Impact of successive bleaching on coral assemblages: Who are the winners and losers on Guam's reefs under climate change?

[1]Raymundo, LJ, [2]Williams, GJ, [1]Burdick, DR

[1]Marine Laboratory, University of Guam, USA

[2]School of Ocean Sciences, Bangor University, UK

UNIVERSITY OF GUAM MARINE LABORATORY

TECHNICAL REPORT # 173

May 2026

TABLE OF CONTENTS

TABLES AND FIGURES

List of Tables

List of Figures

BACKGROUND AND CONTEXT

Coral reefs provide essential ecosystem services to hundreds of millions of people, but the structure and function of these hyper diverse ecosystems is undergoing rapid change as a result of myriad interacting local and global human impacts (Norström et al. 2016; Williams et al. 2019; Woodhead et al. 2019). Most notably are the effects of anthropogenic climate change, leading to elevated ocean temperatures which increase the frequency and magnitude of anomalous ocean warming events (Heron et al. 2016; van Hooidonk et al. 2016). Periods of extreme heat stress in tropical waters can cause a breakdown in the symbiotic relationship between the coral animal and its photosynthetic algal endosymbionts (Brown 1997), leading to localized to widespread coral bleaching events. These events are becoming more frequent (Hughes et al. 2018b) and, in conjunction with local human stressors impacting coastal water quality, are resulting in the mass death of calcifying reef-building corals (Hughes et al. 2017; Gove et al. 2023) and an increase in fleshy non-calcifying benthic organisms such as algae and soft corals (Norström et al. 2009; Graham et al. 2015; Jouffray et al. 2015).

The mass mortality of corals on tropical reefs can have profound impacts on other reef-associated organisms that depend on the corals for food and shelter. For example, mass mortality of corals can lead to a reduced diversity of reef fishes (Richardson et al. 2018; Stuart-Smith et al. 2018), many of which form an essential component of subsistence-based fisheries (Robinson et al. 2019). However, coral bleaching does not always result in mass coral mortality (Fox et al. 2019; Fox et al. 2023) and can result in more subtle changes to reef ecosystem structure that still have notably knock-on effects to overall reef structure and function (Williams and Graham 2019). For example, rather than undergoing wholesale coral loss, coral communities can reorganize to form new assemblages following repeated bleaching disturbance, with the loss of bleaching-vulnerable species and an increase in more bleaching-resistant coral taxa (Loya et al. 2001; Williams et al. 2010; Hughes et al. 2018a; Raj et al. 2021). As coral taxa differ in size and morphology, shifts in coral assemblages lead to changes in these morphological traits (Zawada et al. 2019), altering fine-scale reef habitat structure (Richardson et al. 2017a) and the community composition of reef-associated communities such as fishes (Richardson et al. 2017b). Quantifying such detailed changes in coral assemblage structure on reefs in response to bleaching are rare in the literature, but key if we are to understand how reefs of the future may look and function under continued global change.

The size structure of a coral population can affect its demography and reproductive output and the size-frequency distribution of a coral population is therefore intricately linked to its resilience following disturbance (Shenkar et al. 2005; Dietzel et al. 2020). A decline in smaller colonies can be an indication of recent recruitment failure (Kenyon et al. 2006; Dietzel et al. 2020) and a loss of recovery potential following mass coral bleaching (Graham et al. 2015). Persistence of larger older corals can also mask a loss in absolute abundance of colonies and overall coral population densities (Dietzel et al. 2020). However, collecting information on the size-frequency distributions and density of corals is challenging due to the laborious nature of *in situ* surveys. Surveys of reef condition are often conducted over limited spatial extents and to a low taxonomic resolution, hampering our ability to quantify more detailed changes to coral assemblages over time and in response to disturbance (Ford et al. 2021). Here, we utilize over 20,000 individual coral colony observations collected using photoquadrats across the shallow outer reef slopes along the sheltered west coast of Guam, Micronesia from 2013-2017. These data were collected during a five-year period of acute disturbance events involving coral bleaching from elevated SSTs in 2013, 2014, 2016, and 2017; ENSO-induced repeated extreme low tides in 2014 and 2015; and disease outbreaks in 2016 and 2017 (**Fig. 1**). However, surveys along the exposed east coast of Guam were not included in this analysis, though a limited number of surveys were undertaken when possible. Access to this side of the island was severely limited due to year-round high swell so replicated surveys to the same sites were generally not possible. Collectively, these events resulted in a 34% decline in live coral cover along shallow reef slopes and a 37% decline on reef flats (Raymundo et al. 2017, 2019). Using these data, we quantified how successive coral bleaching events have changed the (1) density of coral communities and (2) susceptibility of individual coral taxa to bleaching over time.

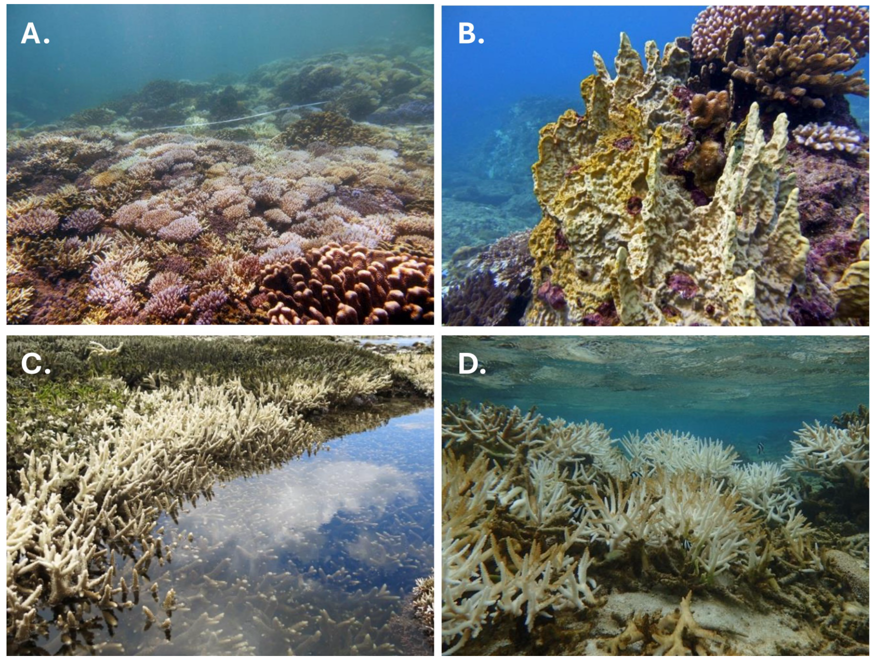

Figure 1. Successive mortality events impacting Guam's reefs. A, B: Island-wide, multi-species bleaching; C: ENSO-induced extreme low tides; D: A White Syndrome outbreak.

METHODS AND RESULTS

Question 1: Impact of successive coral bleaching events on coral community density patterns

METHODS

To characterize the impacts of these mortality events on changes to coral communities over time, we conducted a number of surveys around the coast of Guam between 2013 and 2017, including qualitative reconnaissance surveys as well as quantitative and semi-quantitative surveys of the shallow forereef, reef flat, and highly vulnerable staghorn *Acropora* thickets (summarized in **Fig. 2**). This report is based on benthic photo transect survey data obtained at eight sites located along the shallow outer reef slopes (5-7 m depth) on the west coast of Guam. The eight sites represent a subset of more than 45 randomly allocated survey sites around the island. The sites analyzed in this report were selected based on the availability of photo transect data from both 2013 and 2017, thus allowing us to test for temporal change while minimizing spatial biases. Surveys were conducted by staff and students associated with the Guam Long-Term Monitoring Program, the Raymundo Lab, and the NOAA Pacific Islands Pacific Regional Office—Guam Field Office (Raymundo et al. 2019; Burdick et al. 2023). Transects were not permanently marked but were georeferenced in the field using a hand-held GPS receiver. Surveys were conducted along (n = 3) 25 m (2013) or 30 m (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. In total, three island-wide bleaching events, multiple extreme low tide events, and two disease outbreaks occurred during this period (Raymundo et al. 2019). Surveys in 2013 occurred between the middle and end of the first bleaching event, while surveys in 2017 occurred between the middle and end of the bleaching event and so captured most of the bleaching impacts that occurred that year.

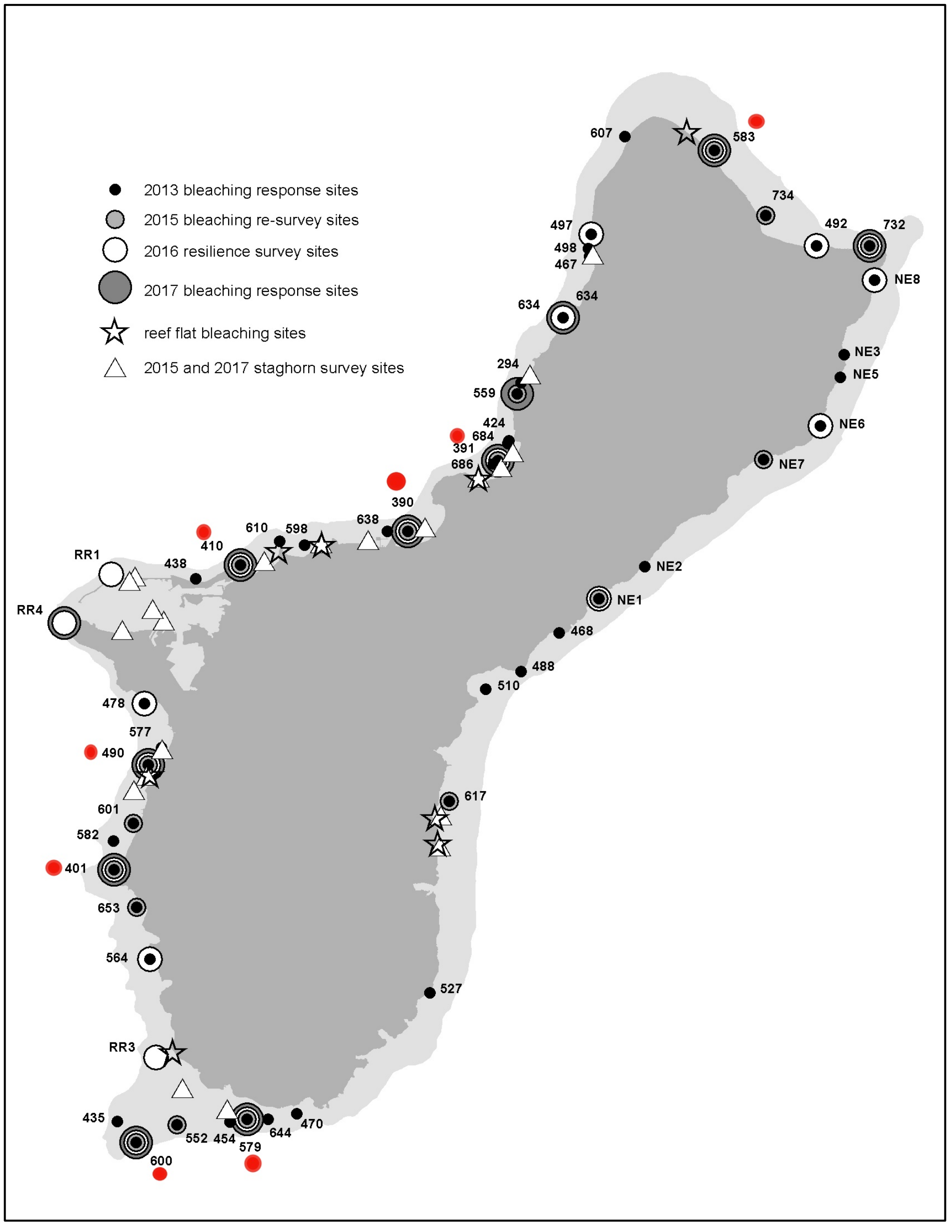

Figure 2: Sites surveyed for bleaching and disease responses across a five-year period, from 2013 through 2017. Sites included in this analysis are identified by red dots.

All post-hoc benthic image analyses were completed using CPCe to generate colony size and condition data for the eight sites. Colonies were included in the assessment if the observer could reasonably assume that the center of colony was located within the image area. Colony diameter (longest planar dimension) was measured to the nearest cm; however, the size of larger, irregularly shaped colonies occurring near the image periphery was likely underestimated, as were small colonies (<5cm) in 2013 surveys, due to the lower camera resolution. Colony density was determined as the number of colonies per image area. A selection of images from each survey year in which the monopod was placed directly on, or immediately adjacent to, the transect tape were each scaled in CPCe. A single image area value for each survey year was arrived at by averaging the image area values generated by CPCe for the selected images (n = 5 in 2013 and n= 8 in 2017). However, it should be noted that image area values varied significantly for images obtained within a survey year, likely owing to differences in reef rugosity and the placement of the monopod (e.g., directly on the substrate or above the substrate to avoid physical damage to fragile colonies). The higher resolution of the camera system used in 2017 (20.2MP vs. 12.1MP) likely allowed the detection of a greater number of smaller (< 5 cm diameter) and otherwise cryptic colonies than in 2013. Because of this, we compared the results obtained with and without colonies < 5 cm in the subsequent analyses. Results are presented separately, below.

RESULTS AND DISCUSSION

A. All colonies included

Mean coral colony density across all coral taxa increased from 1.77 colonies/m^2 in 2013 to 2.68 colonies/m^2 by 2017 (**Fig. 3**). This increase occurred across all coral families, except for the monotypic family Diploastreidae that was recorded as present (as a single colony of *Diploastrea heliopora*) in 2013 but absent in 2017 (**Table 1**). The largest increases in colony density were driven by corals within the families Astrocoeniidae and Psammocoridae, that increased in density by 2.17 and 2.31 colonies/m^2, respectively. At a species taxonomic resolution there was more variability, with 59 of the 81 species increasing and 22 decreasing in density (**Table 2**). Among species for which we had reasonable sample sizes, the largest increases in density were seen in *Cyphastrea* sp., *Echinopora lamellosa*, *Goniopora* sp., *Gardineroseris planulata*, *Leptastrea* sp., *Pavona meandrina*, *Pavona varians*, *Porites annae*, *Porites deformis*, *Psammacora* sp., and *Stylocoeniella armata*. The largest decreases in density were in *Pavona divaricata* and *Pavona maldivensis*, and to a lesser extent several *Acropora* species (*A. cophodactyla*, *A. digitifera*, *A. monticulosa*, *A.* cf. *ocellata*, *A. palmerae-minuta*, *A. verweyi*), *Dipsastraea pallida*, *Pocillopora verrucosa*, and *Porites* sp.- encrusting (**Table 2**). In interpreting these data, it is important to note that both Astrocoeniidae and Psammocoridae are represented in our surveyed reef zone by small, generally cryptic species (Astrocoeniidae, for instance, is represented on Guam by *Stylocoeniella armata*) that would have been difficult to discern using the 12MP camera used in 2013 surveys. Thus, we interpret these increases in density as an artifact of the higher resolution camera used in 2017 surveys. Further, two species: *D. heliopora* and *Lobophyllia corymbosa* were represented by one colony per species observed in 2013 but not in 2017. The extremely limited sample sizes of these two species should not, therefore, be interpreted as their loss or decline from Guam reefs.

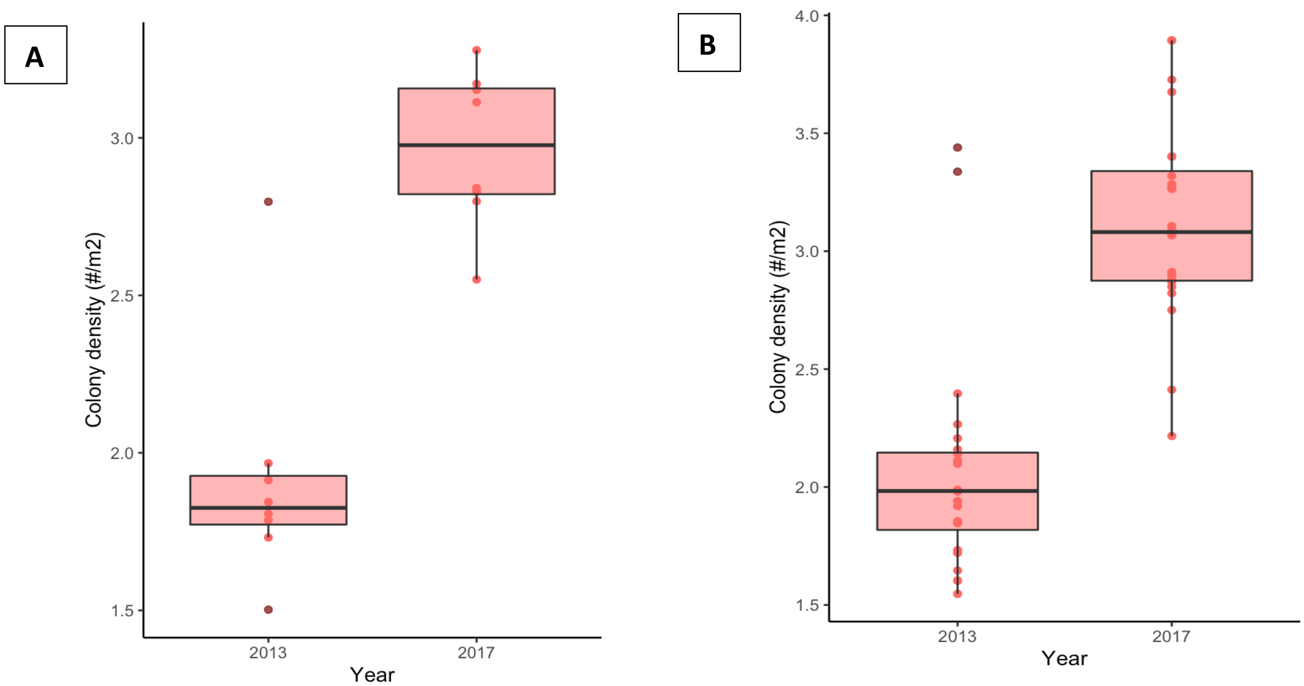

Figure 3. Change in coral colony density (all taxa combined, all colonies included) at eight long-term monitoring reef sites along the west coast of Guam, following successive coral bleaching events between 2013 and 2017 (**A:** dots represent individual site means, n=8; **B:** dots represent individual transect means, n=24). Thick horizontal lines represent the median; thin horizontal lines represent the interquartile range.

Table 1. Change in mean coral colony density (number of colonies / m^2) by coral family at eight long-term monitoring reef sites along the west coast of Guam following successive coral bleaching events between 2013 and 2017. Blue color ramp denotes increase: dark blue, >12% change; medium blue, 5-10% change; and light blue, 1-5% change. Grey signifies a decrease in density. Blank cells = 0 observations.

Species	2013	2017	Δ density	Δ density	Species	2013	2017	Δ density	Δ density
Acanthastrea echinata	1.59	2.51	0.92		*Hydnophora microconos*	1.33	2.40	1.07	
Acropora abrotanoides	1.25	1.65	0.40		*Isopora palifera*	1.42	1.65	0.23	
Acropora azurea	2.40	1.65	-0.74		*Leptastrea purpurea*	3.90	3.30	-0.59	
Acropora cf. *humilis*	1.14	1.89	0.75		*Leptastrea* sp.	3.21	6.36	3.15	
Acropora cf. *nasuta*	1.14	1.65	0.51		*Leptoria phrygia*	2.10	3.69	1.59	
Acropora cophodactyla	1.71		-1.71		*Lobophyllia corymbosa*	1.14		-1.14	
Acropora digitifera	1.14		-1.14		*Lobophyllia hemprichii*	1.14	1.65	0.51	
Acropora globiceps	1.14	1.65	0.51		*Millepora platyphylla*	2.06	2.19	0.13	
Acropora latistella		1.65	1.65		*Montipora* sp.	2.53	2.72	0.18	
Acropora monticulosa	1.14		-1.14		*Pavona bipartita*	2.18	3.58	1.40	
Acropora obtusicaulis	1.14		-1.14		*Pavona chiriquiensis*	3.61	2.67	-0.94	
Acropora palmerae-minuta	1.71		-1.71		*Pavona divaricata*	2.28		-2.28	
Acropora quelchi		1.65	1.65		*Pavona duerdeni*	1.70	2.62	0.92	
Acropora secale	1.42	1.93	0.50		*Pavona maldivensis*	2.85		-2.85	
Acropora sp.-*caespitose*	1.93	2.18	0.25		*Pavona meandrina*		5.51	5.51	
Acropora sp.-*corymbose*	1.22	1.84	0.62		*Pavona varians*	1.63	3.63	2.00	
Acropora surculosa	1.32	1.65	0.34		*Pavona venosa*	1.90	3.30	1.40	
Acropora verweyi	2.93	1.65	-1.27		*Platygyra daedalea*	1.20	2.09	0.89	
Astrea curta	2.72	3.43	0.71		*Platygyra pini*	1.49	2.70	1.22	
Astreopora myriophthalma	2.28	1.65	-0.63		*Platygyra* sp.	1.14	1.65	0.51	
Astreopora sp.	1.52	2.58	1.06		*Pocillopora damicornis-acuta*	1.14	1.65	0.51	
Cyphastrea sp.	1.74	4.52	2.77		*Pocillopora elegans*		1.65	1.65	
Diploastrea heliopora	1.14		-1.14		*Pocillopora grandis*	1.71	1.65	-0.06	
Dipsastraea pallida	1.14		-1.14		*Pocillopora* sp.	1.55	2.05	0.50	
Dipsastraea sp.	2.47	3.77	1.29		*Pocillopora verrucosa*	1.14		-1.14	
Echinophyllia sp.		1.65	1.65		*Porites annae*	1.14	4.33	3.19	
Echinopora lamellosa		3.85	3.85		*Porites deformis*	1.50	4.19	2.69	
Euphyllia glabrescens		1.65	1.65		*Porites densa*		1.65	1.65	
Favites flexuosa	1.71	2.48	0.77		*Porites lichen*		1.65	1.65	
Favites russelli	1.94	3.33	1.39		*Porites rus*	3.43	5.04	1.61	
Fungia sp.	1.77	2.40	0.63		*Porites* sp.-encrusting	1.99		-1.99	
Galaxea fascicularis	3.80	5.58	1.77		*Porites* sp.-massive	2.24	4.20	1.96	
Gardineroseris planulata	1.14	3.30	2.16		*Porites* sp.-other	1.73	2.49	0.76	
Goniastrea edwardsi	1.61	2.57	0.96		*Porites* sp.-submassive	2.02	1.88	-0.14	
Goniastrea pectinata	1.14	2.27	1.13		*Porites vaughani*	1.14	1.65	0.51	
Goniastrea retiformis	2.28	4.08	1.80		*Psammocora profundacella*	1.71		-1.71	
Goniastrea sp.	1.14	2.81	1.67		*Psammocora* sp.	1.64	3.96	2.32	
Goniastrea stelligera	1.56	2.35	0.79		*Stylocoeniella armata*		2.17	2.17	
Goniopora fruticosa	1.27	2.75	1.49		*Stylophora mordax*	1.40	1.84	0.45	
Goniopora sp.	1.22	3.58	2.36		Unidentified coral	1.63	2.36	0.74	
Heliopora coerulea	1.59	1.87	0.28						

All sites showed an increase in mean density between 2013 and 2017, however there was large inter-site variability. Three sites (East Agaña Bay (GUA-390); Adelup (GUA-410); Tumon Bay (GUA-391)) contributed disproportionately to the global trend of increasing colony density, all exceeding an increase of 1.37 colonies / m^2, while one site (Ritidian; GUA-583) showed only a very small increase unlikely to be ecologically meaningful (**Table 3**). For colony density values by species and by site see **Appendix 1**.

Table 2. Change in mean coral colony density (number of colonies / m^2, **all colonies**) by coral species at eight long-term monitoring shallow reef sites (~5 m depth) along the west coast of Guam following successive coral bleaching events between 2013 and 2017. Color ramp denotes either increase (blue) or decrease (grey): dark signifies >12% change; medium, 5-10% change; and light, 1-5% change. Blank cells = 0.

Family	2013	2017	∆ density	∆ density
Acroporidae	1.69	2.03	0.34	
Agariciidae	2.22	3.31	1.10	
Astrocoeniidae		2.17	2.17	
Diploastreidae	1.14		-1.14	
Euphylliidae	3.80	5.14	1.34	
Fungiidae	1.77	2.40	0.63	
Helioporidae	1.59	1.87	0.28	
Lobophylliidae	1.49	2.28	0.79	
Merulinidae	1.85	3.13	1.28	
Milleporidae	2.06	2.19	0.13	
Pocilloporidae	1.42	1.90	0.48	
Poritidae	1.96	3.35	1.39	
Psammocoridae	1.65	3.96	2.31	
Scleractinia incertae sedis	3.29	6.02	2.73	
Unidentified coral	1.63	2.36	0.74	

Table 3. Change in mean coral colony density (number colonies / m^2, all colonies included) by site at eight long-term monitoring shallow reef sites along the west coast of Guam following successive coral bleaching events between 2013 and 2017.

Site	Site Code	2013	2017	∆ Density
East Agana Bay	GUA-390	1.84	3.28	1.43
Tumon Bay	GUA-391	1.79	3.15	1.37
Facpi Point	GUA-401	1.5	2.55	1.05
Adelup	GUA-410	1.73	3.11	1.38
Gaan Point	GUA-490	1.91	2.84	0.93
Achang Bay	GUA-579	1.81	2.8	0.99
Ritidian	GUA-583	2.8	2.83	0.03
Cocos Lagoon South	GUA-600	1.97	3.17	1.2

B. Colonies < 5 cm excluded

Mean coral colony density across all coral taxa increased from 1.57 colonies/m^2 in 2013 to 2.17 colonies/m^2 by 2017 (**Fig. 4**). This increase occurred across all coral families, except for Diploastreidae; present in 2013 (as a single colony; see above explanation) but absent in 2017 (**Table 4**). The largest increases in colony density were driven by corals within the families Psammacoridae, Merulinidae, and Poritidae that increased in density by 1.29, 0.90, and 0.84 colonies/m^2, respectively. At a species taxonomic resolution there was more variability, with 56 of the 76 species increasing and 20 decreasing in density (**Table 5**). And, as explained above, for the taxa represented by adequate sample sizes, the largest increases in density were in *Echinopora lamellosa*, *Gardineroseris planulata*, and *Pavona meandrina*, and to a lesser extent *Acropora latistella*, *Cyphastrea* sp., *Echinophyllia* sp., *Goniastrea retiformis*, *Goniopora* sp., *Leptoria phrygia*, *Pocillopora elegans*, *Porites deformis*, *Porites densa*, *Porites* sp.-massive, and *Psammacora* sp. The largest decreases in density were in *Pavona maldivensis*, and to a lesser extent several *Acropora* species (*A. cophodactyla*, *A. digitifera*, *A. monticulosa*, *A. obtusicaulis*, *A. verweyi*), *Dipsastraea pallida*, *Pavona divaricata*, *Pocillopora verrucosa*, *Porites* sp.-encrusting, and *Psammacora profundacella* (**Table 5**).

All sites showed an increase in mean density between 2013 and 2017, though with large inter-site variability. Three sites: Adelup (GUA-410), East Agaña Bay (GUA-390), and Tumon Bay (GUA-391) contributed disproportionately to the global trend of increasing colony density, all exceeding an increase of 0.85 colonies / m^2 (**Table 6**). For colony density values by species and by site see **Appendix 2**.

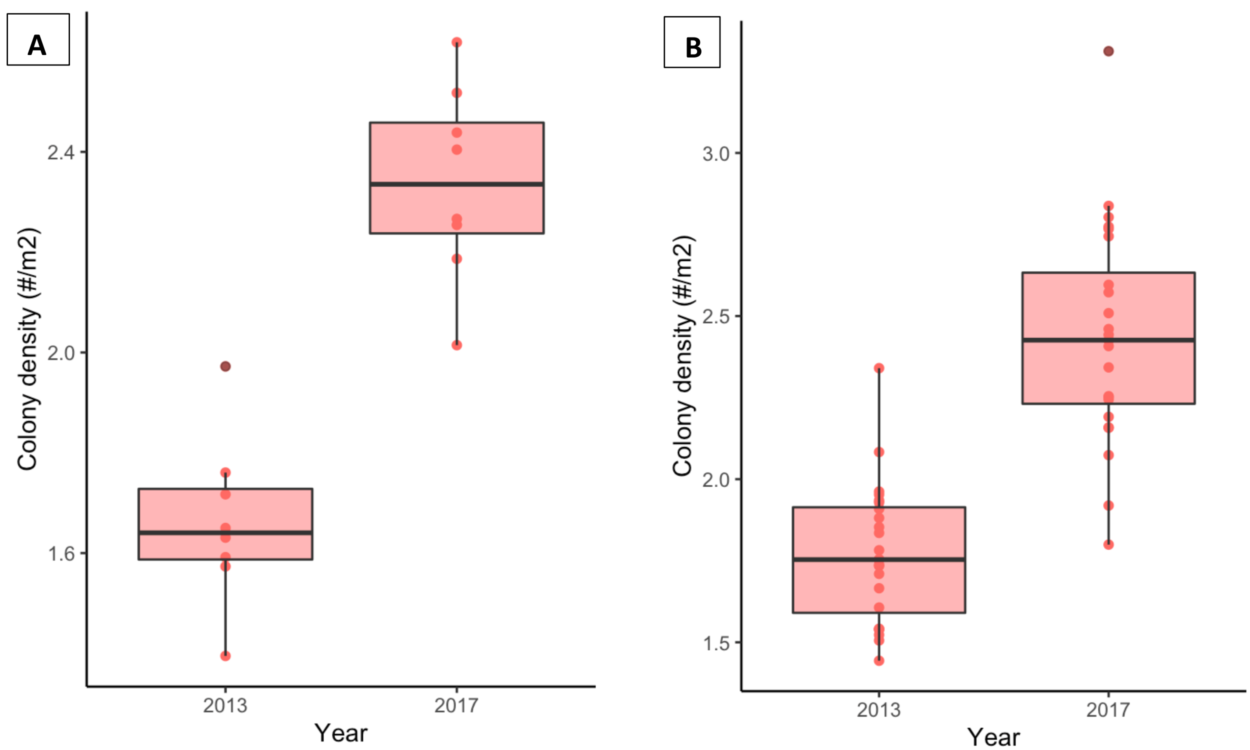

Figure 4. Change in coral colony density (all taxa combined, **colonies < 5cm removed**) at eight long-term monitoring shallow reef sites (~5 m depth) along the west coast of Guam following successive coral bleaching and disease events between 2013 and 2017 (A: dots represent individual site means, n=8; B: dots represent individual transect means, n=24). Thick horizontal lines represent the median; thin horizontal lines represent the interquartile range.

Table 4. Change in mean coral colony density (number colonies / m^2, **colonies < 5cm removed**) by coral family at 8 long-term monitoring shallow reef sites (~5 m depth) along the west coast of Guam following successive coral bleaching events between 2013 and 2017. Color ramp denotes either increase (blue) or decrease (grey). Blank cells = 0.

Family	2013	2017	Δ density	Δ density
Acroporidae	1.63	1.96	0.33	
Agariciidae	1.74	2.51	0.77	
Diploastreidae	1.14		-1.14	
Euphylliidae	3.21	3.85	0.64	
Fungiidae	1.57	1.65	0.09	
Helioporidae	1.35	1.76	0.41	
Lobophylliidae	1.29	1.89	0.60	
Merulinidae	1.56	2.47	0.90	
Milleporidae	1.61	1.96	0.35	
Pocilloporidae	1.42	1.79	0.36	
Poritidae	1.72	2.56	0.84	
Psammocoridae	1.46	2.74	1.29	
Scleractinia incertae sedis	2.18	2.85	0.66	
Unidentified coral	1.65	2.03	0.37	

Table 5. Change in mean coral colony density (number colonies / m^2, colonies **< 5cm removed**) by coral species at eight long-term monitoring shallow reef sites (~5 m depth) along the west coast of Guam following successive coral bleaching and disease events between 2013 and 2017. Color ramp denotes either increase (blue) or decrease (grey); dark signifies >12% change; medium, 5-10% change; and light, 1-5% change. Blank cells = 0.

Species	2013	2017	Δ density	Δ density
Acanthastrea echinata	1.33	1.95	0.62	
Acropora abrotanoides	1.26	1.65	0.40	
Acropora azurea	2.32	1.65	-0.66	
Acropora cf. *humilis*	1.14	1.89	0.75	
Acropora cf. *nasuta*	1.14	1.65	0.51	
Acropora cophodactyla	1.71		-1.71	
Acropora digitifera	1.14		-1.14	
Acropora globiceps	1.14	1.65	0.51	
Acropora latistella		1.65	1.65	
Acropora monticulosa	1.14		-1.14	
Acropora obtusicaulis	1.14		-1.14	
Acropora palmerae-minuta	1.42		-1.42	
Acropora secale	1.42	1.65	0.23	
Acropora sp.-caespitose	1.96	2.37	0.41	
Acropora sp.-corymbose	1.22	1.87	0.64	
Acropora surculosa	1.32	1.65	0.34	
Acropora verweyi	2.74	1.65	-1.09	
Astrea curta	2.01	2.26	0.24	
Astreopora myriophthalma	2.28	1.65	-0.63	
Astreopora sp.	1.46	2.10	0.64	
Cyphastrea sp.	1.51	3.19	1.68	
Diploastrea heliopora	1.14		-1.14	
Dipsastraea pallida	1.14		-1.14	
Dipsastraea sp.	1.78	2.68	0.90	
Echinophyllia sp.		1.65	1.65	
Echinopora lamellosa		3.30	3.30	
Favites flexuosa	1.71	1.65	-0.06	
Favites russelli	1.36	2.22	0.86	
Fungia sp.	1.57	1.65	0.09	
Galaxea fascicularis	3.21	3.85	0.64	
Gardineroseris planulata	1.14	3.30	2.16	
Goniastrea edwardsi	1.40	2.23	0.83	
Goniastrea pectinata	1.14	1.65	0.51	
Goniastrea retiformis	1.95	3.33	1.37	
Goniastrea sp.	1.14	1.65	0.51	
Goniastrea stelligera	1.34	2.11	0.77	
Goniopora fruticosa	1.31	2.30	0.99	
Goniopora sp.	1.14	2.64	1.50	

Species	2013	2017	Δ density	Δ density
Heliopora coerulea	1.35	1.76	0.41	
Hydnophora microconos	1.29	2.14	0.84	
Isopora palifera	1.42	1.65	0.23	
Leptastrea purpurea	2.63	1.65	-0.98	
Leptastrea sp.	2.13	3.00	0.87	
Leptoria phrygia	1.91	3.30	1.40	
Lobophyllia corymbosa	1.14		-1.14	
Lobophyllia hemprichii	1.14	1.65	0.51	
Millepora platyphylla	1.61	1.96	0.35	
Montipora sp.	2.20	2.48	0.28	
Pavona bipartita	2.02	2.64	0.62	
Pavona chiriquiensis	2.15	2.68	0.53	
Pavona divaricata	1.14		-1.14	
Pavona duerdeni	1.58	1.98	0.41	
Pavona maldivensis	2.56		-2.56	
Pavona meandrina		3.30	3.30	
Pavona varians	1.52	2.43	0.91	
Pavona venosa	1.77	1.65	-0.12	
Platygyra daedalea	1.23	1.81	0.58	
Platygyra pini	1.40	2.20	0.80	
Platygyra sp.	1.14	1.65	0.51	
Pocillopora damicornis-acuta	1.14	1.65	0.51	
Pocillopora elegans		1.65	1.65	
Pocillopora grandis	1.71	1.65	-0.06	
Pocillopora sp.	1.56	1.90	0.34	
Pocillopora verrucosa	1.14		-1.14	
Porites annae	1.14	2.04	0.90	
Porites deformis	1.31	3.19	1.88	
Porites densa		1.65	1.65	
Porites rus	2.74	3.37	0.63	
Porites sp.-encrusting	1.99		-1.99	
Porites sp.-massive	2.05	3.09	1.04	
Porites sp.-other	1.19	1.65	0.46	
Porites sp.-submassive	1.65	1.75	0.09	
Psammocora profundacella	1.14		-1.14	
Psammocora sp.	1.50	2.74	1.24	
Stylophora mordax	1.36	1.68	0.33	
Unidentified coral	1.65	2.03	0.37	

Table 6. Change in mean coral colony density (number colonies / m^2, colonies < 5cm removed) at eight long-term monitoring shallow reef sites (~5 m depth) along the west coast of Guam following successive coral bleaching events between 2013 and 2017. Refer to Fig. 1 for site locations.

Site	Site Code	2013	2017	Δ Density
East Agana Bay	GUA-390	1.72	2.62	0.90
Tumon Bay	GUA-391	1.59	2.44	0.85
Facpi Point	GUA-401	1.39	2.01	0.62
Adelup	GUA-410	1.57	2.52	0.94
Gaan Point	GUA-490	1.65	2.27	0.62
Achang Bay	GUA-579	1.63	2.19	0.56
Ritidian	GUA-583	1.97	2.25	0.28
Cocos Lagoon South	GUA-600	1.76	2.40	0.64

Question 2: Impact of successive coral bleaching events on coral taxa bleaching susceptibility

METHODS

The bleaching condition of each coral colony identified in the digital images was scored using three separate indices, including a semi-quantitative index with four broad bleaching categories (no bleaching, pale, partially bleached, whole bleached) that was first used during a bleaching response effort in 2013, a more refined semi-quantitative bleaching condition index developed in 2017 that used seven categories (normal pigmentation, partial colony pale, whole colony pale, partial colony bleached, whole colony bleached, bleached with partial mortality, dead), and a mortality index developed for this analysis that allowed the assessment of recent mortality independent of bleaching condition (no recent mortality, <50% recent partial mortality, 50–95% recent partial mortality, >95% recent partial mortality. Examples of these eleven bleaching severity categories are presented in **Fig. 5**. The three indices reflect the evolution in our approach to assessing bleaching condition, and the use of all three indices in this analysis facilitates direct comparability of data generated from this analysis to data previously generated for other sites surveyed in 2013 that were not included in this analysis. For our final analysis, the values for these three indices were combined post-hoc into 22 separate rankings that accounted for *pigmentation condition* (normal, pale, bleached) as well as the *percent of the colony affected* by the dominant pigmentation condition (partial = <50%, mostly = 50-95% , whole = >95%) and an estimate of the percent of the colony with mortality. The inclusion of the mortality index allowed for the detection of mortality that may not be easily attributed to thermal/light stress, but which may be an indirect result of such stress. For example, patchy tissue loss (i.e., partial mortality) was observed in numerous massive *Porites* colonies during the 2017 bleaching event, but most of these colonies exhibited only tissue discoloration or slight paling, rather than tissue loss in association with fully bleached portions of the colony. Again, we compared the results obtained with and without including colonies < 5 cm in the subsequent analyses.

Figure 5. Eleven bleaching severity categories used in a semi-quantitative assessment in rapid bleaching surveys. A: *Acropora abrotanoides*, normal pigmentation; B: *Pocillopora grandis*, colony partially pale; C: *Leptoria phrygia*, colony mostly pale; D: *Pocillopora verrucosa*, whole colony pale; E: *Gardineroseris planulata*, colony partially bleached; F: *Goniastrea stelligera*, colony partially bleached with <50% mortality; G: *Leptoria phrygia*, colony mostly bleached; H: *Pocillopora meandrina*, whole colony bleached; I: *Montipora* sp., whole colony bleached with <50% mortality; J: *Pocillopora ankeli*, whole colony bleached with <50% mortality; K: *Millepora platyphylla*, whole colony bleached with >50% mortality; L: *Acropora* sp., recent mortality.

RESULTS AND DISCUSSION

A. All colonies included

Of the 9,440 coral colonies examined in 2013, the majority (60.9%) showed no signs of bleaching (**Table 7**). Of those that did show paling/bleaching in 2013, 'partial bleached' and 'whole bleached' were the most prevalent (8.6 and 8.3%, respectively), while 'partial bleached with <50% mortality' and 'mostly pale' were the least prevalent responses (both <1%). By 2017, across the 11,698 coral colonies examined, the majority (65.2%) of colonies still showed no signs of bleaching, representing an increase in prevalence of this response of 4.3% since 2013 (**Table 7**). Of those that showed paling/bleaching in 2017, 'partial bleached' and 'whole bleached' were once again the most prevalent (10.0 and 5.6%, respectively) and 'partial bleached with <50% mortality' and 'mostly pale' were once again the least prevalent responses (both <1% of colonies). The variation in the prevalence of the most common responses (normal, partial bleached, whole bleached) across both sites and transects decreased between 2013 and 2017, although there was still wide variation in responses among sites within both years (**Fig. 6**).

Table 7. Change in coral colony bleaching response at eight monitoring reef sites along the west coast of Guam following coral bleaching events between 2013 and 2017. **Top table:** 11 bleaching response categories; values shown are the mean percentage of colonies by response category (total number of colonies examined in 2013 and 2017 shown). 'Normal' represents no signs of bleaching response. **Bottom table:** Bleaching responses by site, showing percent of total colonies examined exhibiting one of three bleaching categories. Color ramp denotes either increase (blue) or decrease (grey); dark signifies >12% change; medium, 5-10% change; and light, 1-5% change.

Bleaching Severity	2013	# colonies	2017	# colonies	△
Normal	60.9	7841	65.2	5549	4.3
Partial pale	3.7	335	3.2	338	-0.5
Mostly pale	0.7	43	0.5	65	-0.2
Whole pale	4.8	476	4.1	455	-0.7
Partial bleached	8.6	673	5.6	757	-3.0
Partial bleached, <50% mortality	0.3	13	0.1	20	-0.1
Mostly bleached	3.4	324	3.0	352	-0.4
Whole bleached	8.3	1173	10.0	887	1.7
Whole bleached with <50% mortality	5.4	310	3.0	580	-2.4
Whole bleached with >50% mortality	2.1	171	1.7	231	-0.4
Recent whole colony mortality	1.8	339	3.5	206	1.7

Site Name	Site Code	Normal			Partial bleached			Whole bleached		
		2013	2017	△	2013	2017	△	2013	2017	△
West Agaña	GUA-390	72.9	65.4	-7.5	10.6	7.5	-3.1	1.9	11.8	9.9
Tumon Bay	GUA-391	82.4	83.5	1.1	2.0	3.0	1.0	0.9	5.9	5.0
Facpi Point	GUA-401	50.6	67.6	17.0	18.9	3.7	-15.2	9.9	12.9	3.0
Adelup	GUA-410	67.7	65.6	-2.1	20.6	8.2	-12.4	2.0	14.1	12.1
Gaan Point	GUA-490	79.4	69.4	-10.0	3.5	3.8	0.3	2.0	11.8	9.8
Achang Bay	GUA-579	28.6	68.3	39.7	6.5	3.7	-2.8	20.7	9.4	-11.3
Ritidian	GUA-583	89.6	38.4	51.2	2.0	7.9	5.9	0.2	8.6	8.4
Cocos Lagoon South	GUA-600	16.1	63.7	47.6	4.9	7.1	2.2	28.5	5.5	-23.0

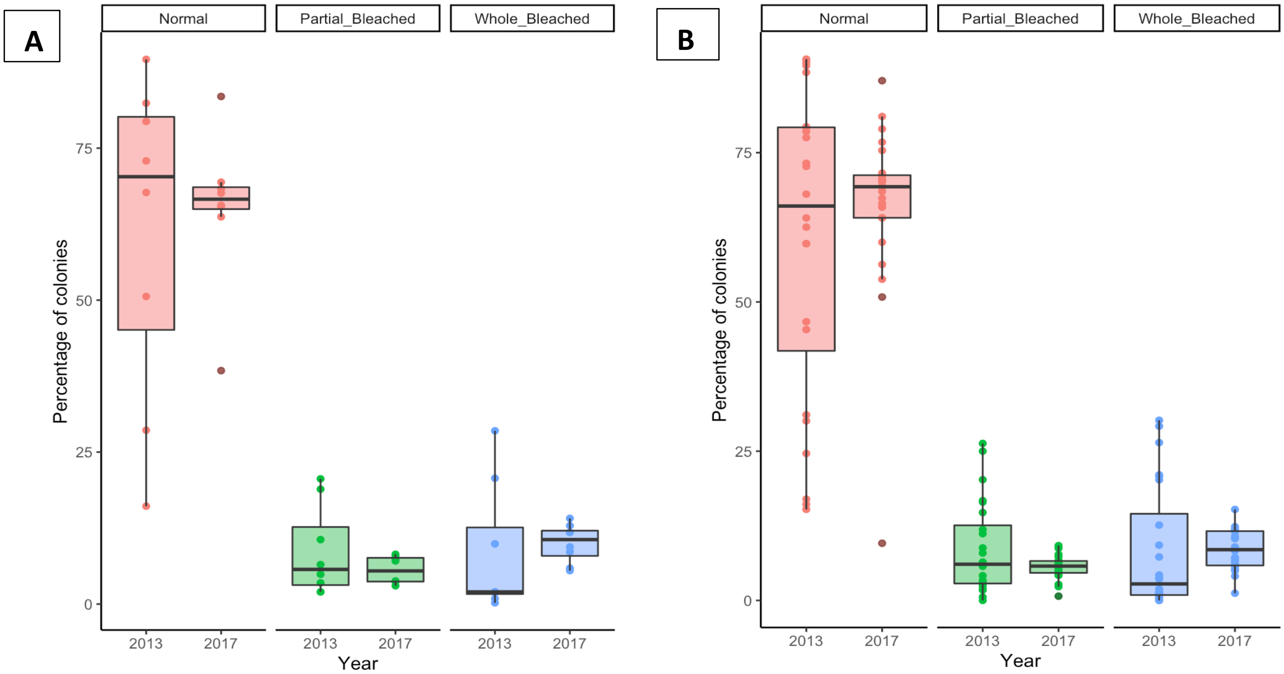

Figure 6. Change in the prevalence of colony bleaching response (all taxa combined) at eight long-term monitoring reef sites along the west coast of Guam following successive coral bleaching events between 2013 and 2017. The three most prevalent responses are shown. (A: dots represent individual site means, n=8; B: dots represent individual transect means, n=24). Thick horizontal lines represent the median; thin horizontal lines represent the interquartile range.

At the site level, there was wide variation in the percentage of ‘normal’ colonies in 2013, ranging from 16.1% at Cocos Lagoon South (GUA-600) to 89.6% at Ritidian (GUA-583) (**Table 7**). By 2017, half the sites displayed an increase in the percentage of ‘normal’ colonies and half, a decrease. Ritidian was no longer the site with the highest percentage of ‘normal’ colonies, instead it was Tumon Bay (GUA-391); Ritidian instead had the lowest percentage (38.4%). The largest increase in the prevalence of ‘normal’ colonies occurred at Cocos Lagoon South and overall variation among sites had decreased substantially, ranging only from 3.0 to 8.2% (**Table 7**). The largest decreases in partial bleaching prevalence occurred at Facpi Pt. (GUA-401) and Adelup (GUA-410). In 2013, the prevalence of percent whole bleached colonies ranged from 0.2% to 28.5%. At two sites (Cocos Lagoon South (GUA-600) and Achang (GUA-579), more than 20% of colonies displayed whole bleaching, while the other six sites all had <10% of colonies with this response (**Table 7**). By 2017, six of the eight sites had experienced an increase in whole colony bleaching prevalence, with the largest increase occurring at Adelup (increasing by 12.1%). The largest decrease in the prevalence of whole colony bleaching occurred at Cocos Lagoon South (-23.0%).

Across coral families, those contributing most to a lack of bleaching response (i.e., normal pigmentation) in both 2013 and 2017 were the Merulinidae and Poritidae, and to a lesser extent the Euphylliidae (**Table 8**). These three families accounted for 66.7% and 66.6% of the normal response prevalence in 2013 and 2017, respectively, and each showed a very consistent prevalence of a normal response between the two survey years. The ‘partial bleached’ response was overwhelmingly driven by the Merulinidae in both 2013 (49.3%) and 2017 (66.7%), representing a mean increase of 17.4% of Merulinidae colonies showing signs of partial bleaching between the two survey years (**Table 8**). The ‘whole bleached’ response was overwhelmingly driven by the Acroporidae (55.1%) and to a lesser extent the Merulinidae (29.5%) in 2013. However, by 2017 the mean prevalence of Acroporidae colonies showing signs of whole bleaching had dropped by 48.1% to just 7.0%. The ‘whole bleaching’ signal in 2017 was instead heavily driven by the Merulinidae whose prevalence increased by 40.2% to 69.7% (**Table 8**). However, it is important to note that we observed much variability in bleaching responses within most families, between genera and even within genera. Thus, a deeper analysis to examine species-level differences would be very useful.

Table 8. Change in coral colony bleaching response by coral family at eight long-term monitoring shallow reef sites along the west coast of Guam following successive coral bleaching events between 2013 and 2017. Values shown are the mean percentage of colonies per response category (with the total number of colonies examined in 2013 and 2017 shown to the left). 'Normal' represents no signs of bleaching response.

Response category	Year	# colonies	Acroporidae	Agariciidae	Astrocoeniidae	Diploastreidae	Euphylliidae	Fungiidae	Helioporidae	Lobophylliidae	Merulinidae	Milleporidae	Pocilloporidae	Poritidae	Psammocoridae	Scleractinia	Unidentified
Normal	2013	5549	8.2	3.4	0	0	15.0	0	1.8	3.2	26.0	0.8	1.2	25.7	1.5	12.8	0.4
	2017	7841	2.7	1.4	0.3	0	13.4	0.1	0.5	3.3	24.0	0.2	2.3	29.2	3.7	18.0	0.8
Partial pale	2013	338	7.4	2.1	0	0	0.6	0.3	0	0.6	60.9	1.2	8.3	10.9	2.4	4.1	1.2
	2017	335	3.6	1.2	0	0	3.9	0	1.5	1.5	60.0	3.9	0.9	11.9	6.6	4.5	0.6
Mostly pale	2013	65	3.1	1.5	0	0	0	0	1.5	7.7	70.8	0	3.1	7.7	3.1	1.5	0
	2017	43	0	0	0	0	4.7	0	0	0	69.8	0	0	9.3	4.7	11.6	0
Whole pale	2013	455	7.3	3.3	0	0	3.1	1.5	0.9	1.8	47.9	0	8.6	23.3	0.7	0.7	1.1
	2017	476	1.7	0.6	1.3	0	5.9	0.4	1.3	2.3	63.4	0	2.1	12.8	4.4	1.5	2.3
Partial bleached	2013	757	12.3	3.8	0	0	1.3	0	0	0	49.3	0.1	5.7	8.5	0.5	18.5	0
	2017	673	4.9	2.8	0.1	0	2.7	0.1	0.3	0.4	66.7	1.3	0.4	10.1	4.0	5.3	0.6
Partial bleached (<50% mortality)	2013	20	20.0	15.0	0	0	0	0	0	0	5.0	0	15.0	45.0	0	0	0
	2017	13	5.0	0	0	0	0	0	0	0	55.0	0	0	5.0	0	0	0
Mostly bleached	2013	352	31.3	5.1	0	0	0.3	0.3	0	0.9	50.0	0	4.8	4.0	0.3	2.0	1.1
	2017	324	4.0	3.7	0	0	1.9	0.0	0	0.6	73.1	0	0.3	6.5	4.0	4.3	1.5
Whole bleached	2013	887	55.1	1.7	0	0	0.7	0.1	0	0.1	29.5	0	3.4	3.9	0.1	0.1	5.2
	2017	1173	7.0	3.6	0	0	1.0	0.4	0.2	0.3	69.7	0.3	1.5	4.3	3.1	0.9	7.7
Whole bleached (<50% mortality)	2013	580	60.9	6.0	0	0	0	0.2	0	0	14.8	0.5	6.7	7.4	0	0	3.4
	2017	310	15.2	5.2	0	0	0.6	0	0.3	0	56.8	0.3	3.5	10.6	2.3	1.0	4.2
Whole bleached (>50% mortality)	2013	231	71.9	9.1	0	0	0.4	0	0	0	6.1	0.4	6.9	4.3	0	0	0.9
	2017	171	40.4	2.3	0	0	0	0	0	0	32.2	1.2	7.0	12.9	0	0	4.1
Recent whole colony mortality	2013	206	80.6	1.0	0	0	0	1.0	0	0	2.4	0	4.9	4.9	0	0	5.3
	2017	339	64.0	0.6	0	0	0.3	0.0	0	0.3	14.5	1.8	7.7	4.7	0	0	6.2

B. Colonies < 5 cm excluded

Of the 6,857 coral colonies examined in 2013, the majority (53.2%) showed no signs of bleaching (**Table 9**). Of those that did show some sign of paling/bleaching in 2013, 'whole bleached' and 'partial bleached' were the most prevalent (10.1 and 9.5%, respectively), while 'partial bleached with <50% mortality' and 'mostly pale' were the least prevalent responses (both <1% of colonies). By 2017 and across the 6,395 coral colonies examined, the majority (59.5%) of colonies still showed no signs of bleaching, representing an increase in prevalence of this response of 6.3% since 2013 (**Table 9**). Of those that did show some sign of paling/bleaching in 2017, 'whole bleached' and 'partial bleached' were once again the most prevalent (11.2 and 7.8%, respectively) and 'partial bleached with <50% mortality' and 'mostly pale' were once again the least prevalent responses (both <1% of colonies). The variation in the prevalence of the most common responses (normal, partial bleached, whole bleached) across both sites and transects was relatively consistent between 2013 and 2017 (**Fig. 7**).

At the site level, there was variation in the percentage of 'normal' colonies in 2013, ranging from only 4.9% at GUA-600 to 20.5% at GUA-390 (**Table 9**). By 2017, half the sites displayed an increase in the percentage of 'normal' colonies and half a decrease. GUA-390 was no longer the site with the highest percentage, instead it was GUA-391 (increased by 10.7% to 26.5%) and GUA-401 had the lowest percentage (4.7%). Partial bleaching in 2013 ranged from 1.9% to 29.5%. By 2017, five sites had experienced an increase in the percentage of partial bleaching. GUA-410 remained the site with the highest prevalence of partial bleaching in both years and experienced very little overall change in prevalence (0.2%), while GUA-401 displayed the largest decrease in prevalence (-14.6%) of any site (**Table 9**). Whole bleaching showed the most dramatic intra-site changes in prevalence between survey years of any of the responses. In 2013, GUA-600 and GUA-579 showed the highest prevalence of whole colony bleaching, both with >20% of colonies bleached (more than double all other sites). By 2017, five sites had experienced an increase in the percentage of both whole and partial colony bleaching (**Table 9**). The percentage of whole bleached colonies at both GUA-600 and GUA-579 had halved to <10% of colonies, and instead sites that had previously had some of the lowest prevalence of whole bleaching in 2013 (GUA-410 and GUA-490) now had among the highest in 2017 (**Table 9**). GUA-600 overall showed the largest decrease in whole bleaching prevalence between survey years (-53.9%) and GUA-410 experienced the largest increase (28.5%).

Table 9. Change in coral colony bleaching response (colonies < 5cm removed) at eight long-term monitoring shallow reef sites along the west coast of Guam following successive coral bleaching events between 2013 and 2017. **Top table:** 11 bleaching response categories scored; values shown are the mean percentage of colonies by response category (with the total number of colonies examined in 2013 and 2017 shown). 'Normal' represents no signs of bleaching response. **Bottom table:** Bleaching responses by site, showing percent of total colonies examined exhibiting one of three bleaching categories. Blue = an increase between survey years; grey = a decrease.

Bleaching Severity	2013	# colonies	2017	# colonies	Δ
Normal	53.2	3649	59.5	3808	6.3
Partial pale	3.6	246	2.9	186	-0.7
Mostly pale	0.8	52	0.3	19	-0.5
Whole pale	4.6	316	3.1	201	-1.5
Partial bleached	9.5	648	7.8	502	-1.6
Partial bleached, <50% mortality	0.3	20	0.2	12	-0.1
Mostly bleached	4.5	310	3.8	240	-0.8
Whole bleached	10.1	695	11.2	715	1.0
Whole bleached with <50% mortality	7.7	528	4.2	270	-3.5
Whole bleached with >50% mortality	3.1	214	2.3	148	-0.8
Recent whole colony mortality	2.6	179	4.6	294	2.0

Site Name	Site Code	Normal			Partial bleached			Whole bleached		
		2013	2017	Δ	2013	2017	Δ	2013	2017	Δ
West Agaña	GUA-390	20.5	18.9	-1.6	18.5	21.9	3.4	2.9	22.7	19.8
Tumon Bay	GUA-391	15.8	26.5	10.7	1.9	10.0	8.1	0.9	10.8	9.9
Facpi Point	GUA-401	7.7	4.7	-3.0	18.2	3.6	-14.6	8.6	6.2	-2.5
Adelup	GUA-410	12.2	19.5	7.3	29.5	29.7	0.2	1.7	30.2	28.5
Gaan Point	GUA-490	14.2	7.9	-6.3	4.9	6.2	1.2	2.3	7.1	4.8
Achang Bay	GUA-579	6.3	8.5	2.2	11.3	6.4	-4.9	24.6	10.3	-14.3
Ritidian	GUA-583	18.4	5.0	-13.4	4.2	12.7	8.6	0.4	8.1	7.7
Cocos Lagoon South	GUA-600	4.9	9.0	4.1	11.6	9.6	-2.0	58.6	4.6	-53.9

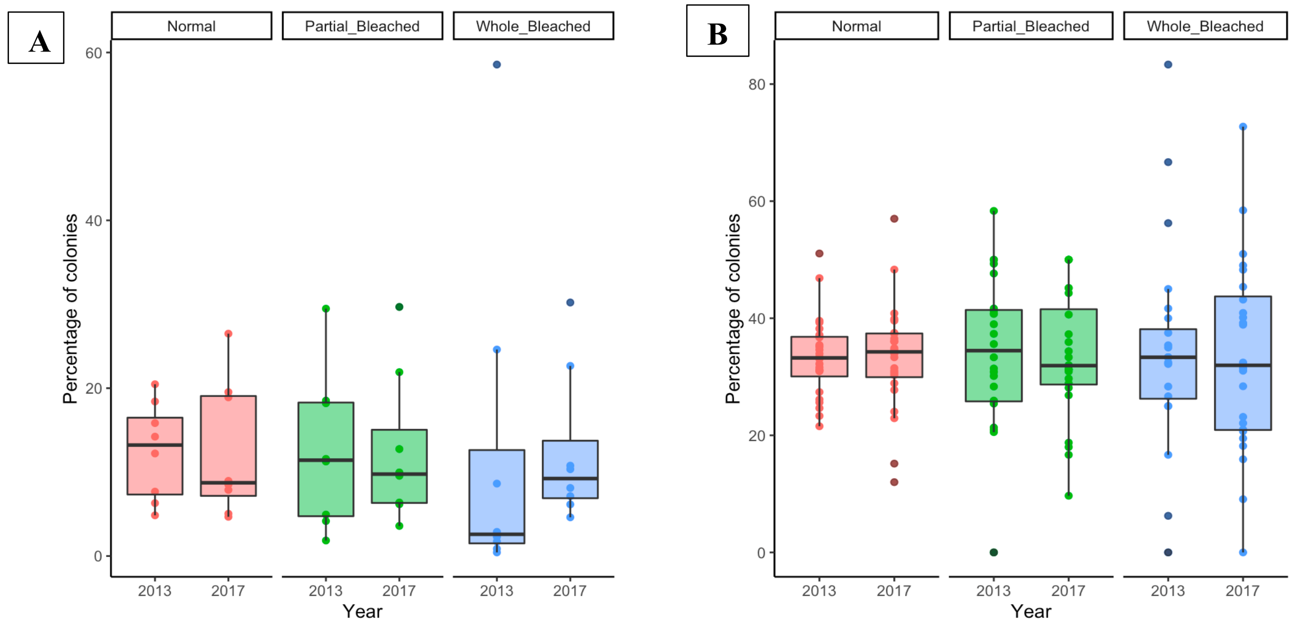

Figure 7. Change in the prevalence of coral colony bleaching response (all taxa combined, **colonies < 5cm removed**) at eight long-term monitoring shallow reef sites along the west coast of Guam following successive coral bleaching events between 2013 and 2017. The three most prevalent responses are shown. (**A:** dots represent individual site means, n=8; **B:** dots represent individual transect means, n=24). Thick horizontal lines represent the median; thin horizontal lines represent the interquartile range.

Table 10. Change in coral colony bleaching response (colonies < 5cm removed) by coral family at 8 long-term monitoring shallow reef sites along the west coast of Guam following successive coral bleaching events between 2013 and 2017. Values shown are the mean percentage of colonies by response category (with the total number of colonies examined in 2013 and 2017 shown to the right). 'Normal' represents no signs of bleaching response.

Response category	Year	# Colonies	Acroporidae	Agariciidae	Diploastreidae	Euphyllidae	Fungiidae	Helioporidae	Lobophyllidae	Merulinidae	Milleporidae	Pocilloporidae	Poritidae	Psammocoridae	Scleractinia incertae sedis	Unidentified
Normal	2013	3649	9.3	2.6	<0.1	18.3	0.0	1.6	3.3	22.1	1.0	1.5	30.3	1.9	7.9	0.2
	2017	3808	3.8	1.3	0.0	18.9	0.0	0.5	2.8	24.3	0.2	2.2	32.9	3.8	8.8	0.4
Partial pale	2013	246	8.5	2.8	0.0	0.8	0.4	0.0	0.8	55.3	1.6	11.0	11.4	2.8	3.7	0.8
	2017	186	6.5	1.1	0.0	3.2	0.0	1.1	1.1	55.4	5.4	0.0	16.1	7.0	3.2	0.0
Mostly pale	2013	52	3.8	1.9	0.0	0.0	0.0	1.9	7.7	65.4	0.0	3.8	9.6	3.8	1.9	0.0
	2017	19	0.0	0.0	0.0	5.3	0.0	0.0	0.0	68.4	0.0	0.0	5.3	5.3	15.8	0.0
Whole pale	2013	316	8.5	3.8	0.0	2.8	1.3	1.3	1.6	44.3	0.0	11.1	23.7	0.6	0.6	0.3
	2017	201	2.0	1.5	0.0	9.0	0.0	1.5	1.5	70.1	0.0	0.5	9.5	3.5	0.5	0.5
Partial bleached	2013	648	13.7	3.9	0.0	1.5	0.0	0.0	0.0	49.8	0.2	6.2	9.1	0.6	15.0	0.0
	2017	502	5.8	2.6	0.0	3.0	0.2	0.2	0.4	68.9	1.6	0.4	10.0	4.4	2.4	0.2
Partial bleached (<50% mortality)	2013	20	20.0	15.0	0.0	0.0	0.0	0.0	0.0	5.0	0.0	15.0	45.0	0.0	0.0	0.0
	2017	12	8.3	0.0	0.0	0.0	0.0	0.0	0.0	83.3	0.0	0.0	8.3	0.0	0.0	0.0
Mostly bleached	2013	310	33.2	4.8	0.0	0.3	0.3	0.0	0.6	50.3	0.0	4.5	3.9	0.3	1.3	0.3
	2017	240	5.0	2.5	0.0	1.7	0.0	0.0	0.4	78.3	0.0	0.0	5.8	3.8	1.7	0.8
Whole bleached	2013	695	59.0	1.9	0.0	0.7	0.1	0.0	0.1	27.6	0.0	3.2	3.0	0.0	0.0	4.3
	2017	715	7.6	1.8	0.0	1.0	0.0	0.1	0.3	78.9	0.4	1.7	2.1	2.7	0.0	3.5
Whole bleached (<50% mortality)	2013	528	61.7	6.3	0.0	0.0	0.2	0.0	0.0	14.6	0.6	6.6	6.8	0.0	0.0	3.2
	2017	270	16.3	5.6	0.0	0.7	0.0	0.4	0.0	57.4	0.4	3.3	9.6	2.2	0.7	3.3
Whole bleached (>50% mortality)	2013	214	71.5	9.8	0.0	0.0	0.0	0.0	0.0	5.6	0.5	7.5	4.2	0.0	0.0	0.9
	2017	148	44.6	2.7	0.0	0.0	0.0	0.0	0.0	29.7	1.4	6.1	12.8	0.0	0.0	2.7
Recent whole colony mortality	2013	179	81.0	1.1	0.0	0.0	1.1	0.0	0.0	2.2	0.0	4.5	5.6	0.0	0.0	4.5
	2017	294	69.0	0.3	0.0	0.3	0.0	0.0	0.0	12.9	2.0	5.8	4.8	0.0	0.0	4.8

Across coral families, those contributing most to a lack of bleaching response (i.e., normal condition) in both 2013 and 2017 were the Poritidae and Merulinidae, and to a lesser extent the Euphylliidae (**Table 10**). These three families accounted for 70.7% and 76.1% of the normal response prevalence in 2013 and 2017, respectively, and each showed a very consistent prevalence of a normal response between the two survey years. The 'partial bleached' response was overwhelmingly driven by the Merulinidae in both 2013 (49.8%) and 2017 (68.9%), representing a mean increase of 19.1% of Merulinidae colonies showing signs of partial bleaching between the two survey years (**Table 10**). The 'whole bleached' response was overwhelmingly driven by the Acroporidae (71.5%) in 2013. However, by 2017 the mean prevalence of Acroporidae colonies showing signs of whole bleaching had dropped to 44.6% (a decrease of 26.9%) and the Merulinidae also contributed to the whole bleaching response, increasing from 5.6% of colonies in 2013 to 29.7% in 2017 (**Table 10**).

SUMMARY & IMPLICATIONS

Between 2013 and 2017, multiple acute disturbance events impacted coral reefs surrounding Guam, Micronesia. These events – elevated SSTs in 2013, 2014, 2016, and 2017; ENSO-induced repeated extreme low tides in 2014 and 2015; and disease outbreaks in 2016 and 2017 -- acted synergistically to impact coral communities island-wide from shallow reef flats to depths of more than 20 m. Surveys were conducted in 2013, 2015, 2016, and 2017 to document the extent of these impacts on coral communities with the objectives of noting potential geographic variation in impacts, differential resilience between coral species, the extent of mortality, and signs of recovery over time. Collectively, these events caused an estimated 34% coral loss on shallow forereef communities and 37% loss on reef flat communities (Raymundo et al. 2017; 2019). This analysis utilizes a subset of these survey dates and sites to examine more nuanced impacts to coral colony density and test for evidence of species-specific shifts in bleaching response over multiple events. Our analyses included a total of 11,698 colonies assessed in 2013 and 9,440 colonies assessed in 2017 observed across eight sites along the western coast of Guam.

Coral colony density responses were clearly evident though a shift in survey methodology between years necessitated that we examine colony count data with and without small colonies <5cm. However, a consistent pattern emerged showing colony density increasing from 2013 to 2017 across all sites (**Tables 1 & 4**). Taxonomically, there were few discernible patterns though *Porites* spp – known to be more heat-resistant -- showed consistent increases in density while several *Acropora* species – known to be highly susceptible to bleaching -- showed declines in density (**Tables 2 & 5**). As stated previously, the camera used in 2013 featured a lower resolution capacity than that used in 2017. We attribute much of the increase in density across these years to the use of the higher resolution camera that allowed the counting of very small colonies; mainly those in Astrocoeniidae and Psammacoridae, both of which are generally bleaching-resistant families. With the removal of colonies <5cm, there were minor shifts in density responses over time, which supports this artifact. In addition, all sites showed an increase in colony density from 2013 to 2017, though variability was high. East Agaña, Adelup, and Tumon Bay sites contributed the most to this increase; these sites are in close proximity to each other along the central-western coast and forereef communities are relatively contiguous. They are also offshore of the areas of highest coastal development. However, the source of these increases could not be fully verified from our methods, aside from the camera resolution issue described above. Shifts in colony counts may be the result of either the fragmentation via partial mortality of larger colonies or recruitment of new colonies as a result of spawning events. However, the former is more likely, given that Guam is known to be recruitment-limited (Birkland and Randall 1981; Minton and Lundren 2006) and repeated heat stress likely reduced reproductive success

(Briggs et al. 2024). Thus, it is more likely that our observed increases in density are the product of colony fragmentation, though an analysis of population size class distribution would help to elucidate this and is planned for the future.

Colonies assessed in 2017 had survived four successive bleaching events. Thus, we asked the question: "did taxa that had previously bleached show greater or lesser bleaching susceptibility, as measured by our semi-quantitative bleaching scores?" Overall, a slightly greater percentage of corals were normally pigmented in 2017 (65.2%) relative to 2013 (60.9%); a 4% increase. And of the 10 remaining categories of bleaching severity, eight showed decreases from 2013 to 2017 in the percentage of colonies displaying bleaching **(Tables 7 & 9)**. Interestingly, the two categories that did display increases between the two years were whole colony bleaching and recent mortality. Of the coral taxa analyzed, Merulinidae showed consistent increases in all bleaching severity categories, with up to 5-fold increases in the percent of colonies bleached in certain categories. In contrast, virtually all other taxa showed decreases in susceptibility across years, with the exception of certain categories among Poritids **(Tables 8 & 10)**. Thus, our data suggest that surviving colonies in most taxa gained some level of resistance to bleaching over time. Highly susceptible colonies across taxa were removed from the population early on, leaving those with higher resistance to survive.

Documenting this rapid succession of unpredictable events was a monumental effort that involved multiple local agencies, working without a dedicated funding source. Slight necessary changes our methodology between years meant that this report describes only a subset of the work that was completed. Despite these challenges, there was a substantial data set accumulated that suggests shifts in Guam's shallow coral community. Coral density increased, though there was little to no evidence that this was the product of recruitment – it was more likely generated from fragmentation of larger colonies. This, in turn, has likely resulted in a decline in reproductive success, as fecundity is linked to colony size (Szmant et al. 1985; Okobo et al. 2007). We found evidence of heat resistance over time in most taxa that we surveyed, though we also noted certain rare species previously observed on Guam that may be nearing functional extirpation. A population size structure analysis would allow us to more fully understand the impacts of these events for the future of Guam's reefs, particularly their capacity to recover via recruitment.

Finally, while this analysis provides a detailed view of a very large dataset, it is important to emphasize that our results presented here only discuss Guam's sheltered western coast. Our limited surveys along the eastern exposed coast showed that most of the bleaching impacts between 2013 and 2017 were seen on this side of the island. We saw a >60% decline in coral cover on the east side, with no discernable change on the west side (Raymundo et al. 2019). The ~34% island-wide average (Raymundo et al. 2019) represents, therefore, a total mean loss of coral cover with a very large standard deviation due to the difference in responses between the east and west sides of the island of Guam. Further, the influence of repeated Crown- of -Thorns (COTS) outbreaks on coral community structure on Guam is well-documented (Randall 1971; Caballes 2009; Tusso et al. 2016), and this has also affected the two coasts differently, primarily due to wave exposure. The lower wave exposure of much of the west coast meant that COTS has impacted shallower areas of the slope, whereas they are generally limited to depths of ≥10 m on the east coast; below wave surge. The co-susceptibility of many coral taxa to COTS and bleaching (Acroporidae, for example) meant that many of the bleaching susceptible taxa at 5-7 m (our survey zone) on the west coast had been eliminated from the population long before our first severe bleaching event in 2013. However, there were still abundant populations of these most susceptible taxa remaining at our survey depth along the east coast and our initial surveys (2013) revealed significant bleaching impacts among these taxa. Unfortunately, the high wave exposure along the eastern coast also prevented repeated and replicated surveys of the east coast sites in 2017; they were entirely excluded from this study. Thus, the reefs we documented that were most impacted by bleaching on Guam could not be comparatively analyzed in this report; instead we focused on shallow west coast reefs that were shaped by decades of COTS predation prior to the onset of severe bleaching. The history and trajectory of these two coasts are different and interesting in their own right, but an examination of the impacts of bleaching on the east coast communities require a different statistical approach.

REFERENCES

Birkeland C, Randall, R H (1981) Coral recruitment patterns at Guam. 4th Int'l. Coral Reef Symp. 2:339–344.

Briggs N D, Page CA, Giuliano C, Alessi C, Hoogenboom M, Bay L K, Randall C J (2024).Dissecting coral recovery: bleaching reduces reproductive output in *Acropora millepora*. Coral Reefs, 43(3), 557–569. https://doi.org/10.1007/s00338-024-02483-y

Brown BE (1997) Coral bleaching: causes and consequences. Coral Reefs 16:129-138

Burdick D, Raymundo LJ, Drake D, Hershberge A (2023) A decade of change on Guam's coral reefs. University of Guam Technical Report 170. 120 pp.

Caballes, C. F. (2009). The role of chemical signals on the feeding behavior of the crown-of-thorns seastar, *Acanthaster planci* (Linnaeus, 1758). MSc Biology Thesis. University of Guam. 164 pp.

Dietzel A, Bode M, Connolly SR, Hughes TP (2020) Long-term shifts in the colony size structure of coral populations along the Great Barrier Reef. Proceedings of the Royal Society B: Biological Sciences 287:20201432

Ford HV, Gove JM, Davies AJ, Graham NAJ, Healey JR, Conklin EJ, Williams GJ (2021) Spatial scaling properties of coral reef benthic communities. Ecography 44:188-198

Fox MD, Carter AL, Edwards CB, Takeshita Y, Johnson MD, Petrovic V, Amir CG, Sala E, Sandin SA, Smith JE (2019) Limited coral mortality following acute thermal stress and widespread bleaching on Palmyra Atoll, central Pacific. Coral Reefs 38:701-712

Fox MD, Guillaume-Castel R, Edwards CB, Glanz J, Gove, JM, Mattias Green JA, Juhlin E., Smith JE, Williams GJ (2023) Ocean currents magnify upwelling and deliver nutritional subsidies to reef-building corals during El Niño heatwaves. Sci Adv 9 (2023). https://doi.org:10.1126/sciadv.add5032

Gove JM, Williams GJ, Lecky J, Brown E, Conklin E, Counsell C, Davis G, Donovan MK, Falinski K, Kramer L, Kozar K, Li N, Maynard JA, McCutcheon A, McKenna SA, Neilson BJ, Safaie A, Teague C, Whittier R, Asner GP (2023). Coral reefs benefit from reduced land-sea impacts under ocean warming. Nature 621, 536-542. https://doi.org:10.1038/s41586-023-06394-w

Graham NAJ, Jennings S, MacNeil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature 518:94-97

Heron SF, Maynard JA, van Hooidonk R, Eakin CM (2016) Warming Trends and Bleaching Stress of the World's Coral Reefs 1985–2012. Scientific Reports 6:38402

Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF, Hoey AS, Hoogenboom MO, Liu G, McWilliam MJ, Pears RJ, Pratchett MS, Skirving WJ, Stella JS, Torda G (2018a) Global warming transforms coral reef assemblages. Nature 556:492-496

Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison H, Hobbs J-PA, Hoey AS, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett M, Schoepf V, Torda G, Wilson SK (2018b) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359:80-83

Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH, Babcock RC, Beger M, Bellwood DR, Berkelmans R, Bridge TC, Butler IR, Byrne M, Cantin NE, Comeau S, Connolly SR, Cumming GS, Dalton SJ, Diaz-Pulido G, Eakin CM, Figueira WF, Gilmour JP, Harrison HB, Heron SF, Hoey AS, Hobbs J-PA, Hoogenboom MO, Kennedy EV, Kuo C-y, Lough JM, Lowe RJ, Liu G, McCulloch MT, Malcolm HA, McWilliam MJ, Pandolfi JM, Pears RJ, Pratchett MS, Schoepf V, Simpson T, Skirving WJ, Sommer B, Torda G, Wachenfeld DR, Willis BL, Wilson SK (2017) Global warming and recurrent mass bleaching of corals. Nature 543:373-377

Jouffray J-B, Nyström M, Norström AV, Williams ID, Wedding LM, Kittinger JN, Williams GJ (2015) Identifying multiple coral reef regimes and their drivers across the Hawaiian archipelago. Philos Trans R Soc Lond, Ser B: Biol Sci 370:20130268

Kenyon JC, Vroom PS, Page KN, Dunlap MJ, Wilkinson CB, Aeby GS (2006) Community structure of hermatypic corals at French frigate shoals, Northwestern Hawaiian Islands: Capacity for resistance and resilience to selective stressors. Pac Sci 60:153-175

Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, van Woesik R (2001) Coral bleaching: the winners and the losers. Ecol Lett 4:122-131

Minton D, Lundgren I (2006) Coral Recruitment and Sedimentation in Asan Bay and War in the Pacific NHP, Guam (N. P. Service, Ed.; pp. 1–28). National Park Service.

Norström AV, Nyström M, Lokrantz J, Folke C (2009) Alternative states on coral reefs: beyond coral - macroalgal phase shifts. Mar Ecol Prog Ser 376:295-306

Norström AV, Nyström M, Jouffray J-B, Folke C, Graham NAJ, Moberg F, Olsson P, Williams GJ (2016) Guiding coral reef futures in the Anthropocene. Front Ecol Environ 14:490-498

Okubo N, Motokawa T, Omori M. (2006) When fragmented coral spawn? Effect of size and timing on survivorship and fecundity of fragmentation in *Acropora formosa*. Marine Biology, 151(1), 353–363. https://doi.org/10.1007/s00227-006-0490-2

Raj KD, Aeby GS, Mathews G, Williams GJ, Caldwell JM, Laju RL, Selva Barath M, Dinesh Kumar P, Arasamuthu A, Gladwin Gnana Asir N, Wedding LM, Davies AJ, Moritsch MM, Patterson Edward JK . (2021) Coral reef resilience differs among islands within the Gulf of Mannar, southeast India, following successive coral bleaching events. Coral Reefs 40, 1029-1044. https://doi.org:10.1007/s00338-021-02102-0

Randall R. 1971. Tanguisson-Tumon, Guam reef corals before, during and after the crown-of-thorns starfish (*Acanthaster planci*) predation. UOGML Technical Report. 119 pp.

Raymundo, LJ, Burdick, D, Lapacek, VA, Miller, R, Brown, V. 2017. Anomalous temperatures and extreme tides: Guam staghorn *Acropora* succumb to a double threat. Marine Ecology Progress Series. 564:47-55.

Raymundo LJ, Burdick D, Hoot WC, Miller RM, Brown V, Reynolds T, Gault J, Idechong J, Fifer J, Williams A (2019) Successive bleaching events cause mass coral mortality in Guam, Micronesia. Coral Reefs 38:677-700

Richardson LE, Graham NAJ, Hoey AS (2017a) Cross-scale habitat structure driven by coral species composition on tropical reefs. Scientific Reports 7:7557

Richardson LE, Graham NAJ, Pratchett MS, Hoey AS (2017b) Structural complexity mediates functional structure of reef fish assemblages among coral habitats. Environ Biol Fishes 100:193-207

Richardson LE, Graham NAJ, Pratchett MS, Eurich JG, Hoey AS (2018) Mass coral bleaching causes biotic homogenization of reef fish assemblages. Global Change Biol 24:3117-3129

Robinson JPW, Wilson SK, Robinson J, Gerry C, Lucas J, Assan C, Govinden R, Jennings S, Graham NAJ (2019) Productive instability of coral reef fisheries after climate-driven regime shifts. Nature Ecology & Evolution 3:183-190

Shenkar N, Fine M, Loya Y (2005) Size matters: bleaching dynamics of the coral Oculina patagonica. Marine Ecology-Progress Series 294:181-188

Stuart-Smith RD, Brown CJ, Ceccarelli DM, Edgar GJ (2018) Ecosystem restructuring along the Great Barrier Reef following mass coral bleaching. Nature 560:92-96

Szmant-Froelich, A., Szmant, A., Szmant-Froelich, A., & Szmant, A. (1985). The effect of colony size on the reproductive ability of the Caribbean coral *Montastrea annularis* (Ellis and Solander). Fifth International Coral Reef Congress, 4, 295–300.

van Hooidonk R, Maynard JA, Tamelander J, Gove JM, Ahmadia G, Raymundo L, Williams GJ, Heron SF, Planes S (2016) Local-scale projections of coral reef futures and implications of the Paris Agreement. Scientific Reports 6:39666

Tusso S, Morcinek K, Vogler C, Schupp P J, Caballes C F, Vargas S, Wörheide G. 2016. Genetic structure of the crown-of-thorns seastar in the Pacific Ocean, with focus on Guam. PeerJ, 2016(5). https://doi.org/10.7717/peerj.1970

Williams GJ, Graham NAJ (2019) Rethinking coral reef functional futures. Funct Ecol 33:942-947

Williams GJ, Knapp IS, Maragos JE, Davy SK (2010) Modeling patterns of coral bleaching at a remote Central Pacific atoll. Mar Pollut Bull 60:1467-1476

Williams GJ, Graham NAJ, Jouffray J-B, Norström AV, Nyström M, Gove JM, Heenan A, Wedding LM (2019) Coral reef ecology in the Anthropocene. Funct Ecol 33:1014-1022

Woodhead AJ, Hicks CC, Norström AV, Williams GJ, Graham NAJ (2019) Coral reef ecosystem services in the Anthropocene. Funct Ecol 33:1023-1034

Zawada KJA, Madin JS, Baird AH, Bridge TCL, Dornelas M (2019) Morphological traits can track coral reef responses to the Anthropocene. Funct Ecol 33:962-975

APPENDICES

Appendix 1. Coral colony density values (number colonies / m^2) by species across sites and years.

	GUA-390		GUA-391		GUA-401		GUA-410		GUA-490		GUA-579		GUA-583		GUA-600	
Species	**2013**	**2017**	**2013**	**2017**	**2013**	**2017**	**2013**	**2017**	**2013**	**2017**	**2013**	**2017**	**2013**	**2017**	**2013**	**2017**
Acanthastrea echinata	1.14	2.57	1.14	1.76	1.14	1.65	1.52	2.70		1.98	2.41	4.24	2.09	2.67	1.71	2.53
Acropora abrotanoides	1.14	1.65						1.65			1.22		1.14	1.65	1.52	1.65
Acropora azurea	1.14							1.65			2.05		1.71		4.68	
Acropora cf. *humilis*	1.14			1.65	1.14	1.65		1.65		3.30	1.14	1.65		1.65	1.14	1.65
Acropora cf. *nasuta*	1.14	1.65		1.65							1.14				1.14	
Acropora cophodactyla															1.71	
Acropora digitifera	1.14															
Acropora globiceps	1.14				1.14	1.65							1.14		1.14	1.65
Acropora latistella				1.65												
Acropora monticulosa															1.14	
Acropora obtusicaulis															1.14	
Acropora palmerae-minuta	1.14				1.14								3.42		1.14	
Acropora quelchi								1.65								
Acropora secale			1.14					1.65			2.28		1.14	2.48	1.14	1.65
Acropora sp.-*caespitose*	1.14				1.14	1.65	1.14	1.65	1.14	1.65	1.14	3.30	2.63	1.89	5.20	2.94
Acropora sp.-*corymbose*	1.14	1.65	1.14			1.65	1.14	2.10	1.14	1.65	1.14		1.14	1.65	1.71	2.31
Acropora surculosa	1.14	1.65		1.65			1.14	1.65			1.60			1.65	1.39	
Acropora verweyi	1.14			1.65							1.14		2.60		6.82	1.65
Astrea curta	1.14	1.65	1.14	1.65	1.14		1.33	2.20			2.97	4.29	7.76	4.04	3.57	6.76
Astreopora myriophthalma			2.28	1.65				1.65								
Astreopora sp.			1.52	1.82	1.68	3.44	1.14	1.65	1.14	3.30	1.14	3.15	1.39	2.62	2.66	2.10
Cyphastrea sp.	2.28	2.48	1.14	2.36	1.14	4.04	1.14	5.16	1.14	4.63	3.42	7.79	2.56	3.49	1.14	6.19
Diploastrea heliopora					1.14											
Dipsastraea pallida			1.14													
Dipsastraea sp.	1.60	2.96	2.25	2.93	1.19	2.20	4.40	6.41	1.94	1.65	3.69	4.35	3.03	5.96	1.69	3.69
Echinophyllia sp.												1.65				
Echinopora lamellosa								4.96				1.65				4.96
Euphyllia glabrescens								1.65								
Favites flexuosa	1.14			1.65		1.65		3.30				3.30			2.28	
Favites russelli	1.14	2.11	1.14	3.76	1.14	1.95	1.80	3.59	1.90	3.30	2.47	3.88	4.48	4.42	1.42	3.63
Fungia sp.									1.77	2.40						
Galaxea fascicularis	8.45	9.19	4.02	9.67	1.90	2.48	2.23	3.25	1.93	3.92	1.90	3.30	6.55	8.26	3.46	4.56
Gardineroseris planulata		3.30							1.14							
Goniastrea edwardsi		1.65	1.90		1.90	1.65	1.14	4.75	1.14	1.65	1.28	2.94		1.78	2.28	3.54
Goniastrea pectinata		1.65				3.30	1.14	2.48				1.65				
Goniastrea retiformis	4.56	7.78	2.22	5.51	1.37	1.65	1.92	5.67	1.80	3.41	2.11	2.77	1.94	2.33	2.36	3.54
Goniastrea sp.		2.48		1.65			1.14	1.65		6.61	1.14					1.65
Goniastrea stelligera	1.37	2.52	1.14	2.60	1.42	1.65	2.35	3.19	1.14	2.06	1.14	1.98	2.41	2.42	1.52	2.40
Goniopora fruticosa			1.37	6.47	1.42	1.65			1.14	1.65	1.14	2.34				1.65
Goniopora sp.		1.65	1.37		1.14					1.65	1.14	4.81				6.19
Heliopora coerulea		1.65	1.14			1.65			2.94	2.54	1.14	1.65		2.06	1.14	1.65
Hydnophora microconos					1.14			1.65		1.65	1.14	1.65	1.57	2.62	1.46	4.40
Isopora palifera													1.42	1.65		
Leptastrea purpurea		3.30	3.90													
Leptastrea sp.	1.95	6.61	2.11	6.94	4.24	7.43	4.47	10.44	1.68	3.51	2.61	5.22	6.10	4.29	2.53	6.42
Leptoria phrygia	1.71	5.51	1.80	3.73	1.42	2.20	4.81	7.09	1.71	1.65	2.37	3.00	1.14	2.51	1.84	3.83
Lobophyllia corymbosa									1.14							
Lobophyllia hemprichii		1.65					1.14			1.65						
Millepora platyphylla	1.39	3.58	1.25	2.40		1.65	1.14	1.65			2.85		4.56		1.14	1.65
Montipora sp.	1.52	2.15	1.63	1.65	1.91	3.25	1.14	2.29	2.28	2.48	3.28	2.68	4.89	3.92	3.62	3.30
Pavona bipartita									2.18	3.58						
Pavona chiriquiensis	3.87	4.29	1.60	2.06	1.63	1.65		2.75	2.47	3.30		1.65	8.46	3.96		1.65
Pavona divaricata									2.28							
Pavona duerdeni		3.30		1.65	1.14			1.65	1.71	1.65	2.28	2.48			1.66	4.96
Pavona maldivensis									2.85							
Pavona meandrina				9.91						1.65						4.96
Pavona varians	1.37	2.48	1.37	2.31	1.14	7.16	1.71	3.30	3.09	6.36	1.14	2.48		1.65		3.30
Pavona venosa	3.42		1.14						1.14							3.30
Platygyra daedalea		1.65		2.20	1.14		1.52	2.06	1.14	1.65	1.14	1.65	1.14	3.30	1.14	
Platygyra pini	1.14	2.75	1.14	1.93	1.14	3.30	1.93	2.48	1.52	1.65	2.07	3.07	1.54	3.48	1.42	2.97
Platygyra sp.						1.65	1.14	1.65								
Pocillopora damicornis-acuta			1.14						1.14		1.14	1.65				
Pocillopora elegans				1.65												
Pocillopora grandis				1.65											1.71	1.65
Pocillopora sp.	2.31	1.96	1.14	1.91	1.55	1.77	1.14	2.46		2.40	2.15	2.41	1.14	1.76	1.45	1.75
Pocillopora verrucosa			1.14													
Porites annae		3.07	1.14	3.30			1.14	6.61								
Porites deformis	1.60	8.48	2.85	2.36	1.14	1.65	1.14		1.14	4.26					1.14	
Porites densa		1.65												1.65		
Porites lichen																1.65
Porites rus	2.23	7.15	4.35	10.27	1.42	3.42	1.71	6.06	8.60	5.11		1.65		1.65	2.28	
Porites sp.-encrusting													2.85		1.14	
Porites sp.-massive	1.52	3.51	2.41	5.16	4.09	6.09	2.37	4.53	2.28	3.11	1.49	3.09	1.59	3.63	2.21	4.49
Porites sp.-other	1.71		2.28	3.72	1.27	1.65	1.14	2.20	2.85	3.23				1.65	1.14	
Porites sp.-submassive		1.65	2.72	1.65	1.14	1.87		1.65	1.90	1.65	3.06	2.40	1.14	1.65	2.16	2.48
Porites vaughani									1.14	1.65						
Psammocora profundacella			1.71													
Psammocora sp.	1.57	7.33	2.01	3.78	1.37	1.65	1.37	3.41	1.97	6.54	1.14	1.65	2.05	4.01		3.30
Stylocoeniella armata				1.65						2.70						
Stylophora mordax					1.71	2.42			1.60	1.65	1.14	1.65		1.65	1.14	
Unidentified coral	1.90	2.25	1.88	2.45	1.71	2.30		2.00	1.63	3.15	1.52	1.65		2.91	1.14	2.20

Appendix 2. Coral colony density values (number colonies / m^2, **colonies < 5cm removed**) by species across sites and years.

	GUA-390		GUA-391		GUA-401		GUA-410		GUA-490		GUA-579		GUA-583		GUA-600	
	2013	2017	2013	2017	2013	2017	2013	2017	2013	2017	2013	2017	2013	2017	2013	2017
Acanthastrea echinata	1.14	1.65	1.14	1.65	1.14		1.14	1.84		1.65	2.10	2.88	1.54	1.65	1.14	2.36
Acropora abrotanoides	1.14	1.65						1.65			1.23		1.14	1.65	1.52	1.65
Acropora azurea	1.14							1.65			2.28		1.63		4.22	
Acropora cf. *humilis*	1.14			1.65	1.14	1.65		1.65		3.30	1.14	1.65		1.65	1.14	1.65
Acropora cf. *nasuta*	1.14	1.65		1.65							1.14				1.14	
Acropora cophodactyla															1.71	
Acropora digitifera	1.14															
Acropora globiceps	1.14				1.14								1.14		1.14	1.65
Acropora latistella				1.65												
Acropora monticulosa															1.14	
Acropora obtusicaulis															1.14	
Acropora palmerae-minuta	1.14				1.14								2.28		1.14	
Acropora secale			1.14					1.65			2.28		1.14	1.65	1.14	1.65
Acropora sp.-*caespitose*	1.14				1.14	1.65			1.14		1.14	3.30	2.41	1.79	4.80	2.73
Acropora sp.-*corymbose*	1.14	1.65						2.06	1.14	1.65	1.14		1.14	1.65	1.57	2.31
Acropora surculosa	1.14	1.65		1.65			1.14	1.65			1.60			1.65	1.39	
Acropora verweyi	1.14										1.14		2.66		6.03	1.65
Astrea curta	1.14	1.65		1.65	1.14		1.14	1.65			2.21	2.81	3.74	2.48	2.71	3.30
Astreopora myriophthalma			2.28					1.65								
Astreopora sp.			1.71	1.65	1.54	2.48	1.14	1.65	1.14	2.48	1.14	2.55	1.27	1.94	2.28	1.95
Cyphastrea sp.	2.28	2.48	1.14	2.10	1.14	2.48	1.14	5.95	1.14	3.30	2.28	2.97	1.85	2.33	1.14	3.95
Diploastrea heliopora					1.14											
Dipsastraea pallida			1.14													
Dipsastraea sp.	1.46	2.84	1.37	1.98	1.14	1.65	2.57	4.46	1.14	1.65	2.79	2.91	2.32	3.33	1.48	2.59
Echinophyllia sp.												1.65				
Echinopora lamellosa								3.30				1.65				4.96
Favites flexuosa	1.14					1.65		1.65				1.65			2.28	
Favites russelli	1.14	1.65	1.14	3.30	1.14	1.65	1.49	2.48	1.60	2.83	1.28	1.79	1.97	2.43	1.14	1.65
Fungia sp.									1.57	1.65						
Galaxea fascicularis	7.10	7.01	3.66	7.31	1.71	2.48	2.16	2.54	1.39	2.54	1.61	2.64	5.53	2.89	2.49	3.40
Gardineroseris planulata		3.30							1.14							
Goniastrea edwardsi					1.14		1.14	3.15	1.14	1.65	1.28	2.57		1.84	2.28	1.93
Goniastrea pectinata						1.65	1.14	1.65				1.65				
Goniastrea retiformis	3.82	4.91	1.74	3.57	1.52		1.71	4.69	1.39	2.80	1.86	2.67	1.39	1.98	2.19	2.66
Goniastrea sp.				1.65			1.14	1.65								1.65
Goniastrea stelligera	1.14	2.20	1.14	2.48	1.52		1.76	2.28	1.14	1.65	1.14	1.65	1.77	2.41	1.14	2.10
Goniopora fruticosa			1.37	4.45	1.42	1.65				1.65	1.14	2.10				1.65
Goniopora sp.		1.65	1.14		1.14					1.65	1.14	3.11				4.13
Heliopora coerulea		1.65	1.14						1.99	2.20	1.14	1.65		1.65	1.14	1.65
Hydnophora microconos					1.14			1.65		1.65	1.14	1.65	1.42	2.42	1.46	3.30
Isopora palifera													1.42	1.65		
Leptastrea purpurea		1.65	2.63													
Leptastrea sp.	1.71	3.30	1.85	2.62	3.06	2.33	2.95	4.70	1.14	1.89	2.47	2.97	2.28	3.41	1.57	2.75
Leptoria phrygia	1.61	4.54	1.75	3.26	1.14	2.48	4.14	6.41	1.71	1.65	2.18	2.80	1.14	2.45	1.57	2.84
Lobophyllia corymbosa									1.14							
Lobophyllia hemprichii		1.65					1.14									
Millepora platyphylla	1.39	2.89	1.25	1.95		1.65	1.14	1.65			2.85		1.90		1.14	1.65
Montipora sp.	1.52	2.01	1.33	1.65	1.83	2.28	1.14	2.03	2.28	2.36	2.75	2.68	3.40	3.85	3.34	2.97
Pavona bipartita									2.02	2.64						
Pavona chiriquiensis	2.85	4.96	1.14	1.65	1.33			2.48	1.71	1.65			3.70	2.64		
Pavona divaricata									1.14							
Pavona duerdeni				1.65	1.14			1.65	1.90	1.65	1.71	2.48			1.55	2.48
Pavona maldivensis									2.56							
Pavona meandrina				4.96						1.65						3.30
Pavona varians	1.37	2.20	1.14	1.65	1.14	2.20	1.52	3.30	2.80	4.34	1.14	1.65				1.65
Pavona venosa	3.04		1.14						1.14							1.65
Platygyra daedalea		1.65		2.20	1.14		1.71	2.06	1.14	1.65	1.14	1.65	1.14	1.65	1.14	
Platygyra pini	1.14	2.39	1.14	1.65	1.14	1.65	1.82	2.15	1.14	1.65	1.86	2.60	1.44	2.55	1.52	2.97
Platygyra sp.							1.14	1.65								
Pocillopora damicornis-acuta									1.14		1.14	1.65				
Pocillopora elegans				1.65												
Pocillopora grandis				1.65											1.71	1.65
Pocillopora sp.	2.34	1.65		2.48	1.37	1.93	1.14	1.99		1.98	1.97	1.90	1.14	1.65	1.40	1.65
Pocillopora verrucosa			1.14													
Porites annae		2.81	1.14	1.65			1.14	1.65								
Porites deformis	1.60	4.60	1.71	1.65	1.14		1.14		1.14	3.30					1.14	
Porites densa		1.65														
Porites rus	2.05	4.46	3.74	5.70	1.42	1.98	1.76	4.17	6.34	3.97		1.65		1.65	1.14	
Porites sp.-encrusting													2.85		1.14	
Porites sp.-massive	1.42	2.60	2.14	3.54	3.59	3.53	2.00	3.27	2.62	2.80	1.33	2.36	1.42	3.30	1.85	3.34
Porites sp.-other	1.33		1.14	1.65	1.14					1.65					1.14	
Porites sp.-submassive		1.65	2.34	1.65	1.14	1.82		1.65	1.14	1.65	2.39	1.65	1.14	1.65	1.77	2.24
Psammocora profundacella			1.14													
Psammocora sp.	1.57	3.10	1.84	2.51	1.14	1.65	1.37	3.14	1.66	4.58	1.14	1.65	1.82	3.30		2.02
Stylophora mordax					1.78	1.78			1.37	1.65	1.14	1.65		1.65	1.14	
Unidentified coral	2.28	1.65	1.60	1.98	1.67	2.06		1.65	1.82	2.27	1.42	1.65		3.30	1.14	1.65