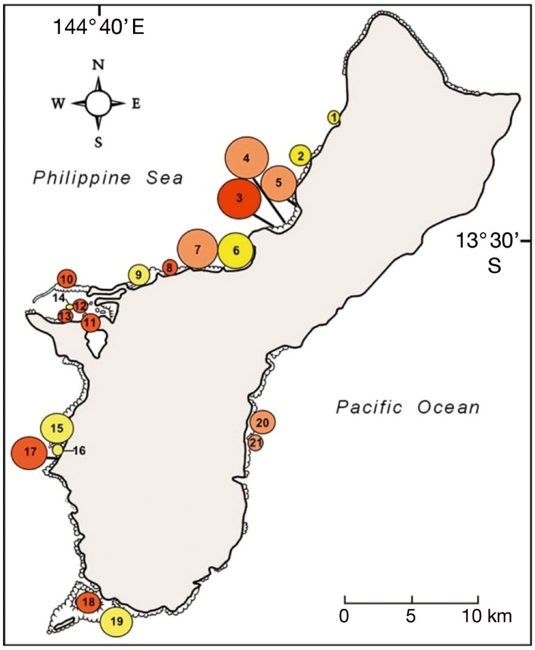

Fig. 3. Location of staghorn *Acropora* communities along Guam shallow reef habitats. Circle diameter is proportional to the areal size of the communities. Color denotes mean relative severity of bleaching: yellow = 1–30%; orange = 31–74%; red = 75–100%. Refer to Table 1 for actual percentages and site names

range of 17.80 ha (low mortality estimate: 47% mortality) to 12.18 ha (high mortality estimate: 63% mortality). Eight of the 21 sites showed an estimated mortality ≥75% (Table 1, Fig. 3). The largest losses were a 77.9 ha thicket of *A.* cf. *pulchra* (Site 3, Fig. 3), with an estimated 75% mortality, and a 24.7 ha thicket of *A. aspera* (Site 17, Fig. 3), which was 100% dead at the time of our surveys. Furthermore, 5 of the 7 sites containing rare staghorn species exhibited 80 to 90% mortality (Sites 10–13 and 18). Only 2 of the 4 rare species, *A. virgata* and *A. austera,* have been observed since the bleaching events, suggesting that the persistence of *A. vaughani* and *A. teres* in Guam is in doubt or that one or more of these species may have already been extirpated from Guam's waters.

Although our calculations of mortality extent are based on semi-quantitative estimates, the detailed survey conducted at West Agaña Bay (Site 7, Fig. 3; Fig. 4A) provided a fully quantitative assessment of bleaching extent during the 2013 episode but before significant mortality had occurred. Within this extensive *A.* cf. *pulchra* bed, bleaching stress and mortality associated with the 2013 event ranged from 11 to 100% along the 12 transects we surveyed, and 5 transect locations exhibited >75% severe bleaching and recent mortality. Corals classified as pale, severely bleached, or recently dead comprised 68 ± 36% (SD) within the surveyed area during the event. By 2015, our estimated mortality for the entire bay (6.4 ha; Table 1), including smaller patches seaward and southward, was 75%. A distinct gradient of bleaching stress and mortality was observed, with nearshore corals faring far worse than those closer to the reef margin ($R^2 = 0.8268$; $p < 0.0001$; Fig. 4B).

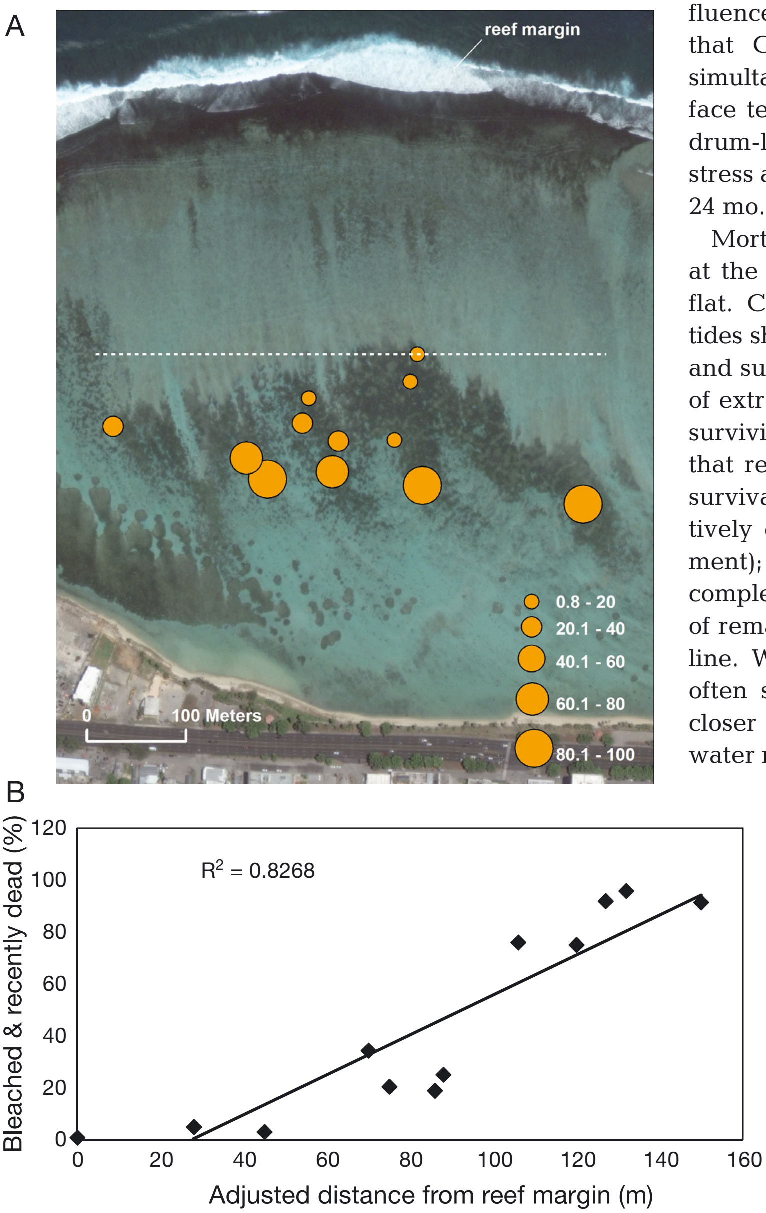

Fig. 4. Bleaching severity along nearshore and offshore gradients within the West Agaña (Site 7) staghorn thicket. (A) Location of survey sites within the thicket (orange circles). Diameter of the circle is proportional to bleaching severity. Dotted line shows the seaward thicket boundary. (B) Regression showing a significant and positive relationship between distance from the outer reef margin and bleaching severity

DISCUSSION

In the western Pacific, the interannual variation in sea level is driven primarily by the ENSO and associated Kelvin waves (Weisberg & Wang 1997). The low sea levels and resulting extreme low tides beginning in 2014 appear to have signified the early stages of the transition to an El Niño phase of the ENSO cycle, which reached a peak in late 2015 and has since begun to diminish (NOAA NOS 2016a). The confluence of these environmental phenomena meant that Guam's shallow staghorn populations were simultaneously exposed to anomalously high sea surface temperatures, increased irradiance due to doldrum-like wave and wind conditions, and exposure stress associated with anomalously low tides for 16 of 24 mo.

Mortality patterns in affected corals were evident at the scales of individual colony, thicket, and reef flat. Colonies subaerially exposed at extreme low tides showed complete mortality of exposed branches and subsequent recovery within months of cessation of extreme low tides. Recovery was principally from surviving reservoirs of tissue below low tide level that resheeted over dead skeleton. Within thickets, survival was higher along the thicket margin (relatively deeper and exposed to greater water movement); the centers of large thickets were nearly or completely devoid of living tissue, with some pockets of remaining live tissue below the low tide exposure line. Within the same reef flat, nearshore thickets often suffered higher mortality than those located closer to the reef margin, where wave energy and water motion were higher.

These observed mortality patterns may be at least partially explained by the degree of water motion and circulation available to corals during extreme events. Water movement around corals serves a variety of functions, including the advection of heat and metabolic by-products away from colonies (Nakamura & van Woesik 2001, Nakamura et al. 2003), facilitation of oxygen transport and photosynthetic efficiency (Finelli et al. 2006), and delivery of carbon as a heterotrophic food source during photoinhibition (Lesser et al. 1994). Thus, water movement was critical to the survival — and ongoing recovery — of bleached thickets. Colonies growing at the same depth, but with greater access to water movement, appeared to have survived heated water better than those bathed in standing water. This pertained to colonies growing at the margins of large thickets as well as those growing in small clumps rather than large thickets. Colonies occurring closer to the reef margin may also have benefitted from the higher mean sea level resulting from the greater wave height at these locations. Greater wave action can also provide moisture to exposed corals during extreme low tides. Indeed, at Site 20 (Fig. 3), for example, temperatures approaching 36°C were recorded on a dive computer within a narrow, well-flushed reef margin channel, yet the staghorns growing there showed no mortality during these events, in contrast to nearby colonies in isolated pools with stagnant water at low tide.

In addition to the multiple environmental processes interacting during a bleaching event, exposure history may also influence mortality patterns. At a number of locations, corals historically growing in areas of high flushing and wave energy bleached more severely when water circulation was also reduced (Mauritius: McClanahan et al. 2005; Guam and northern Marianas: Reynolds 2016; Thailand: Brown et al. 2002; Belize: Castillo & Helmuth 2005). In American Samoa, experimentally stressed corals showed both higher acclimatization capacity and genetically based adaptation when originating from highly variable heat regimes, in contrast to those acclimatized to less variable environments (Palumbi et al. 2014). This could explain the high mortality we observed in the Apra Harbor sites (Sites 10–14, Fig. 3), which were deeper and growing in more constant temperature regimes than those in the west coast shallow reef flats.

The frequency of both anomalously warm water sea level events is expected to increase (Hoegh-Guldberg 1999); indeed, we may already be experiencing the development of a new normal temperature and exposure regime. Increasing frequency of ENSO events and associated extreme low tides are likely to continue to limit upward growth of reef flat corals and kill those exposed for prolonged periods, despite current trends in sea level rise. Indeed, Widlansky et al. (2015) predict that these extreme events, known as taimasa, will double in frequency in the tropical western Pacific. While evidence suggests both acclimatization and adaptation in corals is possible, the short time periods between Guam's temperature anomalies may have precluded acclimatization and adaptive build-up of resistance (Coles & Brown 2003, Guest et al. 2012), resulting in the mass mortality observed. Local extinction is a possibility under the current predictions of increased frequency of sea surface temperature events. This has already been documented for 2 species of *Millepora* in the eastern Pacific (Glynn & de Weerdt 1991) as a consequence of the 1982−1983 ENSO event. In Guam, little historical information is available to quantify previous abundances of staghorn corals, and taxonomic uncertainty presents challenges in interpreting existing historical records. The species we have classified as rare have not been previously recorded elsewhere in the Marianas, and their possible extirpation from Guam as a result of these bleaching events would result in a significant range shift. Low abundance and limited range could reflect poorer competitive ability, lower reproductive capacity, higher susceptibility to stress, or a combination of these factors. It is interesting to note that many of the pre-bleaching populations were located in slightly deeper water with less variable temperature regimes and less wave action (Fig. 3, Sites 10–13).

Repeated incidents of partial mortality will have an impact on reproduction and, thus, the persistence of this functional group. When corals suffer partial mortality, limited energetic resources must be rerouted to tissue regeneration and away from gamete production (Ward et al. 2000, Baird & Marshall 2002). Bleaching mortality also reduces colony size, thereby limiting reproductive capacity (Tsounis et al. 2006, Okubo et al. 2007). The reproductive biology of staghorn *Acropora* is poorly documented in Guam, despite the ecological importance of this functional group, making it challenging to develop effective management options. Efforts are currently underway to determine spawning timing and fecundity, genetic connectivity, bleaching resilience, and management options for remaining populations. A preliminary genetic analysis of *Acropora* cf. *pulchra* suggested very low genetic diversity among Guam populations (Boulay 2015). Populations showed low sexual recruitment and a high clonality due to the likely establishment of populations from transported fragments rather than sexual recruits. Therefore, it is reasonable to assume low variability in genetically based resistance to bleaching and a predominance of asexual propagation via fragmentation. If so, management options should involve identification of particularly resilient populations for additional protection, enhancement of sexual reproduction to introduce genetic diversity, and careful site selection in restoration efforts to optimize environmental conditions.

Despite the extensive mortality we observed, remnant populations have survived and appear to be recovering. Indeed, Renema et al. (2016) argue that the life history strategies of fragmentation, rapid growth, and recovery are key to their persistence over geologic time, particularly in periods of rapid sea level rise. We suggest that these attributes should be utilized in developing restoration approaches and to manage remaining populations. The resilience potential of both local reef zones/habitats and populations requires consideration when developing restoration efforts. Wooldridge & Done (2004) outline a useful decision support tool to aid in the identification of marine preserve networks that could be modified to identify appropriate restoration sites. In Guam, work by Storlazzi et al. (2013) revealed nearshore hydrodynamic events that resulted in rapid short-term water cooling caused by internal bores bringing in cool offshore water during warming events. A better understanding of such phenomena may assist in selecting potential refugia habitats suitable for restoration and enhanced protection.

Predictions of increased frequency and severity of climate change-related events are supported by current evidence. These changes will likely result in a shift in what are currently considered normal conditions for marine flora and fauna. Particularly vulnerable taxa, such as staghorn *Acropora*, may require active management intervention if populations are to adapt and acclimatize to this shift in environmental conditions. To formulate such interventions, it is necessary to increase our predictive power regarding the nature of change that has already begun and its long-term consequences on individual species or functional groups. Approaches such as those discussed by van Oppen et al. (2015) offer intriguing options for enhancing resilience in vulnerable systems. Ultimately, however, reducing carbon dioxide concentrations is the only solution to slowing the alarming rate of change and providing species with enough time to adapt to changes that have already been set in motion.

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