



# Coral bleaching variability during the 2017 global bleaching event on a remote, uninhabited island in the western Pacific: Farallon de Medinilla, Commonwealth of the Northern Mariana Islands

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**ABSTRACT.**—A survey conducted in Fall 2017 by US Navy scientists around the small, uninhabited island of Farallon de Medinilla (FDM) documented severe bleaching related to extended regional heat stress. Three of the dominant scleractinian genera at FDM, *Pocillopora*, *Leptastrea*, and *Astreopora*, were severely impacted, with more than 90% of colonies from many species exhibiting bleaching. In contrast, several species of *Porites* corals, another dominant genus at FDM, fared better, with less bleaching (7%–68% by species) than the island average (78%). Bleaching was somewhat higher at shallower depths (<10 m depth stratum, compared to 10–20 m depth stratum) and on the leeward of the island. Surveying FDM presented logistical challenges including a compressed time window for survey execution, periods of strong currents >1 knot that precluded diving, rare but potentially hazardous ordnance items, survey requirements for georeferenced imagery, and quantitative data collection. The survey protocol designed to accommodate these challenges is presented here, as are lessons from an unsuccessful attempt to delineate bleached coral colonies in photographs using automated object-based image analysis.

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Scleractinian (hard) corals contain symbiotic dinoflagellate algae of the genus *Symbiodinium*, which supply the majority of energy required by most host corals for metabolism, growth, calcification, and reproduction (Roth 2014). This symbiotic relationship drives the relatively high productivity of coral ecosystems in oligotrophic portions of the oceans, although corals also feed heterotrophically to different extents, which vary across time and space (Houlbrèque and Ferrier-Pagès 2009). Despite its importance, the coral-*Symbiodinium* symbiosis is tenuous and can be disturbed by a range of stressors, leading corals to expel their symbionts and become “bleached” (e.g., Brown 1997). Bleached corals can die from starvation (Anthony et

al. 2009) or disease (Brandt and McManus 2009); cellular damage from heat stress that causes bleaching can also drive coral mortality (Jones 2008, Ainsworth et al. 2011). On large spatial scales, mass bleaching events are recognized as historically new phenomena driven by warm-water stress associated with heat waves driven by El Niño events and/or global warming (Hughes et al. 2018). Coral mortality associated with these mass bleaching events is widely recognized as the major threat to coral survival worldwide (Hoegh-Guldberg 2011).

Given the global importance of reef-building corals (*see* Knowlton 2001), understanding, predicting, and, ultimately, preventing coral bleaching is a critical topic in marine science research, with many hundreds of scientific articles published describing coral bleaching from the scale of subcellular physiology to global-scale observations. From this body of work, evidence has emerged that demonstrates a number of factors that contribute to coral resistance and resilience (survival and recovery) to bleaching, ranging from the physiology of individual corals to ecological conditions. Indeed, the response of corals to a given warm-water event is highly variable both between and within species, and ultimately these differences are expected to lead to changes in coral reef communities as bleaching events become more common (e.g., van Woesik et al. 2011). Here, a brief overview of the general understanding of factors that affect coral bleaching is provided, to place into context the observational data reported below.

Coral bleaching is generally considered a response to the toxic buildup of oxygen radicals produced by overactive photosynthesis in *Symbiodinium* (Weis 2008), triggered on reef-wide and larger scales by warm water and/or light stress (Roth 2014). Physical oceanographic conditions on a range of scales influence the stress that corals experience; enhanced water movement at reef- and island-scales can reduce overall heat stress by stirring up cooler, deeper water (Storlazzi et al. 2013, Wall et al. 2015) and on fine scales can reduce boundary layers and increase diffusion of damaging oxygen radicals from corals (Nakamura and Van Woesik 2001, Marshall and Schuttenberg 2006). Other co-occurring stressors can also affect bleaching response; for example, nutrient enrichment appears to exacerbate bleaching (Wooldridge 2009), possibly by increasing *Symbiodinium* populations and thus production of reactive oxygen under heat and/or light stress (Cunning and Baker 2013). In contrast, suspended sediment can in some circumstances alleviate bleaching by reducing light stress and/or by providing an alternative source of food particles to bleached corals (Anthony et al. 2007). Differences in coral physiology also affect coral survival through bleaching events; corals with more fat stores (Grottoli et al. 2004) and/or those that can maintain energy by increasing heterotrophy (Grottoli et al. 2006) may survive better than others. Some corals may resist bleaching by increased production of photoprotective compounds that reduce light transmission to symbionts (Smith et al. 2013), or survive by preventing physiological damage through production of heat shock proteins and other compounds (Baird et al. 2009). Taken together, variations in physical and biological conditions across regional to subcolony scales ultimately lead to variability in bleaching responses and survival. This manuscript presents observations of bleaching at a remote island that may serve as a bleaching refuge compared to other islands in the region.

**STUDY SITE.**—Farallon de Medinilla (FDM) is an uninhabited island approximately 2.8 km in length, located in the western Pacific Ocean near the middle of the

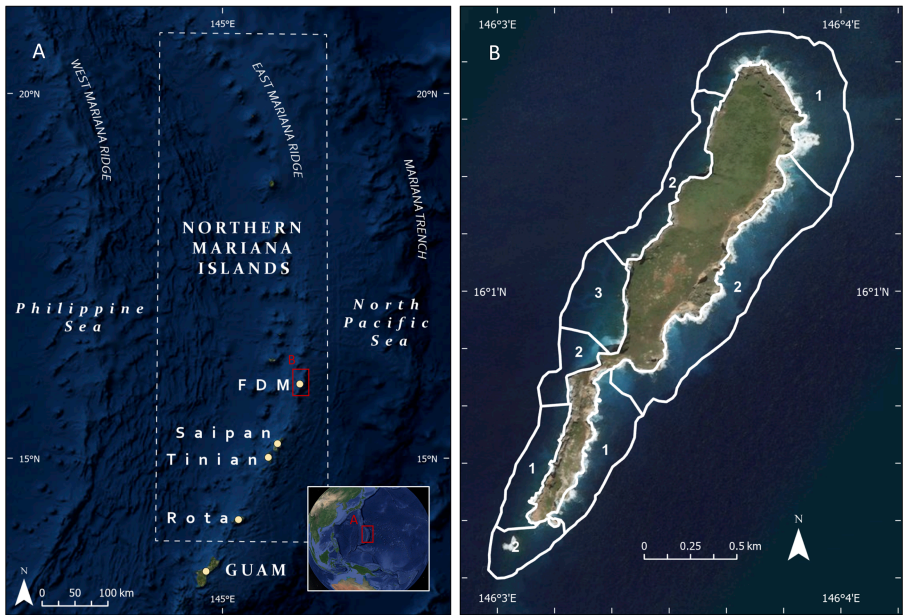


Figure 1. (A) Regional map of the Northern Mariana Islands, with inset indicating location of (A) within the western Pacific Ocean, and (B) aerial view of Farallon de Medinilla (FDM), Commonwealth of the Northern Mariana Islands with generalized habitat types: (1) sediment and rubble with approximately 0% coral cover (not surveyed), (2) scattered coral communities with generally <15% cover, and (3) constructional coral reef with 25%–50% coral cover (Google Earth).

Commonwealth of the Northern Mariana Islands (CNMI) archipelago, 278 km north of Guam and 83 km north of Saipan, the closest inhabited island (Fig. 1A). The island is comprised of limestone that forms plunging cliffs on all sides. Underwater, previously eroded cliff blocks and exposed limestone substrates host variable densities of corals, ranging between approximately 0% and 50% cover (Figs. 1B and 2). Only one portion of the island contains a classic framework-building constructional coral reef, located near the middle of the leeward (western) side of the island (Fig. 1B). This reef includes specimens of massive *Porites* spp. that exceed 250 cm in their maximum dimension and could be several hundred years old (McCutcheon et al. 2015).

FDM is a physically unprotected island located within one of the most active typhoon regions in the world. It is routinely subject to extreme waves and strong currents (Smith and Marx 2016). Buoy data from two stations north of Saipan and Guam show that most wave energy approaches this region from the northeast, with average annual significant wave heights of approximately 1.5–2 m and maximum significant wave heights exceeding 6 m in some time periods (Coastal Data Information Program 2020). In this region, typhoons generally approach from the southeast and rarely from other directions; thus as with typical wave impacts, the western portion of the island is more protected from typhoon impacts (Joint Typhoon Warning Center 2018).

FDM has been used by the United States Department of Defense (DoD) as a live and inert ordnance training and testing range for the US Navy since 1971. The DoD funded 14 marine ecological surveys at FDM between 1997 and 2012, including

7 surveys conducted by scientists from the National Oceanic and Atmospheric Administration (NOAA), the US Fish and Wildlife Service, the CNMI government, and the University of Hawaii; as summarized in Smith and Marx (2016), those surveys found little to no evidence of negative impacts to corals associated with ordnance use at the island. Indeed, Smith and Marx (2016) showed that DoD training activities and a three-mile restricted access zone around the island had served as a deterrent to fishers between 1997 and 2010, with healthier fish populations compared to those at inhabited islands in the region. Qualitative fish community and behavior observations by US Navy scientists in 2012 and 2017 and personal communication with four Saipan residents, who requested not to be identified, indicate that the island has been periodically targeted by commercial spearfishers visiting from inhabited islands since approximately 2010. However, using limited unbaited video of fish assemblages captured in 2017, Houk and Hernandez-Ortiz (2019) found that “healthy fish populations may exist” at FDM, despite this more recent targeted spearfishing. In addition to relatively reduced fishing pressure, the island is not affected by other local-scale anthropogenic impacts such as anchor damage, improper refuse disposal, or sewage, agricultural, and roadway runoff, which can affect reefs adjacent to inhabited islands. These factors have overall created a *de facto* marine protected area at FDM (Smith and Marx 2016).

**HEAT STRESS HISTORY AND BLEACHING ASSESSMENT.**—Marine resources were surveyed at FDM approximately annually between 1997 and 2012 and in 2017, with particular focus on assessing impacts from DoD training (Online Supplementary Material). Over this time period, satellite-estimated water temperatures from the Northern Mariana Islands Coral Reef Watch Virtual Station indicated that bleaching was likely (Alert Level 1) at FDM in 2001, 2003, 2007, 2009, and 2016, and that more severe coral bleaching and mortality was likely (Alert Level 2) at FDM in 2013, 2014, and 2017 (Coral Reef Watch 2013, Liu et al. 2013). Prior to the 2017 survey, when extensive bleaching was recorded, the only other year during which bleaching was observed at FDM was 2007; however, surveys were not conducted between 2013 and 2016. The 2017 FDM survey coincided with the second of two peaks of heat stress that occurred in this region in 2017 (Online Supplement Fig. 1), and was the strongest heating event registered until that time by the Northern Mariana Islands Coral Reef Watch Virtual Station (Coral Reef Watch 2013, Liu et al. 2013). By 1 October, the final day of this survey, the Northern Mariana Islands had experienced more than 10 wks (73 d) of heat stress that exceeded 4 Degree Heating Weeks (DHW; Alert Level 1), above which coral bleaching is likely, and more than 7 wks (54 d) of heat stress that exceeded 8 DHW (Alert Level 2), above which coral mortality is likely (Coral Reef Watch 2013, Liu et al. 2013). The 2017 FDM survey was conducted primarily to assess the condition of Endangered Species Act (ESA) listed corals and coral reef habitat at FDM (Online Supplementary Material). However, because the survey coincided with a strong regional bleaching event associated with the latter portion of a lengthy worldwide bleaching event that stretched from 2014 to 2017 (Eakin et al. 2019), further analysis was conducted to assess how corals at FDM responded to this regional bleaching event. Differences in bleaching response across FDM between taxa as well as depth, exposure, and generalized habitat survey strata are presented here. These results are then discussed in context of the coral bleaching literature.



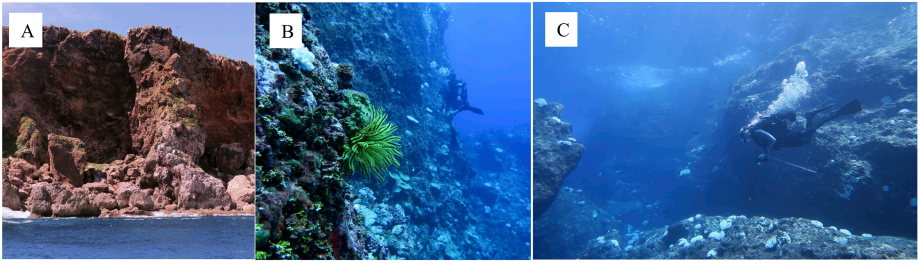


Figure 2. (A) Typical view of FDM seacliffs. (B) Underwater plunging seacliffs. (C) Example FDM underwater scene with scattered corals on eroded cliff blocks.

As part of data reanalysis for this manuscript, object-based image analysis (OBIA) was tested to determine if that approach could automate coral bleaching analysis. In contrast to pixel-based image analysis, OBIA groups pixels into spatially contiguous segments or objects in order to achieve image classification. This approach is increasingly used in automated habitat classification and mapping, especially in ultra-high spatial resolution imagery, with demonstrated superior results compared to pixel-based analysis approaches (Blaschke et al. 2014). The imagery-intensive approach used in this study, used to maximize survey coverage within a restricted time window, would benefit from automated analysis methods to reduce the labor involved in manual annotation of large amounts of imagery.

## MATERIALS AND METHODS

**DIVE SURVEY.**—The marine survey was conducted from 27 September to 1 October, 2017, during a short time window of 5 d when the training range was closed. The survey was staged from a large vessel that held station on the lee of the island, and dives were conducted between the submerged cliff and up to 300 m offshore from a more maneuverable rigid hull inflatable boat (RHIB). Navy marine ecologists were accompanied by US Navy Explosive Ordnance Disposal (EOD) divers during the survey to ensure safety. Divers were equipped with tank-mounted diver propulsion devices during some of the dives in more exposed areas. Fair weather and moderate sea state conditions during the survey period enabled all areas around the island to be surveyed.

The survey protocol was designed to gather quantitative data despite challenging oceanographic and logistical constraints. The protocol thus included in situ rapid assessment combined with collection of scaled and georeferenced photographs that could be analyzed postsurvey and archived for future reference. The survey focused on coral-bearing substrates to assess species composition and coral condition, and included directed searches for ESA-listed corals, the major regulatory driver for this survey (Online Supplementary Material). Regions dominated by unconsolidated sediment were not surveyed in 2017 (Region 1 in Fig. 1B, Online Supplemental Fig. 2).

One underwater camera was fitted with a 94 cm metal monopod (Fig. 2) to set the perpendicular offset distance and acquire scaled photoquadrat images of the benthos. Photoquadrats collected using the monopod produced an image footprint of  $1.5 \times 1.0$  m based on camera parameters and offset distance, when the camera was oriented nadir to the sea floor. Photoquadrats were placed every few meters along

Table 1. Summary of transects and photoquadrats completed during 2017 FDM survey within each stratum compared across different physical categories, with total transects and photoquadrats for each category/stratum set. As used in this survey, depths of 10 m or less were defined as shallow; depths between 10 and 20 m were defined as deep. The north, east, and south sides of the island were considered exposed; the west side was considered sheltered.

Physical category	Stratum	Transects	Photoquadrats
Depth	Deep	18	261
	Shallow	30	413
Physical exposure	Exposed	23	332
	Sheltered	25	342
Generalized reef type	Coral communities	43	605
	Constructional reef	5	69
Total per physical category		48	674

diver-defined survey transects to capture image data in representative areas that supported live coral cover. Transects were oriented roughly parallel to the shoreline at 6–20 m depths, and located to cover as much of the island as possible, excluding regions without corals (Table 1, Online Supplemental Fig. 2; Carilli et al. 2018). Percent cover of hard substrate and coral on hard substrate was visually assessed in situ across each dive site by the same diver throughout the survey period to ensure consistency. Directed searches for ESA-listed species and collection of supplemental coral species photographs using a second underwater camera were conducted during photoquadrat transect surveys.

Each diver wore an acoustic transponder to provide range and bearing from the dive boat, which was equipped with the fixed base transponder of a micro ultra-short baseline (USBL) underwater positioning system (SeaTrac by Blueprint Subsea). A topside computer and specialized software (NavPoint by Blueprint Subsea) converted diver relative positions into geographic coordinates (latitude and longitude) during the dives. Dive tracks, saved as National Marine Electronics Association (NMEA) strings of diver positions associated with timestamps, were captured using the program Tera Term (by Tera Term Project). Photographs taken by the divers were then georeferenced to these diver location tracks via timestamp matching, using the program HoudahGeo (by Houdah Software).

MANUAL IMAGE ANALYSIS.—In photoquadrat images, scleractinian coral colonies that could theoretically be identified were annotated with a number. A total of 3498 coral colony targets were annotated on 674 photoquadrats representing 48 transects in the study (Table 1). Subsequently, colonies were identified to the lowest possible taxonomic level by visual comparison of survey imagery with photographs, descriptions in the published literature including Veron (2000), Veron et al. (2018), and Wallace (1999), and species lists for the Mariana Islands in Randall (1995). A custom document was also compiled with example images of individual species from the survey and closest match identifications based on visual comparison to published literature. This document and independent analysis of the same group of photographs by at least two analysts were used to check the accuracy of taxonomic identifications. Health status of corals was assessed by visually interpreting coral condition in imagery and assigning each coral colony to one of seven categories: healthy, pale, mottled, bleached, diseased, broken, or recently dead. Taxa names and health status were then recorded in spreadsheets (Carilli et al. 2018).

**OBJECT-BASED IMAGE ANALYSIS.**—We conducted preliminary tests of OBIA algorithms using eCognition software (Trimble Navigation Ltd) on a subset of imagery with the aim of delineating coral colonies and classifying them as 100% bleached, partially bleached, or not bleached. Tests focused on exploiting color and texture differences in RGB imagery using multiresolution segmentation and tests of the scale parameter in controlling the delineation of object “primitives” (homogenous pixel groups).

**DATA ANALYSIS.**—Statistical analysis was conducted in R v3.4.3 (R Core Team 2018). To test whether there were significant associations between coral taxa and health status, proportions of corals in any given taxa that were unhealthy (bleached, pale, mottled, diseased, dead, or broken) vs healthy were compared across taxa using a chi-squared test ( $df = 79$ ), and the significance of the resulting chi-squared value was evaluated using the `pchisq` function. For this analysis, most taxa were compared at species level, followed by genus level, with one unknown category (see Online Supplemental Table 1). Differences between individual taxa were compared using pairwise chi-squared tests (3160 combinations,  $df = 1$ ,  $P_{\text{critical}} = 1.58 \times 10^{-5}$  using a Bonferroni adjustment). The critical chi-squared value ( $\chi^2_{\text{critical}}$ ) for each pairwise comparison was determined as 18.7 to achieve  $P < P_{\text{critical}}$  using different values for  $\chi^2_{\text{critical}}$  and the `pchisq` function.

To compare bleaching (completely bleached as well as both completely and partially bleached) between surveyed strata [shallow and deep, exposed and protected, within and outside of the constructional reef habitat (Fig. 1)], transect-level averages were used as individual data points and the means of strata were compared using unpaired *t*-tests in R. All datasets compared using *t*-tests were normal according to `shapiro.test` in R.

## RESULTS

**CORAL IDENTIFICATION.**—In total, 3104 coral colonies were identified in the photoquadrat imagery to the lowest possible taxonomic classification and assigned a health status code. Many taxa were determined to be unique species but could not be identified beyond genus (and in one case, not even to genus; Carilli et al. 2018). An additional 393 colonies captured in imagery were not able to be identified due to insufficient image clarity. A total of 3163 coral colonies were assigned health status codes (some colonies were clearly bleached, for example, though we could not identify them).

**PATTERNS OF SPECIES COMPOSITION.**—By frequency, massive *Porites* spp. corals were the most abundant at FDM during the 2017 survey (21.6% of all colonies), followed by *Pocillopora meandrina* (13.8% of all colonies) and *Leptastrea purpurea* (9.4% of all colonies). *Porites* spp. corals were particularly abundant in the constructional reef habitat in the protected lee of the island (36.3% of all colonies in that region) and least abundant within coral communities in exposed portions of the island (16.3% of all colonies in that region), where *P. meandrina* was the most common coral taxon (17.5% of all colonies in that region; coral genera proportions are shown in Fig. 3). Colonies of massive *Porites* spp. within the constructional reef habitat frequently exceeded 150 cm in their maximum dimension and in some cases exceeded 250 cm. Massive *Porites* spp. from Guam showed extension rates ranging from 0.8 to 1.9 cm

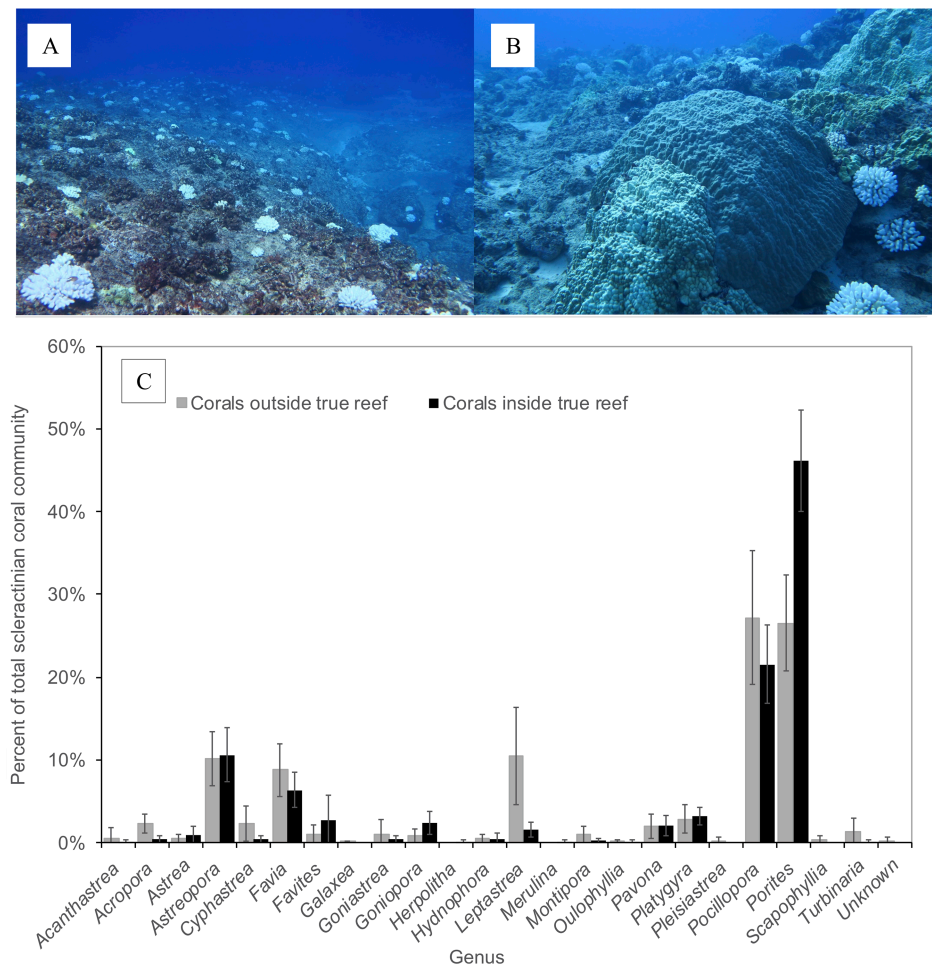


Figure 3. Examples of (A) typical cliff-block substrate around FDM with scattered, nonreef-building coral community, (B) typical portion of the single true coral reef near the center of the lee of the island, (C) abundance of scleractinian coral genera in these two major habitat types at FDM, shown as means where error bars represent standard deviation across transects.

yr<sup>-1</sup> (McCutcheon et al. 2015); if these *Porites* spp. corals at FDM grow at similar rates, the largest colonies could range from approximately 130 to over 300 yrs in age.

**CORAL TAXONOMIC DIVERSITY AND ENDANGERED SPECIES.**—Approximately 89 unique taxa of scleractinian corals were identified at FDM during the 2017 survey. These include 3 likely new, undescribed, species of *Acropora* corals, 11 other species of *Acropora* that could not be identified but are probably not new, 4 *Favia* species, 4 *Favites* species, and 3 *Montipora* species that could not be definitively identified beyond the genus level. One ESA-listed coral (*Acropora globiceps*) was tentatively identified in low abundance (Online Supplement Table 1; Carilli et al. 2018). Several coral colonies were captured in photographs that look very similar to the coral *Pavona diffluens*, which is ESA-listed in the Indian Ocean and Red Sea; that coral is not

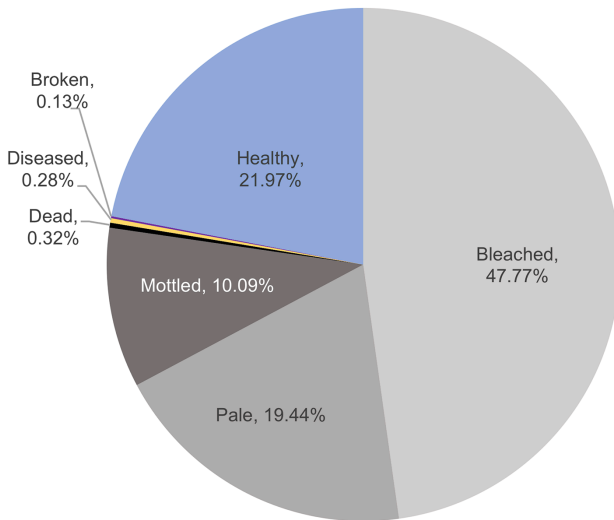


Figure 4. Overall health status of all corals identified in photoquadrat imagery.

officially recognized as existing in the Pacific Ocean and is therefore referred to as *Pavona cf. diffluens* here (Online Supplement Table 1; Carilli et al. 2018).

**CORAL HEALTH AND CONDITION.**—Most corals at FDM were classified as unhealthy during the 2017 survey (78%; Fig. 4). Of these, the largest proportion (47.8%) were completely bleached, followed by pale (19.4%) and mottled (partially bleached; 10.1%). Only a very small number of corals were classified as diseased (0.3%), recently dead (0.3%), or broken (0.1%); thus, some degree of coral bleaching (reduced *Symbiodinium* spp. populations) caused by thermal stress was the major contributor to overall poor coral health status recorded during this survey.

There were significant differences in the proportion of healthy vs unhealthy corals across coral taxa ( $\chi^2 = 1079$ ,  $df = 79$ ,  $P = 2.5 \times 10^{-175}$ ), with some taxa exhibiting a larger proportion of unhealthy or healthy corals than the overall average across the island. Of the 3160 pairwise comparisons between individual coral taxa, 338 pairs were significantly different. Most of these differences were driven by *Pocillopora* spp., *Astreopora* spp., and *L. purpurea* having higher proportions of unhealthy corals compared to other taxa (e.g., 97.9% of *P. meandrina* were unhealthy, with 93.9% fully bleached), and by colonies of *Favia* spp., *Porites* spp., and one *Favites* species, which were observed to be generally healthier compared to other taxa (e.g., *Porites rus* was only 6.9% unhealthy; Table 2).

For corals that were 100% bleached, no differences were observed with depth, however fewer corals were 100% bleached in the exposed stratum than the protected stratum (Table 3, Fig. 5). When considering all levels of bleaching (100% bleached, mottled, and pale, combined), significantly fewer corals in both the deeper and more exposed strata were bleached (Table 3, Fig. 5). No significant differences in bleaching were detected between corals in the constructional reef habitat and distributed coral community habitats.



Table 2. Summary of chi-squared ( $\chi^2$ ) test results for those coral taxa (column 1) where the observed proportion of unhealthy colonies either exceeded or fell below the expected proportion by more than 1 standard deviation across taxa (column 2), and the total number of taxa from which each given taxon was significantly different (column 3). Also listed are the relative abundances of each taxon presented [as a percent of all colonies across the island (column 4)], and the percentage of all colonies of each taxon that were categorized either as bleached, pale, or mottled (column 5).

Coral taxon	Larger proportion of colonies more healthy or less healthy than expected ( $\chi^2$ )	Number of other coral taxa with significantly different health status (pairwise $\chi^2$ )	Percent of total colonies observed at FDM in 2017	Percent of colonies bleached, pale or mottled
<i>Astreopora cucullata</i>	Less healthy	6	3.4%	97.2%
<i>Astreopora myriophthalama</i>	Less healthy	7	6.3%	96.9%
<i>Leptastrea purpurea</i>	Less healthy	7	9.4%	92.1%
<i>Pocillopora</i> juvenile	Less healthy	7	3.7%	98.3%
<i>Pocillopora meandrina</i>	Less healthy	79 (all other taxa)	13.8%	97.2%
<i>Pocillopora verrucosa</i>	Less healthy	7	4.3%	93.9%
<i>Pocillopora</i> hybrid #1	Less healthy	5	2.7%	97.6%
<i>Favia matthai</i>	More healthy	15	2.1%	39.4%
<i>Favia</i> unknown #2	More healthy	79 (all other taxa)	2.5%	18.2%
<i>Favites</i> unknown #1	More healthy	75	1.4%	19%
<i>Porites rus</i>	More healthy	79 (all other taxa)	0.9%	6.9%
<i>Porites solida</i>	More healthy	19	4.8%	49.3%
<i>Porites</i> massive	More healthy	7	21.6%	68.3%

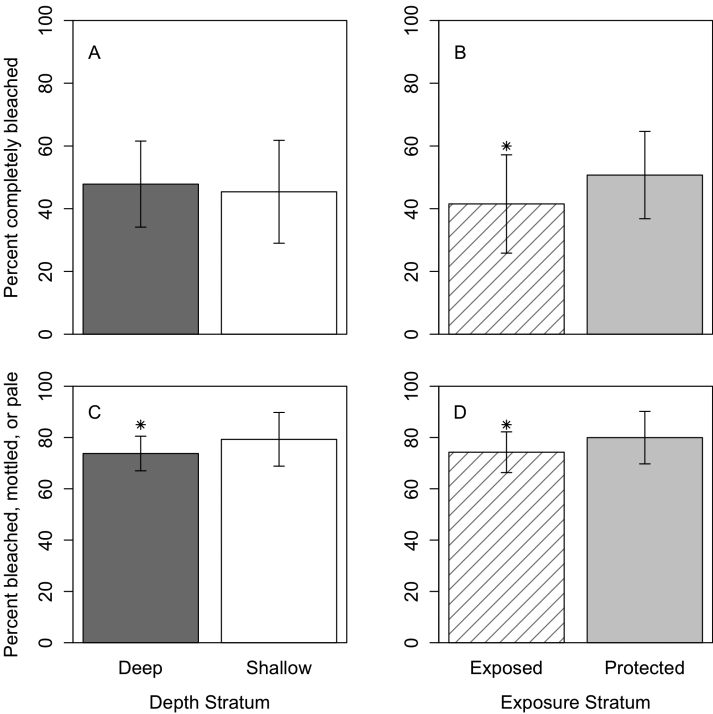


Figure 5. Barplots depicting the mean bleaching conditions in (A, C) deep (about 10–20 m) and shallow (about <10 m) depth strata, and (B, D) protected (west) and exposed (north, east, and south) strata. Asterisks denote strata with significantly less bleaching on average. Error bars denote standard deviation from the mean.

Table 3. Summary of bleaching prevalence: mean (standard deviation) percentage of corals bleached in deep (about 10–20 m) and shallow (approximately <10 m) depth strata, protected (west) and exposed (east and south) portions of the island, and corals in the constructional reef habitat in the center leeward portion of the island (Fig. 1) and those outside of this habitat. Asterisks indicate pairs of strata that were significantly different.

Physical category	Stratum	Completey bleached	Bleached, mottled, and pale
Depth	Deep	47.8% (13.7%)	73.8% (6.8%)*
	Shallow	45.5% (16.4%)	79.3% (10.4%)*
Physical exposure	Exposed	41.5% (15.7%)*	74.3% (7.9%)*
	Sheltered	50.7% (13.9%)*	79.9% (10.2%)*
Generalized reef type	Coral communities	48.7% (10.7%)	82.2% (5.8%)
	Constructional reef	45.2% (15.8%)	75.6% (9.2%)

TESTS OF AUTOMATED CORAL BLEACHING ASSESSMENT USING OBIA.—Most OBIA settings used for this project led to poor results in (1) delineating colony boundaries in nonbleached coral from background and (2) differentiating bleached coral and sand. Such delineation errors would produce incorrect results when assessing areal proportions of bleached corals. Only very low scale parameters, defining tiny object sizes (i.e., one or several image pixels representing objects less than 0.1 cm), were successful in defining object primitives that correctly captured coral colony and other habitat type edges. In future work, very small object primitives could potentially be iteratively merged to accurately define coral colonies, and then subjected to classification of bleaching categories.

## DISCUSSION

RAPID IMAGERY COLLECTION METHODS FOR MONITORING REMOTE CORAL REEFS.—The methods used here, to capture scaled and georeferenced photoquadrat imagery using a minimal amount of equipment (camera with small monopod, compact USBL diver tracker system), can be especially useful for rapid but thorough data collection on remote islands with limited survey duration (e.g., Preskitt et al. 2004, Molloy et al. 2013). For the most confident taxonomic identification in corals, sampling and microscopic analysis of skeletal morphology is required, but paired colony-scale and close-up imagery can be sufficient in many cases. For this survey, time constraints precluded collecting detailed photographs of all species, which may have enabled identification of more colonies or unknown taxa. Therefore, close-up, high-resolution photographs of all coral taxa present at a site, allowing for more accurate species-level identification of corals in photoquadrats, would be another useful addition to this methodology.

REGIONAL AND ISLAND-SCALE BLEACHING PATTERNS.—The coral survey at FDM was conducted during a widespread regional bleaching event, with Coral Reef Watch Bleaching Alert Level 2 (mortality likely) stress predicted at virtual stations during this time period in the Northern Mariana Islands (9 wks), Guam (7 wks), Palau (3 wks), and the Western (8 wks) and Eastern (10 wks) Federated States of Micronesia (Coral Reef Watch 2013; Online Supplement Fig. 3). This regional bleaching event occurred (starting around July 2017) after the global 2017 bleaching event had generally ended (around May 2017; NOAA 2017, Eakin et al. 2019). During the 2017 FDM

bleaching event, corals living on the more exposed portions of the island had lower bleaching incidence than protected corals (Fig. 5), and less bleaching was observed in the relatively deeper corals (approximately 10–20 m depth stratum) than shallower corals (<10 m depth; Fig. 5). These observations are consistent with the literature from other reefs around the world and experimental studies, where bleaching incidence is generally lower when corals are exposed to more vigorous water motion (e.g., Marshall and Schuttenberg 2006), and/or are exposed to cooler (deeper) waters, and/or less solar irradiance (e.g., Smith et al. 2014, Coelho et al. 2017, Muir et al. 2017).

Other regional-scale bleaching events in this area occurred in 2013 and 2014, when the Northern Mariana Islands experienced approximately 8 and 10 wks, respectively, of Alert Level 2 bleaching stress (Coral Reef Watch 2013; Online Supplement Fig. 3). In Guam, high mortality of *Acropora* branching corals was caused by the 2013 and 2014 bleaching events, particularly in locations with restricted water flow (Raymundo et al. 2017). Heron et al. (2016) similarly reported that corals at three islands just north of FDM had high mortality of particularly susceptible taxa after the 2013 bleaching event, and found that, similar to FDM, the bleaching incidence in 2014 was correlated with exposure (for example, high bleaching inside a circulation-restricted caldera on Maug island).

Although no surveys occurred at FDM between 2013 and 2016, overall coral cover appeared to have remained the same or slightly increased between earlier surveys and 2017 (Carilli et al. 2018), suggesting that regional heat stress events that occurred between the 2012 and 2017 surveys did not cause significant mortality at FDM. Interestingly, the average level of bleaching at FDM in 2017 (including pale and mottled corals) of 77.3%, with approximately 13 DHW of accumulated heat stress, echoes regional-wide patterns between coral-bleaching occurrence and DHW observed across the Northern Mariana Islands during the 2014 bleaching event (see figure 4 in Heron et al. 2016). Taken together, these observations suggest that FDM corals may respond to heat stress similarly to coral communities at other Northern Mariana Islands (similar resistance) but could possibly be more resilient and thus survive that stress.

**CORAL RECOVERY POTENTIAL AT FDM.**—Considering what is known about coral bleaching, the physical conditions at FDM could lead to higher survival and recovery of corals from bleaching compared to other islands in the Mariana Archipelago. These conditions include the high energy environment at FDM, which (1) may increase coral feeding opportunities through enhanced zooplankton stocks (e.g., Williams et al. 2018), (2) may reduce heat stress by stirring up cooler, deeper water (e.g., Hasegawa et al. 2004), and/or (3) could reduce boundary layers adjacent to coral tissues and thus increase diffusion of damaging oxygen radicals away from corals during bleaching (Nakamura and Van Woesik 2001, Marshall and Schuttenberg 2006). Indeed, Raymundo et al. (2017) found that *Acropora* corals situated in channels and thus better flushed with oceanic water survived bleaching events in 2013 and 2014 on Guam that caused mass mortality of corals in more restricted pools. The frequent typhoons that affect FDM can also provide beneficial cooling that may curtail or even prevent development of heat stress events (Carrigan and Puotinen 2011).

The lack of other co-occurring stressors at FDM, prevalent at inhabited islands, and in some cases occurring naturally at larger uninhabited islands, may also confer increased potential for coral resilience to bleaching at FDM. For example, coral

resilience to heat stress-induced bleaching decreases when combined with additional stress from local impacts (Carilli et al. 2009) such as sedimentation (Bessell-Browne et al. 2017) and nutrient pollution (Wooldridge 2009). Further, coral disease often drives mortality after bleaching, and disease tends to be exacerbated by these and other factors including (1) algal contact (Nugues et al. 2004), which increases when grazers are overfished (McManus et al. 2000), (2) increased transmission associated with dive tourism (Lamb et al. 2014), (3) land-based runoff (Haapkylä et al. 2011), (4) nutrient pollution (Vega Thurber et al. 2014), and (5) plastic pollution (Lamb et al. 2018). On FDM, these latter stressors are nonexistent, while algal contact with corals is likely minimized by healthy fish stocks (Smith and Marx 2016).

Overall, the natural conditions at FDM could impart more resilience to bleaching than at locations with suboptimal local conditions. Indeed, historical observations support this interpretation. Smith and Marx observed extensive bleaching of scleractinian and alcyonacean (soft) corals at both FDM and in Apra Harbor, Guam (278 km south of FDM) during a regional bleaching event in 2007, with annual maximum heat stress up to 8 DHW (Alert Level 2, mortality likely) at FDM, and 4 DHW (Alert Level 1, bleaching likely) near Apra Harbor (Coral Reef Watch 2013). However, in 2008, corals at FDM showed virtually 100% recovery, but a subjectively high proportion (>60%) of scleractinian and alcyonacean corals at study sites in Apra Harbor, Guam were dead and overgrown with algae (S Smith and D Marx, NIWC Pacific, pers observ). Compared to full recovery of corals at FDM, the death of corals in Apra Harbor after the 2007 bleaching event, despite experiencing lower levels of heat stress, suggests that conditions at FDM could be more conducive to coral recovery after bleaching than in Apra Harbor. Apra Harbor is a semienclosed lagoonal area, which is relatively protected from open ocean conditions compared to FDM, and receives sediment-laden runoff from the urbanized Piti-Asan watershed (Prouty et al. 2014), but supports extensive reefs and most of the dive tourism on the island of Guam (Sellers 2013).

**BLEACHING AND CORAL COMMUNITY COMPOSITION.**—It is unknown how corals at FDM have fared in the interim since the 2017 survey, however, if the 2017 bleaching event or future bleaching events cause mortality, the overall coral community composition may change over time in response to bleaching. Similar to observations at other Northern Mariana Islands in 2014 (Heron et al. 2016), many *Pocillopora* spp. corals exhibited high levels of bleaching at FDM in 2017, as did many *Astreopora* and *Leptastrea* corals (Table 2). Surveys in May 2018 in Saipan (83 km south of FDM) documented the recent death of approximately 90% of branching *Acropora* spp. and 70% of *Pocillopora* spp. corals across the island (S McKagan, NOAA, pers comm via AJ Reyes; D Fenner, NOAA, pers observ), presumably associated with the regional 2017 bleaching event. In contrast, *Astreopora* corals, also common at Saipan, were alive in 2018 (D Fenner, NOAA, pers observ). While no direct information on bleaching on Saipan was obtained, assuming that *Acropora*, *Pocillopora*, and *Astreopora* corals bleached at similar levels in Saipan as at FDM in 2017, these observations are consistent with previous studies that have found branching corals such as *Acropora* and *Pocillopora* generally less resilient to bleaching compared to other growth forms (Marshall and Baird 2000, McClanahan et al. 2007, Baker et al. 2008).

With high levels of bleaching observed in *Pocillopora* (branching), *Astreopora* (massive), and *Leptastrea* (encrusting) corals at FDM in 2017 (Table 2), the proportion

of *Astreopora* and *Leptastrea*, along with other massive and encrusting corals, may increase compared to branching corals like *Pocillopora* if taxonomic patterns of bleaching recovery at FDM mirror those at other reefs.

Future surveys should continue to quantify coral communities at FDM to test for recovery and assess potential coral community shifts related to global change. Given the remote, high-energy environment at FDM and other small uninhabited islands in the Northern Mariana Islands, coral communities may be more resilient than at larger inhabited islands in the archipelago, potentially behaving as climate refuges for corals in the Mariana Islands.

**AUTOMATED CLASSIFICATION APPROACHES.**—OBIA methods have been used for coral and benthic habitat mapping in aerial and satellite imagery (e.g., Phinn et al. 2012) and more recently explored for coral bleaching assessments in aerial imagery (e.g., Levy et al. 2018, Roelfsema et al. 2018). Classification accuracy is not high in these studies and methods for mapping at the colony-level are in their infancy. Levy et al. (2018) conducted a similar test to that completed here using aerial drone imagery at Kaneohe Bay, Oahu, Hawaii and likewise found that at present, human interpretation and digitization of coral colony boundaries is still the most reliable process for colony-level assessment, although these methods are hugely time-consuming.

Although OBIA methods are not currently able to delineate individual coral colonies, once refined, such methods offer enormous potential gains in efficiency for quantifying characteristics such as coral health at fine scales (i.e., colony level) across broad regions, and improve our ability to test more complex hypotheses (*see*, for example, the patterns in coral distribution observed after manually delineating corals in photomosaics at Palmyra atoll; Edwards et al. 2017). This is important for natural resources management and monitoring, especially in conjunction with rapid in situ assessment and in response to tracking and documenting regional coral bleaching events.

Some technical modifications that may improve OBIA methods for coral colony delineation include using 3D imagery [produced from stereo photographs or video using structure-from-motion (SfM) methods]. Incorporating surface relief has resulted in substantially improved classification and delineation of plant canopies using OBIA (e.g., O'Neil-Dunne et al. 2013), and could improve detection of coral colony boundaries by improving edge detection. Underwater hyperspectral imaging (UHI) could also be used to greatly expand spectral data content in imagery. Such data could be used to enhance classification based on a more complete range of spectral and textural differences between corals and background. Incorporating such information together with in situ-collected training data in a machine-learning based OBIA approach also offers new potential in automated, quantitative assessment of coral bleaching at the colony level. Such approaches increase the computing load and complexity of a project; however, as techniques improve, these methods will substantially increase the area over which quantitative surveys can be conducted and may revolutionize coral reef studies.

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## LITERATURE CITED

- Ainsworth TD, Wasmund K, Ukani L, Seneca F, Yellowlees D, Miller D, Leggat W. 2011. Defining the tipping point. A complex cellular life/death balance in corals in response to stress. *Sci Rep.* 1:160. <https://doi.org/10.1038/srep00160>
- Anthony KR, Connolly SR, Hoegh-Guldberg O. 2007. Bleaching, energetics, and coral mortality risk: effects of temperature, light, and sediment regime. *Limnol Oceanogr.* 52(2):716–726. <https://doi.org/10.4319/lo.2007.52.2.0716>
- Anthony KR, Hoogenboom MO, Maynard JA, Grottoli AG, Middlebrook R. 2009. Energetics approach to predicting mortality risk from environmental stress: a case study of coral bleaching. *Funct Ecol.* 23(3):539–550. <https://doi.org/10.1111/j.1365-2435.2008.01531.x>
- Baker AC, Glynn PW, Riegl B. 2008. Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. *Estuar Coast Shelf Sci.* 80:435–471. <https://doi.org/10.1016/j.ecss.2008.09.003>
- Baird AH, Bhagooli R, Ralph PJ, Takahashi S. 2009. Coral bleaching: the role of the host. *Trends Ecol Evol.* 24:16–20. <https://doi.org/10.1016/j.tree.2008.09.005>
- Bessell-Browne P, Negri AP, Fisher R, Clode PL, Jones R. 2017. Cumulative impacts: thermally bleached corals have reduced capacity to clear deposited sediment. *Sci Rep.* 7(1):2716. <https://doi.org/10.1038/s41598-017-02810-0>
- Blaschke T, Hay GJ, Kelly M, Lang S, Hofmann P, Addink E, Feitosa RQ, Van der Meer F, Van der Werff H, Van Coillie F, et al. 2014. Geographic object-based image analysis - towards a new paradigm. *ISPRS J Photogramm Remote Sens.* 87:180–191. <https://doi.org/10.1016/j.isprsjprs.2013.09.014>
- Brandt ME, McManus JW. 2009. Disease incidence is related to bleaching extent in reef-building corals. *Ecology.* 90(10):2859–2867. <https://doi.org/10.1890/08-0445.1>
- Brown BE. 1997. Coral bleaching: causes and consequences. *Coral Reefs.* 16:S129–S138. <https://doi.org/10.1007/s003380050249>
- Carilli JE, Norris RD, Black BA, Walsh SM, McField M. 2009. Local stressors reduce coral resilience to bleaching. *PLOS ONE.* 4(7):e6324. <https://doi.org/10.1371/journal.pone.0006324>
- Carilli J, Smith SH, Marx D Jr, Bolick L, Fenner D. 2018. Farallon de Medinilla 2017 species level coral reef survey report. Prepared for US Pacific Fleet. Space and Naval Warfare Systems Center Pacific Technical Report 3156. 80 p. Available from: <https://apps.dtic.mil/dtic/tr/fulltext/u2/1069450.pdf>
- Carrigan AD, Puotinen ML. 2011. Assessing the potential for tropical cyclone induced sea surface cooling to reduce thermal stress on the world's coral reefs. *Geophys Res Lett.* 38:L23604. <https://doi.org/10.1029/2011GL049722>
- Coastal Data Information Program. 2020. Station data from Buoy 196 (Ritidian Point, Guam) and 197 (Tanapag, Saipan). Accessed 8 April, 2020. Available from: <http://cdip.ucsd.edu>
- Coelho V, Fenner D, Caruso C, Bayles B, Huang Y, Birkeland C. 2017. Shading as a mitigation tool for coral bleaching in three common Indo-Pacific species. *J Exp Mar Biol Ecol.* 497:152–163. <https://doi.org/10.1016/j.jembe.2017.09.016>
- Coral Reef Watch. 2013. NOAA Coral Reef Watch daily global 5-km satellite virtual station time series data for Northern Mariana Islands, 8 June, 2017–1 October, 2017. Accessed 24 August, 2018. Available from: <http://coralreefwatch.noaa.gov/vs/index.php>
- Cunning R, Baker AC. 2013. Excess algal symbionts increase the susceptibility of reef corals to bleaching. *Nat Clim Chang.* 3(3):259–262. <https://doi.org/10.1038/nclimate1711>

- Eakin CM, Sweatman HP, Brainard RE. 2019. The 2014–2017 global-scale coral bleaching event: insights and impacts. *Coral Reefs*. 38(4):539–545. <https://doi.org/10.1007/s00338-019-01844-2>
- Edwards CB, Eynaud Y, Williams GJ, Pedersen NE, Zgliczynski BJ, Gleason AC, Smith JE, Sandin SA. 2017. Large-area imaging reveals biologically driven non-random spatial patterns of corals at a remote reef. *Coral Reefs*. 36(4):1291–1305. <https://doi.org/10.1007/s00338-017-1624-3>
- Grottoli AG, Rodrigues LJ, Juarez C. 2004. Lipids and stable carbon isotopes in two species of Hawaiian corals, *Porites compressa* and *Montipora verrucosa*, following a bleaching event. *Mar Biol*. 145(3):621–631. <https://doi.org/10.1007/s00227-004-1337-3>
- Grottoli AG, Rodrigues LJ, Palardy JE. 2006. Heterotrophic plasticity and resilience in bleached corals. *Nature*. 440(7088):1186. <https://doi.org/10.1038/nature04565>
- Haapkylä J, Unsworth RK, Flavell M, Bourne DG, Schaffelke B, Willis BL. 2011. Seasonal rainfall and runoff promote coral disease on an inshore reef. *PLOS ONE*. 6(2):e16893. <https://doi.org/10.1371/journal.pone.0016893>
- Hasegawa D, Yamazaki H, Lueck RG, Seuront L. 2004. How islands stir and fertilize the upper ocean. *Geophys Res Lett*. 31: L16303. <https://doi.org/10.1029/2004GL020143>
- Heron SE, Johnston L, Liu G, Geiger EF, Maynard JA, De La Cour JL, Johnson S, Okano R, Benavente D, Burgess TF, et al. 2016. Validation of reef-scale thermal stress satellite products for coral bleaching monitoring. *Remote Sens*. 8(1):59. <https://doi.org/10.3390/rs8010059>
- Hoegh-Guldberg O. 2011. Coral reef ecosystems and anthropogenic climate change. *Reg Environ Change*. 11:215–227. <https://doi.org/10.1007/s10113-010-0189-2>
- Houk P, Hernandez-Ortiz D. 2019. Farallon de Medinilla fish video analysis. Prepared by Marine Laboratory, University of Guam, for Naval Facilities Engineering Command Marianas. 26 p.
- Houlbrèque F, Ferrier-Pagès C. 2009. Heterotrophy in tropical scleractinian corals. *Biol Rev Camb Philos Soc*. 84(1):1–7. <https://doi.org/10.1111/j.1469-185X.2008.00058.x>
- Hughes TP, Anderson KD, Connolly SR, Heron SE, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC, et al. 2018. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science*. 359(6371):80–83. <https://doi.org/10.1126/science.aan8048>
- Joint Typhoon Warning Center. 2018. Western North Pacific best track data. Accessed 15 August, 2018. Available from: <http://www.metoc.navy.mil/jtwc/jtwc.html?western-pacific>
- Jones RJ. 2008. Coral bleaching, bleaching-induced mortality, and the adaptive significance of the bleaching response. *Mar Biol*. 154:65–80. <https://doi.org/10.1007/s00227-007-0900-0>
- Knowlton N. 2001. The future of coral reefs. *PNAS*. 98(10):5419–5425. <https://doi.org/10.1073/pnas.091092998>
- Lamb JB, True JD, Piromvaragorn S, Willis BL. 2014. Scuba diving damage and intensity of tourist activities increases coral disease prevalence. *Biol Conserv*. 178:88–96. <https://doi.org/10.1016/j.biocon.2014.06.027>
- Lamb JB, Willis BL, Fiorenza EA, Couch CS, Howard R, Rader DN, True JD, Kelly LA, Ahmad A, Jompa J, et al. 2018. Plastic waste associated with disease on coral reefs. *Science*. 359(6374):460–462. <https://doi.org/10.1126/science.aar3320>
- Levy J, Hunter C, Lukaczyk T, Franklin EC. 2018. Assessing the spatial distribution of coral bleaching using small unmanned aerial systems. *Coral Reefs*. 37(2):373–387. <https://doi.org/10.1007/s00338-018-1662-5>
- Liu G, Rauen Zahn JL, Heron SE, Eakin CM, Skirving WJ, Christensen T, Strong AE, Li J. 2013. NOAA coral reef watch 50 km satellite sea surface temperature-based decision support system for coral bleaching management. NOAA Technical Report. NESDIS 143.
- Marshall PA, Baird AH. 2000. Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs*. 19:155–163. <https://doi.org/10.1007/s003380000086>
- Marshall PA, Schuttenberg HZ. 2006. A reef manager's guide to coral bleaching. Townsville, QLD, Australia: Great Barrier Reef Marine Park Authority.

- McClanahan TR, Ateweberhan M, Graham NAJ, Wilson SK, Sebastian CR, Guillaume MMM, Bruggemann JH. 2007. Western Indian Ocean coral communities: bleaching responses and susceptibility to extinction. *Mar Ecol Prog Ser.* 337:1–13. <https://doi.org/10.3354/meps337001>
- McCutcheon AL, Raymundo LJ, Jenson JW, Prouty NG, Lander MA, Randall RH. 2015. Testing the strontium/calcium proxy for sea surface temperature reconstruction in the coral *Porites lutea*. University of Guam Marine Laboratory Technical Report 159, Water and Environmental Research Institute Technical Report 152.
- McManus JW, Menez LA, Kesner-Reyes KN, Vergara SG, Ablan MC. 2000. Coral reef fishing and coral-algal phase shifts: implications for global reef status. *ICES J Mar Sci.* 57(3):572–578. <https://doi.org/10.1006/jmsc.2000.0720>
- Molloy PP, Evanson M, Nellas AC, Rist JL, Marcus JE, Koldewey HJ, Vincent ACJ. 2013. How much sampling does it take to detect trends in coral-reef habitat using photoquadrat surveys? *Aquat Conserv.* 23(6):820–837. <https://doi.org/10.1002/aqc.2372>
- Muir PR, Marshall PA, Abdullah A, Aguirre JD. 2017. Species identity and depth predict bleaching severity in reef-building corals: shall the deep inherit the earth? *Proc Biol Sci.* 284:20171551. <https://doi.org/10.1098/rspb.2017.1551>
- Nakamura T, Van Woesik R. 2001. Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. *Mar Ecol Prog Ser.* 212:301–304. <https://doi.org/10.3354/meps212301>
- NOAA. 2017. Global coral bleaching event likely ending. Accessed 24 August, 2018. Available from: <https://www.noaa.gov/media-release/global-coral-bleaching-event-likely-ending>
- Nugues MM, Smith GW, Van Hooideonk RJ, Seabra MI, Bak RP. 2004. Algal contact as a trigger for coral disease. *Ecol Lett.* 7(10):919–923. <https://doi.org/10.1111/j.1461-0248.2004.00651.x>
- O'Neil-Dunne JP, MacFaden SW, Royar AR, Pelletier KC. 2013. An object-based system for LiDAR data fusion and feature extraction. *Geocarto Int.* 28(3):227–242. <https://doi.org/10.1080/10106049.2012.689015>
- Phinn SR, Roelfsema CM, Mumby PJ. 2012. Multi-scale, object-based image analysis for mapping geomorphic and ecological zones on coral reefs. *Int J Remote Sens.* 33(12):3768–3797. <https://doi.org/10.1080/01431161.2011.633122>
- Preskitt LB, Vroom PS, Smith CM. 2004. A rapid ecological assessment (REA) quantitative survey method for benthic algae using photoquadrats with Scuba. *Pac Sci.* 58(2):201–209. <https://doi.org/10.1353/psc.2004.0021>
- Prouty NG, Storlazzi CD, McCutcheon AL, Jenson JW. 2014. Historic impact of watershed change and sedimentation to reefs along west-central Guam. *Coral Reefs.* 33(3):733–749. <https://doi.org/10.1007/s00338-014-1166-x>
- R Core Team. 2018. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available from: <https://www.R-project.org/>
- Randall RH. 1995. Biogeography of reef-building corals in the Mariana and Palau Islands in relation to back-arc rifting and the formation of the Eastern Philippine Sea. *Nat Hist Res.* 3(2):193–210.
- Raymundo LJ, Burdick D, Lapacek VA, Miller R, Brown V. 2017. Anomalous temperatures and extreme tides: Guam staghorn *Acropora* succumb to a double threat. *Mar Ecol Prog Ser.* 564:47–55. <https://doi.org/10.3354/meps12005>
- Roelfsema C, Kovacs E, Ortiz JC, Wolff NH, Callaghan D, Wettle M, Ronan M, Hamylton SM, Mumby PJ, Phinn S. 2018. Coral reef habitat mapping: a combination of object-based image analysis and ecological modelling. *Remote Sens Environ.* 208:27–41. <https://doi.org/10.1016/j.rse.2018.02.005>
- Roth MS. 2014. The engine of the reef: photobiology of the coral–algal symbiosis. *Front Microbiol.* 5:422. <https://doi.org/10.3389/fmicb.2014.00422>
- Sellers KE. 2013. Dive industry use patterns and economic dependency on Apra Harbor's coral reefs. Miami: Open Access Theses, University of Miami. 418.

- Smith EG, D'Angelo C, Salih A, Wiedenmann J. 2013. Screening by coral green fluorescent protein (GFP)-like chromoproteins supports a role in photoprotection of zooxanthellae. *Coral Reefs*. 32(2):463–474. <https://doi.org/10.1007/s00338-012-0994-9>
- Smith TB, Glynn PW, Maté JL, Toth LT, Gyory J. 2014. A depth refugium from catastrophic coral bleaching prevents regional extinction. *Ecology*. 95(6):1663–1673. <https://doi.org/10.1890/13-0468.1>
- Smith SH, Marx DE Jr. 2016. De-facto marine protection from a Navy bombing range: Farallon De Medinilla, Mariana Archipelago, 1997 to 2012. *Mar Pollut Bull*. 102(1):187–198. <https://doi.org/10.1016/j.marpolbul.2015.07.023>
- Storlazzi CD, Field ME, Cheriton OM, Presto MK, Logan JB. 2013. Rapid fluctuations in flow and water-column properties in Asan Bay, Guam: implications for selective resilience of coral reefs in warming seas. *Coral Reefs*. 32:949–961. <https://doi.org/10.1007/s00338-013-1061-x>
- van Woesik R, Sakai K, Ganase A, Loya Y. 2011. Revisiting the winners and the losers a decade after coral bleaching. *Mar Ecol Prog Ser*. 434:67–76. <https://doi.org/10.3354/meps09203>
- Vega Thurber RL, Burkepile DE, Fuchs C, Shantz AA, McMinds R, Zaneveld JR. 2014. Chronic nutrient enrichment increases prevalence and severity of coral disease and bleaching. *Glob Change Biol*. 20(2):544–554. <https://doi.org/10.1111/gcb.12450>
- Veron JEN. 2000. *Corals of the world*. Vol. 1–3. Townsville: Australian Institute of Marine Science. 1382 p.
- Veron JEN, Stafford-Smith MG, Turak E, DeVantier LM. 2018. *Corals of the world*. Accessed 15 September, 2018. Version 0.01 (Beta). Current version available from: <http://coralsoft-heworld.org/>
- Wall M, Puthim L, Schmidt GM, Jantzen C, Khokiattiwong S, Richter C. 2015. Large-amplitude internal waves benefit corals during thermal stress. *Proc R Soc Lond B Biol Sci*. 282:20140650. <https://doi.org/10.1098/rspb.2014.0650>
- Wallace C. 1999. *Staghorns of the world: a revision of the coral genus Acropora* (Scleractinia: Astrocoeniina; Acroporidae) worldwide, with emphasis on morphology, phylogeny, and biogeography. Melbourne: CSIRO. 438 p.
- Weis VM. 2008. Cellular mechanisms of Cnidarian bleaching: stress causes the collapse of symbiosis. *J Exp Biol*. 211:3059–3066. <https://doi.org/10.1242/jeb.009597>
- Williams GJ, Sandin SA, Zgliczynski BJ, Fox MD, Gove JM, Rogers JS, Furby KA, Hartmann AC, Caldwell ZR, Price NN, et al. 2018. Biophysical drivers of coral trophic depth zonation. *Mar Biol*. 165(4):60. <https://doi.org/10.1007/s00227-018-3314-2>
- Wooldridge SA. 2009. Water quality and coral bleaching thresholds: formalising the linkage for the inshore reefs of the Great Barrier Reef, Australia. *Mar Pollut Bull*. 58(5):745–751. <https://doi.org/10.1016/j.marpolbul.2008.12.013>

