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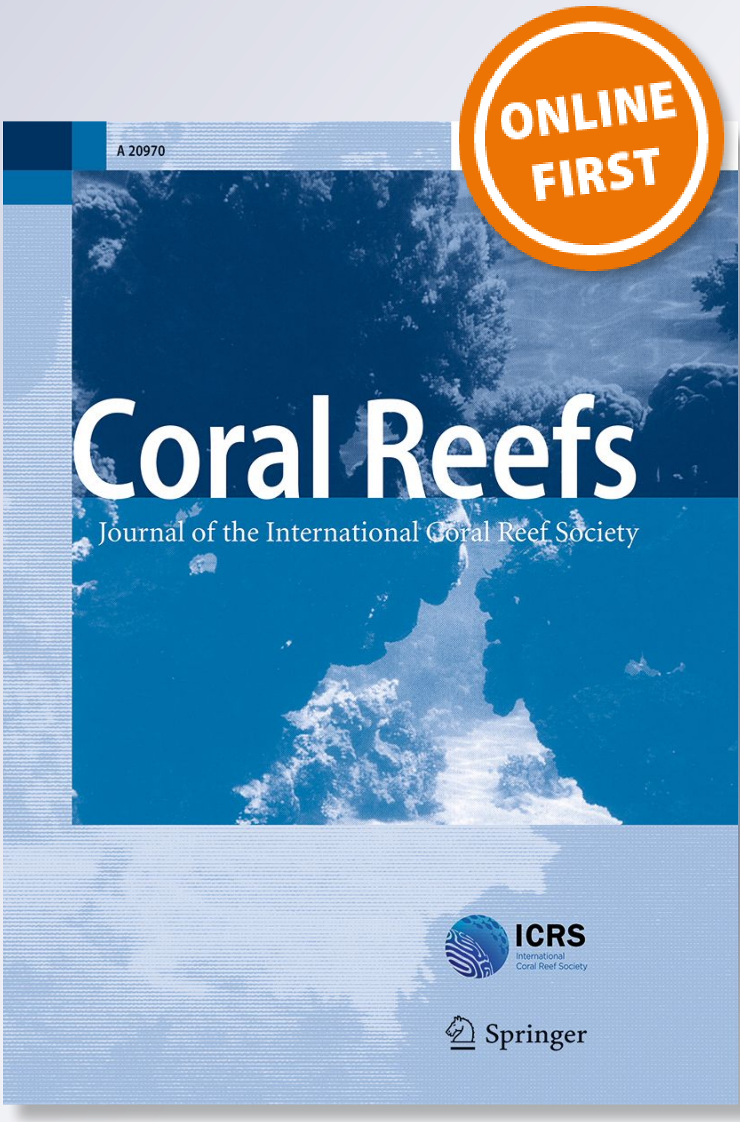

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REPORT

Successive bleaching events cause mass coral mortality in Guam, Micronesia

L. J. Raymundo[1] · D. Burdick[1] · W. C. Hoot[2] · R. M. Miller[1] · V. Brown[3] · T. Reynolds[1] · J. Gault[1] · J. Idechong[1] · J. Fifer[1,4] · A. Williams[1]

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Abstract The reefs of Guam, a high island in the Western Pacific, were impacted by an unprecedented succession of extreme environmental events beginning in 2013. Elevated SSTs induced severe island-wide bleaching in 2013, 2014, 2016, and 2017. Additionally, a major ENSO event triggered extreme low tides beginning in 2014 and extending through 2015, causing additional coral mortality from subaerial exposure on shallow reef flat platforms. Here, we present the results of preliminary analyses of environmental and biological data collected during each of these events. Accumulated heat stress in 2013 was the highest since satellite measurements began, but this record was exceeded in 2017. Overall, live coral cover declined by 37% at shallow reef flat sites along the western coast, and by 34% at shallow seaward slope sites around the island. Staghorn *Acropora* communities lost an estimated 36% live coral cover by 2017. Shallow seaward slope communities along the eastern windward coast were particularly devastated, with an estimated 60% of live coral cover lost between 2013 and 2017. Preliminary evidence suggests that some coral species are at high risk of extirpation from Guam's waters. In light of predictions of the near-future onset of severe annual bleaching, and the possibility that the events of 2013–2017 may signal the early arrival of these conditions, the persistence of Guam's current reef assemblages is in question. Here, we present detailed documentation of ongoing changes to community structure and the status of vulnerable reef taxa, as well as a critical assessment of our response protocol, which evolved annually as bleaching events unfolded. Such documentation and analysis are critical to formulating effective management strategies for the conservation of remaining reef diversity and function.

Keywords Guam · Mariana Islands · Bleaching mortality · Rapid response

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Introduction

Small islands are likely to be disproportionately impacted by climate change-related stressors, as their high reef-to-land area and heavy dependence on shallow marine ecosystems increase their vulnerability to the decline and loss of these ecosystems. Many such islands have experienced gradual declines in health, diversity, and productivity in recent decades, principally from local anthropogenic stressors. However, recent climate change-related shifts in sea surface temperature have added a global stressor to this list, with sudden and devastating consequences in some areas. The U.S. Territory of Guam (13°28′N, 144°46′E), the southernmost island in the Mariana Archipelago, lies just outside the Indo-Pacific center of reef biodiversity (Roberts et al. 2002) and hosts approximately 350 species of shallow-water scleractinian corals (Randall 2003). Like many small islands in the tropical Pacific, the condition of Guam's coral reefs has gradually declined since the 1960s from repeated *Acanthaster planci* outbreaks, worsening water quality, and high fishing pressure from a growing population (Chesher 1969; Randall and Holloman 1974; Colgan 1987; Burdick et al. 2008; Caballes 2009; McNeil et al. 2015). The recent superimposition of warming sea surface temperatures and other unpredicted stressors onto these already stressed communities had devastating effects on Guam's reefs. These events triggered an evaluation of our current approach to reef management and conservation, and highlighted an urgent need to develop a strategy for coping with climate-related change. Our experiences, and the evaluation of our response strategy, provide important documentation of climate change impacts to small island ecosystems.

Prior to 2013, coral reefs in Guam had been mildly affected by anomalous sea surface warming, relative to other sites in the Western Pacific. Paulay and Benayahu (1999) described the first recorded bleaching event in Guam in 1994 as affecting reefs island-wide but resulting in little mortality. While the authors did not believe the event was associated with unusually high sea surface temperatures at the time of the study, a later review of Pathfinder sea surface temperature measurements indicated that the bleaching threshold used for Guam for the period 1985–2003 (29.9 °C) was exceeded in 1994 (Burdick et al. 2008). Birkeland et al. (2000) and Richmond et al. (2002) mentioned coral bleaching in association with the historic 1997–1998 El Niño Southern Oscillation (ENSO) event, but mortality was limited and the overall impact was considered mild compared to the significant impacts observed in nearby Palau (Bruno et al. 2001) and at other reef locations around world (Wilkinson 2000). Burdick et al. (2008) reported bleaching on Guam's reefs in 2006 and 2007, but mortality was limited primarily to *Acropora* along the reef margin.

Although the frequency and severity of mass coral bleaching events on Guam's reefs has increased in recent decades, impacts were limited. However, a severe bleaching event in 2013, and subsequent events in 2014, 2016, and 2017, elevated concern among managers and researchers regarding the high potential for these events to drive a rapid and significant loss in coral cover, change in species composition, and decline in overall reef condition. Concern was also raised regarding the potential for the onset of near-annual frequency of heat stress events occurring earlier than had previously been predicted for the region (Donner et al. 2005; Donner 2009; van Hooidonk et al. 2016). In addition to the repeated heat stress events, a year-long ENSO-related period of extreme low tides began in late 2014 and extended into 2015, resulting in further coral mortality on Guam's shallow reef flat platforms. Here, we present summaries of these annual events, our assessment of the current state of reefs in Guam, and an analysis of the methods we utilized to respond to these events, which will be incorporated into future management protocols.

Materials and methods

The severity, scale, and repetitive nature of these bleaching events necessitated the development of multiple survey approaches, to maximize the quality of data collected given limited time and resources. These surveys and our assessment of their utility are described in Table S1. An intensive, island-wide survey approach was formulated by the authors in 2013, based on qualitative reconnaissance assessments of a subset of sites where bleaching was first detected, and informed by a draft bleaching response plan previously developed by the Guam Bureau of Statistics and Plans (BSP) and the National Oceanic and Atmospheric Administration (NOAA) Fisheries Guam Field Office, with support from the NOAA Coral Reef Conservation Program. However, time and resources were not available to achieve the same scale of sampling effort for subsequent years, and thus, a scaled-down effort was adopted for a smaller number of sites during these events. Surveys were conducted by a team of managers and scientists from government agencies (BSP, NOAA Fisheries, Guam Environmental Protection Agency, National Parks Service) and academe (University of Guam). In addition, an existing reef flat long-term monitoring program tracked bleaching events at five monitored sites throughout the entire period. Shallow staghorn *Acropora* communities were particularly vulnerable and were initially spot surveyed for bleaching impacts in 2014, and later quantitatively surveyed for the extent of loss in 2014–2015 and again in 2017. In 2016, a rapid reef flat site assessment protocol was developed and tested for "canary sites"—those sites intended to serve as part of an early warning system to guide decisions on further actions. Figure 1 provides the locations along the coast of Guam where these different surveys were conducted. Prevalence of bleaching and bleaching mortality were calculated for all species encountered in these surveys as:

$$\frac{\#\text{ of colonies or }\%\text{ of coral cover with bleaching or bleaching mortality}}{\#\text{ of colonies counted}} \times 100$$

Seaward slope surveys

Shallow seaward slope surveys were undertaken in 2013, 2015, 2016, and 2017 using generally the same protocols; details of modifications are described where appropriate. All sites were at approximately 5 m depth and included reef fronts of fringing platform reefs, shallow reaches of apron reefs, and shallow veneering communities at the cliff base along the northeastern coast; surveys did not include sheltered environments such as lagoons. Sites were located in the field using a handheld GPS receiver, and divers entered the water at a safe distance immediately seaward of the site and navigated to the target depth. Surveys were conducted along ($n = 3$) 25 m (2013 and 2015) or 30 m (2016 and 2017) transects placed along the target depth contour, clockwise around the island during all survey periods. Benthic photo-transect surveys were conducted using a compact point-and-shoot camera (Canon PowerShot SD940 IS in 2013, Canon PowerShot S120 in 2015, and Sony Cybershot RX100 in 2016 and 2017) to obtain an image every meter along each transect at 1 m above the substrate. Semiquantitative coral community bleaching assessments carried out in 2017 were conducted by one diver (either DB or LJR) swimming off-transect (in the general vicinity) for 20 min and recording the bleaching condition of each haphazardly encountered coral. Corals were identified to the lowest taxon possible and scored according to the following bleaching severity categories: normal (normal pigmentation), partial colony paling (such as on surfaces directly exposed to insolation), whole colony paling, partial bleaching (on surfaces directly exposed to insolation), whole colony bleaching, partial bleaching-associated mortality (on surfaces directly exposed to insolation), and whole colony bleaching-associated mortality. These in situ observations were augmented by photo-documentation of additional colonies not assessed on-site; bleaching condition was assessed from these photographs using the same categories presented above and combined with the in situ observations into a single database.

In 2013, benthic photo-transect surveys were carried out between October and December at 46 sites around Guam in response to observations of bleaching at multiple sites around the island in August. Forty-one of these sites were among the 52 sites visited during a NOAA Pacific Islands Fisheries Science Center (PIFSC) reef fish community assessment in 2011 (see Williams et al. 2012). The NOAA PIFSC sites were generated using a depth-stratified random sampling design. We located these sites using waypoints provided by NOAA PIFSC, keeping our survey sites to 5 m depth. The locations of seven additional sites were randomly generated along the northeast coast using ArcGIS, as the NOAA PIFSC surveys underrepresented this portion of the coastline.

In 2015, benthic photo-transect surveys were carried out between June and September at a randomized subset ($n = 17$) of the 2013 survey sites. The objective of these surveys was to assess cumulative impacts of 2013 and 2014, and to establish a new baseline of coral cover, species composition, and condition against which recovery or future impacts could be measured. Coral quadrat surveys were conducted along the same transects as the benthic photo-transect surveys, to assess the size and condition of coral colonies within ($n = 6$) 0.25 m^2 quadrats placed every 5 m along each transect. Colony size was visually estimated and binned ($\leq$ 10 cm, 11–30 cm, 31–60 cm, 61–100 cm, 101–200 cm, > 200 cm). Health impacts were recorded and the percentage of colony affected was estimated. Partial and full-colony mortality were assessed and ascribed to bleaching-associated mortality from the 2013 and 2014 events based on expert assessment of the pattern and estimated timing of the mortality. Partial mortality was characterized as low ($\leq$ 10%), medium (10–50%), or high (> 50%).

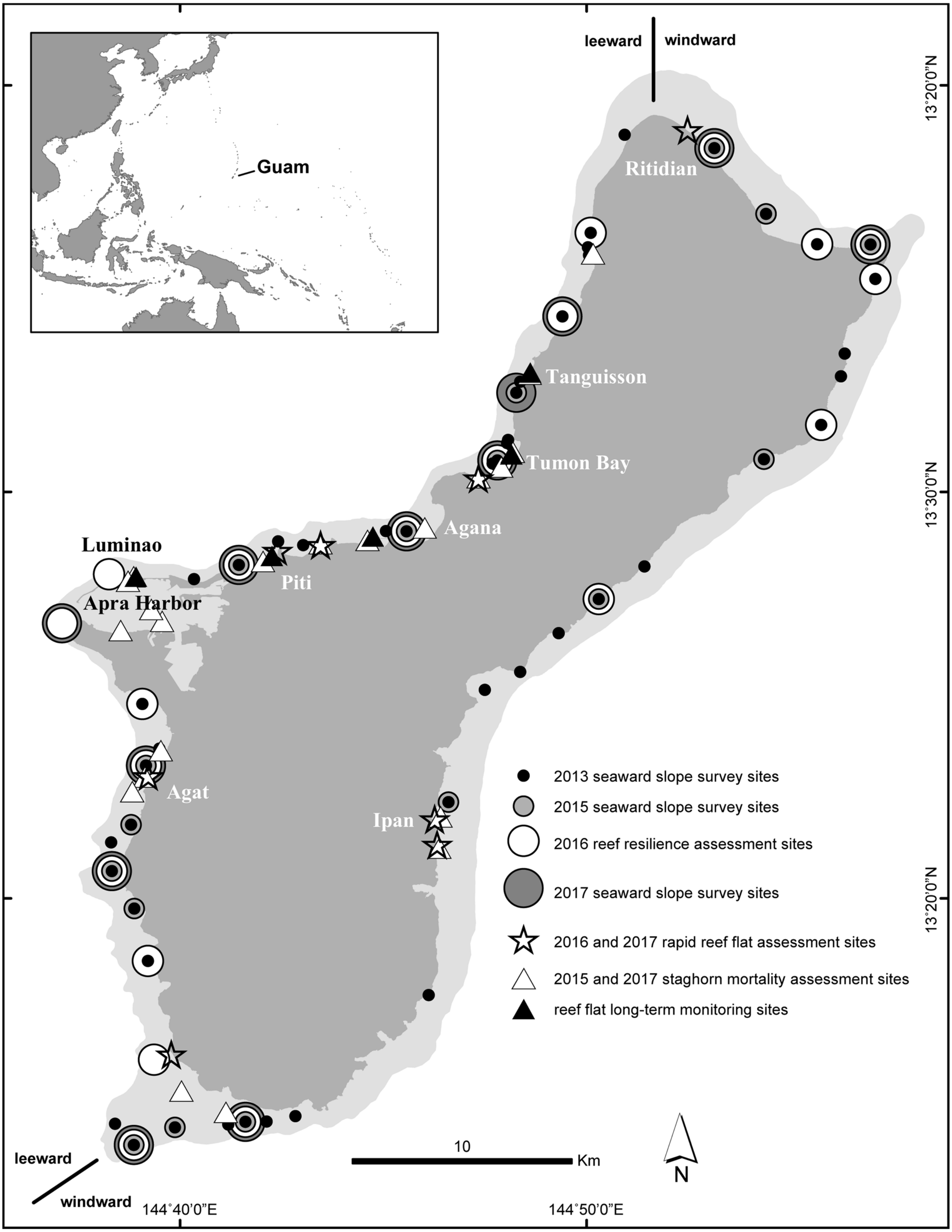
Benthic photo-transects were carried out at 20 sites around the island between July 2016 and January 2017, including 17 of the sites surveyed in 2013 and four new sites, in conjunction with a NOAA Saltonstall-Kennedy Grant-funded reef resilience assessment led by Dr. Jeffrey Maynard and DB. The resilience assessment sites were selected from the 2013 bleaching assessment sites in a non-random manner to achieve an even distribution of sites around the island, with priority placed on those sites that had been surveyed in both 2013 and 2015. Persistent poor water conditions prevented surveys at five of the sites along the east coast.

In 2017, benthic photo-transect surveys and semiquantitative coral community bleaching assessments were carried out at 12 sites in October in response to observations of bleaching at multiple sites around the island. Several sites, including most sites on the windward eastern coast, could not be accessed due to hazardous water conditions.

Images from photo-transect surveys were color-corrected using Adobe Photoshop Lightroom 6.0 and analyzed for percent cover using CPCe 4.1. The benthic feature at each randomly generated point (16 points per image) was identified to the lowest possible taxonomic level. Points that fell on a portion of a coral colony that exhibited non-normal pigmentation or exhibited bleaching-associated mortality were classified as pale, bleached, or recently dead in order to generate estimates of the percent of bleaching-impacted coral cover.

Reef flat long-term monitoring

A long-term monitoring program for reef flat platforms along Guam's western coastline was established in 2009.


leeward
windward
Guam
13°20'0"N
Ritidian
Tanguisson
Tumon Bay
13°30'0"N
Agana
Luminao
Piti
Apra Harbor
Agat
Ipan
2013 seaward slope survey sites
2015 seaward slope survey sites
2016 reef resilience assessment sites
2017 seaward slope survey sites
2016 and 2017 rapid reef flat assessment sites
2015 and 2017 staghorn mortality assessment sites
reef flat long-term monitoring sites
13°20'0"N
10
Km
N
leeward
windward
144°40'0"E
144°50'0"E

◀**Fig. 1** Map of Guam, showing location of survey sites for the shallow seaward slope, rapid reef flat sites, and staghorn mortality assessments, and reef flat long-term monitoring bleaching surveys

Five reef flats are monitored three to four times per year, along ($n = 3$) permanent 20 m × 1 m belt transects per site. Two of these sites (Luminao and Piti Bomb Holes) are dominated by *Porites*; Tanguisson, Tumon Bay and West Agaña are dominated by large staghorn *Acropora* thickets and *Pavona* spp. The line-intercept method was used to characterize benthic composition; live hard coral cover data from this data set were analyzed to examine changes over time between 2012 (prior to bleaching onset) and 2017. At one site (West Agaña), transect markers were lost in a storm in 2013 and redeployed in approximately the same positions; thus, only data from 2014–2017 were used in this analysis.

Assessment of staghorn *Acropora* loss

The areal extent of all known staghorn *Acropora* populations ($n = 21$) around Guam was previously determined using ArcGIS heads-up digitization of a 2011 Worldview-2 satellite image mosaic, and ground-truthed by in-water surveys carried out between 2009 and 2013 (described in Raymundo et al. 2017). A rapid, semiquantitative assessment of the extent of mortality and condition of these communities was undertaken from November 2014 to February 2015, after anecdotal reports of severe bleaching in 2014 (Fig. 1). Surveys were carried out while snorkeling, as these communities are primarily restricted to shallow reef flats and lagoonal patch reefs. Surveys involved visual estimation of percent and patterns of mortality for all populations, verification of species composition, and georeferenced photo-documentation to further develop the spatial data layer compiled prior to bleaching. Post-bleaching areal extent was calculated by multiplying percent mortality estimates by pre-bleaching areal extent. Coral loss was then calculated as the difference between pre- and post-bleaching area values, with a margin of 10% variation from the mean to account for uncertainty that is inherent in visual estimates (Raymundo et al. 2017). An assessment of 13 individual staghorn *Acropora* colonies tagged for reproductive activity in Tumon Bay Marine Preserve was undertaken in July 2014, when bleaching was observed within this population. Colonies were individually inspected for percent of the colony affected and bleaching severity (pale, bleached, partially dead).

Repeated mortality events following the completion of surveys in 2015 prompted a second set of surveys of the same 21 populations in 2017. All populations except those in Apra Harbor were assessed from February to May, prior to bleaching season. Surveys at Apra Harbor sites surveys took place in October, during the height of the bleaching event. These surveys scored coral condition as live or dead at 16 points within replicate 0.25 m^2 quadrats placed on staghorn thickets. Quadrats were placed every 1–2 m along a visually estimated transect that bisected the thicket; one or more additional transects perpendicular to the first were also assessed for larger thickets. Percent mortality was then calculated as:

$$\frac{\#\text{ of points of dead skeleton or rubble}}{16} \times 100$$

and average mortality per thicket was then calculated from the replicate quadrats. Additional data on coral condition collected within quadrats included species composition, recovery via recruitment or resheeting, disease, predation, percent rubble (a sign that the thicket was breaking down), and recruitment of other species onto dead skeleton. As above, total coral loss per site was calculated as the pre-bleaching areal extent (assuming 100% coral cover within thickets) minus percent mortality per thicket, and expressed in ha.

Rapid reef flat site assessments

Eight shallow reef flat sites were selected in 2016 for rapid assessment of bleaching severity during the bleaching event (Fig. 1). Sites were selected based on accessibility and species composition. The selected coral communities were predicted to respond quickly to bleaching and thus provide a rapid means of tracking the scope and severity of the bleaching event as it progressed.

Reef flat sites were surveyed on multiple occasions between August and December 2016 and between September and November 2017, corresponding to warming events during each of these years. Snorkelers conducted 20-minute timed swims along ($n = 3$) parallel 1 m-wide belt transects, at 1–1.5 m depth. The start and end coordinates for each transect were recorded using a handheld Garmin GPS attached to a float. Survey area was calculated by multiplying the transect length by 1 m width. Transect length and the distance between transects were dependent on the spatial extent of target coral communities, and thus varied across sites. Re-surveys started at the same coordinate and compass heading. In 2016, two sites were surveyed twice and two were surveyed three times; the remaining four sites were each surveyed four times over the five-month period, for a total of 26 surveys. In 2017, all sites but one were surveyed twice, for a total of 15 surveys. The total reef area surveyed in 2016 was 791 m^2, with a mean of 98 m^2 ± 62 m^2 surveyed per site. In 2017, we surveyed a total reef area of 916 m^2, with a mean of 116 m^2 ± 54 m^2 per site. All coral colonies within each belt were identified to species, where possible, and characterized by the severity of bleaching (no bleaching, partial colony paling, partial colony bleaching, whole colony paling, whole colony bleaching, and partial or whole colony mortality). Bleaching prevalence was calculated as:

$$\frac{\#\text{ of points of dead skeleton or rubble}}{16} \times 100$$

A bleaching mortality index (BMI) (McClanahan et al. 2004) was calculated for all genera with more than 5 colonies counted across all surveys accomplished in September for each year (2016 and 2017), using the formula:

$$\mathrm{BMI} = \frac{(0c1 + 1c2 + 2c3 + 3c4)}{3}$$

Bleaching severity categories used in our study were pooled to fit into the four bleaching categories used in the index: c1 = unbleached; c2 = moderate (partial colony paling; partial colony bleaching; whole colony paling); c3 = severe (whole colony bleaching; partial colony mortality); c4 = dead (whole colony mortality).

Environmental parameter data

Satellite-derived sea surface temperature (SST) and degree heating weeks (DHW) data, bleaching alerts, and predictions were accessed via NOAA Coral Reef Watch (2017). Temperatures and sea level were also monitored using the NOAA Tide Gauge in Apra Harbor (NOAA CO-OPS 2018a, b). Temperature and wave data from wave buoys located near Ipan, eastern Guam, and Ritidian, northern Guam, were monitored at PACIOOS (2018), and quality-controlled datasets were obtained for analysis from NOAA (2018a, b). Tropical cyclone records between 2013 and 2017, for all systems within 200 nm of Guam, were gathered from NOAA Digital Coast Historic Hurricane Tracks Viewer (NOAA 2019). Reef flat temperatures have been monitored at three reef flat long-term monitoring sites since 2009, using Onset® Hobo pendant loggers installed at approximately 1 m depth. Additional loggers were installed at three rapid reef flat assessment sites at the same depth during 2016 and 2017 bleaching events.

Statistical analyses

Seaward slope percent coral cover and percent bleaching-impacted coral cover values were square-root-transformed and pooled at the site level. Values were tested for normality using a Shapiro–Wilk test and for homoscedasticity using the modified Levene equal-variance test. The R package Partiallyoverlapping, which was developed for comparing samples with a mix of paired and unpaired observations based on method presented in Derrick et al. (2017), was used to perform two-sample comparisons for sites between each possible sample year combination. Comparisons between windward and leeward sites within the same sampling year were made using an equal-variance *t* test or Aspin–Welch unequal-variance test for normally distributed data, or a Mann–Whitney U test for non-normal data.

Reef flat long-term monitoring live hard coral cover data were square-root-transformed to meet the assumptions of normality and homoscedasticity and were examined via a two-way ANOVA using DataDesk V8.0.3 software®, with year and site as predictors.

Results

Synopsis of events in 2013

Environmental parameters

Satellite-derived SST first exceeded the predicted coral bleaching threshold for Guam (30 °C) on 1 June. NOAA CRW issued a Bleaching Watch (0 °C < HotSpot < 1 °C) on 11 June, and SST remained below 30 °C until 14 July. Temperatures reached Alert Level 1 levels ($4 \leq$ DHW ≤ 8) on 13 August, and Alert Level 2 (≥ 8 DHW) on 3 September; Alert Level 2 status continued through most of October. A maximum SST of 31.5 °C was recorded on 31 August (Fig. 2, 2013). Maximum recorded in situ temperatures of 31.5 °C were recorded from the Ipan buoy (southeastern Guam; Fig. 1) in both August and September, 32.6 °C from the Ritidian buoy (northwestern Guam; Fig. 1) in September, and 34 °C from the Luminao (central western Guam; Fig. 1) reef flat logger in July. Accumulated heat stress reached a peak of 12 DHW in early October and did not fully dissipate until late December. Temperatures remained above 29 °C through 19 December, with brief declines as low-pressure systems passed nearby. A pair of cyclones in mid-October caused southwest wave heights in excess of 5 m and resulted in a brief hiatus from high temperatures (Fig. 2, 2013). Wave heights on western exposures were variable; however, wave heights on eastern exposures stayed below 2 m through most of the bleaching period.

Seaward slope surveys

The island-wide mean percentage of shallow (5 m depth) seaward slope coral cover that was pale or bleached in 2013 was 20% ± 16%; an additional 11% ± 9% of coral cover exhibited bleaching-associated mortality, for a total of 32% ± 19% of coral cover that was impacted by the

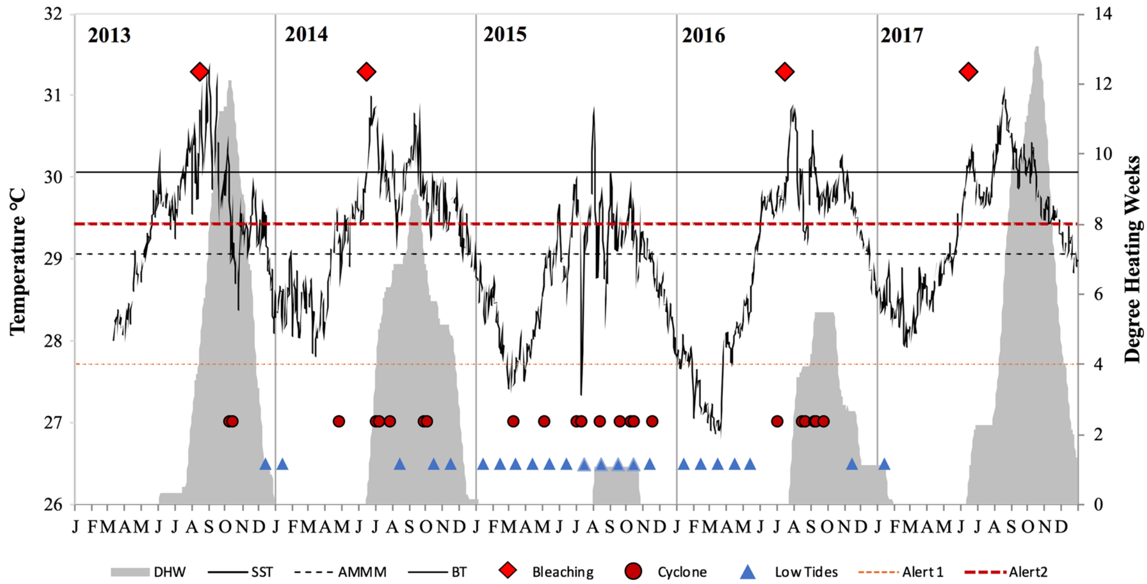


Fig. 2 2013–2017 time series of running 7-d mean sea surface temperature (SST) from the NOAA CRW virtual station for Guam plotted against annual maximum monthly mean SST (AMMM), bleaching threshold (BT), and degree heating weeks (DHW) for 2013–2017. Diamonds indicate observed bleaching events; circles represent cyclone events, and triangles are periods of extreme low tides

bleaching event (Fig. 3). The percentage of pale or bleached coral cover was greater for eastern windward sites (31 ± 17%) than for western leeward sites (11 ± 7%) ($U = 87$, $Z = 3.75$, $p < 0.001$), but there was no significant difference between the percentage of coral cover with bleaching-associated mortality at eastern (10 ± 7%) versus western sites (12 ± 10%)($t(43) = 0.48$, $p < 0.001$) (Fig. 3).

Synopsis of events in 2014

Environmental parameters

The onset of the sea surface temperature anomaly occurred early in the year, less than six months after dissipation of the previous event, with satellite-derived SST first exceeding the 30 °C bleaching threshold on 25 May, and a maximum SST of 31 °C recorded on 20 June (Fig. 2, 2014). Satellite-derived temperatures remained between 29 °C and 30 °C through December; however, temperatures recorded by in situ loggers exceeded 31 °C periodically between June and September. Accumulated heat stress reached a peak of 9 DHW in mid-September and dissipated by mid-December. Periodic low-pressure systems were associated with increased wave heights and decreased temperatures in July, August, and October (Fig. 2, 2014). As the El Niño event developed in 2014, sea levels began to decrease around Guam, resulting in extreme low tides beginning in August (Figure S1, 2014).

Prior to 2015, the NOAA CRW automated operational Satellite Bleaching Alert email system was based on measurements obtained at a single stationary 50 km satellite grid cell. In 2014, this alert system issued a Bleaching Watch for Guam in mid-May, as SST first reached the maximum monthly mean within the grid cell. A Bleaching Warning was issued between mid-June and early July, corresponding to SST values between 30.0 and 30.6 °C. Bleaching Watch conditions continued through late November, but accumulated heat stress never exceeded 3 DHW. NOAA CRW has since migrated to a higher resolution product that utilizes a grid of 5 km cells extending across a larger area around each jurisdiction. The retrospective SST measurements presented above and associated CRW alerts based on the 5 km product indicated that the 2014 temperature anomaly was of significantly greater magnitude and duration than that recorded by the 50 km product. The 5 km product signaled the onset of Bleaching Watch conditions in early April. Alert Level 1 conditions were reached on 29 June, and after brief declines in SST, Alert Level 2 conditions persisted from late August through September. Bleaching Watch conditions did not dissipate until the end of December.

Reef flat bleaching observations

Anecdotal observations and photo-documentation by LJR, DB, and VB confirmed that paling, bleaching, and bleaching-associated mortality affected multiple coral species at several shallow reef flat sites within six months

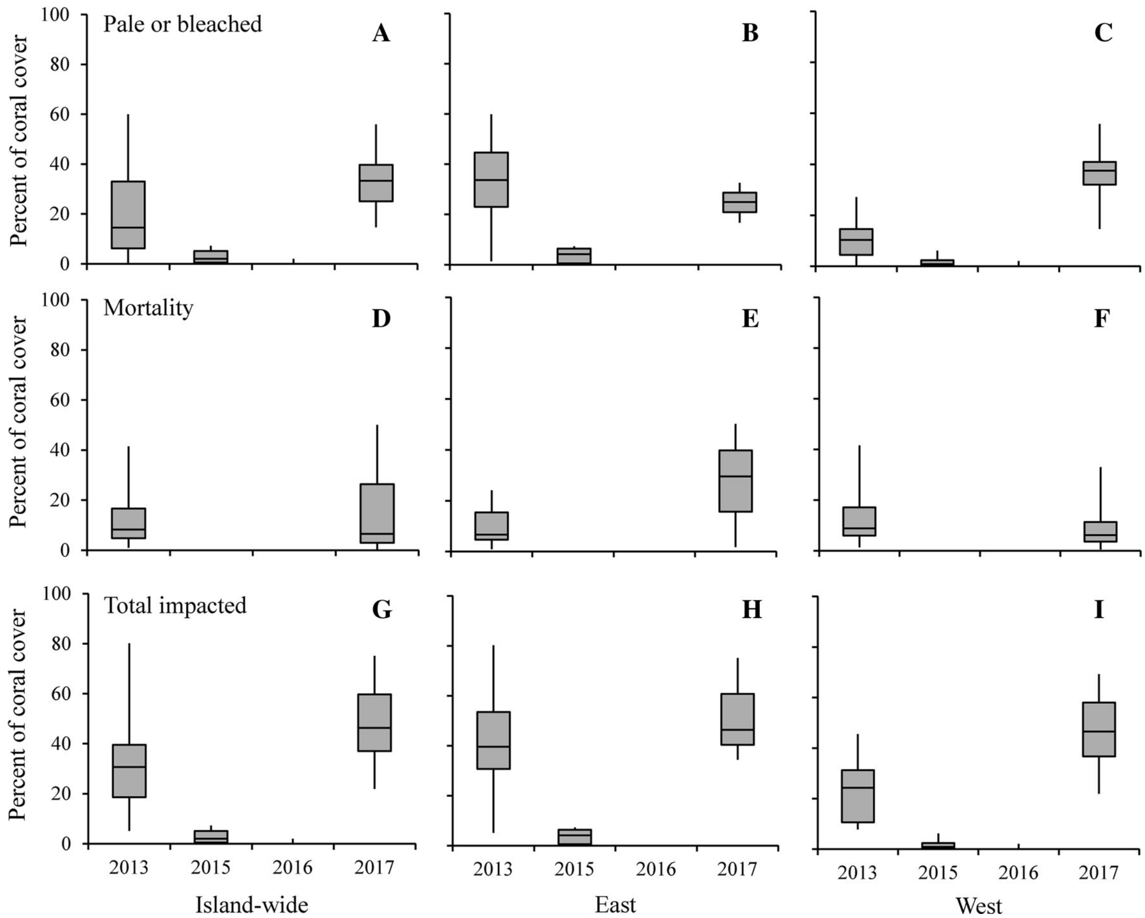


Fig. 3 Box plots of percentage of bleaching-impacted coral cover values from shallow (5 m) seaward slope benthic photo-transects surveys in 2013, 2015, 2016, and 2017. The percent of coral cover exhibiting paling or bleaching is presented for all sites island-wide (**a**), eastern windward sites (**b**), and western leeward sites; the percent of coral cover exhibiting bleaching-associated mortality is presented for all sites island-wide (**d**), eastern sites (**e**), and western sites (**f**); and the percentage of coral cover exhibiting paling, bleaching, or bleaching-associated mortality is presented for all sites island-wide (**g**), eastern sites (**h**), and western sites (**i**). Data were obtained from a total of 46 sites (21 east, 25 west) in 2013, 17 sites (9 east, 8 west) in 2015, 19 sites (7 east, 12 west) in 2016, and 11 sites (3 east, 8 west) in 2017

of the previous bleaching event. Nearshore staghorn *Acropora* communities were particularly affected, with LR and VB observing bleaching and associated mortality of *A. muricata*, *A.* cf. *intermedia*, and *A.* cf. *pulchra* between May and July; 62% of tagged *Acropora* cf. *pulchra* and *A.* cf. *intermedia* colonies were affected.

Synopsis of events in 2015

Environmental parameters

Guam experienced frequent weather disturbances in 2015, including close approaches by six cyclones. Three others passed close enough to affect weather conditions in Guam (Fig. 2, 2015). Decreased SST and high wave heights were associated with these events. Satellite-derived sea surface temperature reached 29 °C in May and exceeded the 30 °C bleaching threshold briefly in July and August, reaching a peak of 30.8 °C on 31 July; conditions warranted Bleaching Warning status for a total of eleven days (Fig. 2, 2015). Data collection at the buoys was inconsistent in 2015 due to impacts from disturbances; data are not presented here for this year. With the onset of a strong ENSO event, sea level decreased by 0.35 m between late 2014 and 2015. Mean low water declined to -0.15 m in December 2015 (Fig. S1, 2015), and extreme low tide values in excess of -0.1 m were recorded every month in 2015, with peak values in excess of -0.3 m below mean sea level in October and November. These ENSO-associated extreme low tide events repeatedly subaerially exposed shallow reef flat coral communities throughout the year, causing mortality of the top several inches of exposed tissue. Partial mortality was particularly pronounced during the summer months, triggered by a combination of exposure for several afternoon hours on consecutive days and doldrum-like wind conditions resulting in reduced water circulation (Fig. S2).

Seaward slope surveys

Seaward slope surveys took place from mid-June to mid-September, when signs of heat stress would be expected. Coral quadrat and photo-transect surveys yielded similar bleaching prevalence values (pale and bleached colonies), with island-wide means of 3 ± 3% and 3 ± 2% (n = 3851 colonies censused), respectively. Bleaching was not reported by the authors or other observers (such as Guam's Eyes of The Reef participants) at other reef areas during the period coinciding with the temperature anomaly. The results of the quadrat surveys indicated that an average of 13 ± 9% of observed colonies exhibited partial to full-colony mortality attributable to the 2013 and 2014 events. The prevalence of mortality attributed to the 2013 and 2014 events was similar for the eastern windward and western leeward sites (14 ± 12% and 12 ± 4%, respectively) (Fig. 3).

Staghorn Acropora populations

Prior to 2013, staghorn populations covered a total of 33.3 ha and were composed of monospecific, or occasionally mixed-species, stands. Eight species had been identified from Guam: *Acropora* cf. *pulchra, A.* cf. *intermedia, A. muricata,* and *A. aspera* existed in extensive thickets up to 7.8 ha in area, while *A. vaughani, A. virgata, A. austera,* and *A. teres* were rarer, and limited to individual colonies or small thickets of < 12 m^2 at several sites. In 2015, two species, *A. aspera* and *A. virgata,* were observed in one site each, and a third species, *A. teres*, was observed at two sites. *Acropora vaughani* was not observed in 2015 and has not been seen since, which suggests that it may be extirpated from Guam's waters. Of the remaining three staghorn species, *A.* cf. *pulchra* was the most common, found in 16 of the 21 sites surveyed (Raymundo et al. 2017).

Surveys in 2015 documented cumulative mortality from both elevated SSTs and the onset of extreme low tides across 2013 and 2014; thus, it was not possible to attribute mortality within these populations to specific years or events. Cumulative mortality from the 2013–2015 events, which was first reported in Raymundo et al. (2017), was estimated at 53% ± 10%. One extensive population suffered complete mortality, and live coral cover at eight others was estimated to have decreased by 70% or more.

Synopsis of events in 2016

Environmental parameters

Conditions around Guam warranted Bleaching Watch status by 18 May. Sea surface temperature reached 30 °C, and a Bleaching Warning was issued on 19 July. A maximum SST of 30.9 °C was recorded on 25 July (Fig. 2, 2016). In situ temperatures above 30 °C were recorded at the Ipan buoy starting on 30 May, and the maximum reef flat temperature recorded was 35.6 °C, in July, from Tumon Bay (West-central Guam). The Ritidian buoy was offline until 16 June but recorded in situ temperatures above 30 °C beginning on 28 June and maximum temperatures above 32 °C in July and August (Fig. 2, 2016). Conditions reached Alert Level 1 for seventeen days starting on 27 August, and accumulated heat stress peaked at 5.5 DHW between 9 September and 10 October. Sea surface temperature decreased after tropical disturbances and monsoons in August and September, but remained elevated through 19 December.

Seaward slope surveys

In contrast to observations at reef flat sites, heat stress-associated bleaching was very low along the shallow seaward slope, with the percent of pale or bleached coral cover at 0.1 ± 0.5%, and no bleaching-associated mortality (Fig. 3). Similar to the 2015 bleaching site re-surveys, the 2016 reef resilience surveys began prior to the onset of the temperature anomaly but continued into months during which bleaching would be expected.

Reef flat rapid site assessments

A total of 13,640 observations were made on corals during 26 surveys at eight reef flat sites, representing 18 coral genera and at least 37 species. Bleaching prevalence across all sites and survey dates was 46% ± 17% (mean ± SD). Average bleaching prevalence across sites between August and September was 53% ± 15%, and from October to December mean prevalence dropped to 39% ± 16% as water temperatures cooled. The most severe bleaching impacts captured by these surveys were reported at Agat (Fig. 1), where a maximum temperature of 35.3 °C was recorded in July; impacts at this site included 70% of colonies impacted by paling, bleaching, and mortality in August, 78% impacted in September, 56% in October, and 58% in December (refer to Table 1). Significantly, this site also exhibited the complete loss of an extensive staghorn bed, documented in the 2015 staghorn surveys (see 2015 Synopsis). *Goniastrea, Acropora,* and *Isopora* showed the highest BMIs, but the two most common genera, *Porites* and *Leptastrea*, showed relatively low BMIs (Table 2).

Synopsis of events in 2017

Environmental parameters

Sea surface temperature exceeded 29 °C on 30 April and 30 °C on 8 June. Water conditions were calm and no

Table 1 Mean bleaching prevalence (± SD) and mean bleaching mortality prevalence (± SD) for each coral taxon assessed in 2017

Taxon	Survey	Reef zone	No. sites, west	No. sites, east	Total no. colonies	Bleaching prev.	Bleaching mortality prev.
Scleractinian taxa							
Acanthastrea echinata	1	s	5	2	68	19 ± 29	0.9 ± 3
Acropora abrotanoides	1	s	5	4	87	8 ± 16	45 ± 46
Acropora aspera	2	f	1	0	121	Na	61 ± 0
Acropora austera	2	f, l, s	5	0	45	13 ± 23	51 ± 15
Acropora cf. *azurea*	1	s	7	1	29	12 ± 25	36 ± 40
Acropora cerealis	1	s	4	2	26	25 ± 37	17 ± 32
Acropora cophodactyla	1	s	2	0	5	0	15 ± 38
Acropora digitifera	1	s	5	2	11	25 ± 43	14 ± 33
Acropora globiceps	1	s	6	3	64	21 ± 29	43 ± 40
Acropora humilis	1	s	6	2	103	15 ± 19	44 ± 36
Acropora cf. *intermedia*	2	f, l	5	0	141	18 ± 36	54 ± 23
Acropora latistella	1	s	2	0	3	15 ± 38	0
Acropora monticulosa	1	s	1	0	1	8 ± 28	0
Acropora muricata	2	f, l	7	0	104	Na	59 ± 13
	3	f	1	0	86	84 ± 0	15 ± 0
Acropora cf. *nasuta*	1	s	2	1	5	10 ± 29	13 ± 32
Acropora cf. *pulchra*	2	f, l	15	1	853	Na	56 ± 13
	3	f	3	0	140	60 ± 35	13 ± 12
Acropora secale	1	s	6	2	109	12 ± 23	40 ± 44
Acropora surculosa	1	s	8	4	128	51 ± 34	29 ± 31
Acropora tenuis	1	s	5	1	14	15 ± 32	31 ± 44
Acropora teres	2	f	1	0	5	Na	44 ± 0
Acropora valida	1	s	5	2	25	23 ± 35	23 ± 44
Acropora verweyi	1	s	2	3	59	7 ± 14	18 ± 35
Acropora virgata	2	l	1	0	3	Na	92 ± 0
Acropora sp. "quelchi"	1	s	1	2	3	8 ± 28	0
Acropora sp. "wardii"	1	s	5	1	8	31 ± 48	15 ± 38
Acropora sp. 1	1	s	0	1	3	0	8 ± 28
Acropora spp. caespitose	1	s	7	4	174	23 ± 33	40 ± 42
Acropora spp. corymbose	1	s	4	2	80	4 ± 7	40 ± 45
Acropora spp. other	1	s	3	2	30	0.4 ± 2	38 ± 50
Astrea curta	1	s	6	3	52	45 ± 40	5 ± 11
Astreopora elliptica	1	s	2	1	10	13 ± 32	3 ± 10
Astreopora gracilis	1	s	1	0	3	8 ± 28	0
Astreopora listeri	1	s	4	3	28	26 ± 43	8 ± 27
Astreopora myriopthalma	1	s	8	4	163	35 ± 25	0
Astreopora ocellata	1	s	2	0	20	13 ± 32	0
Astreopora randalli	1	s	4	2	17	33 ± 43	0
Astreopora spp.	1	s	6	2	202	36 ± 40	0.3 ± 1
Coscinaraea columna	1	s	4	1	5	39 ± 51	0
Cycloseris sp.	1	s	1	0	1	8 ± 28	0
Cyphastrea chalcidicum	1	s	5	3	23	20 ± 31	0
Cyphastrea serailia	1	s	8	3	33	19 ± 31	0
Cyphastrea spp.	1	s	3	2	48	13 ± 22	2 ± 6
Diploastrea heliopora	1	s	7	2	79	8 ± 13	0
Dipsastrea danae	1	s	4	2	35	23 ± 37	3 ± 9

Table 1 continued

Taxon	Survey	Reef zone	No. sites, west	No. sites, east	Total no. colonies	Bleaching prev.	Bleaching mortality prev.
Dipsastrea favus	1	s	9	3	144	70 ± 30	0.3 ± 1
Dipsastrea helianthoides	1	s	3	3	48	25 ± 39	13 ± 28
Dipsastrea matthaii	1	s	1	0	1	0	0
	3	f	1	0	1	0 ± 0	0
Dipsastrea pallida	1	s	6	3	99	63 ± 46	0.4 ± 1
Dipsastrea sp. 1	1	s	3	0	6	0	0
Dipsastrea spp.	1	s	7	4	511	20 ± 38	0
Echinophyllia echinata	1	s	1	0	1	8 ± 28	0
Echinopora pacificus	1	s	3	2	6	27 ± 44	12 ± 30
Euphyllia glabrescens	1	s	1	0	1	0	0
Favites flexuosa	1	s	5	2	18	37 ± 47	8 ± 28
Favites rotundata	1	s	0	2	14	3 ± 11	0
Favites russelli	1	s	6	2	65	47 ± 41	0
Favites spp.	1	s	3	0	10	20 ± 38	0
Fungia fungites	1	s	2	0	14	10 ± 29	0
Fungia granulosa	1	s	1	0	1	0	0
Fungia paumotensis	1	s	1	0	2	8 ± 28	0
Fungia scutaria	1	s	3	0	10	12 ± 30	0
Galaxea fascicularis	1	s	9	4	322	9 ± 13	1 ± 4
Gardineroseris planulata	1	s	6	1	22	54 ± 52	0
Goniastrea edwardsii	1	s	9	2	250	56 ± 31	17 ± 25
	3	f	1	0	3	33 ± 0	0
Goniastrea minuta	1	s	1	0	1	0	8 ± 28
Goniastrea pectinata	1	s	7	2	50	43 ± 48	24 ± 43
Goniastrea retiformis	1	s	9	3	351	50 ± 28	16 ± 20
	3	f	4	2	17	57 ± 49	0
Goniastrea stelligera	1	s	8	4	172	35 ± 33	25 ± 35
Goniopora fruticosa	1	s	5	1	41	1 ± 4	0
Goniopora minor	1	s	2	0	6	0	0
Goniopora somaliensis	1	s	1	0	2	8 ± 28	0
Goniopora tenuidens	1	s	1	0	1	0	0
Goniopora spp.	1	s	7	2	42	8 ± 20	4 ± 14
Herpolitha limax	1	s	6	0	7	31 ± 48	0
Hydnophora microconos	1	s	7	4	93	66 ± 41	2 ± 5
Isopora palifera	1	s	0	1	42	1 ± 4	2 ± 7
	3	f	1	1	197	55 ± 0	1 ± 0
Leptastrea pruinosa	1	s	1	1	3	0	0
Leptastrea purpurea	1	s	9	4	415	13 ± 15	0 ± 1
	3	f	6	2	2060	15 ± 18	0 ± 0
Leptastrea spp.	1	s	4	2	23	7 ± 18	0
Leptastrea transversa	1	s	4	3	16	22 ± 38	0
Leptoria phrygia	1	s	8	4	436	74 ± 27	3 ± 5
Lobophyllia hemprichii	1	s	8	2	46	77 ± 44	0 ± 1
Lobophyllia sp.	1	s	1	0	8	3 ± 10	1 ± 4
Merulina ampliata	1	s	4	1	9	19 ± 38	8 ± 28
Montipora caliculata	1	s	3	0	5	23 ± 44	0
Montipora danae	1	s	1	0	1	8 ± 28	0

Table 1 continued

Taxon	Survey	Reef zone	No. sites, west	No. sites, east	Total no. colonies	Bleaching prev.	Bleaching mortality prev.
Montipora foveolata	1	s	5	2	48	35 ± 42	17 ± 29
Montipora grisea	1	s	3	0	4	0	19 ± 38
Montipora hoffmeisteri	1	s	5	2	47	36 ± 40	17 ± 26
Montipora informis	1	s	1	0	3	3 ± 9	0
Montipora monasteriata	1	s	1	0	4	4 ± 14	4 ± 14
Montipora planiuscula	1	s	1	0	1	0	0
Montipora tuberculosa	1	s	4	1	7	8 ± 19	12 ± 30
Montipora verrucosa	1	s	8	4	138	42 ± 36	50 ± 36
Montipora spp.	1	s	9	3	370	51 ± 33	35 ± 33
Oulophyllia crispa	1	s	6	4	24	68 ± 47	2 ± 6
Pachyseris speciosa	1	s	2	0	3	15 ± 37	0
Pavona bipartita	1	s	2	0	6	8 ± 19	4 ± 14
Pavona chiriquiensis	1	s	5	2	45	24 ± 30	0
Pavona decussata	3	f	2	1	214	6 ± 8	0
Pavona cf. *diffluens*	1	s	1	0	1	8 ± 28	0
Pavona divaricata	3	f	1	1	39	63 ± 52	0
Pavona duerdeni	1	s	6	4	43	66 ± 46	11 ± 28
Pavona maldivensis	1	s	3	1	8	21 ± 38	10 ± 24
Pavona sp. 1 "white collines"	1	s	1	0	1	8 ± 28	0
Pavona spp.	1	s	7	2	24	0	0
Pavona varians	1	s	8	2	46	28 ± 32	0
Pavona venosa	1	s	4	0	15	4 ± 14	0
	3	f	1	0	1	0 ± 0	0
Platygyra daedalea	1	s	8	4	146	55 ± 35	17 ± 28
Platygyra pini	1	s	9	4	242	## ± 21	10 ± 17
	3	f	2	0	21	39 ± 56	0
Plesiastrea versipora	1	s	1	1	2	8 ± 28	0
Pocillopora ankeli	1	s	6	1	30	38 ± 45	10 ± 17
	3	f	1	0	8	13 ± 0	0
Pocillopora damicornis	1	s	4	1	26	8 ± 28	4 ± 16
	3	f	6	2	497	60 ± 24	0 ± 0
Pocillopora danae	1	s	1	0	1	8 ± 28	0
Pocillopora elegans	1	s	4	2	24	29 ± 43	9 ± 22
Pocillopora grandis	1	s	7	4	98	41 ± 48	28 ± 32
Pocillopora cf. *ligulata*	1	s	5	3	21	41 ± 48	4 ± 14
Pocillopora meandrina	1	s	8	4	184	31 ± 25	39 ± 32
Pocillopora setchelli	1	s	1	1	9	1 ± 4	8 ± 28
Pocillopora verrucosa	1	s	9	4	304	41 ± 16	32 ± 24
	3	f	2	0	5	75 ± 33	0
Pocillopora woodjonesi	1	s	0	1	2	0	8 ± 28
Pocillopora spp.	1	s	7	2	119	24 ± 28	30 ± 42
Porites annae	1	s	4	0	33	0 ± 1	0
	3	f	4	2	38	41 ± 44	0
Porites australiensis	1	s	5	0	9	4 ± 14	0
	3	f	1	0	4	## ± 0	0
Porites cylindrica	1	s	2	0	2	0	0
	3	f	2	0	476	37 ± 25	0 ± 0

Table 1 continued

Taxon	Survey	Reef zone	No. sites, west	No. sites, east	Total no. colonies	Bleaching prev.	Bleaching mortality prev.
Porites deformis	1	s	8	0	56	9 ± 28	0
Porites densa	1	s	2	1	9	3 ± 9	0
Porites lichen	1	s	5	3	47	24 ± 27	21 ± 26
Porites lobata	1	s	1	0	2	0	0
Porites lutea	1	s	4	0	15	10 ± 29	3 ± 6
Porites sp. 1	1	s	1	0	2	4 ± 14	0
Porites spp. massive	1	s	9	4	1099	35 ± 10	12 ± 8
	3	f	5	2	645	49 ± 26	0.1 ± 0.3
Porites spp. submassive	1	s	1	2	20	13 ± 29	3 ± 9
Porites spp. other	1	s	3	1	12	3 ± 9	8 ± 28
Porites cf. *myrmiodonensis*	1	s	3	0	6	8 ± 28	9 ± 28
	3	f	1	0	58	55 ± 0	29 ± 0
Porites rus	1	s	9	2	312	2 ± 3	0
	3	f	2	0	87	63 ± 52	4 ± 6
Porites vaughani	3	f	1	0	3	67 ± 0	0
Psammocora contigua	1	s	4	0	10	18 ± 37	0
	3	f	2	1	15	0 ± 0	0
Psammocora haimeana	1	s	3	1	5	27 ± 44	4 ± 14
Psammocora nierstraszi	1	s	5	1	20	29 ± 46	0
Psammocora profundacella	1	s	4	2	12	35 ± 47	0
Psammocora stellata	3	f	1	0	1	## ± 0	0
Psammocora sp. 1	1	s	1	0	1	0	0
Psammocora spp.	1	s	6	1	35	26 ± 34	1 ± 4
Sandalolitha dentata	1	s	1	0	1	8 ± 28	0
Scapophyllia cylindrica	1	s	0	1	1	0	8 ± 28
Stylocoeniella armata	1	s	3	0	5	12 ± 30	0 ± 0
	3	f	1	0	1	## ± 0	0
Stylocoeniella guentheri	1	s	1	0	2	0	0
Stylophora sp. "mordax"	1	s	5	4	133	8 ± 15	61 ± 44
	3	f	1	0	3	0 ± 0	100 ± 0
Turbinaria reniformis	1	s	1	1	3	8 ± 28	0
Turbinaria stellulata	1	s	1	1	4	12 ± 30	0
Non-scleractinian taxa							
Sinularia spp.	3	f	4	0	239	86 ± 14	0
Heliopora coerulea	1	s	3	3	63	25 ± 32	0
	3	f	3	0	40	20 ± 17	0
Millepora dichotoma	1	s	1	0	11	2 ± 8	0
Millepora platyphylla	1	s	8	4	122	53 ± 41	0
Millepora tuberosa	1	s	1	0	1	8 ± 28	0

Mean bleaching prevalence was calculated as the percentage of total observed colonies recorded as pale or bleached, averaged across all survey sites; colony assessments were pooled within sites. Staghorn mortality assessments were not conducted during a bleaching events, and thus, bleaching prevalence is not included here (these cases are denoted as "Na"). Mean bleaching mortality prevalence was calculated as the percentage of total observed colonies with partial to full-colony bleaching mortality, averaged across all survey sites. Survey methods are denoted as 1 = off-transect coral condition assessment during island-wide bleaching assessments (5 m and 12 m data pooled), 2 = reef flat staghorn mortality assessment, and 3 = rapid reef flat site assessment. Reef zones are denoted as l = lagoon patch reef, f = reef flat platform, and s = seaward slope

Table 2 Bleaching mortality index (after McClanahan et al. 2004) calculated for genera surveyed at eight rapid reef flat assessment sites in 2016 and 2017

Genus	2016			2017		
	BMI	*n*	% of total	BMI	*n*	% of total
Goniastrea	25.93	9	0.2	18.33	20	0.4
Platygyra	0.00	0	0.0	23.81	21	0.4
Psammocora	10.71	28	0.6	3.51	19	0.4
Heliopora	4.27	39	0.8	7.50	40	0.8
Acropora	24.65	169	3.5	36.26	273	5.5
Pavona	3.57	196	4.1	4.10	260	5.2
Sinularia	15.71	227	4.7	30.82	239	4.8
Isopora	24.16	229	4.8	18.95	197	3.9
Pocillopora	15.03	408	8.5	15.20	544	10.9
Porites	9.57	1337	28.0	18.73	1315	26.4
Leptastrea	5.56	2139	44.7	2.20	2060	41.3
Total colony count		4781			4988	

N = total number of colonies of each genus assessed during the September surveys in each year; % of total is the percent contribution of that number to the total population of colonies counted

storms or significant monsoons or cyclones developed (Fig. 2, 2017). Both satellite-derived and buoy temperatures exceeded 31 °C in August. Maximum in situ reef flat temperatures of 34.4 °C and 34.8 °C were recorded from Tumon Bay in June and August, and 35 °C in Agat in June. Conditions warranted Alert Level 1 on 6 August, Alert Level 2 on 22 August, and remained at Alert Level 2 status for 57 d. Temperatures remained above 29 °C through the end of the year, and bleached corals were observed at depths in excess of 30 m in October. Accumulated heat stress reached a peak of 13 DHW in mid-October, exceeding the previous record high of 12 DHW in 2013 (Fig. 2, 2017).

Seaward slope surveys

The impacts of the 2017 bleaching event on shallow seaward slope communities exceeded those observed in 2013, with an island-wide mean of 33 ± 12% pale or bleached coral cover and an additional 15 ± 17% of coral cover exhibiting bleaching-associated mortality (Fig. 3). In total, 48 ± 17% of coral cover was impacted by the 2017 bleaching event, compared to the 32 ± 19% of coral cover impacted by the 2013 bleaching event ($t(39.2) = 2.61$, $p = 0.013$). In contrast to the pattern observed in 2013, percentages of pale, bleached, or recently killed coral cover at the seaward slope sites during the 2017 bleaching event were similar for both the eastern windward (52 ± 21%) and western leeward coral communities (46 ± 17; $t(9) = 2.26$, $p = 0.66$) (Fig. 3). We recognize, however, that the limited number of windward sites ($n = 3$; Fig. 1) likely affected this comparison. Observations from semi-quantitative, off-transect surveys revealed prevalence of pale, bleached, and/or bleaching mortality was 61 ± 12%, slightly greater than the severity calculated from photo-transects ($t(11.7) = 2.19$, $p < 0.001$).

Semiquantitative, off-transect surveys also revealed that 92% of all surveyed coral taxa and 98% of coral genera exhibited paling, bleaching, or bleaching-associated mortality (summarized in Table 1). The five coral genera with the highest percentages of normally pigmented colonies were as follows: *Galaxea* (94%, $n = 322$), *Goniopora* (92%, $n = 92$), *Leptastrea* (88%, $n = 457$), *Diploastrea* (81%, $n = 80$), and *Cyphastrea* (64%, $n = 104$). (This excludes *Euphyllia,* which was represented by a single unbleached colony seen in one site.) In contrast, the five coral genera with the highest percentage of full-colony bleaching-associated mortality include *Acropora* (55%, $n = 967$), *Stylophora* (35%, $n = 133$), *Montipora* (23%, $n = 62$), and *Millepora* (21%, $n = 134$), and *Isopora* (19%, $n = 42$). The genus *Porites*, dominated by massive species at these depths, also had a relatively high proportion of normally pigmented colonies (64%, $n = 1627$), but this was lower than expected, given that *Porites* is generally thought to be bleaching resistant.

Staghorn Acropora populations

All 21 staghorn populations re-assessed in 2017 showed reductions live cover ranging from 29 to 100%. Four populations were devoid of any living tissue and consisted of standing dead skeleton or rubble piles, three others showed > 70% dead skeleton within the existing areal extent, while seven populations showed > 50% live cover (Fig. 4). Overall, surveys revealed a reduction in total area of live coral cover from 33.3 ha prior to 2013 to an

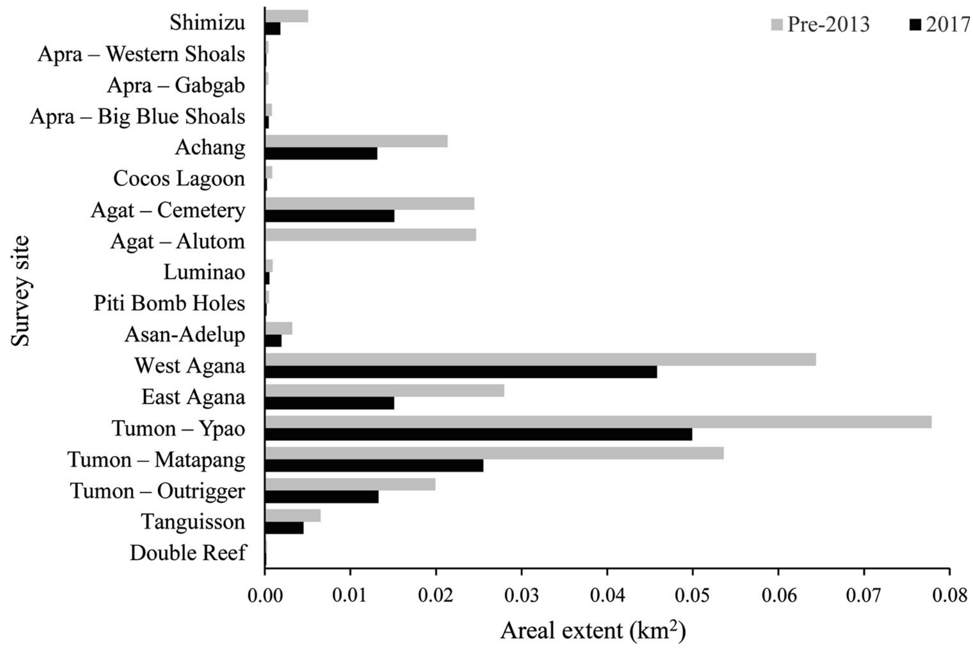


Fig. 4 Change in estimated areal population size in 18 surveyed staghorn *Acropora* populations around Guam. The graph depicts the areal extent of the sites surveyed prior to 2013 compared to the estimated extent in 2017 calculated from bleaching mortality. Populations with an original size < 100 m^2 are excluded here (n = 3)

estimated live cover of 21.3 ha, a loss of 36%. Recovery, via resheeting over dead skeleton or larval recruitment onto dead skeleton by other species, was observed in seven populations with extensive thickets, though only one staghorn recruit was seen in one site. Populations with high mortality subjected to physical disturbance (high wave energy or high human use) were reduced to rubble and showed no recovery.

Rapid reef flat site assessments

A total of 9670 observations were made during 15 surveys at the eight sites, representing 18 coral genera and at least 35 species. Mean bleaching prevalence across surveyed reef flat sites for all surveys was 35 ± 4%. Mean bleaching prevalence across sites for September was 40 ± 7%, and for October to November was 29 ± 5%. As in 2016, the most severe bleaching was observed in Agat; bleaching prevalence at this site was 74% in late September. BMIs were higher in *Acropora, Heliopora, Porites,* and *Sinularia* than those calculated for 2016, but lower in *Psammocora, Goniastrea*, and *Isopora* (Table 2). Other genera showed similar responses between years.

Cumulative impacts to coral cover

Reef flat communities

Live coral cover on monitored shallow reef flats declined by 36% between 2012 (pre-bleaching) and 2017 (F = 6.135; p = 0.023) (Table 3). Sites dominated by staghorn *Acropora* showed substantial cumulative loss (between 43 and 80%), which represented a statistically significant overall decline at two sites (West Agaña and Tanguisson: F = 17.07; p = <0.0001) (Fig. 4). In contrast, coral cover at sites dominated by *Porites* did not decline significantly and at one site, the Piti Bomb Holes Marine Preserve, cover increased slightly (by 4%). Interestingly, Tumon, located in the heart of the tourism district and Guam's most prominent marine preserve, exhibited the widest annual fluctuation in coral cover, showing a total estimated loss of 49%, but recovering between bleaching events in 2015 and 2017, with a net gain of 24% during these two years. The extreme low tide episodes recurring throughout 2015 contributed to the mortality rate, despite the fact that 2015 was not a significant bleaching year. Staghorn *Acropora* were particularly impacted by subaerial exposure; the monitored West Agaña site declined from 29 to 7% live coral cover across the January, May, and December survey periods, with the majority of the loss from the site's primary staghorn thicket (Table 3, Fig. 4).

Shallow seaward slope communities

Mean coral cover at the shallow seaward slope sites declined from 25 ± 13 to 18 ± 8%, (t(36.7) = 2.66, p = 0.012) between 2013 and 2015, and from 18 ± 8 to 13 ± 8% between 2015 and 2016 (t(20.1) = 2.35, p = 0.029) (Fig. 5). No statistically significant difference in seaward slope coral cover was detected between 2016 and 2017 (t(15.3) = 1.39, p < 0.183). When considering the entire 2013–2017 period, island-wide mean coral cover at the shallow seaward slope sites declined by 34% (from 25 ± 13 to 17 ± 9%, t(38.9) = 2.24, p = 0.031). The

Table 3 Change in live coral cover within five monitored reef flats along western Guam, 2012–2017

Year	Tanguisson	% Change	Tumon	% Change	West Agaña	% Change	Piti	% Change	Luminao	% Change
2012	29.3	Na	52.8	Na		Na	29.9	Na	35.2	Na
2013	20.0	**− 9.3**	45.4	**− 7.4**		Na	28.8	**− 1.1**	40.6	5.4
2014	13.8	**− 6.2**	26.7	**− 18.7**	29.3	Na	31.8	3.0	27.1	**− 13.5**
2015	13.6	**− 0.2**	40.7	14.0	29.3	0.0	28.0	**− 3.8**	24.7	**− 2.4**
2016	8.9	**− 4.7**	16.7	**− 24.0**	16.5	**− 12.8**	30.5	2.5	27.2	2.5
2017	5.8	**− 3.1**	27.0	10.3	16.6	0.1	34.0	3.5	28.3	**− 0.2**
Net change per site		**− 23.5**		**− 1.5**		**− 12.7**		4.1		**− 8.3**
Total % change per site		**− 80.2**		**− 48.9**		**− 43.3**		13.7		**− 19.6**

$N = 3$ transects per site. Mean % cover taken during the last quarter surveys for each year presented here. Numbers in bold represent net losses in cover between years

Mean % change across sites: − 35.7%

decline in coral cover as a result of the 2013 and 2014 events was greatest at the eastern windward sites (− 45%, from 29 ± 13 to 16 ± 7%, $t(16) = 3.57$, $p = 0.003$), while no significant difference in coral cover was detected at the western leeward sites over the same time period ($t(19.4) = 0.68$, $p = 0.51$). The disparity observed in impacts to coral cover between eastern windward and western leeward sites between 2013 and 2017 was even greater than that observed between 2013 and 2015, with a 59% decline (from 29 ± 13 to 12 ± 1%, $t(16.6) = 6.05$, $p < 0.001$) at the eastern sites and no significant difference in coral cover observed at western sites ($t(20.4) = 0.9$, $p = 0.377$). However, it should be noted that the small sample size of eastern seaward slope sites surveyed in 2017 may not be representative of the full extent of the windward side of the island.

Staghorn Acropora populations

All known staghorn populations were assessed in 2015 and 2017. Total live coral cover loss was estimated at 53% in 2015 and 36% in 2017, based on the total 33.3 ha areal extent measured prior to 2013. All populations experienced bleaching-induced mortality in similar patterns. Large thickets (≥ 0.3 ha in size; 11 out of the 21 sites) showed high mortality in the center of the stands, with remaining live tissue limited to thicket margins. In sites that had experienced high storm-driven wave energy, thickets with high mortality were reduced to rubble, with no signs of recovery. Outbreaks of a rapidly progressing white syndrome were observed in Tumon in 2016 (18.7% prevalence), and in three sites in 2017 (Tumon, Tanguisson, and Apra Harbor; 13.4%, 10.2%, and 24% prevalence, respectively) during the bleaching season, which caused additional mortality. Resheeting over dead skeleton was observed by 2017 in thickets with large central dead patches, which accounted for lower total mortality estimated in 2017. However, three species, *Acropora aspera, A. virgata*, and *A. teres,* were all reduced to a single stand, with estimated mean mortalities of 62% ± 37%, 92% ± 10%, and 44% ± 23%, respectively. One species, *Acropora vaughani*, possessed no live tissue in 2017, though isolated clumps were observed in Apra Harbor in 2015; it is likely extirpated from Guam.

Evidence of species replacements within staghorn thickets was observed at three sites with high mortality but remaining intact structure. Recruits of several common reef flat species: *Porites cylindrica, Pavona decussata, P. divaricata, Pocillopora damicornis, Psammocora contigua*, and *Leptastrea purpurea* recruited onto standing dead skeletal structure and had begun consolidating it during the 2017 surveys.

Discussion

A recent study of coral cores by Cybulski (2016) noted dominance by *Acropora* on Guam reefs for the previous 500 yrs, with a human disturbance-driven shift to Pocilloporidae 100 yrs ago. The author noted no evidence of significant bleaching-related mortality within the 500 yr period, indicating that the magnitude of recent heat stress impacts is unprecedented over at least 500 yrs. The level of heat stress associated with the 2013 sea surface temperature anomaly around the island was the highest since satellite measurements began, but this record was exceeded in 2017. Lower-magnitude, but still historically significant, heat stress events occurred in two of the three intervening years. Guam was impacted by warming events two years prior to the 2015-16 ENSO event that affected other countries in the region, and this effect was prolonged through 2017, during the subsequent La Niña. The ENSO

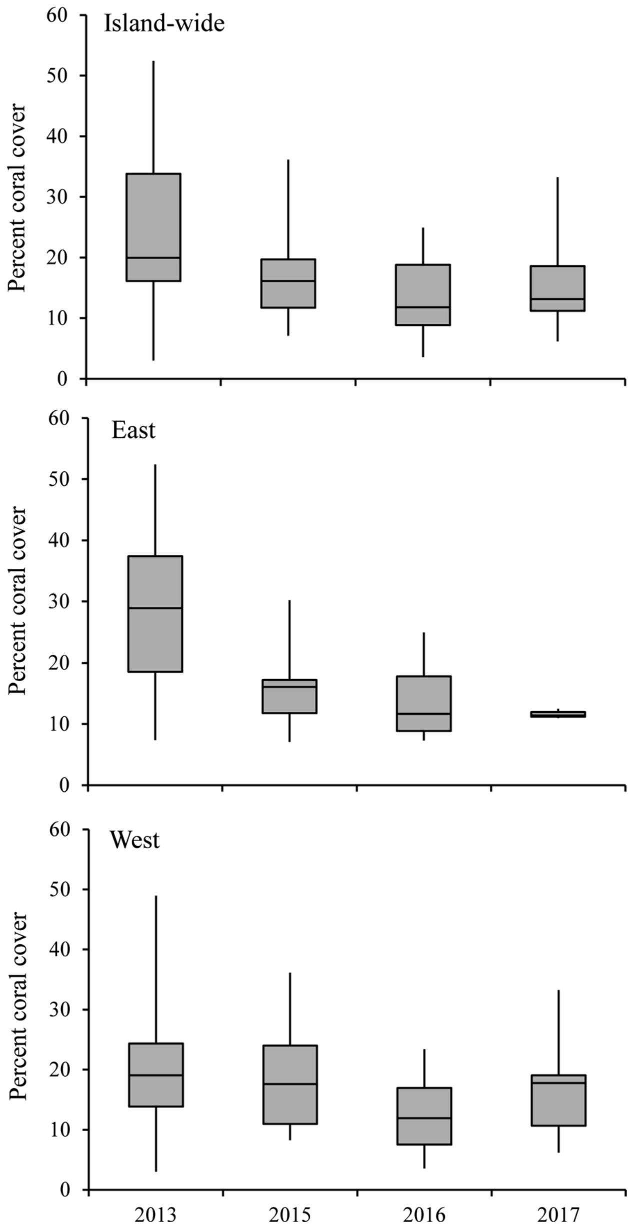


Fig. 5 Box plots of percent coral cover values from shallow (5 m) seaward slope benthic photo-transect surveys between 2013 and 2017 for all sites island-wide, eastern windward sites, and western leeward sites. Data were obtained from a total of 46 sites (21 east, 25 west) in 2013, 17 sites (9 east, 8 west) in 2015, 19 sites (7 east, 12 west) in 2016, and 11 sites (3 east, 8 west) in 2017

event itself triggered repeated extreme tide episodes that killed exposed corals, which were then subjected to further warming in the subsequent year.

Differential responses to events

The past five years of repeated, anomalous environmental events triggered profound and sudden change in the structure, and likely the function, of Guam's reefs. Coral cover on monitored reef flats along the western coast declined 37% by 2017. Staghorn *Acropora* communities were particularly devastated; three experienced complete mortality. Nearly a third of coral cover was lost island-wide along the shallow seaward slope between 2013 and 2017, with approximately 60% of coral cover lost along the eastern windward coast. An earlier analysis of 2013 data concluded that the difference in bleaching prevalence observed between windward and leeward sites was, in part, attributable to the greater proportion of bleaching-susceptible taxa (primarily acroporids) within shallow windward coral communities (Reynolds 2016).

The decline in shallow seaward slope coral cover observed between 2015 and 2016 did not appear directly associated with thermal stress-driven mortality, as bleaching prevalence at seaward slope sites during this period was very low and no mortality was reported. The cause of this decline could not be determined from this preliminary analysis, but observations by LR, DB, and WH suggest that some of the mortality may have been attributed to elevated coral disease (white syndrome) and corallivorous snail (mainly *Drupella*) predation. The minimal bleaching prevalence at seaward slope sites in 2016 was in contrast to significant bleaching impacts recorded at reef flat sites that same year. Thus, our data suggest differential responses to heat stress between reef flat and seaward slope coral communities. Differences in environment (such as water circulation), species-specific responses of dominant taxa, and a latent effect of the 2015 extreme low tide events on the bleaching susceptibility of reef flat corals could have contributed to the mortality differences we observed between these distinct reef zones. No significant decline in coral cover was observed at shallow seaward slope sites between 2016 and 2017, despite the more severe thermal stress experienced in 2017. However, the 2017 bleaching response surveys were carried out while the event was ongoing; quantitative surveys were not conducted following the complete dissipation of thermal stress in late 2017. The higher percentage of bleaching-impacted coral cover recorded during the 2017 event, and qualitative observations of catastrophic mortality of shallow-water *Acropora* species at several seaward slope sites in 2018, suggest a loss in coral cover at shallow seaward slopes comparable to the 2013 event.

A critical methods analysis

This assessment of recent bleaching-associated impacts to Guam's coral reefs relied upon quantitative or semiquantitative datasets generated by five separate survey types that involved a total of seven individual survey methods (summarized in Table S1). The sampling approaches included that used by an existing long-term monitoring program of benthic cover and coral size/condition data at high priority reef flat sites, and four that were developed specifically to assess bleaching severity and bleaching-associated impacts to benthic cover during and after the events documented above. These survey methodologies were developed and implemented in succession, as the Guam Coral Reef Response Team adaptively allocated limited field survey capacity based on need, and as informed by personal observations and preliminary analysis of existing data.

The implementation of different survey methods to document the extent and severity of coral bleaching events on Guam resulted from:

(1) The need to take advantage of data produced by an existing survey effort though this program was not specifically designed to assess bleaching impacts as they are occurring;
(2) The need for methods appropriate for particular reef zones or communities;
(3) Limited personnel and resources available to carry out surveys; and
(4) The timing of the surveys, also related to resource availability.

Multiple sampling approaches and survey methods are often necessary to understand the impacts of acute disturbances, such as coral bleaching events, across distinct coral reef communities and at different spatial and temporal scales. However, the integration of multiple datasets into a single, comprehensive analysis requires an understanding of the limits of each methodology and the potential biases that manifest in the generated datasets. A critical analysis of these methods, and the datasets they generate, can inform changes to an approach to assessing the impacts of acute disturbances, with the aim of maximizing data accuracy and comparability. Here, we present a qualitative analysis of the sampling approaches and survey methods used in the present study, with recommendations for improving comparability of datasets generated by different methodologies across different reef communities, as well as suggestions for further evaluating the comparability of these data. Our rationale explaining the order of implementation of survey methods is as follows:

2013 The island-wide randomized approach targeting the seaward slope maximized overlap with randomly generated sites surveyed by NOAA PIRSC in 2011. Reconnaissance indicated this zone was most severely impacted by bleaching stress; significant mortality had not yet been observed at the reef flat/staghorn areas being monitored when this decision was made.

2014 The NOAA CRW automated system did not catch the warming event in time to allow for team mobilization; as stated above, the 2014 bleaching event occurred six months after the 2013 event. Documentation of 2014 events was thus limited to bleaching reconnaissance and limited personal observations. Subsequent improvements in the accuracy of the NOAA CRW early warning system in 2015 greatly increased our capacity to mobilize for future events.

2015 Resources were available for a subset of the island-wide seaward slope sites surveyed in 2013; these were prioritized to assess the cumulative impacts of the 2013 and 2014 events and to establish a new baseline against which recovery and future impacts could be evaluated. Observations of the rapid onset of bleaching mortality among a small number of staghorn communities in 2014 triggered the island-wide staghorn coral mortality assessment in 2015 to address this major knowledge gap. The geographic scale of the effort and limited staff availability necessitated the adoption of a rapid assessment protocol that took advantage of existing geospatial data developed by the Guam Long-Term Monitoring Program.

2016 As Co-PI on a NOAA Saltonstall-Kennedy reef resilience assessment project, DB helped develop a sampling strategy that maximized overlap between resilience assessment sites and seaward slope sites surveyed in 2013 and 2015. Resilience assessment field surveys conducted at the beginning of the bleaching season were fortuitous in that the data collected at both the seaward slope and lower depths provided a good record of the limited impact of the 2016 temperature anomaly on these communities. In contrast, significant bleaching and mortality was observed at rapid reef flat canary sites. Though semiquantitative, data generated allowed BMI values to be derived, BMI was not initially incorporated into our protocol but it provided a tractable and rapid post hoc assessment of genera at risk, and will be utilized as part of our standard protocol in the future.

2017 Significant bleaching had not been observed at the reef flat canary sites when Response Team members observed severe bleaching along the seaward slope. Those observations and NOAA CRW predictions informed the timing of the re-survey of sites previously visited in 2013, 2015, and 2016. Additional mortality observed at several staghorn sites as a result of extreme low tides in 2015, and bleaching and disease in 2016, necessitated the re-survey of all major staghorn communities around the island. A more quantitative approach to assessing staghorn condition was implemented at this time.

We identify the following specific issues with our multiple survey bleaching response approach and highlight changes we are incorporating to address these issues.

- Two metrics were used to assess bleaching prevalence from photo-quadrats: percentage of total colonies and percentage of total coral cover. A preliminary analysis of data collected using both methods in 2013 suggests that these values were significantly different for the same sites. These differences are likely related to the sensitivity of each measure to community composition and size structure. We intend to quantitatively evaluate these data sets to determine the nature and consistency of these differences across taxa and population size distributions, as they potentially influence our interpretation of the data and subsequent management decisions.

- The two methods used to assess staghorn mortality in 2015 versus 2017 were not comparable quantitatively. The 2015 method allowed for a very rapid assessment of a large number of sites in a very short period, which was the intention of the surveys. However, the 2017 assessments provided a more quantitative reference point for future assessments of the condition of remaining staghorn beds. An effort to re-map the areal extent of these beds is planned, but because satellite-based photo-imagery cannot distinguish live versus dead coral cover, these surveys will require in-water ground-truthing.
- The use of quasi-permanent transect locations based on GPS coordinates introduced additional variance into key parameters such as species composition, and undoubtedly lowered statistical power.
- The ability of the canary sites to detect island-wide bleaching across reef zones was called into question in 2017. NOAA CRW products showed that thermal stress for Guam peaked in October, when mean bleaching prevalence at the canary sites was 29%. However, BMI calculated after the events revealed differential generic responses between 2016 and 2017, with three key genera, *Acropora, Porites*, and *Sinularia,* showing much more severe responses in 2017. Further, October seaward slope assessments estimated bleaching and bleaching mortality to be 48%, with observations of bleaching to 40 m. These widely varying responses between reef zones suggested that reef flat rapid assessments may not adequately inform bleaching response efforts for seaward slope sites. We plan to incorporate the use of the BMI as part of our rapid response protocol, as its utility as a means of identifying taxa at particular risk and comparing taxon performance between reef zones makes it a valuable addition to our toolbox. We also intend to establish permanent transects at these sites for future assessments and to add shore-accessible seaward slope sites to canary sites for rapid reconnaissance.
- The Guam Coral Bleaching Response Plan (Hoot and Burdick 2017) was designed to leverage existing mechanisms, such as projections provided by NOAA CRW and temperature data from in situ loggers deployed in long-term monitoring programs. In general, in situ loggers recorded maximum temperatures of 1–2 °C higher than satellite-derived SSTs. Thus, these loggers may provide an effective local early warning system at scales relevant to individual coral communities, in conjunction with CRW alerts.

A schematic of our response protocol is presented in Fig. 6 as a decision tree to guide activities according to both event severity and resource availability. This protocol, the bleaching response plan, and the formation of an interagency Guam Coral Reef Response Team have allowed local managers and researchers to proactively plan for events before they occur and mobilize rapidly, thus increasing effective resource allocation and improving consistency among response efforts. However, maintaining flexibility is key to success, given limited resources. As overall improvements to our bleaching response, we will (a) align reef flat, canary, and staghorn sites where possible and appropriate; (b) align semiquantitative bleaching condition assessments for all surveys and zones, to the extent possible (i.e., standardize coral condition categories, survey area, and survey duration); (c) conduct power analyses prior to surveys to determine appropriate sample sizes; (d) conduct rapid calibration protocols between methods and among personnel and discuss calibration results, to better standardize surveys; and (d) coordinate data collection efforts for other projects to maximize site overlap and timing to extent possible.

In summary, the use of multiple survey methods is often necessary in order to adequately sample different reef communities within distinct reef environments, and to take advantage of data that may not have been collected for the same purpose. Our results show that these different reef communities can respond to an acute disturbance in significantly different ways, and data collected for a single reef community type, however broadly distributed it may be within a biogeographic region, may not be representative of other reef communities and thus may not provide an adequate measure of the totality of impacts to the reef areas within that region.

The results of Jokiel et al. (2015) indicate that estimates of broad-level parameters generated from different survey methods, such as coral cover, appear to be relatively consistent across most methods. However, their results also indicate that measures of diversity can differ significantly between methods. While the impacts of recent bleaching events on the diversity of corals on Guam's reefs were not assessed in this study, further analysis will include an examination of impacts to diversity, and thus should consider known biases in estimates generated by different sampling approaches.

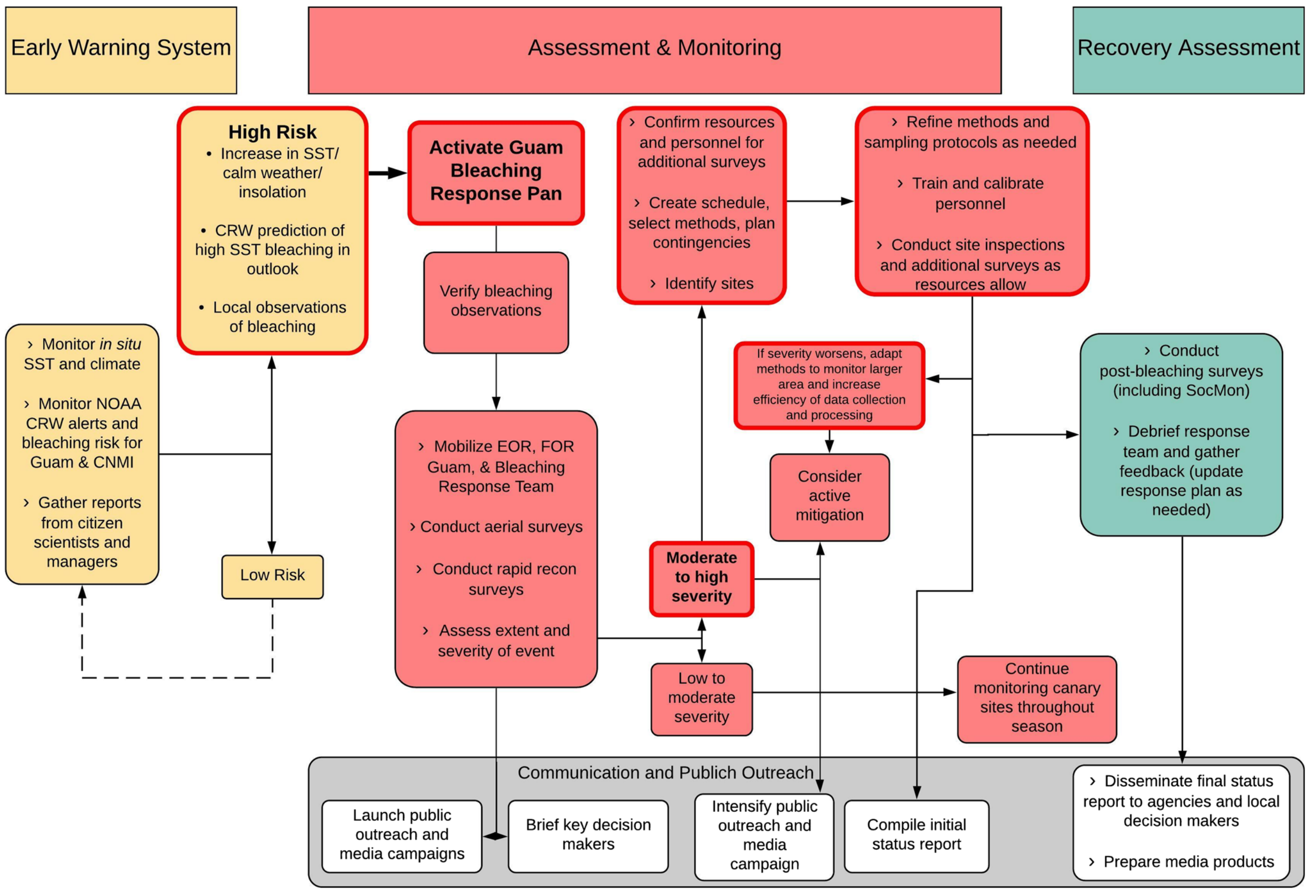


Fig. 6 A flowchart developed by the Guam Coral Reef Response Team as a decision tree for coral bleaching response, included in the Guam Coral Bleaching Response Plan (Hoot and Burdick 2017)

Species loss and the trajectory of change

The possible extirpation of one species, *Acropora vaughani,* was noted in our surveys, and three others, *A. aspera, A. teres,* and *A. virgata,* are reduced to single stands. Wallace (1999) synonymized *Acropora virgata* with *A. formosa* (now *A. muricata*) but Guam colonies, which are identical to Dana's *A. virgata*, are morphologically distinct from *A. muricata*. This taxonomic quandary is illustrative of the difficulty in ascertaining scleractinian coral species boundaries, and the challenge this presents for coral species conservation. Our analyses and recent post-bleaching observations suggest that other species may also be at high risk. Three previously common species: *Stylophora pistillata* f. *mordax* and the caespitose *Acropora* cf. *azurea* and *A. verweyi* have been greatly reduced across multiple sites. *Stylophora pistillata* f. *mordax* declined precipitously in 2017, and few living colonies were observed during multiple visits to various sites in 2018. *Acropora* cf. *azurea* and *A. verweyi*, typically found at 1–4 m depth along exposed seaward slopes, were locally abundant prior to 2013 (refer to Fig. 7a, d, f). While bleaching impacts recorded during the event were not exceptional for these two species, observations in 2018 at previously surveyed sites, and at other reef areas where these species were locally abundant, suggest catastrophic ($> 95\%$) mortality. This apparent discrepancy may be a result of the relatively low number of colonies encountered during surveys, which were conducted at depths slightly greater than their preferred range, or a sharp increase in mortality following survey completion. Observations of significant mortality among colonies of the major structure-providing species, *Acropora abrotanoides* (Fig. 7d), as well as other species, such as *Acropora monticulosa* and *Acropora palmerae*, once common features of Guam's reef front and shallow slope zone, have also raised concern about the long-term viability of these species. Thus, "safety in numbers" (Birkeland et al. 2013a, b) may not be providing a refuge from extirpation for these key, highly susceptible species. *Montipora verrucosa* and other encrusting *Montipora* species also exhibited high rates of mortality, although field observations of mortality early in bleaching events, and the difficulty in detecting dead *Montipora* colonies in benthic photo-transect images, suggest that actual mortality rates

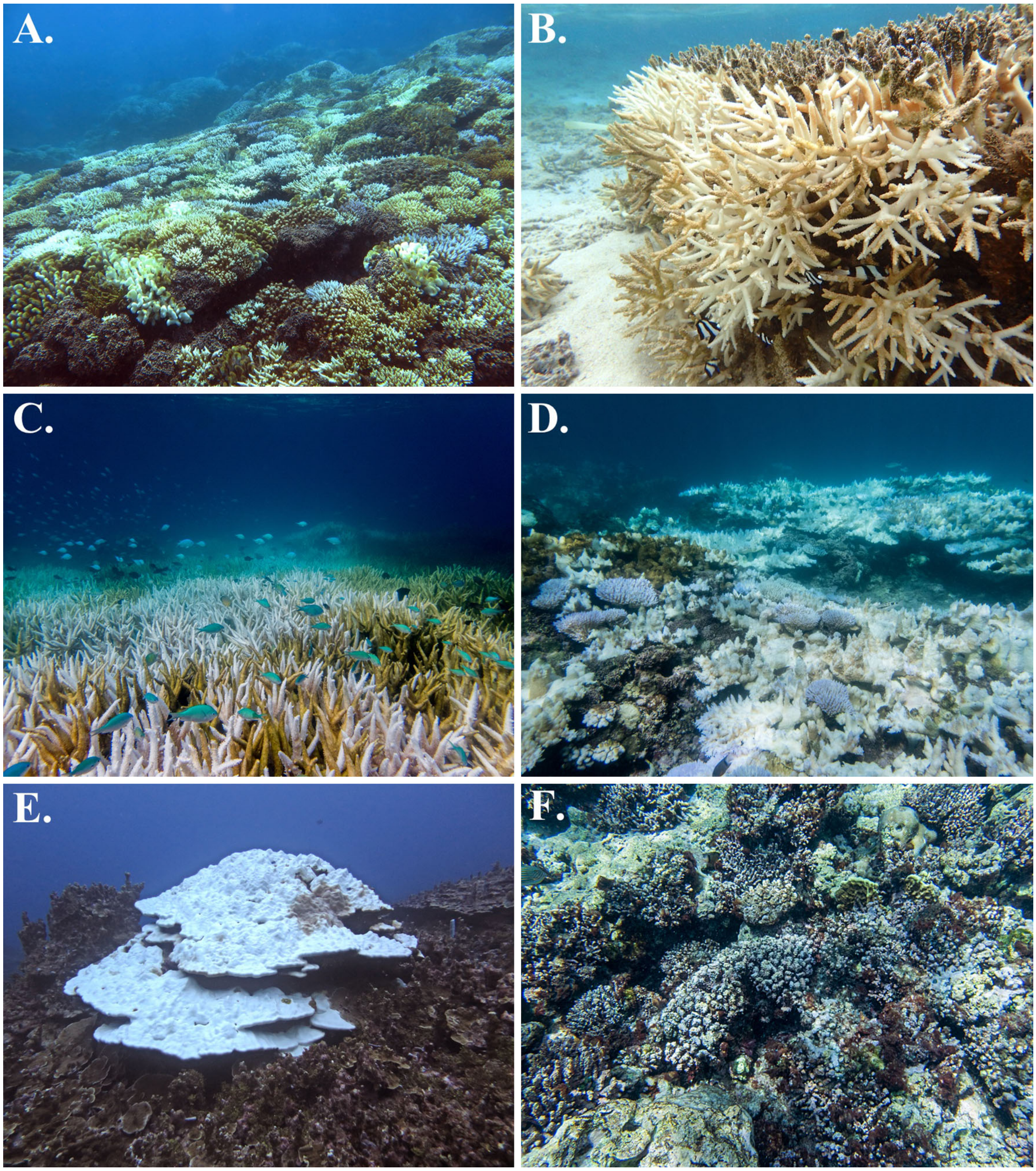


Fig. 7 Extent of bleaching within the different coral community types on Guam. **a** Mixed *Acropora–Pocillopora* eastern exposure shallow seaward slope community bleaching in 2013. **b** Staghorn *Acropora pulchra* thicket bleaching on a reef flat in 2016. **c** Staghorn *Acropora muricata* bleaching in Apra Harbor in 2017. **d** Eastern exposure *Acropora abrotanoides* community bleaching in 2017. **e** Western exposure *Porites* community in 2017, showing bleached massive *Porites* sp. **f** Bleaching mortality of mixed *Acropora–Pocillopora* eastern exposure shallow seaward slope community in 2018. Photo credits: D. Burdick, W. Hoot, L. Raymundo

among *Montipora* species were likely greater than what we report here.

The trajectory and character of change in Guam reef communities that has been initiated by the onset of repeated, severe coral bleaching events will be a focus of future analyses. For example, dead staghorn communities that have already been reduced to rubble at several sites may persist in this flattened state, as rubble is an unstable recruitment substrate (Raymundo et al. 2007; Birkeland et al. 2013a, b). The flattening of these stands may, in turn, reduce the ability of reef flat platforms to dissipate wave energy, particularly during storms (Ferrario et al. 2014; van Beukering et al. 2007), and will likely impact the populations of fish species that utilize staghorn *Acropora* thickets for one or more phases of their life history. Colonies that remained secured to existing substrate began resheeting within months after warming subsided, via an apparent "phoenix effect" (Dias-Pulido 2009; Roff et al. 2014). This phenomenon involves the survival of residual tissue deep in the skeleton, thus providing a tissue "reservoir" for regrowth. Observations suggest resheeting of dead skeleton was largely responsible for the increase in coral cover in the Tumon Bay and West Agaña thickets from 2016 to 2017, despite the severe temperature anomaly in 2017 (Table 2). This effect was enhanced at sites that were well flushed, as increased water movement likely mitigated warming impacts by improving coral resilience to heat stress (Nakamura and van Woesik 2001; Fifer 2018). However, recruitment of other species onto dead staghorn skeleton was also common, suggesting that colonies that do not resheet may be replaced by developing communities comprised of *Pavona, Pocillopora,* and *Porites.*

Coral diversity declines northward along the Mariana Arc, a pattern primarily driven by the general northward decrease in island size and differences in habitat type and availability between the older, primarily carbonate islands in the south and the younger, volcanically active islands in the north (Richmond et al. 2008, Brainard et al. 2012). A recent analysis of larval transport pathways in the region concluded that Guam populations of coral taxa with pelagic larval durations < 20 d are primarily self-seeding, and that there is a northward bias in larval transport within the archipelago (Kendall and Poti 2015). The implications of these findings, in light of recent coral bleaching-associated impacts to Guam's coral communities, are twofold: Recovery following mass coral mortality events via larval import for these taxa is likely to be negligible on Guam, and as vulnerable coral populations decline on the high diversity coral reefs of Guam, their ability to act as a larval source for the northern reefs of the Mariana Archipelago will decrease in the coming decades.

The future of Guam's reefs

Ocean warming events of unprecedented frequency and magnitude resulted in significant declines in coral cover at reef flat and shallow seaward slope sites around Guam. The variability in response to thermal stress between leeward and windward communities appeared driven in part by differences in the proportion of bleaching-susceptible taxa, while variation in the responses of reef flat and seaward slope communities may be driven by differences in community composition and the environmental regimes of these distinct reef zones. Other environmental drivers of bleaching patterns, such as cyclonic activity, wave height, the timing and severity of anomalous warming, have not yet been examined, but will be considered in future analyses. Other possible drivers of the declines we observed, such as disease, predation, and local stressors, must also be considered.

The full impact to the diversity, structure, and function of Guam's coral reefs from the mortality documented in this study, and implications for the future of Guam's coral reef ecosystem, remains unresolved. However, projections of increasing bleaching frequency raise concern that coral recovery will not keep pace with mortality. Should this occur, the result will be a net loss in cover until a currently undefined threshold is reached, beyond which recovery may not be possible at timescales relevant to present human communities. Van Hooidonk et al. (2016) predicted that annual severe bleaching in the Mariana Islands could begin by the early 2020s, but the events documented here suggest that even this alarming estimation may have overestimated the time that Guam's shallow-water corals have to acclimate and adapt to rapidly warming ocean temperatures. Detailed documentation of ongoing changes to community structure, key ecological processes, and the status of vulnerable reef taxa is critical to formulating effective management strategies for the conservation of remaining reef diversity and function. Guam is likely a sentinel for the type of near-future change that awaits other small islands throughout the global range of coral reefs. The lessons we learned from documenting and responding to this experience may thus provide guidance and insight for scientists and managers who are challenged by similar impacts.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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