Human and natural drivers of coral reef resilience to climate-induced coral bleaching in Guam; identifying potential climate refugia

Performance Progress Report for Grant No. NA 18NOS4820106 for the period from 08/01/2018-07/31/2019

Final Report

Award Recipient: SymbioSeas - Project PIs: Dr. Gareth Williams and Dr. Jeffrey Maynard

Brief Project Summary: This proposed project involves collaboratively working with resource managers in Guam to achieve these two outcomes: **1**) increase our knowledge of the human and natural drivers of coral reef resilience to climate-induced coral bleaching in Guam, and **2**) guide management planning and decision-making to promote reef recovery. These outcomes will be achieved through our team's planned applied research under 6 project objectives, and via our 7th objective (cross-cutting) of engaging with managers throughout the project. We will develop: Objectives 1 and 2) syntheses of >10 years monitoring data collected by local (University of Guam, our team) and regional (NOAA) agencies to produce quantitative summaries of spatial and temporal change in reef condition around Guam, **3**) data layers and maps of key anthropogenic drivers (e.g. coastal development) that act as 'stress-reinforcing' factors of reef decline under the threat of climate change, **4**) data layers and maps of upwelling, which can act as a 'stress-mitigating' factor of reef decline under the threat of climate change, **5**) statistical models that link reef change over space and time (Obj. 1) to gradients in human and natural drivers (Obj. 2 – 3) to identify the key drivers/characteristics explaining: a) spatial variation in bleaching prevalence and severity across sites, b) spatial variation in bleaching-induced mortality and d) spatial variation in reef recovery post-bleaching, and **6**) a quantitative analysis to identify which and why some reef sites around Guam may appear to deviate in a positive way from the mean (so called 'bright spots') and thus have the potential to serve as refugia under future climate change. **7**) Meetings with managers will be held near the conclusion of the project and will also include representatives from conservation and community organizations, as well as community members. The full-day workshop will include time to present and discuss results and tailor planned project outputs to meet manager needs.

Introduction:

Coral reef resilience is the capacity of a reef to resist or recover from degradation and maintain provision of ecosystem goods and services. Resilience-based management (RBM) has been developed to overcome the challenges of supporting ecosystem resilience in this era of rapid change. RBM involves the application of resilience theory and tools to deliver ecosystem-based management outcomes into the future. RBM of coral reefs can include assessing spatial variation in resilience potential and then targeting and tailoring appropriate actions to preserve or restore the resilience of reefs. Resilience assessments involve measuring or assessing resilience indicators (e.g., coral disease, coral recruitment and herbivorous fish biomass) and producing an aggregate score that expresses resilience potential for all sites as relative to the site with the highest (assessed) resilience potential.

This project team completed a resilience assessment in 2017 for Guam based on data collected in 2016 (Figure 1). The results have a strong spatial pattern with resilience being assessed as higher in the northern half of Guam and lower in the southern half and this was true for both depths (Figure 1). For both depths and with very few exceptions, scores were medium-high or high for resilience indicators in northern Guam and medium-low or low in southern Guam.

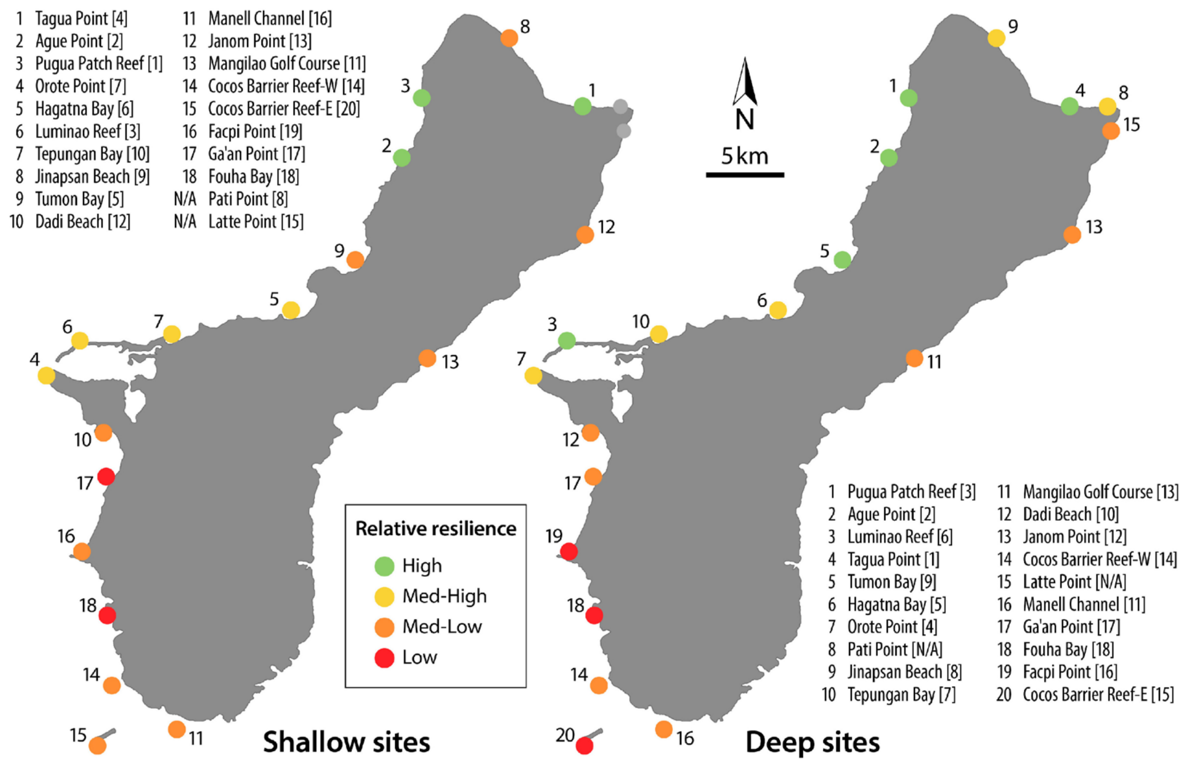

Figure 1. Spatial variation in relative resilience for both depths. Sites are ranked from highest to lowest relative resilience (from Maynard et al. 2018; CRCP TM 29).

The resilience assessment results were communicated via a PowerPoint presentation to community groups, conservationists and natural resource managers in Guam during a workshop in April of 2017 (Figure 2).

Figure 2. Attendees of a climate change and coral reefs workshop in Guam in April of 2017, co-hosted by Co-PIs Laurie Raymundo and David Burdick, working with Jeffrey Maynard on a project funded by the Pacific Islands Climate Science Consortium.

The April 2017 workshop was focused on climate model projections of coral bleaching conditions for Guam. Participants were very interested in the resilience assessment results, which led to a discussion of next steps for research on reef resilience in Guam. Some highlights from discussions held at the workshop are listed below - all represent identified needs for future research and work.

1) The resilience assessment conducted to date in Guam (results shown in Figure 1) is not spatially continuous (much coral reef monitoring data available for Guam was not included, hence this project's objectives 1-4);

2) When assessing resilience within the IPCC vulnerability assessment framework, resilience is a combination of the ecological capacity to resist and recover (assessed for 20 sites, see Figure 1) AND the extent to which anthropogenic stress impacts resilience (hence this project's objective 3).

3) Resilience 'potential', which is what has been assessed to date, is more limited in its potential conservation and management utility than 'demonstrated resilience', where spatial variation in actual resistance and recovery is measured (hence this project's objective 4-6).

4) State-of-art projections of coral reef futures (as in van Hooidonk, Maynard, Williams et al. 2016) do not resolve local features, such as upwelling, that can mitigate thermal stress, so projections are less accurate in upwelling areas (hence this project's objective 4).

5) Participants expressed it would be extremely useful to have a workshop specifically focused on integrating data layers to better understand resilience, identify characteristics driving observed patterns in resilience (resistance and recovery), and identify potential refugia (hence this project's objective 7).

The April 2017 workshop discussions that led to the five identified needs presented just above is the background to why the priority under Climate Change for Guam from the FY18 CRCP Domestic Grants Program Federal Funding Opportunity was as follows:

CC-Guam: a) Projects that examine mechanisms or characteristics explaining the resilience of certain coral species or coral reef sites to climate-related impacts and studies of reef sites with the potential to serve as refugia including mesophotic reefs and highly turbid sites (e.g. Apra Harbor). b) Projects that develop and apply innovative approaches and novel technologies to protect Guam's coral reefs from climate change impacts.

This project sought to meet all of the 5 needs identified at the April 2017 workshop, essentially using the 2016 resilience assessment as a foundation upon which to build a greater body of information on the climate resilience and vulnerability of coral reefs in Guam.

The overarching project goal was to identify and explain patterns in reef resilience in Guam and then identify refugia that represent conservation and management priorities. This was achieved through innovative approaches that combine novel spatial and statistical modeling. The specific project objectives are listed below. The first 6 objectives are presented in the order in which our team progressed through the planned work. The 7th objective is cross-cutting and took place throughout the project (and is ongoing) as we collaborate with manager colleagues and share results with community members.

Objective 1 – Quantify baseline reef condition in Guam prior to the 2013/2014 bleaching event

Objective 2 – Quantify spatial patterns in bleaching prevalence and benthic change between pre- and post-bleaching years

Objective 3 – Quantify spatial patterns in anthropogenic stress that are 'stress-reinforcing' factors that contribute to reef decline under the threat of climate change

Objective 4 – Quantify spatial patterns in upwelling, which is a 'stress-mitigating' factor that supports resilience to climate change

Objective 5 – Develop statistical models that compare and evaluate predictors of reef change in Guam under climate change

Objective 6 – Identify potential reef refugia, 'bright spots' where management investment may reap the greatest returns in long-term provision of ecosystem goods and services.

[Cross-cutting] Objective 7 – Communicate with the scientific and management community and community members in Guam to share project results and identify pathways to action, and ensure project methods and results are formally published with open access.

Methods and results: Each of the seven project objectives re-appears below, and then below each objective we describe the results.

Objective 1: *Quantify baseline reef condition in Guam prior to the 2013/2014 bleaching event*

Methods

Benthic community data synthesis – NOAA towed-diver data

Benthic communities around Guam were quantified in 2003, 2005, 2007, 2009, 2011, 2014, and 2017 by NOAA towed-divers, a spatially expansive method that is effective at characterizing benthic communities at a coarse taxonomic resolution (hard coral, crustose coralline algae, and macroalgae) (Kenyon et al. 2006). In short, SCUBA divers were towed at the end of a 60 m line behind a small boat along a targeted depth contour of 15 m at a speed of ~3 km hr -1 (**Fig. 3**). The divers used a towboard to steer that was equipped with a SeaBird™ SBE39 high-resolution temperature-depth recorder and bottom timer (Richards et al. 2011). Importantly, because towed-diver surveys are able to access exposed coasts (e.g. windward-facing shores and high swell conditions) that cannot always be surveyed using other free-swimming techniques, they provide a more representative estimation of island-mean condition (Williams et al. 2015). The diver made efforts to maneuver the towboard at a distance of ~1 m above the seafloor, visually estimating the percent cover of benthic functional groups over an estimated 10 m swath (5 m on either side of the tow line). Around Guam, the mean depth captured by the towboard surveys from 2003 to 2011 was 14.2 m. To control for potential effects of habitat type and depth, the benthic observation data were filtered to include only those tows crossing the fore reef habitat within a depth range of 12 to 16 m (2 m either side of the mean depth) over consolidated hard (habitable) substrate. Although the towed divers also recorded percent cover of sand, rubble, and 'other', these categories were not investigated in detail here.

Benthic community data – University of Guam

The University of Guam monitoring program collected benthic community data using the photoquadrat method at 48 sites (3 x 30 m photo transects per site) across depths of 5-8 m in 2013 during the bleaching event. The percentage cover of different benthic organisms was determined post-hoc using Coral Point Count (Kohler and Gill 2006) and the proportion of corals that were paling, bleached, and showed signs of bleaching-induced mortality was quantified (all three bleaching metrics were subsequently combined to give a measure of 'overall bleaching impact'). Here we focused on the cover of the same core benthic taxa documented by the NOAA towed-diver surveys, namely hard corals, crustose coralline algae, and macroalgae, but were also able to quantify the cover of fleshy turf algae. In 2015, 17 of the 48 survey sites were re-surveyed to assess reef recovery. These data offered a complimentary shallow reef component to the NOAA towed-diver surveys as well as providing data during two years (2013, 2015) that the NOAA towed-diver surveys were absent.

Benthic community data – spatial processing

We gridded Guam's fore reef habitat into 100 m cells (n = 1,337), starting due north of the island's center and running around the circumference of the coastline in ArcGIS (ver. 10.5) using a custom Python script (Aston et al. 2019). We then spatially joined each towed-diver observation (by survey year) to each grid cell to examine for spatial autocorrelation in the long-term mean benthic data (2003-2011) using two spatial statistical techniques – empirical semivariance (Meisel and Turner 1998) and lacunarity (Gefen et al. 1983; Mandelbrot 1983; Plotnick et al. 1993) within a custom R function (Gove et al. 2015). Both techniques indicated a dramatic decrease in spatial autocorrelation beyond linear distances around the island of 2300 m (**Fig. 4 & 5**). We took the entire circumference of Guam's coastline (along the 15 m depth contour) and divided it by this number, giving us 58 discrete sectors each of which was 2.3 km wide. Benthic cover values were then averaged within each sector by survey year for both core data sites (NOAA and University of Guam) and these data formed the basis of all subsequent spatial analyses.

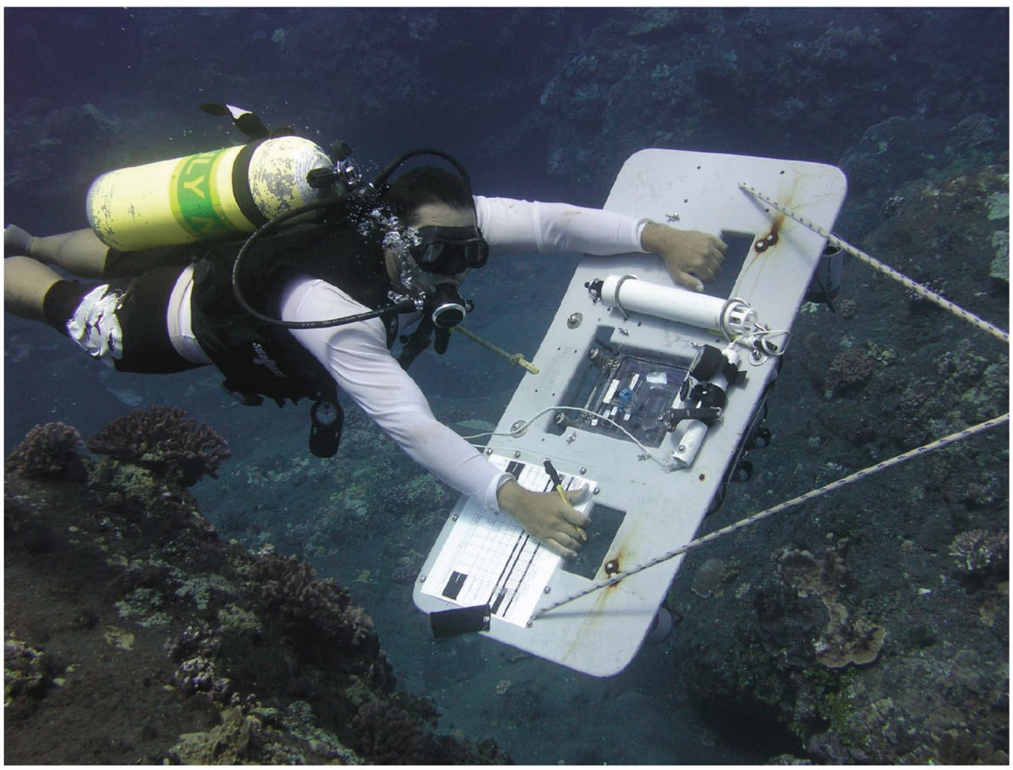

Figure 3. A NOAA towed-diver equipped with instrumented towboard (taken from Richards et al. 2011).

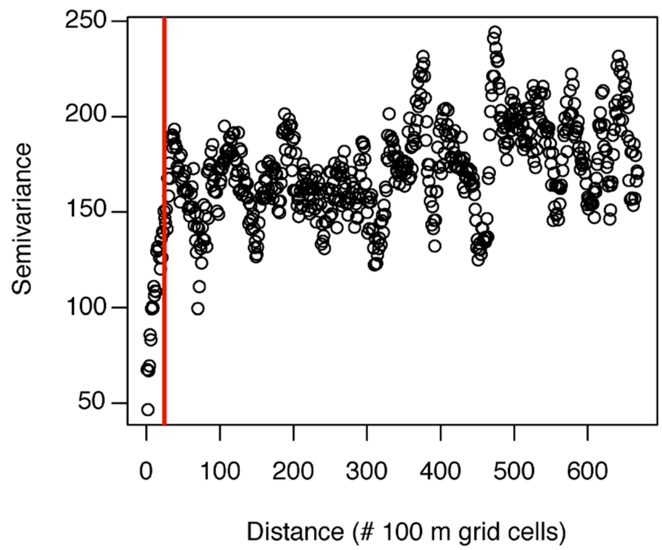

Figure 4. Semivariance curve to quantify the spatial autocorrelation in hard coral cover with increasing distance (number of 100 m grid cells) around the circumference of Guam. Vertical red line indicates the inflection point in the distance that signifies spatial independence (i.e. the distance at which there is no longer appreciable spatial autocorrelation), which here equals 2300 m.

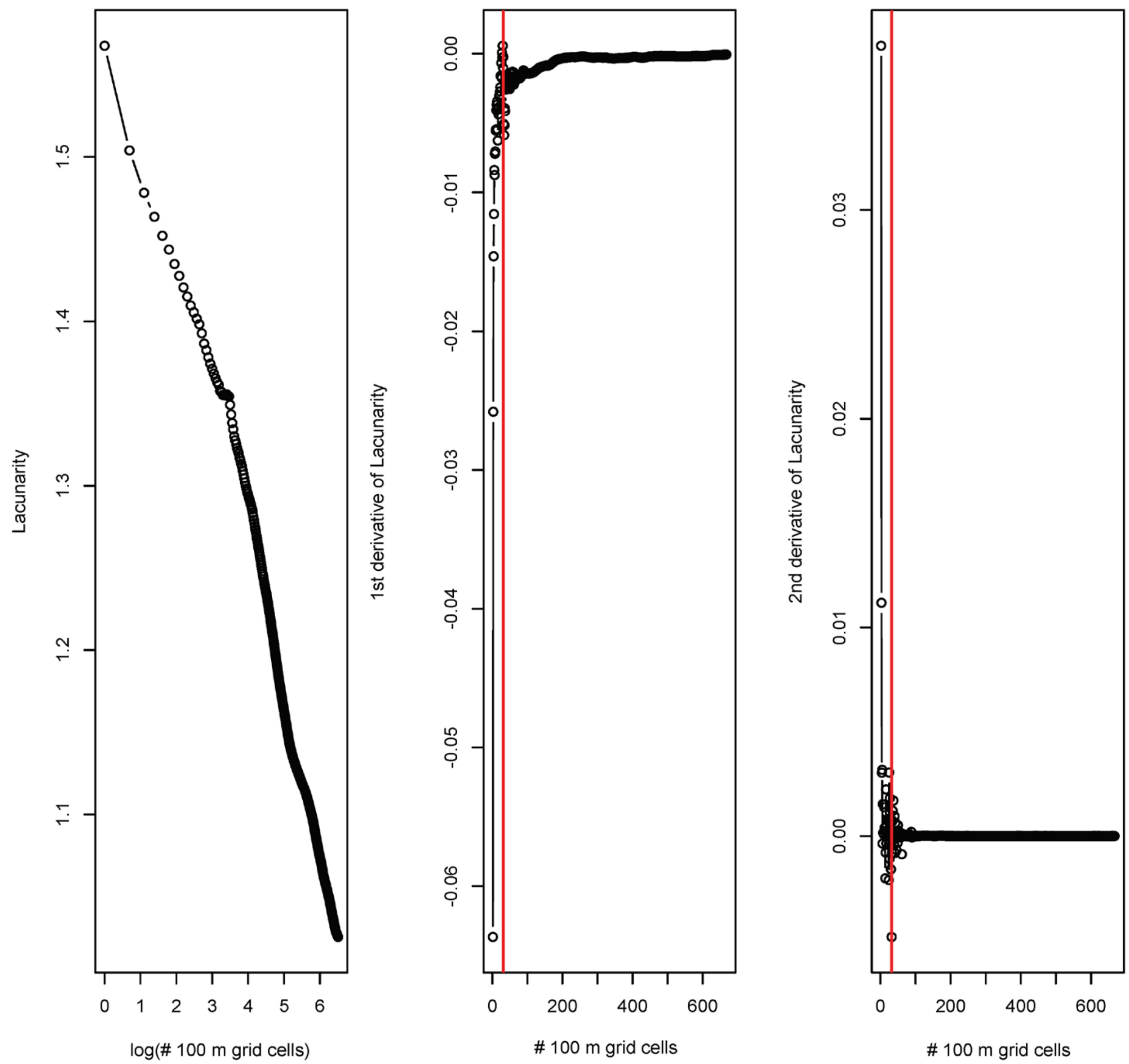

Figure 5. Lacunarity analyses to quantify the spatial autocorrelation in hard coral cover with increasing distance (number of 100 m grid cells) around the circumference of Guam. Vertical red line indicates the inflection point in the distance that signifies spatial independence (i.e. the distance at which there is no longer appreciable spatial autocorrelation), which here equals 2300 m.

Results

Long-term mean benthic community patterns on Guam's ***deep reefs*** *prior to the 2013 bleaching event (NOAA data)*

Prior to the 2013 coral bleaching event, there were clear intra-island gradients in benthic cover. Long-term mean (2003-2011) coral cover around Guam was 16.7% and was highest (up to 41.7%) within pockets along the west to eastern coasts, and generally lowest (down to 2.5%) in the southeastern to southwestern parts of the coastline (**Fig. 6**). Long-term mean crustose coralline algae (CCA) cover around Guam was 7.6% and highest (up to 16.3%) along the northern half of the island, particularly along the northwestern to northern coastline. CCA cover was lowest (<1%) along parts of the southeast and southwest coastline (**Fig. 6**). Long-term mean macroalgae cover around Guam was 38.8% and was highest (up to 70.4%) along parts of the southeastern and western coastlines. The lowest macroalgae cover (down to 13.2%) was located along parts of the northwestern coastline (**Fig. 6**).

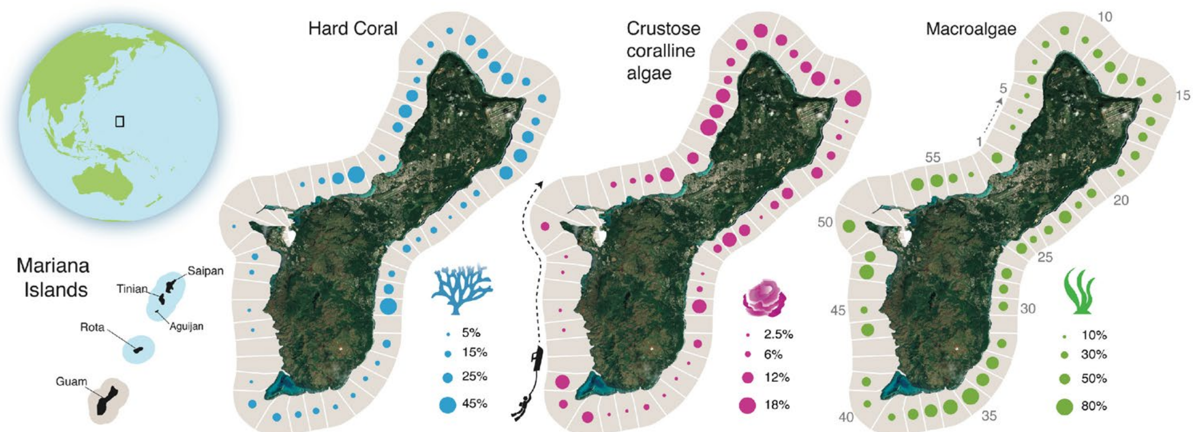

Figure 6. Long-term mean (2003-2011) within-island variation in benthic functional group cover among 58 discrete 2.3 km sectors around the circumference (~134 linear km) of Guam's seascape. Blank sectors indicate an absence of benthic data.

Impact of the 2013 bleaching event on Guam's ***shallow reefs*** *(University of Guam data)*

During the 2013 bleaching event there was clear within-island variation in bleaching-induced coral mortality and overall bleaching impact to Guam's shallow (5-8 m depth) reefs (**Fig. 7**). Mean bleaching-induced mortality at the island scale equaled 10.6% and ranged from 1.0% to 27.2% among sectors. Particularly high levels of bleaching-induced coral mortality occurred along portions of the south (sectors 38-40) and west (sectors 46 and 48) coasts, while the northern coast and pockets along the central east and west coasts showed the lowest levels (**Fig. 7**). Mean overall bleaching impact (bleaching mortality plus colonies also showing signs of paling or bleached appearance) at the island scale equaled 30.3%, and ranged from 5.1% to 75.0% among sectors. General within-island patterns mirrored those of the bleaching-induced mortality patterns (**Fig. 7**).

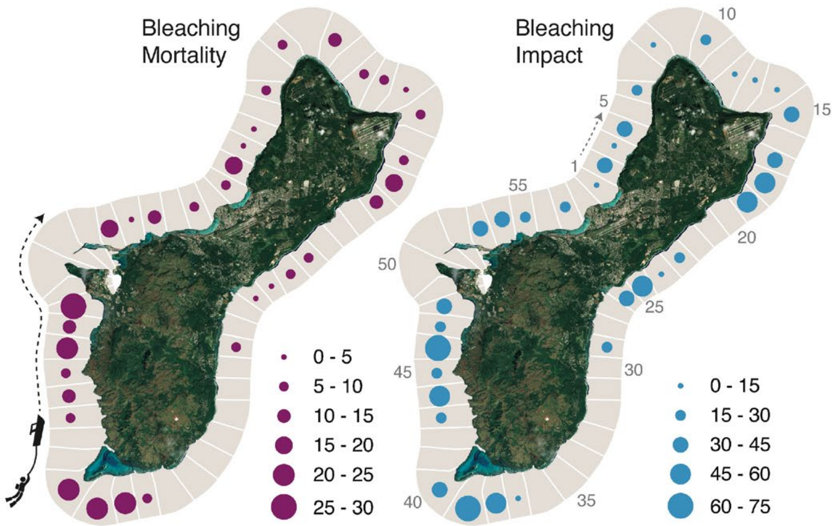

Figure 7. Within-island variation in bleaching-induced mortality (% colonies) and overall bleaching impact (bleaching mortality plus % colonies showing signs of paling or bleached appearance) on Guam's shallow reefs in 2013 among 58 discrete 2.3 km sectors. Blank sectors indicate an absence of bleaching data.

*Initial bleaching impact to Guam's **deep reefs**: change in benthic cover between the long-term mean (2003-2011) and <1 year post-bleaching in 2014 (NOAA data)*

Many island sectors around Guam showed signs of reef decline following the 2013 bleaching event. Within the 33 island sectors containing data in both time points, the most striking change was a substantial loss of crustose coralline algae (CCA) and a subsequent increase in macroalage. Hard coral cover declined by ≥10% in 15% of the 33 sectors, with loss occurring along the northeastern to southeastern coastline (**Fig. 8**). Hard coral cover concurrently showed an appreciable increase of ≥10% in 18% of the 33 sectors scattered along the southeast to southwestern coasts. CCA cover declined by ≥10% in 88% of the 33 island sectors, with loss scattered all around the island. Macroalgae subsequently showed an increase in cover of ≥10% in 70% of the 33 sectors running all around the island; only 1 island sector (sector 6) showed any appreciable drop in macroalgae cover (**Fig. 8**).

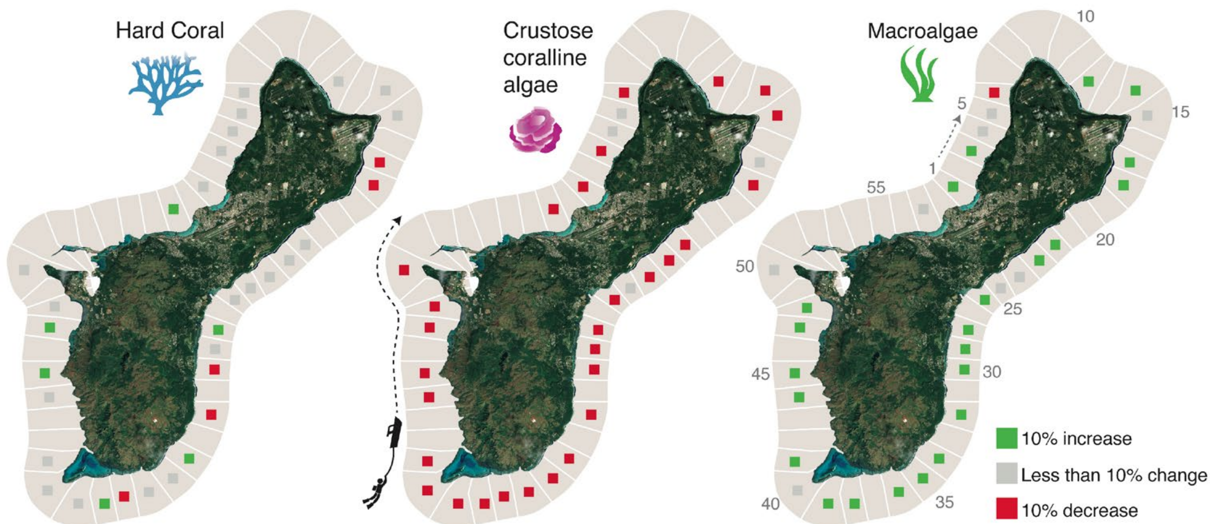

Figure 8. Change in benthic cover between the long-term mean pre-bleaching (2003-2011) and <1 year post-bleaching in 2014. For each discrete sector, we show the mean percentage cover change, set at a threshold of 10% (this is the power of the towed-diver observer technique to accurately document benthic change). Note the loss of hard coral is emphasized within 5 of the sectors (sectors 17, 18, 30, 32 and 37), the extensive loss of crustose coralline algae cover in 29 sectors, and the increase in macroalgae in 23 of the island sectors. Blank sector indicates an absence of benthic data in the sector in at least one of the survey years meaning a change value could not be computed.

*Initial recovery of Guam's **deep reefs**: change in benthic cover between the 2014 (< 1 year post-bleaching) and 2017 (NOAA data)*

Within the 30 island sectors containing data in both time points, hard coral cover recovery was focused in 7 sectors around the northern and southeastern coasts (sectors 3, 4, 6, 12, 14, 29 and 32) (**Fig. 9**), with a maximum increase in cover of 28.1% within any single sector. Crustose coralline algae (CCA) recovery was focused in 2 sectors (sectors 2 and 6) in the northwest, with a maximum increase in cover of 23.1%. Declines in macroalgae cover (as a sign of reef recovery) occurred in 16 sectors – within 14 sectors along the southeast to southwest coastline (occurring between sectors 26 to 43), as well as in two sectors in the north (sectors 12 and 14) (**Fig. 9**), with a maximum decline of 62.3% within any single sector.

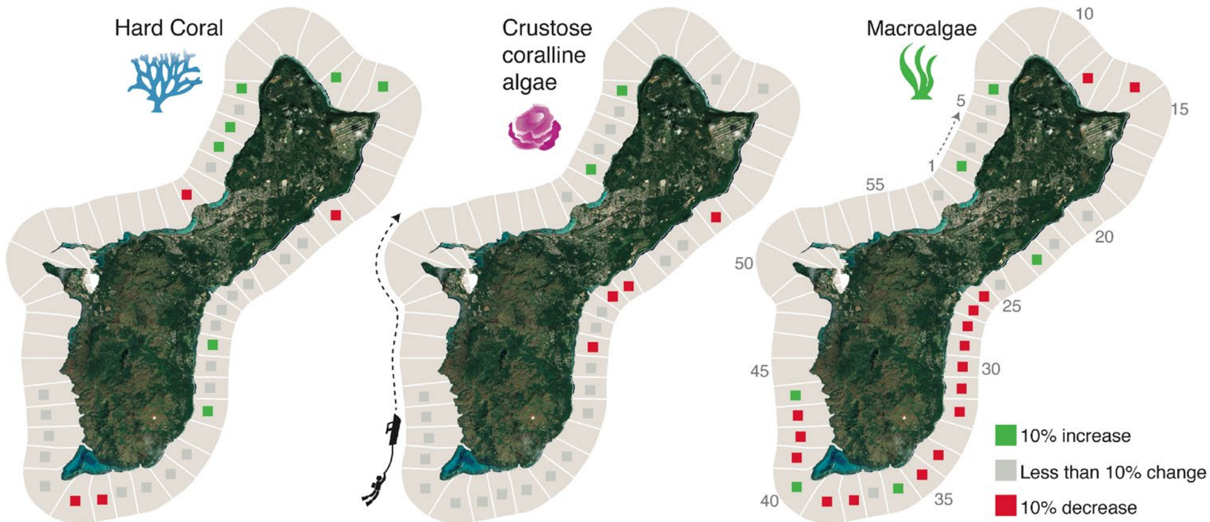

Figure 9. Change in benthic cover between 2014 (<1 year recovery potential) and 2017 (4 years recovery potential). Hard coral recovery was concentrated in 7 core sectors (sectors 3, 4, 6, 12, 14, 29 and 32) and crustose coralline algae (CCA) recovery was concentrated in 2 core sectors (sectors 2 and 6). However, there was continued decline in hard coral within 4 core sectors scattered around the island (sectors 20, 38, 39 and 58) and CCA in 4 core sectors situated along the eastern coast (sectors 20, 25, 26 and 29). Macroalgae decline was focused along the southeast to southwest coastline within 14 core sectors, as well as in two sectors in the north (sectors 12 and 14). Note the continued increase in macroalgae cover in 6 core sectors scattered around the island (sectors 2, 6, 23, 36, 40 and 44). Blank sector indicates an absence of benthic data in the sector in at least one of the survey years meaning a change value could not be computed.

Objectives 2 and 4. *Quantify spatial patterns in bleaching prevalence and benthic change between pre- and post-bleaching years. &. Quantify spatial patterns in upwelling, which is a 'stress-mitigating' factor that supports resilience to climate change.*

Methods

Degree Heating Weeks (DHW)

Degree Heating Week data was provided to our team by NOAA Coral Reef Watch, at 5-km resolution, following methods published within these websites — https://coralreefwatch.noaa.gov/satellite/index.php.

Local human impacts: Integrated local threat

Anthropogenic stress increases sensitivity of coral reefs to the thermal stress events that cause mass coral bleaching. Data on anthropogenic stress patterns can be used in combination with data on resistance and recovery to identify priority areas to reduce stress as part of a Guam-wide effort to support resilience and reduce vulnerability to climate change. The Integrated Local Threat metric was developed for Reefs at Risk Revisited (Burke et al. 2011) and includes overfishing and destructive fishing, marine-based pollution, watershed-based pollution, and coastal development. The ILT data as a raster was converted to points at the resolution of the sectors and then spatially joined to each sector giving us a count, mean and SD. The following categorical breaks were used, following the methods in Reefs at Risk Revisited.

0-100 = Low threat
100-1000 = Medium threat
1000-1500 = High threat
1500 = Very high threat

Tidal energy dissipation (upwelling potential)

State-of-art projections of exposure to coral bleaching conditions in the coming decades (van Hooidonk et al. 2016) do not resolve features, such as upwelling, that can mitigate the effects of thermal stress. Understanding upwelling patterns provides a more detailed view of how exposure to future thermal stress events may shape coral reef communities. Upwelling can temporarily reduce the thermal stress on tropical corals by bringing cool, deep water onto the reef (Storlazzi et al. 2013). These turbulent wave fronts result from the breaking of internal waves traveling along the thermocline and drive an up-slope transport of deep water from beneath the thermocline that, as well as being cooler than ambient surface water, is also typically nutrient rich (Leichter et al. 2003) and may contain higher concentrations of zooplankton and particulate matter (Sevadjian et al. 2012). Upwelling can offer thermal and energetic reprieve to corals during periods of thermal stress and can reduce bleaching prevalence and severity (Wall et al. 2015). Internal waves are a common feature on many coral reef systems, including coastal reefs in Florida (Leichter et al. 1996), low-lying offshore islands such as those in the Andaman Sea (Roder et al. 2010), high-islands such as Oahu in the north Pacific (Sevadjian et al. 2012) and Moorea in the South Pacific (Leichter et al. 2012), and at isolated oceanic atolls, such as Palmyra Atoll in the central Pacific (Gove et al. 2015; Williams et al. 2018). To estimate likely zones of upwelling by the internal tide and internal waves around Guam, we quantified tidal energy dissipation – the dissipation of energy in deep waters that is indicative of deep-water waves breaking and subsequently moving some of the water up the reef slope in to the shallows.

Tidal energy dissipation estimates were calculated using a modified version (Green and Nycander 2013) of an existing parameterization (Zaron and Egbert 2006). The conversion vector was thus given by:

$$E(x,y) = C\rho \frac{(\nabla h)^2 N_b N_a}{h 8 \omega \pi^2} U^2$$

where C~50 is a constant, ρ is the density of seawater, h(x,y) is the water depth, Nb(x,y) is the buoyancy frequency, N, calculated at the sea bed ($N^2 = g/\rho\ \partial\rho/\partial z$), Na(x,y) is the vertically averaged buoyancy frequency throughout the water column, ω is the frequency of the tidal constituent under consideration (here taken to be 2π/(12.42 x 3600), representing the dominating M2 tide), and U(x,y) is the amplitude of the tidal transport vectors. The bathymetry data for h came from GEBCO 2014 (www.gebco.org), tidal transports were taken from the inverse solution in the Pacific Ocean ATLAS (http://volkov.oce.orst.edu/tides/PO.html), and stratification came from the WOCE database (https://www.nodc.noaa.gov/woce/wdiu/).

The conversion was calculated "offline" (Green and Nycander 2013) – their method 1.ii) at the 30" horizontal resolution of the bathymetry, and all other variables were interpolated to the bathymetric grid using linear interpolation before the computation. Note that throughout this study we only investigate the magnitude of the conversion vector.

Surface wave power

Wave power is often a core driver of coral reef ecosystem benthic structure. Where wave power peaks, benthic competitors with wave tolerant, low-lying morphologies such as turf algae and crustose coralline algae (CCA) dominate (Williams et al. 2013; Gove et al. 2015). Where wave power is low, larger upright benthic competitors such as hard corals and macroalgae that are vulnerable to physical dislodgement and damage from water-borne projectiles (Engelen et al. 2005; Madin 2005; Madin et al. 2014) can gain competitive dominance (Williams et al. 2013; Gove et al. 2015).

We calculated integrated surface wave power (kWh m-1) for all island sectors using a 3-h output from NOAA's Wave Watch III global, full-spectral wave model (WWIII; http://polar.ncep.noaa.gov/waves/wavewatch). To link the 50-km resolution WWIII model output to the 58 island sectors, we used an incident wave swath method (Aston et al. 2019). First, we calculated wave power from significant wave height (H_s), peak period (T_p) and peak direction (D_p) (Tolman 2014). Wave power ($W\ m^{-1}$) is the energy flux per unit of wave crest, defined as:

$$WP = \frac{\rho g^2 T_p H_s^2}{64\pi}$$

where ρ is the density of seawater ($1024\ kg\ m^{-3}$) and g is the acceleration of gravity ($9.8\ m\ s^{-2}$). Wave power combines wave height and period and thus provides a more representative metric of the most powerful wave events than either Hs or Tp alone. For 447 equally spaced locations along the 15-m depth contour of Guam (every ~300 m), we created a 360° radial plot of line length 100 km. Where these lines intersected land on Guam itself that degree bin was removed, leaving only the angles open to exposure in the incident wave swath. For each of these exposed degree bins, wave power and its corresponding direction were selected at each time-step for the closest WWIII pixel. We summed yearly values for the period 2003 – 2011 to give a single number representing the mean annual cumulative wave power, or the annual wave energy flux ($kWh\ m^{-1}$) and calculated a yearly average for each of the 447 equally spaced locations. The next step was to create a 250 m buffer around each of our 447 locations and used a spatial join to assign their wave power values to individual island sectors. When sectors contained values from more than one 250 m buffer, an average was taken.

Results

There were clear within-island gradients in stress-reinforcing factors around Guam (**Fig. 10, 11**). Integrated local threat, an integrated measure of local human impacts, was classed as 'very high' along the central western and eastern coasts, 'high' along the remainder of the eastern and western coasts, and 'medium' along the north and south coast (**Fig. 10**). No areas around Guam were classed as 'low' integrated local threat. Exposure to degree heating weeks (DHW) in 2013 generally showed little within-island variation, although the variation that did exist showed similar patterns overall to gradients in integrated local threat. DHW exposure remained emphasized on the central western coast (4.5-5.0 DHW), but patchier along the central eastern coast and in places dropped to 4.0-4.5 (**Fig. 10**). The lowest DHW exposure (3.5-4.0) occurred along the north and southwestern coasts.

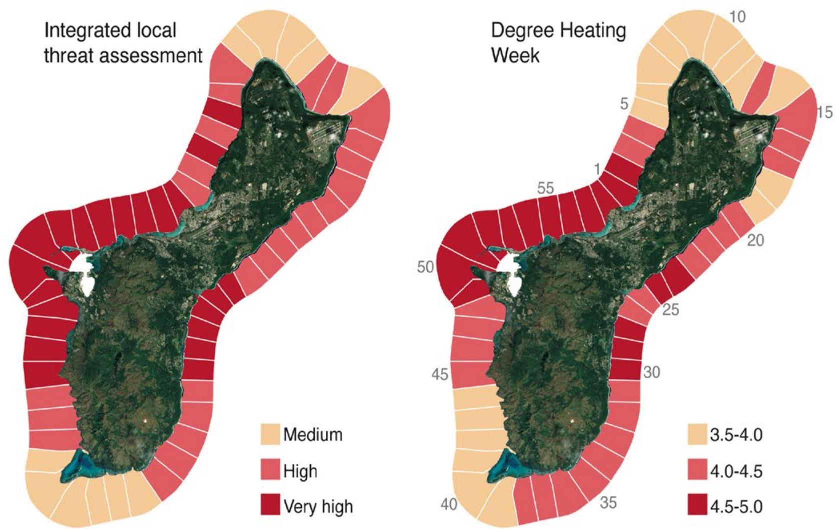

Figure 10. Within-island variation in local human impacts ("integrated local threat") around Guam (left) and the variation in Degree Heating Weeks (DHW) around the circumference of Guam during the 2013 ocean-warming event (right). Note the higher DHW along the western coast and in pockets of the eastern coast, and lower values along the north and southwest coastline.

There were clear within-island gradients in tidal energy dissipation, as a proxy for upwelling potential, and surface wave power (**Fig. 11**). Tidal energy dissipation peaked at >2 W m^2 along the south to southwestern coast and was generally low (0-0.5 W m^2) everywhere else. Surface wave power showed an equally simplistic gradient, with the eastern coastline more exposed than the western (**Fig. 11**). Along the eastern coast, however, there were pockets of variation, with a single sector on the north coast (sector 10) experiencing the highest exposure levels (100-1204 kWh m^{-1}), and a small section (sectors 38-40) of the south coast experiencing medium to low exposure (<404 kWh m^{-1}). In contrast, the western coast experienced a far more homogenous low exposure to surface wave power. Thus, a section of the southwestern coastline experiences both high upwelling potential and low exposure to surface waves (sectors 41-46) (**Fig. 11**).

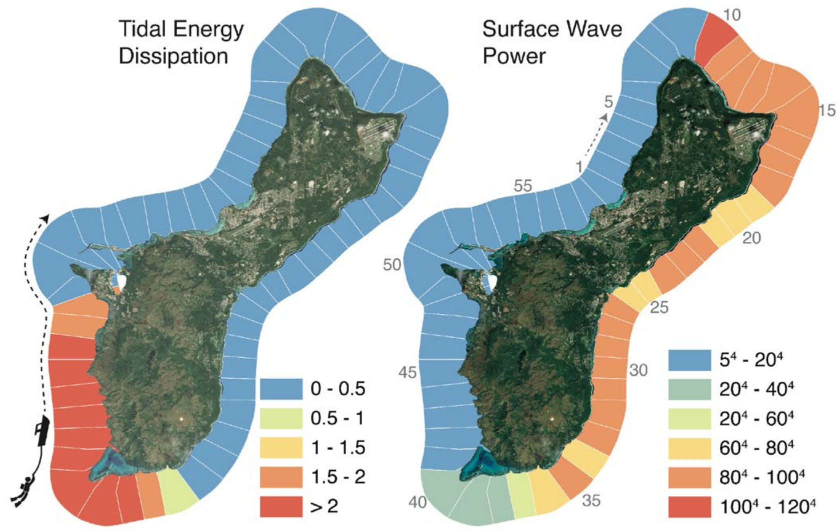

Figure 11. Within-island gradients in tidal energy dissipation (W m^2) as an indicator of upwelling potential (left) and long-term climatology of surface wave power (kWh m^{-1}) (right). Note the high potential for upwelling along the south and south-west coasts of Guam relative to the rest of the island and the high surface wave power in the north-east and down the eastern coast of Guam relative to the rest of the island. Also note the southern-western flank of coastline where upwelling is maximized and surface wave energy is minimized.

Objective 3. *Quantify spatial patterns in anthropogenic stress that are 'stress-reinforcing' factors that contribute to reef decline under the threat of climate change*

Methods

We constructed a series of statistical models to test for a link between our four key response variables (1. pre-bleaching long-term mean benthic community patterns, 2. impact of the 2013 bleaching event on shallow reefs, 3. impact of the 2013 bleaching event on deep reefs, and 4. the initial recovery of deep reefs post-bleaching) and our four stress-reinforcing (integrated local threat, degree heating weeks, surface wave power) and stress-mitigating (tidal energy dissipation) factors. To do this we used distance-based modeling methods, specifically distance-based linear models (McArdle and Anderson 2001). A key advantage of these distance-based, permutational modeling techniques is that they make no prior assumption about the distribution of the response variable data, and thus normality does not need to be satisfied. For each model, the predictor variables were normalized and assessed for pairwise co-linearity using Pearson's correlation values ($r = <0.62$ in all cases). Models were constructed using Euclidean similarity matrices and 10,000 permutations of the raw data. Model selection was based on step-wise selection of the predictors (in a conditional manner) and Akaike's information criterion (Akaike 1973) with a second-order bias correction was applied (AICc) (Hurvich and Tsai 1989) to account for the small sample size.

Results

On Guam's shallow reefs, bleaching-induced mortality in 2013 was best explained by gradients in tidal energy dissipation and variations in integrated local threat, which together explained 36.8% of the within-island variation (Table 1). In general, bleaching-induced mortality was higher where there was higher tidal energy dissipation and lower integrated local threat. Similarly, overall bleaching impact in 2013 was positively correlated with tidal energy dissipation, explaining 11.0% of the within-island variation (Table 1).

On Guam's deeper reefs, change in hard coral cover between pre- (2003-2011) and post-bleaching (2014) was best explained by within-island variations in surface wave power. Loss of coral cover was higher where surface wave power was higher, however the model only explained 10% of the within-island variation (Table 1). Change in CCA cover over the same time period was best explained by gradients in integrated local threat and degree heating weeks, with the two predictors explaining 15.6% of the within-island variation. In general, with the loss of CCA cover was higher where degree heating weeks was higher and integrated local threat was lower. Change in macroalgae cover was best explained by gradients in integrated local threat; increases in macroalgae cover was higher where integrated local threat was lower, however the model only explained 8.7% of the within-island variation (Table 1).

Four years post-bleaching, change in coral cover on Guam's deep reefs remained hard to predict, with higher tidal energy dissipation explaining 8.0% of the within-island variation (Table 1). In general, increases in coral cover were higher where tidal energy dissipation was lower, although the relationship was weak and hard to interpret. Changes in CCA cover over the same time period were best explained by gradients in surface wave power. Increases in CCA cover were higher where surface wave power was lower, explaining 17.2% of the within-island variation (Table 1). Change in macroalgae cover over the same time period was best explained by gradients in surface wave power and tidal energy dissipation, with these two predictors explaining 30.4% of the within-island variation (Table 1). The greatest decreases in macroalage cover were where surface wave power was higher and where tidal energy dissipation was higher.

Table 1. Model output summaries relating within-island spatiotemporal variations in bleaching response and benthic community change on Guam's shallow and deep reefs. CCA, crustose coralline algae; ITL, integrated local threat; DHW, Degree Heating Week; SW, surface wave power; TED, tidal energy dissipation. Variation explained shows individual predictor contributions to overall model performance in parentheses when more than one predictor formed the optimal model.

Benthic group	Response variable	Habitat	Data source	Predictors included	Optimal model	Variation explained (R^2)
Hard coral	Bleaching-induced mortality	Shallow fore-reef	University Guam	ILT+DHW+SW+TED	TED+ILT	(28.5, 8.3) 36.8
Hard coral	Overall bleaching impact	Shallow fore-reef	University Guam	ILT+DHW+SW+TED	TED	11.0
Hard coral	Δ (2003-2011) to 2014	Deeper fore-reef	NOAA towboard	ILT+DHW+SW+TED	SW	10.0
CCA	Δ (2003-2011) to 2014	Deeper fore-reef	NOAA towboard	ILT+DHW+SW+TED	ILT+DHW	(8.8, 6.8) 15.6
Macroalgae	Δ (2003-2011) to 2014	Deeper fore-reef	NOAA towboard	ILT+DHW+SW+TED	ILT	8.7
Hard coral	Δ 2014 to 2017	Deeper fore-reef	NOAA towboard	ILT+DHW+SW+TED	TED	8.0
CCA	Δ 2014 to 2017	Deeper fore-reef	NOAA towboard	ILT+DHW+SW+TED	SW	17.2
Macroalgae	Δ 2014 to 2017	Deeper fore-reef	NOAA towboard	ILT+DHW+SW+TED	SW+TED	(17.1, 13.3) 30.4

Objectives 5 and 6. *Develop statistical models that compare and evaluate predictors of reef change in Guam under climate change. &. Identify potential reef refugia, 'bright spots' where management investment may reap the greatest returns in long-term provision of ecosystem goods and services.*

Methods

Here we defined a 'bright spot' as an above average increase (>1SD of the mean) in hard coral and CCA cover or an above average decrease in macroalgae cover. Conversely, we defined a 'dark spot' as an above average decrease (>1SD of the mean) in hard coral and CCA cover or an above average increase in macroalgae cover.

Results

*Guam's **deep reef** status in 2017 – 4 years post-bleaching (NOAA data)*

Four years after the 2013 bleaching event, mean hard coral cover around Guam equaled 19.8%, crustose coralline algae (CCA) equaled 5.1%, and macroalgae equaled 30.2%. The highest hard coral cover occurred along parts of the northwestern and southeastern coastlines (**Fig. 12**), reaching a maximum of 42.8% within any single sector. The highest CCA cover occurred along pockets of the northwestern and eastern coasts, reaching a maximum of 25% within any single sector. Finally, macroalgae cover was highest predominantly along parts of the southern coast (**Fig. 12**), reaching a maximum of 87.5% within any single sector.

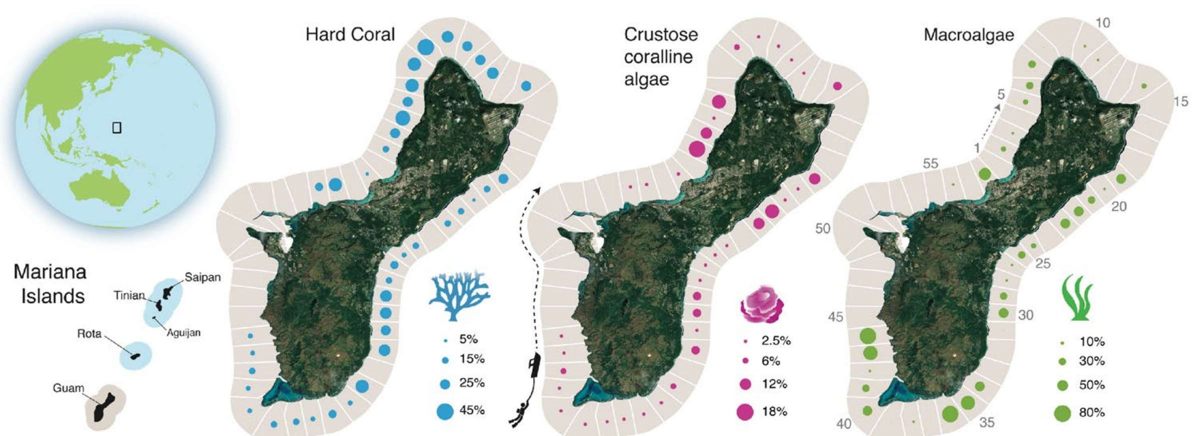

Figure 12. Within-island variation in benthic functional group cover among 58 discrete 2.3 km sectors around the circumference (~134 linear km) of Guam's seascape in 2017. Blank sectors indicate an absence of benthic data.

Guam's coral reef bright and dark spots

Of the 30 island sectors containing data for both time points, there were 3 hard coral bright spots – sectors 6 (northwest), 29 and 32 (both in the southeast) and 4 crustose coralline algae bright spots – sectors 2, 3, 5 and 6 (all concentrated in the northwest) (**Fig. 13**). Additionally, there were 6 macroalgae bright spots – sectors 12 (north), 27, 28, and 32 (southeast), and 38 and 41 (south). There were 3 hard coral dark spots – sectors 20 (east), 38 and 39 (south) and 58 (west), and 4 CCA dark spots – sectors 20, 25, 26, and 29, that were all concentrated along the central eastern coast (**Fig. 13**). There were 6 macroalgae dark spots where macroalgae continued to increase in cover scattered all around the island – sectors 2, 6, 24, 36, 40, and 44.

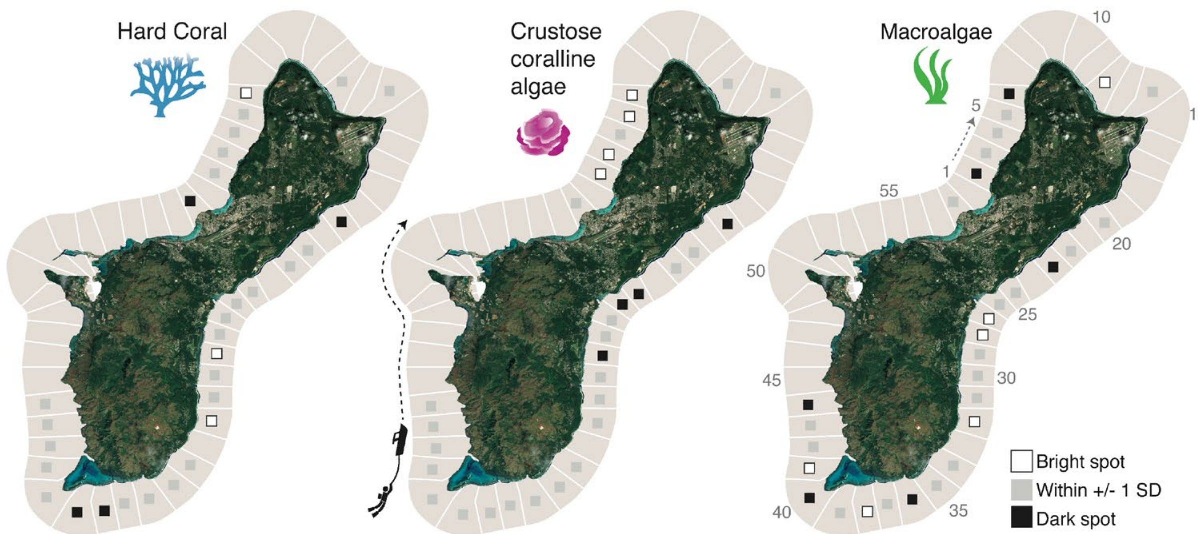

Figure 13. Island sectors around Guam that showed a higher than average or lower than average change in benthic cover between 2014 (<1 year recovery potential) and 2017 (4 years recovery potential). Here we defined a 'bright spot' as an above average increase (>1SD of the mean) in hard coral and CCA cover or an above average decrease in macroalgae cover. Conversely, we defined a 'dark spot' as an above average decrease (>1SD of the mean) in hard coral and CCA cover or an above average increase in macroalgae cover.

Objective 7. - Communicate with the scientific and management community and community members in Guam to share project results and identify pathways to action, and ensure project methods and results are formally published with open access.

The project results have been shared with managers in Guam and CNMI through sharing of the results in meetings led by local project partners, including Dr. Laurie Raymundo. These efforts are ongoing; presentations scheduled for September and October of 2019 were canceled due to some managers having other engagements. Our team will be presenting the results again in November and December of 2019. Our team is also compiling these and other data layers to prepare for a restoration planning workshop that will include all U.S. coral reef jurisdictions in the Pacific, scheduled for the first week of May, 2020 in Honolulu. The bright spots data layers developed during this project for Guam will then be considered to inform prioritizing coral reef sites for restoration.

This final grant report, once posted to CoRIS, will become the open access report the international scientific and management community will be able to access to learn about and share the project methods and results.

Next steps:

The applied research presented within this project report will be continued during FY19 under a CRCP-funded project led by this team, entitled: Mapping climate resilience and vulnerability for the coral reefs of Guam to aid in prioritizing restoration sites. Nursery-raised corals have recently been transplanted in Guam based only on where nursery managers thought transplants would be most likely to survive in the near term. Nursery managers and resource managers are collaborating with this project team and state that future out-planting will benefit greatly from strategic planning. Our project team will develop spatially continuous data on climate vulnerability for the reefs surrounding Guam. We will then develop a Restoration Priority index in a workshop setting with managers and stakeholders based on climate and social vulnerability, human use patterns and impacts, access, and the economic/cultural value of reefs. Developing and combining these data layers ensures strategic planning precedes outplanting.

The results from this FY18-funded project will be combined with the results from the FY19-funded project and shared within a NOAA CRCP Tech Memo we will prepare and publish with CRCP in late 2020.

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Supplemental Material

Supplemental Table 1. Island sector centroids.

GRID_ID	CENT_LAT_UTM	CENT_LON_UTM	CENT_LAT_WGS	CENT_LON_WGS
1	261002.6851	1494809.525	144.7919458	13.51178428
2	262023.0512	1496897.194	144.8011949	13.53073054
3	263048.7602	1498948.91	144.8104975	13.5493523
4	264101.3158	1500998.864	144.8200495	13.56796014
5	264955.6944	1503129.687	144.8277656	13.58728257
6	265672.1669	1505303.448	144.8342053	13.60698183
7	265581.1504	1507728.738	144.8331648	13.62888893
8	266815.5793	1509628.716	144.8444135	13.64615602
9	268707.0113	1511041.947	144.8617746	13.65907714
10	270981.7626	1510089.938	144.8828707	13.65065513
11	272380.6362	1508238.093	144.8959446	13.63403149
12	273822.9425	1506390.369	144.9094173	13.61744765
13	275825.0218	1505342.042	144.9279967	13.60812947
14	278263.8632	1504904.122	144.9505622	13.60435862
15	279161.4031	1502840.314	144.9590138	13.58577702
16	278039.0484	1500703.735	144.9488114	13.5663847
17	276993.6794	1498673.165	144.9393135	13.54795604
18	276185.1222	1496489.222	144.9320159	13.52815939
19	274423.4557	1495006.851	144.9158626	13.51462925
20	272547.8397	1493661.293	144.8986483	13.50232577
21	270670.1895	1492324.107	144.8814163	13.49009678
22	268938.0154	1490827.511	144.8655421	13.47643785
23	267297.1217	1489232.05	144.8505205	13.46189204
24	265558.4338	1487712.292	144.8345917	13.44802193
25	263513.4277	1486643.719	144.8158002	13.43820334
26	261676.9066	1485258.315	144.7989611	13.42553752
27	260343.4336	1483359.319	144.7868095	13.40827098
28	259575.2731	1481177.032	144.7799004	13.38849035
29	259153.7533	1478909.087	144.7761983	13.36796389
30	258985.3115	1476604.514	144.7748348	13.34712701
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32	258799.5245	1472012.589	144.7735001	13.30562106
33	258049.0408	1469819.277	144.7667575	13.28574242
34	256927.6501	1467810.812	144.7565792	13.26750385
35	255444.0928	1466047.757	144.7430412	13.25145298
36	253536.0724	1464672.515	144.7255577	13.23887092
37	251258.0225	1464239.34	144.7045837	13.23476907
38	249024.5399	1463796.893	144.6840225	13.23058549
39	246710.5484	1463316.05	144.6627233	13.22604663
40	244597.9074	1464575.382	144.6431308	13.23724539
41	244763.6773	1466961.336	144.6444521	13.2588161
42	245100.8077	1469214.653	144.6473656	13.27920324
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46	244539.3819	1478692.794	144.6413571	13.36478829
47	244889.8507	1480966.32	144.6443914	13.38535919
48	245357.4104	1483244.663	144.6485062	13.40598374
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55	252633.8062	1491437.142	144.71496	13.48062147
56	254914.4303	1491763.709	144.7359877	13.48376287
57	257113.0851	1492421.908	144.7562315	13.48989223
58	259268.0064	1493246.375	144.7760588	13.49751882