AN ABSTRACT OF THE THESIS OF Travis C. Reynolds for the Master of Science in Biology presented April 25th 2016.

Title: Environmental Factors Explain Coral Demography and Coral Bleaching Patterns in Guam

Approved: ______________________________
Laurie J. Raymundo, Chair, Thesis Committee

In the Mariana Islands, coral bleaching is an increasing threat to coral ecosystem stability. Between August and October 2013, a severe bleaching event impacted Guam reefs and coincided with local offshore sea surface temperatures exceeding the maximum monthly mean by 0.5–1.6 ° C. During this time, doldrum conditions likely increased bleaching intensity from calming seas and low cloud cover. The bleaching event provided an opportunity to understand relationships between ocean warming and Mariana coral demography. This research uses coral life-history to explain how environmental processes influence reef growth and bleaching prevalence around the island. Between October and December 2013, 46 shallow reef sites (2 – 6 m depth) around Guam were surveyed to estimate benthic communities and record bleaching prevalence in coral populations. Using island geology (volcanic vs. limestone; distance to river) and wave exposure gradients (leeward vs. windward; fetch estimates), four biogeographic regions (northwest, northeast, southeast, southwest) were determined *a priori* and evaluated for significant relationships between the local environment and ocean warming. Island-wide, 49% of the coral cover bleached and was most severe in southeastern reefs (79%). Bleaching followed a consistent pattern with higher prevalence occurring in high diversity, windward reefs and lower prevalence in low diversity, leeward reefs. Environmental interdependencies were strongly related to differences in coral life-history. Windward reefs are wave exposed and species with competitive life-histories (faster growing, broadcast spawners, and complex morphology) persist while stress tolerant life-histories (slow growing, brooder, and simple morphology) thrived along leeward reefs in low wave exposure. A bleaching mortality index was estimated for Guam corals and revealed Acroporidae and Pocilloporidae species were most influenced by temperature stress while Faviidae and Portidae species were less influenced. This widely corroborated result is consistent over several regional bleaching events and reveals windward reef communities are highly vulnerable to ocean warming. This is most true for several species of caespitose *Acropora*, encrusting *Montipora*, corymbose *Pocillopora* and *Stylophora mordax*.

TO THE OFFICE OF GRADUATE STUDIES

The members of the committee approve the thesis of Travis C. Reynolds presented April 25th, 2016.

Laurie J. Raymundo, Ph.D., Chair

Peter Houk, Ph. D., Member

Danial Lindstrom, Ph.D., Member

David Burdick, M.S., Member

ACCEPTED:

John A. Peterson, Ph.D. Date
Assistant Vice President of Graduate Studies,
Sponsored Programs and Research

ENVIRONMENTAL FACTORS AND TAXONOMY EXPLAIN CORAL BLEACHING PATTERNS IN GUAM

BY

TRAVIS C. REYNOLDS

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Acknowledgments

This is dedicated to my family who could never be here and for my friends that motivated me to finish.

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I. Introduction

1.1 *Study Overview*

Modern reef structures represent deposited coral assemblages growing over geologic time in response to environmental regimes (Adey 1978). Coral assemblages, in turn, are driven by species-based life-histories that reflect evolutionary responses of fitness-limiting strategies to forcing environments (Darling *et al.* 2012). For instance, species with mounding morphologies typically grow slowly and are often stress resilient, whereby, faster growing, branching species are superior competitors but have low stress-tolerances. Since the Paleozoic, holobiont (host coral and endosymbiotic zooxanthellae) symbiosis has endured to form accreting assemblages and reef structures, despite several mass extinction and climate change (Pandolfi 1999; Hughes et al. 2003). However, accelerated ocean warming associated with modern climate change threatens reef deposition and accretion by selecting against stress-intolerant species (*i.e.*, *Acropora* and *Pocillopora* in the Indo-Pacific).

Coral bleaching is a complex stress response within the holobiont (Hoegh-Guldberg and Smith 1989). Widespread coral bleaching coincides with persistent (*i.e.*, weeks) high irradiance and sea surface temperatures (SST) 1-2 C° higher than the maximum monthly mean (Glynn 1993; Hoegh-Guldberg 1999; Hughes *et al.* 2003). Severe ocean warming events have coincided with Pacific El Niño and La Niña Southern Oscillations (ENSO) (Glynn 1993; Wilkinson 1998), resulting in global bleaching events. But locally, a coral assemblage's thermal history defines bleaching extent and severity (Marshall and Baird 2000). For instance, van Woesik et al. 2012 show that during a recent 2010 bleaching event in Palau, Micronesia, coral assemblages in protected lagoons and bays were less impacted by thermal bleaching compared with outer reefs.

These differential responses were a suspected artifact of more extreme thermal histories in the lagoons, and higher turbidity levels which can limited bleaching response (Cacciapaglia and van Woesik 2016). While climate change is increasingly problematic, direct management is daunting – often unrealistic with current political-economic challenges (see stratosphere injections; Kwiatkowski *et al.* 2015). Therefore, reef managers limited mainly to observation rather than direct intervention, often ask: (*i*) how to monitor and forecast ocean warming, (*ii*) how the global climate influences a region's thermal history, (*iii*) what is the expected, species-based holobiont response, and (*iv*) and how might the local environment influence bleaching response? This thesis addresses these questions using data from a 2013 bleaching event on Guam, the largest island in Micronesia (560 km^2) and southernmost island in the Mariana archipelago. I test the extent to which ocean warming, coral assemblage composition and demography, and environmental regimes influenced coral bleaching prevalence.

1.2 *Ocean warming and management responses*

Ocean warming has increased mean SST across the oceans by 0.6 C° over the past century (IPCC 2014). Although climate change research has advanced, management of coral bleaching events is typically limited to reducing carbon emissions, monitoring, forecasting, and reinvigorating management of synergistic localized stressors (Wooldridge 2009; Cox *et al.* 2002). Thus, management of mass coral bleaching events can be characterized as indirect. In contrast, most other stressors on reefs have direct management options: reef eutrophication and disease epizootics, crown-of-thorns starfish outbreaks, and overfishing (Hughes *et al.* 2003). Respectively, refining waste treatment and limiting toxic runoff improves reef health (Vega Thurber *et al.* 2014), starfish removal and *in situ* lethal injection limit otherwise severe outbreaks

(Rivera-Posada *et al.* 2013), and establishing catch limits and marine sanctuaries are direct solutions (Pauly *et al.* 2002). In contrast, mass coral mortality from thermal bleaching reduces coral cover quickly (16% between 1997/1998; Wilkinson 1998) and is considered unmanageable under current climate projections (IPCC 2014). Therefore, researchers must advance climate science by forecasting pattern trends to mediate negative responses to bleaching.

Researchers use both experimental manipulations and monitoring data to identify how corals and coral assemblages respond to bleaching events. Tracking biological response offers an improved means to characterize acclimatization/adaptation (van Woesik *et al.* 2011; Guest *et al.* 2012; Pratchett *et al.* 2013), and develop management strategies promoting reef growth and species diversity (Graham *et al.* 2014). Central to these studies are remotely sensed data that forecast ocean warming. Climate modeling is continuously improving ocean temperature monitoring and forecasting (Donner 2009; Eakin *et al.* 2009; Kleypas *et al.* 2015). Satellite-derived oceanographic data are essential in describing coral bleaching patterns across space and time (Eakin *et al.* 2009; Oliver *et al.* 2009). NOAA's Coral Reef Watch (CRW) uses near-real time satellite SST and a rolling climatology (long-term baseline) forecast bleaching hotspots based upon Degree Heating Weeks that indicate both the magnitude and duration of thermal stress (DHW; Eakin *et al.* 2009, Lui *et al.* 2006). Thus, bleaching hotspots have positive temperature anomalies that have exceeded local maximum monthly mean SST for a period of 12 weeks. CRW has a newly unveiled 5 km product that adds depth and resolution to the previous 50 km model and better delineates temperature anomalies (coralreefwatch.noaa.gov). Remote sensing improves bleaching forecasting, but reef hydrodynamics, solar irradiance, and watershed influence are all important in refining global predictions at the local scale (Liu et al. 2003). Therefore, it is imperative to track reef assemblages across space and through time to improve our understanding, and management, of bleaching prevalence (Baird and Marshall 2002; van Woesik *et al.* 2011).

1.3 *Global and local climate determine bleaching patterns in Micronesia*

El niño southern oscillation (ENSO) predicts the occurrences of global bleaching events. The positive El Niño phase begins when the Southern Oscillation Index (SOI), a differential sea surface pressure estimate between Darwin, Australia and Tahiti, is positive over an extended period of time (McPhaden 2004). During positive phases, winds die down, and major oceanic surface current systems slow. This drives heavy rainfall over the Americas but contributes to drier conditions in western Pacific. Together these conditions lead to increases in global sea surface temperature. The La Niña phase, measured as extended negative SOI, shifts the Pacific Warm Pool (PWP) to the western Pacific Ocean and bleaching in the Indo-Pacific, Indian Ocean, and Caribbean intensifies (McPhaden 1999). The 1997/1998 ENSO was the strongest recorded and subsequent bleaching-related mortality reduced global reef cover by 16% (Wilkinson 1998). However, longer-term modes such as the Interdecadal Pacific Oscillation (IPO; Mantua *et al.* 1997), Atlantic Multidecadal Oscillation (AMO; Schlesinger and Ramankutty 1994, Enfield *et al.* 2001), and Indian Ocean Dipole (IOD; Saji *et al.* 1999) influence the severity of regional ENSO events as well (Kleypas *et al.* 2015). Interdecadal modes have global and regional consequences. For example, the AMO clearly impacts north Atlantic climate, but also Asian monsoon conditions affecting Indo-Pacific reefs (Lu *et al.* 2006). In the Pacific, the positive phase of the IPO appears to have a secondary contribution to the severity of past ENSO events (Mantua and Hare 2002, Geouro *et al.* 2000, Kleypas *et al.* 2015). Interconnection between ENSO and the PDO have long been known to drive temperature anomalies that differ based upon geographic location, but recent ocean warming is altering historical climate patterns (Donner *et al.* 2005; Thompson and van Woesik 2009; van Woesik *et al.* 2012).

Micronesia, a west Pacific region that includes the Palauan, Marianas, Caroline, and Marshall islands share a rich regional marine species pool, but historical bleaching patterns differed between eastern and western islands. In the eastern Pacific (eastern Caroline and Marshall islands), bleaching return frequency is predicted to be high (< 5yr) and highly correlated with El Niño events. Western Micronesian (western Micronesia, Palauan, Mariana islands) bleaching frequency is predicted to be much lower, occurring in 50-year intervals (Thompson and van Woesik 2009). Climate drives regional ocean temperature warming, but locally, coral temperature sensitivity influences bleaching prevalence, and these can be influenced by local events.

Several environmental factors refine coral bleaching response to global thermal stress events, but weather appears to be most influential. Reef eutrophication (Wooldridge 2009; Wagner *et al.* 2010; Wiedenmann et al. 2012), upwelling of cold water that causes rapid SST flux (Coles and Jokiel 1977; Jaap 1979), salinity decline in the upper isobath (Goreau 1964, Egana and DiSalvo 1982), and aerial exposure during extreme low tides (Glynn 1991) can all induce or augment bleaching at an individual reef scale. Thermal stress is a seasonal phenomena, however, the onset of severe global bleaching is an anomalous atmosphere/ocean interconnection response (Glynn 1991, Hughes et al. 2003). In summer months when SST is highest, bleaching intensifies during periods of clear calm weather (Eakin et al. 2009). These doldrum-like conditions are characterized by limited ocean circulation and increased solar insolation (Mumby et al. 2001; Eakin et al. 2009). Low regional wind circulation translates into increased solar insolation from ultraviolet (UV) radiation, specifically the 280-400nm band (Gleason 1993, Gleason and Wellington 1993, Mumby et al. 2001). Together, high temperature destabilizes coral symbiosis while excessive irradiance directly impairs the photosynthetic apparatus in zooxanthellae (Gleason 1993), leading to an organismal responses to climate stress (Glynn 1991, Hughes et al. 2003).

1.4 Organismal response to climate stress

Photosynthetic efficiency is highest near the upper thermal tolerance of corals (Jokiel and Coles 1977), where over 95% of fixed carbon is assimilated for calcification (Muscatine 1990). Zooxanthellae selectively translocate photosynthates (amino acids, sugars, carbohydrates, and peptide bonds) to the coral for energy (Hoegh-Guldberg 1999). In return, the coral provides protection and stability for zooxanthellae, while host metabolic waste products, nitrogen and phosphorus – limiting nutrients in oligotrophic reefs – are recycled by endosymbionts (Muscatine and Porter 1977, Glynn 1993; Hoegh-Guldberg 1999). When a coral's thermal limit is surpassed, solar insolation becomes a liability and causes photo-inhibition within the symbiont's chloroplast (specifically, the thylakoid membrane where light reactions Photosystem I and Photosystem II (PSII) are embedded; Jones *et al.* 1998). Following temperature and light stress, harmful superoxides and oxygen radicals are overproduced, accumulating in PSII; subsequently, electron transport needed to energize dark reactions and CO_2 fixation is impaired (Iglesias-Prieto *et al.* 1992; Asada 1999). Bleaching begins if the oxidative stress rate is higher than the photosynthetic repair rate (Baird *et al.* 2009). Surpassing this threshold results in zooxanthellae expulsion and/or lost photo-protective pigmentation. Prolonged photosystem impairment leads to whole or partial colony mortality (Baird and Marshall 2002), lowered immunity (Williams and Bunkley-Williams 1990, Bruno *et al.* 2007), reduced growth and calcification (Glynn 1993), and suppressed reproduction (Jokiel and Coles 1990; Baird and Marshall 2002).

Host corals have morphological and physiological traits that also limit photosynthetic impairment. Depth, hydrodynamics, light regimes, and other local environmental determinants of bleaching prevalence noted above, act differently upon colony morphology and coral physiology. Over geologic time, coral species radiation reveals two modes reflected in modern phylogenies: *robusta* and *complexa* (Storlarski *et al.* 2011, Kerr 2005). Interestingly, both modes reveal similar character traits. Both Portidae and Acroporidae are located within *complexa*. *Porites* are often massive forming and stress-tolerant while *Acropora* and *Montipora* have complex morphologies and are highly susceptible to temperature stress. In *robusta*, massive *Dipsastrea* (Pacific *Favia*; Huang *et al.* 2014) are stress-tolerant while most Pocilloporidae species have complex morphologies and are more susceptible to temperature stress (Gleason 1993, Loya *et al.* 2001, Marshall and Baird 2002). Consequently, physiological traits also reflect intercolonial shape – branching morphologies have thinner tissue and less photo-protective pigments to limit temperature stress than massive species (Baird *et al.* 2009). Clearly the host can influence bleaching response, but reef-wide, differential bleaching susceptibility is also environmentally influenced.

1.5 Reef assembly and paleoecology of the Mariana islands

The Mariana Archipelago is a reef system in the tropical Western Pacific where volcanism, tectonic uplift, interannual climate and trade wind-driven wave exposure have influenced reef assembly since the Paleogene. The northern islands recently emerged during late Cenozoic arc-volcanism and are geomorphologically different from the southern islands (Randall

1995). In the southern islands, topographically complex watersheds formed amongst volcanic deposits, while flat, uplifted limestone plateaus dominate the emergent landscape. Guam is a mix of raised limestone and volcanic watersheds. Persistent trade-winds blow across this part of the Pacific, resulting in wave energy regimes with highest exposure along the windward, eastern side and calmer conditions on the leeward, western side. Both geomorphology and wave energy regimes influence coral community zonation in this region. Among southern Marianas coral reefs, Houk and van Woesik (2009) found strong environmental and weak biological regulation in coral communities, which were associated with reef geomorphology. Localized stressors such as watersheds were secondary drivers that acted upon assemblages once geomorphology was accounted for. Yet, the existing literature has not formally explained the presence and distribution of reef types on Guam, an island with significantly more igneous rock basement, thereby a more distinct geomorphological presence. More significantly, given the limited influence of thermal bleaching events to the Mariana archipelago to date, no studies exist to describe how ecological-environmental affinities may determine bleaching prevalence.

1.6 2013 bleaching event on Guam

In 2013, a neutral ENSO year, the Mariana archipelago endured the first recorded severe bleaching event, lasting 12 DHW (Reynolds *et al.* 2014). SST rose above 30°C June 2013; by late July SST rose to 31°C and fluctuated between 31 and 33°C through October 2013 (Figure 1). The first signs of bleaching occurred in early August, peaking by mid October 2013 prior to Typhoon San Francisco forming southwest of Guam. This led to water temperatures normalizing by December when only larger massive coral species still showed paling, as other corals were

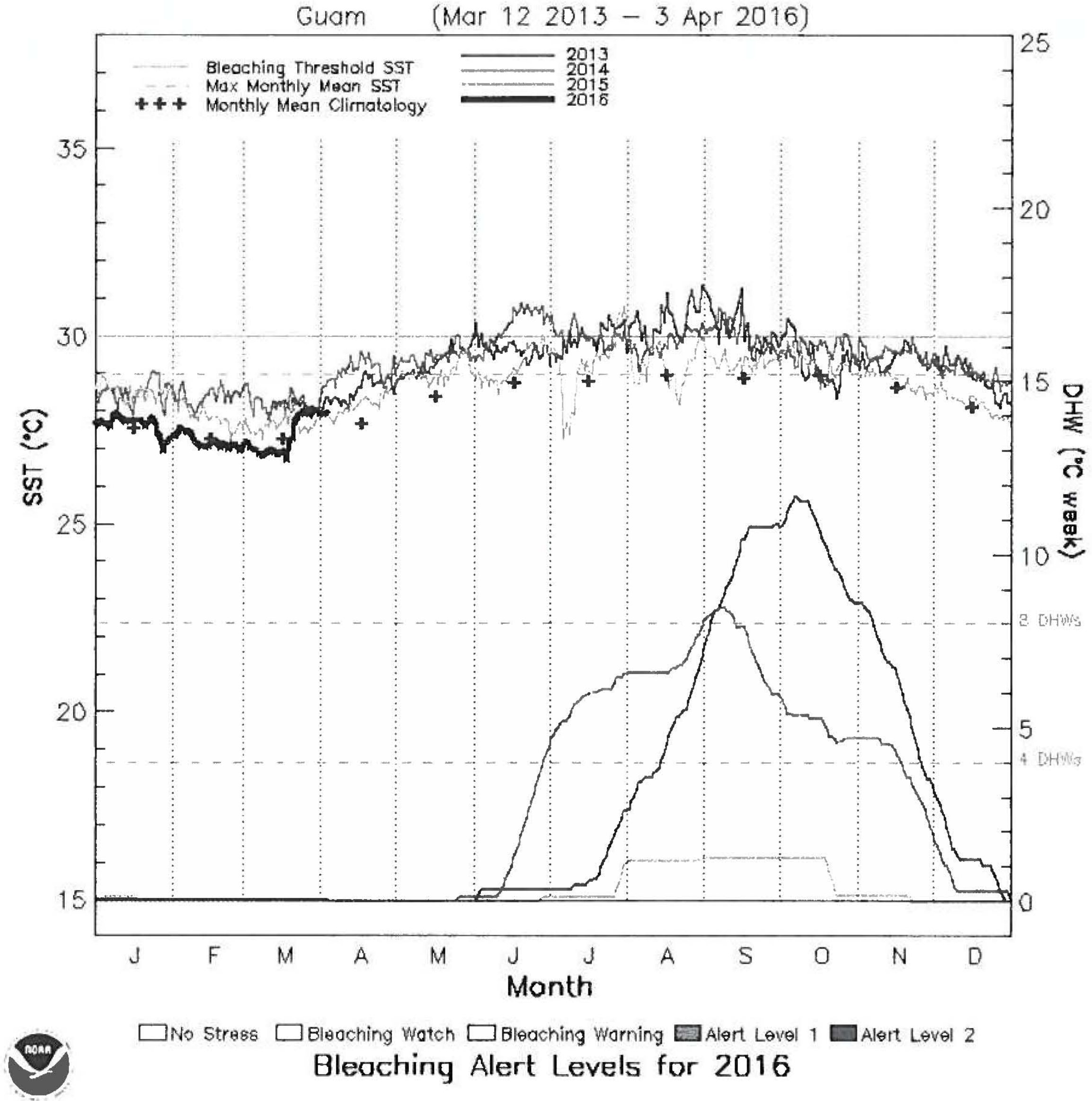


Figure 1. A temperature chart of the 2013 bleaching event with recent heating events in DHW (coralreefwatch.org). The 2013 event is ~12 DHW, three orders higher than 2014 – the next highest anomalous warming period in 15 years. In 2015, reefs did not bleach.

dead or fully recovered. Doldrum conditions were noted during August and September and likely increased bleaching intensity. In response to the bleaching event, Guam was opportunistically surveyed to characterize coral demography and estimate bleaching prevalence in the shallow fore reef (3-6m).

The present thesis coupled several biological measures from coral assemblages (coral abundance, colony density, Shannon diversity, species richness) with environmental measures (wave energy and river distance regimes) to examine their interdependencies. The lack of any previous bleaching events of major significance, the high coral diversity (~ 257 species; Randall 1988), and complex, high-island geology make Guam ideal to examine the role of environmental processes in shaping bleaching responses during a widespread, regional event. This study serves to refine our understanding of how environmental processes determine species composition and bleaching prevalence. Previously, Paulay and Benayahu 1999, Porter *et al.* 2004, Burdick *et al.* 2008, and Reef Base (reefbase.com) recorded the few quantitative bleaching observations in the Mariana Islands (Appendix 1). The 2013 bleaching event allowed us to establish a spatially explicit baseline assessment of Guam's shallow coral communities and quantify ocean warming responses.

1.7 Research objectives and hypotheses

My objectives were to: (*i*) characterize Guam's biogeographic regions by examining relationships between island geology, wave energy, and coral abundances, (*ii*) estimate the extent of the coral bleaching on Guam, and determine if there were spatial differences in prevalence, (iii) synthesize the extent to which favorable conditions for coral growth may have been coupled (or decoupled) with bleaching responses. Sequentially, I address three null hypotheses.

My first hypothesis seeks to define how environmental factors dictate the distribution of coral species abundances around Guam. The null model (H_{01}) states '*that coral assemblages are randomly distribution across wave energy regimes and geological foundations on Guam'*. Accepting the alternative requires evidence for environmental-ecological coupling, and will result in both univariate and multivariate testing to determine how species abundances, percent cover of major benthic substrates, or species diversity responded to environmental factors.

My second hypothesis states that '*coral bleaching prevalence during the 2015 thermal stress event on Guam was homogenous with respect to environmental factors*. If this hypothesis is rejected, multivariate testing will be used to examine the relationships between bleaching prevalence, wave energy, and island geology. In addition, a third hypothesis will be tested to help synthesize the contributions of both environment and biological factors in determining coral bleaching patterns.

My final hypothesis asks if coral growth patterns, environmental regimes, and coral bleaching prevalence around Guam were related. This null model (H_{03}) states that '*coral bleaching prevalence was coupled with both coral abundance patterns and environmental regimes'*. Rejecting this hypothesis would indicate that either biological or environmental history plays a stronger role in determining bleaching response patterns.

II. Methods

2.1 *Site description and biogeographic regions around Guam*

Guam is the oldest (~43 Ma), largest (~540 km^2) and southernmost island in the Marianas Archipelago (13.5° N, 144.8° E). Guam's present day geology is centrally divided along the partially emergent Pago-Adelup Fault, which separates southern volcanic watersheds from uplifted, northern limestone deposits. Trade-wind driven wave exposure further divides the island between eastern-windward and western-leeward coastline (Figure 2).

Southern Guam has complex topography, perforated and scoured by 96 rivers and streams within 14 large watersheds that subdivide into many smaller drainage basins. Southwest Guam's coastline extends from northern Orote peninsula (a Mariana Limestone outcrop), to southern Cocos Island's (an emergent Holocene coral bank) leeward, barrier reef. Protected from trade-wind influence, southwestern reefs fringe along unconsolidated inland features and maintain the lowest island-wide benthic calcification rates and wave energy regimes (long-period south-southwestern swell from passing typhoons prevail 7% of year; Houk and van Woesik 2010; Williams *et al.* 2012). Because Eocene-Oligocene volcanic basement predominates – sediments erode from Quaternary alluvial deposits, and are intensified with poor land-use to transport land-based sediment to the ocean, regularly inundate estuaries. Sediment accumulates along discharge points and re-suspends during storm events, smothering nearby reefs (Wolanski *et al.* 2003).

The island's southeastern (SE) tip includes Cocos Island, a small island separated from Guam by the only true lagoon system where mangroves still exist. The SE coast has well-defined, wave-exposed spur-and-groove reefs that extend from southern Cocos Island to the north end of Pago Bay. Semi-consolidated, east and south-facing coastline with moderate wave exposure ameliorates sedimentation stress from the islands watersheds on the SE coast. Moderate sediment influences may be more of a beneficial nutrient source on the SE coast as opposed to southwestern reefs where sedimentation acts as a chronic anthropogenic stressors due to low wave energy.

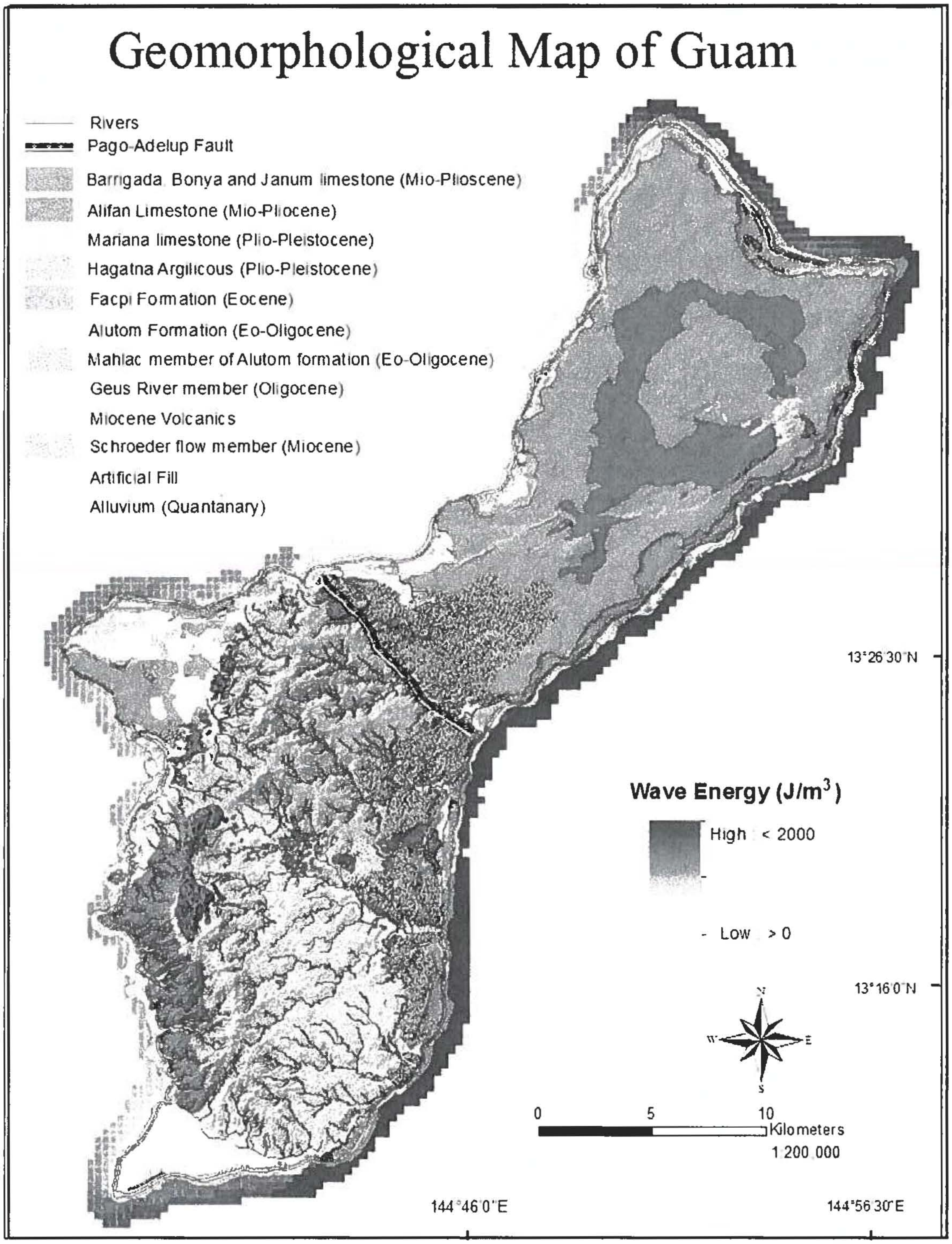


Figure 2. Guam's geologic and wave exposure regimes in a paleoecological context

Northern Guam's geology is uplifted, fractured Plio-Pleistocene limestone that encases the island's aquifer. This freshwater lens also seeps into northern reefs as submarine discharge which occurs more intensely on the leeward coast. Houk and van Woesik (2009) found that monospecific stands of *Porites rus*, *Pavona* spp., and *Porites* spp. thrive in limestone watersheds with aquifer connections and low wave energy. Rivers and streams are absent causing watershed boundaries to be less defined, yet slight, subsurface contour changes along antecedent volcanic slopes delineate six subsurface drainage basins. Surface water containing pollutants (reviewed by Porter *et al.* 2005) percolate into the water table, eventually seeping across reefs. The northeastern coast has mainly non-constructional incipient reef assemblages, as wave energy is higher and more direct. In sum, fringing reefs are narrow to non-existent on the NE coast, but begin to increase in complexity along the northern coastline. The northeast zone is least accessible by fishermen from high wave exposure, federally protected coastline and reef preserve (Anderson Air Force base, Pati Point Marine Preserve), and far distances from boat launching ramps.

Finally, the northwest region extends roughly from northwest point to a mid-island artificial barrier in the south. Along this coastline, much of the reef habitat is uniform, with embayments being very different with *P. rus*. Population density is highest along the northwest coast, but this is mainly due to high population along embayments with sparse settlement along northern military land. Consequently, northwest fringing reefs are more intensely impacted from overfishing, tourism, and coastal urbanization. Together, the geological and trade-wind driven wave exposure differences defined four biophysical regions *a priori*: (1) volcanic/windward (SE), (2) volcanic/leeward (SW), (3) limestone/leeward (NW), (4) limestone/windward (NE) (Figure 3; Table 1).

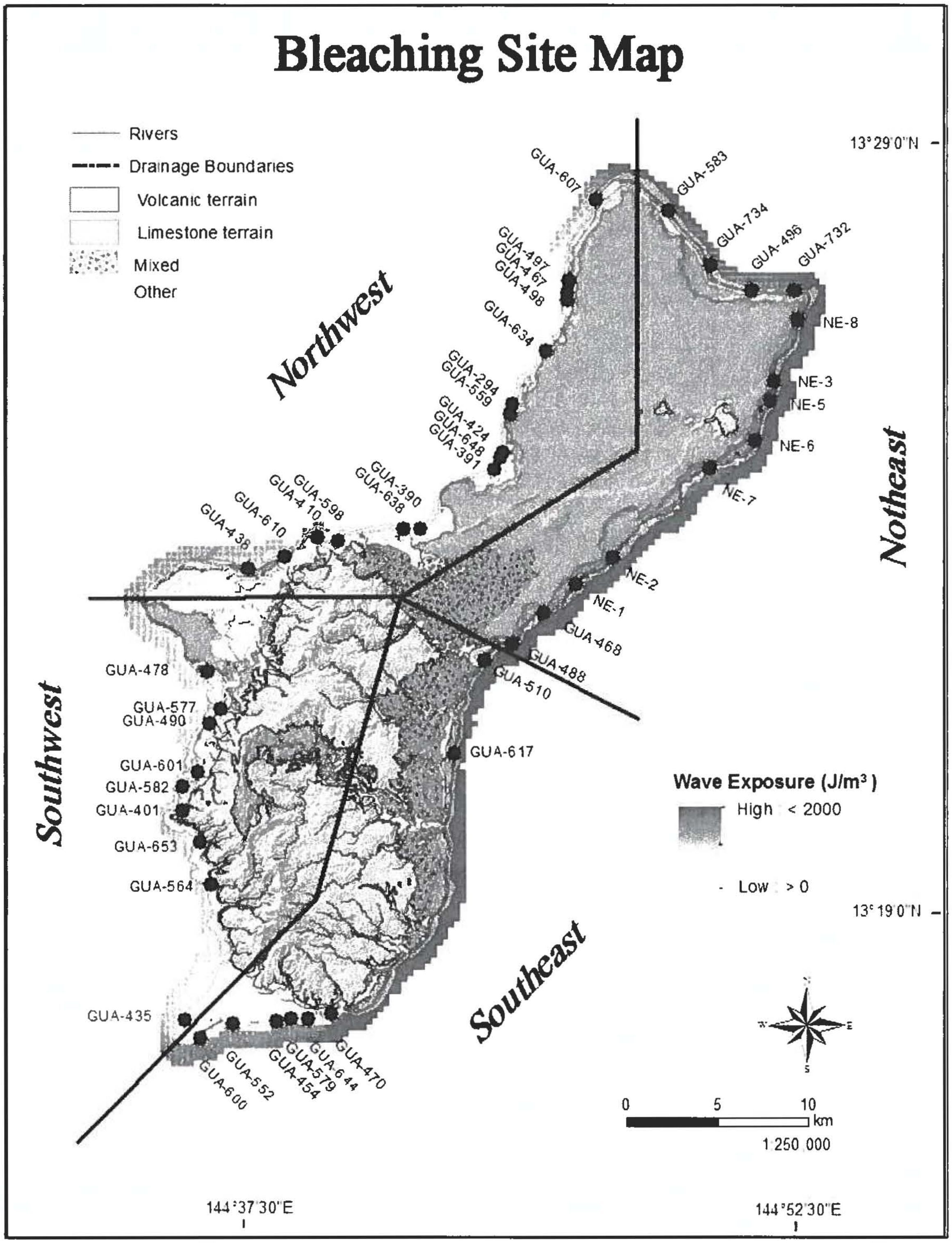


Figure 3. 2013 site map of 46 shallow reef sites among 4 biogeographic regions.

Table 1. Major influences (environmental and anthropogenic) among coastal zones

Regions	n	Wave Energy	Geology	Impacts
Southeast	8	Moderate	Volcanic/ Mixed	Larger watersheds, mixed geology and moderately exosed reefs, Consolidated Hagatna Argilicious member is along coast. Lower fishing pressure, coastal population density/urbanizatinon exist in this region
Southwest	9	Low-Moderate	Volcanic	Chronic sedimentation, unconsolidated coast, mixed geology in north, steep volcanic slope, moderate coastal urbanization/population denisty along Agat. Heavy fishing pressure, chronic sedimentation, and variable exposure exist here.
Northwest	16	Low-Moderate	Limestone	Topography is mixed in southern portion, but consolidated Mariana Limestone north of Tumon. This region has the highest coastal urbanization/population density, a higher portion of freshwater seeps, and highest fishing pressure.
Northeast	13	High	Limestone	Topography is entirely consolidated north of Pago Bay and wraps along north-facing reefs. This region is largely protected from access. Low fishing presssure, eutrophication, coastal urbanization/population denisty and high wave exposure exist here.

2.2 Sampling design

A random stratified sampling design assessed bleaching prevalence in the four, *a priori* biogeographic regions (described in 2.1). Randomized sampling locations were first defined by CRED NOAA Coral Reef Ecosystem Division's (CRED; Williams et al. 2012) when examining fish assemblages around Guam. Experimental design and site selection were modified from the 2011 CRED study by selecting a random subset of 46 shallow (2 – 6 m) sites. Because 2011 CRED surveys did not sufficiently sample northeastern shallow reef surveys due to adverse conditions, 7 additional sites were added along this coastline to even out the sampling effort (Figure 3). At each site, coral demographic data were collected along with benthic substrate composition and bleaching severity estimates.

2.3 Ecological Data Collection

Coral demographic and bleaching surveys were conducted between October and December 2013, during the end of the thermal stress event on Guam. At each 1 m interval along (3) 25 m transect lines per site, a 0.7 x 1 m framed photoquadrat was taken (50 m^2 of substrate). Photographs were analyzed using the Coral Point Count Software (CPC; Kohler and Gill 2006). Analyses first identified every coral colony (> 36,000) whose center point resided within the photograph to genus and functional group. Functional groups were based upon colony morphologies, and were recorded as massive, caespitose, corymbose, table-forming, or encrusting. Second, colony size was estimated within CPC using the following elliptical area equation:

$$\text{elliptical area} = \pi * a * b$$

Where *a* and *b* are half the maximum diameter and the diameter perpendicular to the coral colony. These measurements provided estimates of coral abundance and density.

Bleaching severity was also measured in CPCE to estimate a bleaching mortality index (BMI; Baird and Marshall 2002). This classification system divides severity into 4 hierarchical categories based on pigmentation response/mortality: 1 = no bleaching; 2 = < 50% colony pigmentation response/mortality; 3 = > 50% colony pigmentation response/mortality; 4 = bleaching-induced colony mortality. Bleaching susceptibility was calculated using the bleaching mortality index (BMI) that weights the proportion of bleached colonies by bleaching severity. A BMI for the 25 most abundant coral taxa was estimated from the following equation:

$$\text{BMI} = \frac{0c_1+1c_2+2c_3+3c_4}{3}$$

C1 – C4 correspond to bleaching categories in the same sequence. Bleaching-related mortality accounts for more weight in this index. Colony bleaching responses were further categorized as low and high severity and also as a bleaching prevalence metric. Bleaching prevalence was quantified in terms of both abundance (relative proportion of coral area bleached) and density (relative proportion of colonies bleached).

Last, benthic substrate abundances were estimated using the same photographs. Benthic substrates were identified under each of 15 random points per photograph generated by CPCE, using the following categories: corals (to genus level/species group), turf algae, macroalgae, fleshy coralline algae, crustose coralline algae (CCA), sand, rubble, and other invertebrates. A total of 375 data points per transect; 1125 points per site were analyzed. Site averages, standard deviations, and standard errors were then calculated per site.

2.4 Environmental Data Collection

Two key environmental datasets were generated to understand how long-term forcing influenced reef composition and bleaching prevalence. These were river distances (km) and wave exposure (J/km^3). Using a geographic information system, river distances were measured between a site and its nearest river source. This metric represents a sites direct influence to watershed-based freshwater inputs. Only sites in southern Guam had river distances. Wave energy was determined by fetch estimates (Ekebom et al. 2003) and 10-year mean windspeeds from the Guam airport, based upon angle of exposure. Fetch is the distance of unobstructed open water. Wave heights were calculated following Ekebom et al. (2003). Other geographic information systems layers and spatial datasets were acquired from Hydroguam.net. These included watershed size, urban development, human population density, distance to major fishing access, and other common anthropogenic indicators. However, a full understanding of the entire suite of anthropogenic stressors is beyond the scope of this thesis.

2.5 Statistical Analysis

To analyze coral assemblage distribution across Guam, standard multivariate analyses techniques were applied to test if coral species abundances varied predictably across environmental regimes (Anderson, Gorlet *et al.* 2008). Biological data (*e.g.*, coral assemblage data, bleaching prevalence data) were aggregated, square root-transformed, and Bray-Curtis similarity matrices were calculated to define the ecological distances between sites. Prior to comparisons, multivariate homogeneity tests were conducted to determine if similarity measures (*i.e.*, dependent variables) were evenly distributed across the environmental factors being examined. ANOSIM tests with subsequent graphic interpretations using principal coordinate ordination plots (PCO) were conducted. ANOSIM tests explored the main environmental factors influencing assemblage structure around Guam. PCO plots were based on actual distance similarities between ordinates and have 'eigenvalues' associated with axis scores. PCO1 and PCO2 represents directional axis variation in a plot. Crossed multivariate designs examined whether coral assemblages were significantly different across environmental regions. Vector overlays were used to depict genera contributing the most toward spatial differences, or bleaching prevalence across environmental regimes. All analyses were performed using PRIMER 6 & PERMANOVA software. Additional univariate test were employed to examine bleaching prevalence patterns and interdependencies between the environment and coral distribution. Appropriate transformations were used when necessary and non-parametric equivalent test were employed when model assumptions failed.

III. Results

3.1 Resolving coral taxonomic relationships around Guam

Benthic data highlighted lowest coral coverage in the SW region of Guam (16 ± 3% SD), where turf and macroalgae dominated the substrate (Figure 4). SW reefs were generally dominated by *Poritidae* and small *Faviidae* species, but coral composition varied between Agat Bay (GUA-478 to GUA-582), reefs south of Facpi and outside narrow west-facing embayments (between GUA-653 and GUA-564), and the western side of Cocos Island (GUA-435). Agat Bay was predominantly *Porites rus* habitat with ~14-19% ± 2-4% SD cover. Outside of the embayment from Anai Island (GUA- 582) to Coco's Island (GUA-435), coral cover and

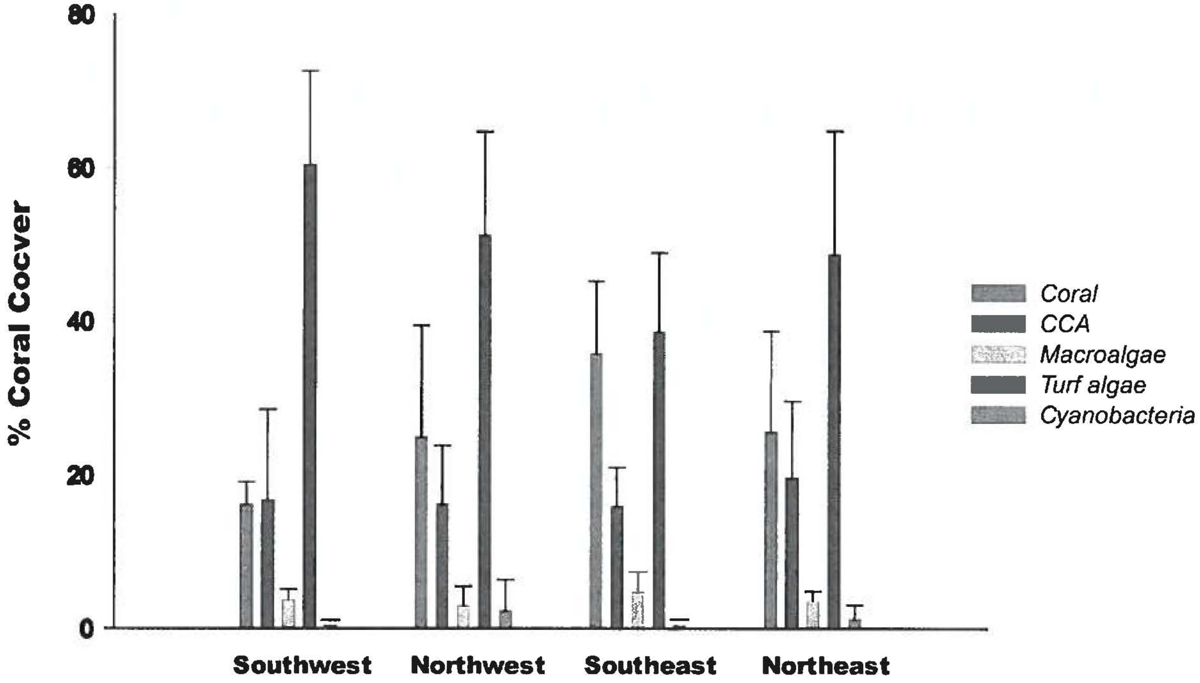


Figure 4. Dominant benthic substrate (% cover ± SD) within Guam's four biophysical regions. Clear differences exist between regions with higher coral cover and lower turfing algae in southeastern Guam. Relationships are ambiguous between macroalgae and CCA, however cyanobacteria is more abundant along northwestern reefs.

diversity were restricted, with reefs characterized by massive *Porites*, *P. rus*, and *Goniastrea spp.*. This was the least diverse region (Shannon-Weaver Evenness H' of 1.3 ± 0.4 SD), and site-level species abundances were least similar (mean similarity: 46.48; Table 2b). Reefs were associated with small watersheds (mean area of 7.4 km^2 ± 2.3 SD) with numerous coastal discharge points and altered land-use.

The NW and NE coastlines had similar coral cover (24-26% ± 13-14% SD, respectively, Figure 4), but species abundances differed across watershed drainage features. For instance, two embayments on the NW coastline, Tumon and East Agana Bay (GUA-424, GUA-648, and GUA-391), both had prolific mono-stands of *Porites rus* associated with large topographic drainage regions and minimal wave exposure (wave energy = 77 ± 7 SD J/m^3). Smaller drainages with low wave exposure also supported limited *Porites rus* growth elsewhere, such as Double Reef (~5% cover). Elsewhere along the NW coast, coral assemblages were often compromised of mixed *Leptoria*, *Porites* (both massive *Porites* and *P. rus*), *Goniastrea* and *Millepora* corals. On north facing reefs, coral cover and diversity varied widely (~21% ± 13% cover SD, GUA-598 to GUA-438), as benthos coupled with increased wave exposure (~159 ± 38 J/m^3 SD) and increased complexity of watershed geology (*i.e.*, Hagåtña argillaceous member).

Wave energy was consistently highest for NE reefs (1410 ± 410 J/m^3 SD), where mixed assemblages of encrusting *Montipora* spp., corymbose *Acropora* spp., arborescent *Acropora* spp., massive *Dipsastrea* spp. (Pacific *Favia*), caespitose *Acropora* spp., encrusting *Leptastrea* spp., and *Goniastrea* spp. were observed. While similar sets of species existed on the NW and NE coastline, species abundance shifted, and *Acropora* and *Montipora* became dominant with higher wave energy on the NE compared to NW (Figure 5). Higher diversity was also found along the NE coastline (Shannon-Weaver Evenness H' of 2.1 ± 0.25 SD). Clearly the NE had

Table 2. SIMPER analysis results revealing *A*) dominant genera around Guam by island side and *B*) species/morphological group assemblages by biogeographic zone. Species abundances contributing between 50 – 60 % of cumulative variation for each region is listed along with the respective species abundances and % of contributed variation.

A) Wind Side Relationships (Genus)

Average Dissimilarity = 52.2

Leeward Windward

Genus	Average Abundance	Average Abundance	Average Dissimilarity	Contribution (%)	Cumulative Contribution (%)
Acropora	**0.1**	**0.5**	**7.9**	**15.2**	**15.2**
Porites	**0.6**	**0.3**	**6.5**	**12.5**	**27.7**
Montipora	**0.1**	**0.4**	**4.7**	**8.9**	**36.6**
Goniastrea	**0.3**	**0.3**	**4.0**	**7.6**	**44.2**
Leptoria	**0.3**	**0.1**	**3.7**	**7.1**	**51.3**

B) Biogeographic Relationships (species/morphological group)

Northwest

Average Similarity = 57.3

Species	Average Abundance	Contribution (%)	Cumulative Contribution (%)
Leptoria phrygia	**0.4**	**14.4**	**14.4**
massive *Porites*	**0.3**	**11.5**	**25.9**
Porites rus	**0.3**	**10.4**	**36.3**
***Goniastrea* spp.**	**0.3**	**9.4**	**45.7**
***Millepora* spp.**	**0.3**	**9.2**	**54.9**

(Continued)

Northeast

Average Similarity = 61.44

Species	**Average Abundance**	**Contribution (%)**	**Cumulative Contribution (%)**
encrusting *Montipora*	**0.4**	**11.5**	**11.5**
corymbose *Acropora*	**0.3**	**8.6**	**20.2**
Acropora abrotanoides	**0.3**	**7.9**	**28.0**
massive *Dipsastrea*	**0.2**	**7.5**	**35.5**
caespitose *Acropora*	**0.2**	**6.8**	**42.3**
encrusting *Leptastrea*	**0.2**	**6.2**	**48.5**
***Goniastrea* spp.**	**0.2**	**5.7**	**54.3**

Southeast

Average Similarity = 63.68

Species	**Average Abundance**	**Contribution (%)**	**Cumulative Contribution (%)**
caespitose *Acropora*	**0.4**	**10.0**	**10.0**
encrusting *Montipora*	**0.4**	**9.7**	**19.7**
***Goniastrea* spp.**	**0.3**	**9.6**	**29.3**
Leptoria phrygia	**0.2**	**7.7**	**37.0**
Acropora *abrotanoides*	**0.2**	**6.6**	**43.6**
corymbose *Acropora*	**0.2**	**5.7**	**49.3**
***Pocillopora* spp.**	**0.2**	**5.7**	**55.0**

Southwest

Average Similarity = 46.48

Species	**Average Abundance**	**Contribution (%)**	**Cumulative Contribution (%)**
massive Porites	**0.5**	**27.8**	**27.8**
Porites rus	**0.4**	**20.5**	**48.2**
Goniastrea spp.	**0.3**	**7.2**	**55.4**

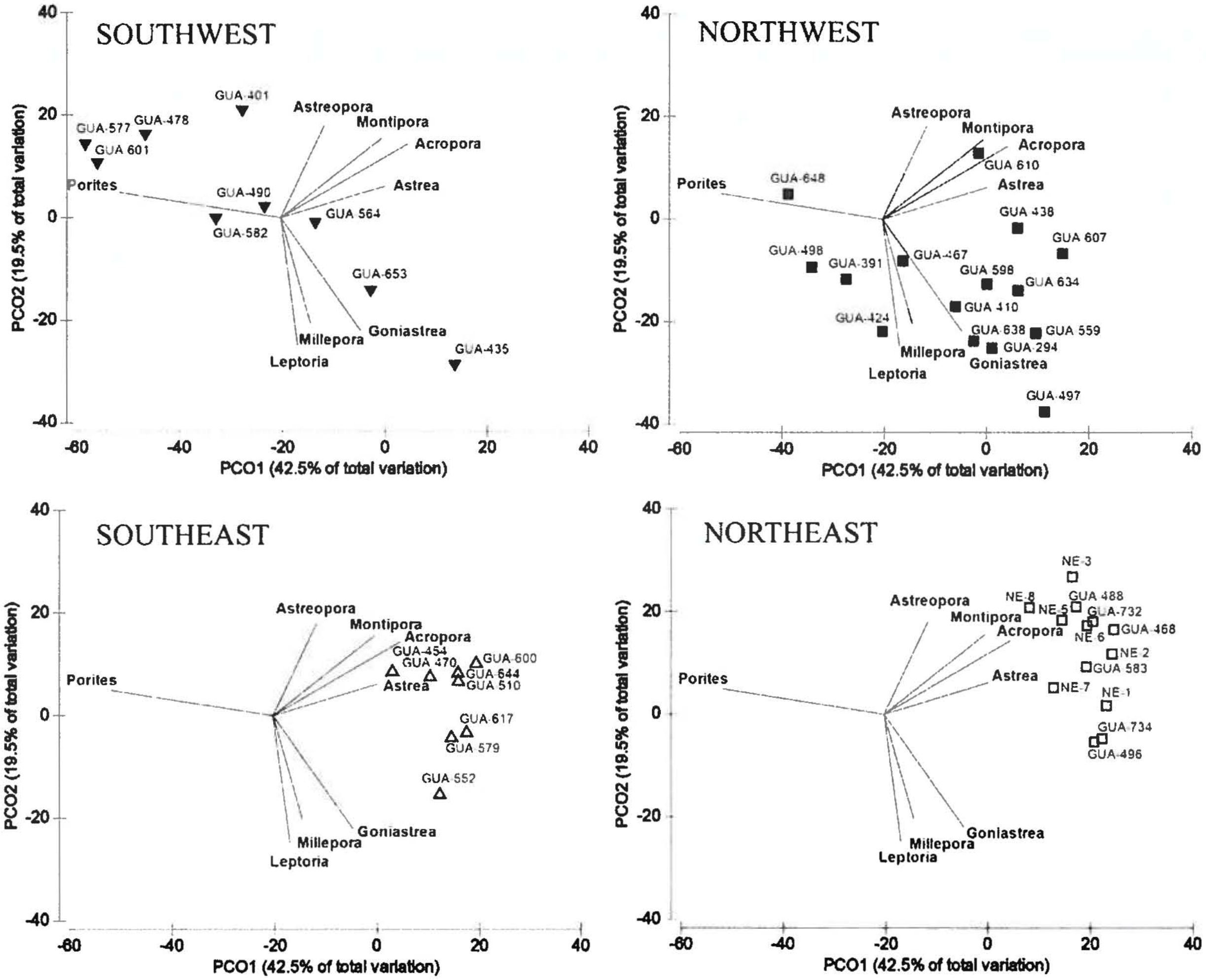


Figure 5. PCO plot highlighting abundance trends around Guam. Significant differences were attributed to both geology (limestone vs. volcanic) and wave exposure regimes (leeward vs. windward) (PERMANOVA, F-statistic > 3.0, $p < 0.05$, for both comparisons). Additionally, there was a significant interactive effect (F-Statistic = 3.4, $p = 0.003$) highlighting regional differences among coral assemblages. Vectors display corals that were significant drivers of these trends (Spearman Correlation coefficients > 0.6).

favorable foundations for modern coral growth, however inter-site variation was high as evidenced by the large error bars, often > 40% of the mean coral and major-substrate coverage on the NE (Figure 2).

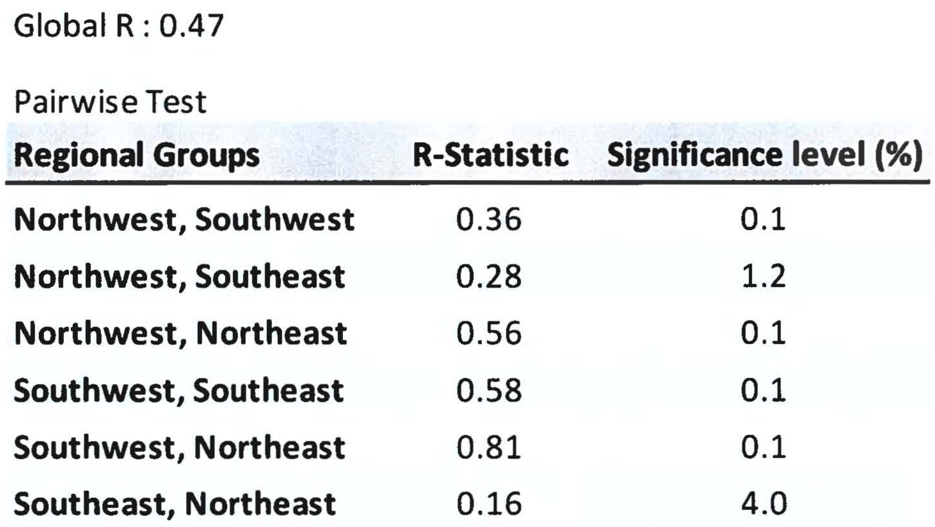
SE Guam had both the highest coral diversity (Kruskall-Wallis, $p < 0.001$, Shannon-Weaver Evenness H' of 2.2 ± 0.3 SD) and coral cover (Kruskall-Wallis, $p < 0.001$, mean cover of 33.3% ± 11.3% SD). Environmental heterogeneity along this coast was also high due to variable wave exposure (889 ± 693 J/m^3), larger complex watersheds (30.3 km^2 ± 17.9 SD) and mixed volcanic and limestone bedrock (Figure 5). Increased environmental variation was largely due to south facing sites adjacent to Coco's lagoon (GUA-600 to GUA-470), where lower wave energy persist, and two east-facing sites between Ipan (GUA-617) and Pago Bay (GUA-510) with higher than average wave exposure. Reefs along the SE were mainly characterized by caespitose *Acropora* and encrusting *Montipora* spp., but mixed species assemblages commonly found around Guam were also abundant, such as *Pocillopora* spp., *Goniastrea* spp., *Leptoria phrygia* and other *Acropora* morphologies (*i.e.*, arborescent and corymbose *Acropora*) (Table 2b).

Multivariate examinations revealed distinct east/west differentiation among dominant coral genera that corresponded with wave exposed/protected environments. This pattern was evidenced by differences in *Acropora*, *Porites*, *Leptoria*, *Astrea* (Pacific *Montastrea*) and *Montipora* abundances. *Porites* and *Leptoria* corals had the greatest proportional abundances on leeward Guam, while *Acropora* and *Montipora* had the greatest proportional abundances along windward reefs (Figure 5). Furthermore, north facing sites GUA-607 (Ritidian), GUA-438 (Orote), GUA-610 (Piti) along the NW coast all experience higher wave exposure (215 ± 56 J/m^3 at north facing reefs and 98 ± 26 J/m^3 along west facing reefs,) and had assemblages that were more similar to eastern, exposed reefs. However, proportional abundances between island sides revealed non-significant differences in coral growth capacity as leeward coral cover was 21.7% ± 12.2% SD while windward cover was 28.5% ± 12.7% SD. While multivariate coral assemblages were significantly different across all of the island sectors, the degree of ecological separation differed widely (Table 3, global $R = 0.47$, $p < 0.001$, ANOSIM tests of multivariate similarity). Due to the above noted differences in coral growth and species abundances, SW reefs were clearly distinct from others, SE and NE were least distinct, and NW versus SE and NE were moderately distinct (Table 3).

3.2 *Resolving bleaching prevalence patterns around Guam.*

The 2013 bleaching event in Guam was similar to historical bleaching patterns across the world in that coral stress response was highly variable across reefscapes (Figure 6). It was unique because reefs experienced their first major thermal stress event in over a decade (Paulay and Benayahu 1999). Island-wide estimates of coral bleaching were 49% ± 20% SD, with significant variation across biogeographic regions and sites (Kruskal-Wallis tests of comparison, $p < 0.001$, Figure 6). On the leeward side, 40% ± 19% SD of the coral bleached, while 60% ± 16% SD coral bleached on the windward island side. Dunn's post-hoc multiple comparisons showed that there was significantly higher bleaching prevalence on the SE compared to all other regions (76% ± 8% SD, $p < 0.001$). Bleaching was similar elsewhere on the SW, NW, and NE (41% ± 25% SD, 39% ± 15% SD, 50% ± 11% SD respectively). Encrusting *Montipora* and caespitose *Acropora* corals were the most susceptible to bleaching with a bleaching mortality index (BMI) > 90, while *P. rus* and *Leptastrea purpurea* were the least susceptible with a BMI < 5 (Table 4a). Several corals such as *Stylophora pistallata* ($n = 67$) and *Hydnophora microconus*

Table 3. ANOSIM showing significant regional coral community differences and separation among all pairwise comparisons



Global R : 0.47

Pairwise Test

Regional Groups	**R-Statistic**	**Significance level (%)**
Northwest, Southwest	0.36	0.1
Northwest, Southeast	0.28	1.2
Northwest, Northeast	0.56	0.1
Southwest, Southeast	0.58	0.1
Southwest, Northeast	0.81	0.1
Southeast, Northeast	0.16	4.0

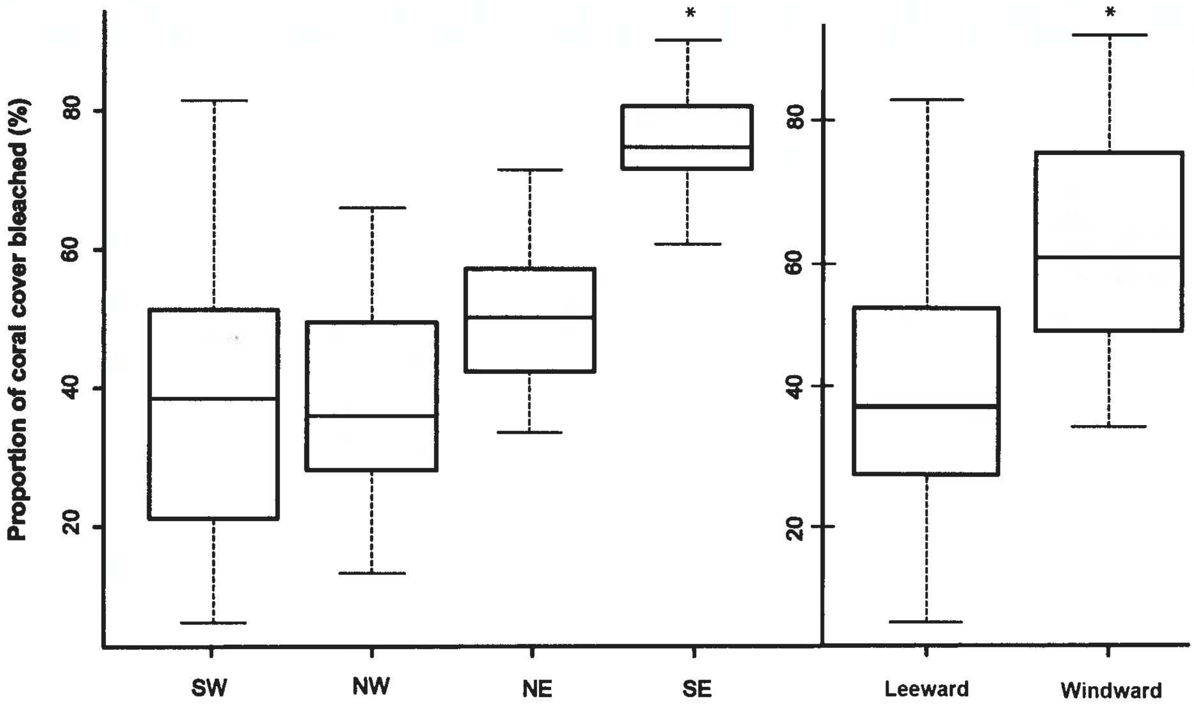


Figure 6. Above boxplot shows summary statistics for bleaching patterns across each biogeographic region. Regional differences in proportion of coral cover bleached exist (Kruskall-Wallis $p < 0.001^*$) and only southeast Guam bleaching was significantly higher compared to other regions (Dunn's multiple comparison). A t-test revealed bleaching on the windward coral reefs was significantly higher ($p < 0.001^*$).

Table 4a. Bleaching Mortality Index based on functional species group and colony proportions.

Genus/Species	Morphology	Functional Group (Darling et al. 2011)	*n*	Normal (%)	Moderate (%)	Severe (%)	Dead (%)	Colonies bleached (%)	Relative abundance (%)	BMI
Montipora	Encrusting	Generalist, Stress-Tolerant, Competitive	*1930*	22.1	11.5	61.0	5.4	77.9	11.1	99
Acropora	Caespitose	Competitive	*4054*	24.0	28.0	37.4	10.6	76.0	6.8	90
Stylophora mordax	Corymbose	Competitive*	*67*	22.4	28.4	44.8	4.5	77.6	0.2	88
Pocillopora (high-relief)	Corymbose	Competitive	*226*	23.5	34.5	38.5	3.5	76.5	2.2	81
Pocillopora (low-relief)	Corymbose	Competitive	*1655*	31.9	26.7	31.9	9.5	68.1	2.9	79
Astrea (Montastrea curta)	Encrusting	Stress-Tolerant	*534*	31.3	20.4	47.6	0.7	68.7	1.1	79
Goniastrea stelligera	Encusting	Stress-Tolerant	*590*	31.5	24.4	41.7	2.4	68.5	2.1	77
Platygyra	Massive	Stress-Tolerant	*461*	33.8	28.9	37.1	0.2	66.2	1.1	69
Hydnophora microconus	Massive	Stress-Tolerant	*143*	30.8	46.9	22.4	0.0	69.2	0.8	61
Leptoria phrygia	Massive	Stress-Tolerant	*1519*	37.9	35.0	26.9	0.3	62.1	7.5	60
Acropora	Arborescent	Competitive*	*279*	42.3	39.8	16.5	1.4	57.7	6.6	51
Millepora	Arborescent	*non-scleractin*	*381*	55.6	24.1	12.3	7.9	44.4	6.7	48
Heliopora coerulea	Arborescent	*non-scleractin*	*82*	62.2	13.4	24.4	0.0	37.8	1.0	41
Acropora	Corymbose	Competitive	*1291*	59.1	27.7	8.1	5.1	40.9	3.2	39
Cyphastrea	Encrusting	Stress-Tolerant	*178*	62.9	20.2	16.9	0.0	37.1	0.3	36
Goniastrea	Encrusting, Massive	Stress-Tolerant	*2877*	69.3	13.0	16.8	0.9	30.7	12.9	33
Astreopora	Massive	Stress-Tolerant	*431*	70.3	22.0	5.8	1.9	29.7	1.5	26
Acanthastrea	Encrusting	Stress-Tolerant	*650*	71.2	22.6	6.0	0.2	28.8	0.5	23
Porites	Massive	Stress-Tolerant	*1972*	77.9	13.4	6.1	2.6	22.1	9.9	22
Dipsastrea (Pacific *Favia*)	Massive	Stress-Tolerant	*5314*	76.7	18.1	5.1	0.1	23.3	2.8	19
Goniopora	Encrusting	Stress-Tolerant	*107*	86.0	7.5	6.5	0.0	14.0	0.3	14
Galaxea fasicularis	Caespitose	Stress-Tolerant, Generalist	*2380*	85.0	10.8	3.4	0.8	15.0	1.1	13
Pavona	Encrusting	Stress-Tolerant	*861*	92.6	4.6	2.8	0.0	7.4	0.8	7
Porites	Arborescent	Weedy	*1526*	97.2	2.2	0.5	0.1	2.8	8.9	2
Leptastrea	Encrusting	Weedy	*4411*	99.0	0.0	1.0	0.0	1.0	3.3	1

not addressed in Darling et al. 2011, trait-based estimation only

Table 4b. Bleaching Mortality Index based on genus and colony proportions.

Genus	Morphology	Functional Group (Darling et al. 2011)	n	Normal (%)	Moderate (%)	Severe (%)	Dead (%)	Colonies bleached (%)	Relative abundance (%)	BMI
Montipora	Encrusting	Generalist, Stress-Tolerant, Competitive	1930	22.1	11.5	61.0	5.4	77.9	11.1	99
Stylophora	Corymbose	Competitive	67	22.4	28.4	44.8	4.5	77.6	0.2	88
Pocillopora	Corymbose	Competitive	1881	30.9	27.6	32.7	8.8	69.1	5.1	80
Astrea (Montastrea)	Encrusting	Stress-Tolerant	534	31.3	20.4	47.6	0.7	68.7	1.1	79
Acropora	Caespitose, Corymbose, Arborescent	Competitive	5853	33.3	28.8	29.2	8.7	66.7	18.4	76
Platygyra	Massive	Stress-Tolerant	461	33.8	28.9	37.1	0.2	66.2	1.1	69
Hydnophora	Massive	Stress-Tolerant	143	30.8	46.9	22.4	0.0	69.2	0.8	61
Leptoria	Massive	Stress-Tolerant	1519	37.9	35.0	26.9	0.3	62.1	7.5	60
Millepora	Encrusting, Arborescent	*non-scleractin*	381	55.6	24.1	12.3	7.9	44.4	6.7	48
Heliopora	Arborescent	*non-scleractin*	82	62.2	13.4	24.4	0.0	37.8	0.5	41
Goniastrea	Encusting, Massive	Stress-Tolerant	3467	62.8	14.9	21.1	1.2	37.2	15.0	40
Cyphastrea	Encrusting	Stress-Tolerant	178	62.9	20.2	16.9	0.0	37.1	0.3	36
Astreopora	Massive	Stress-Tolerant	431	70.3	22.0	5.8	1.9	29.7	1.5	26
Acanthastrea	Encrusting	Stress-Tolerant	650	71.2	22.6	6.0	0.2	28.8	0.5	23
Dipsastrea (Favia)	Massive	Stress-Tolerant	5314	76.7	18.1	5.1	0.1	23.3	2.8	19
Porites	Arborescent, Massive, Encrusting	Weedy, Stress-Tolerant	4559	81.9	10.8	5.9	1.4	18.1	21.4	18
Goniopora	Encrusting	Stress-Tolerant	107	86.0	7.5	6.5	0.0	14.0	0.3	14
Galaxea	Caespitose	Stress-Tolerant	2380	85.0	10.8	3.4	0.8	15.0	1.1	13
Pavona	Encrusting	Stress-Tolerant	861	92.6	4.6	2.8	0.0	7.4	0.8	7
Leptastrea	Encrusting	Weedy	4411	99.7	0.2	0.1	0.0	0.3	3.3	0

(n = 143) were locally rare and retained higher BMI values (> 60). In terms of functional groups, this study found agreement between coral stress tolerance and bleaching prevalence (Table 4a and 4b). On average, coral classified as competitive had highest BMI (> 50), and corals classified as weedy and stress-tolerant had lower BMI values (< 50). Because 2013 surveys occurred during the climax of thermal stress, differential death rates were recorded and *Pocillopora*, *Acropora* and *Millipora* experienced mortality the fastest (8-9% early mortality) compared with < 1% early mortality of *P. rus* and *L. purpurea* (Table 4b).

Spatial patterns in bleaching prevalence were very similar to coral abundance distributions reported above. Multivariate analyses using species-based bleaching prevalence data revealed strong influences of wave exposure, with higher bleaching prevalence on the east versus west, and weaker influences of island geology, with higher bleaching prevalence within the southeast region. Furthermore, the coral taxon driving the spatial differences in assemblage structure were also drivers of bleaching prevalence patterns (Figure 7). Mann-Whitney comparisons showed significantly higher bleaching among *Porites* and *Leptoria* on the west ($p <$ 0.005 and $p = 0.023$, respectively), which followed their abundances. In contrast, *Acropora*, *Montipora*, and *Dipsastrea* (Pacific *Favia*) populations were more abundant and had higher bleaching prevalence on the eastern windward reefs ($p < 0.01$ for all comparison, Mann-Whitney U-tests). Based upon BMI indices, the most susceptible taxon were generally more abundant along windward reefs, but not all corals showed similar trends between abundance and bleaching prevalence. *Pocillopora* and *Goniastrea* populations had similar coverage around the island (< 10 %), but bleaching prevalence was higher on the windward coast ($p < 0.03$ for both, Mann-Whitney U-test). The general findings were that coral bleaching and species abundance patterns were linked for dominant corals with strong affinities to either high or low wave energy

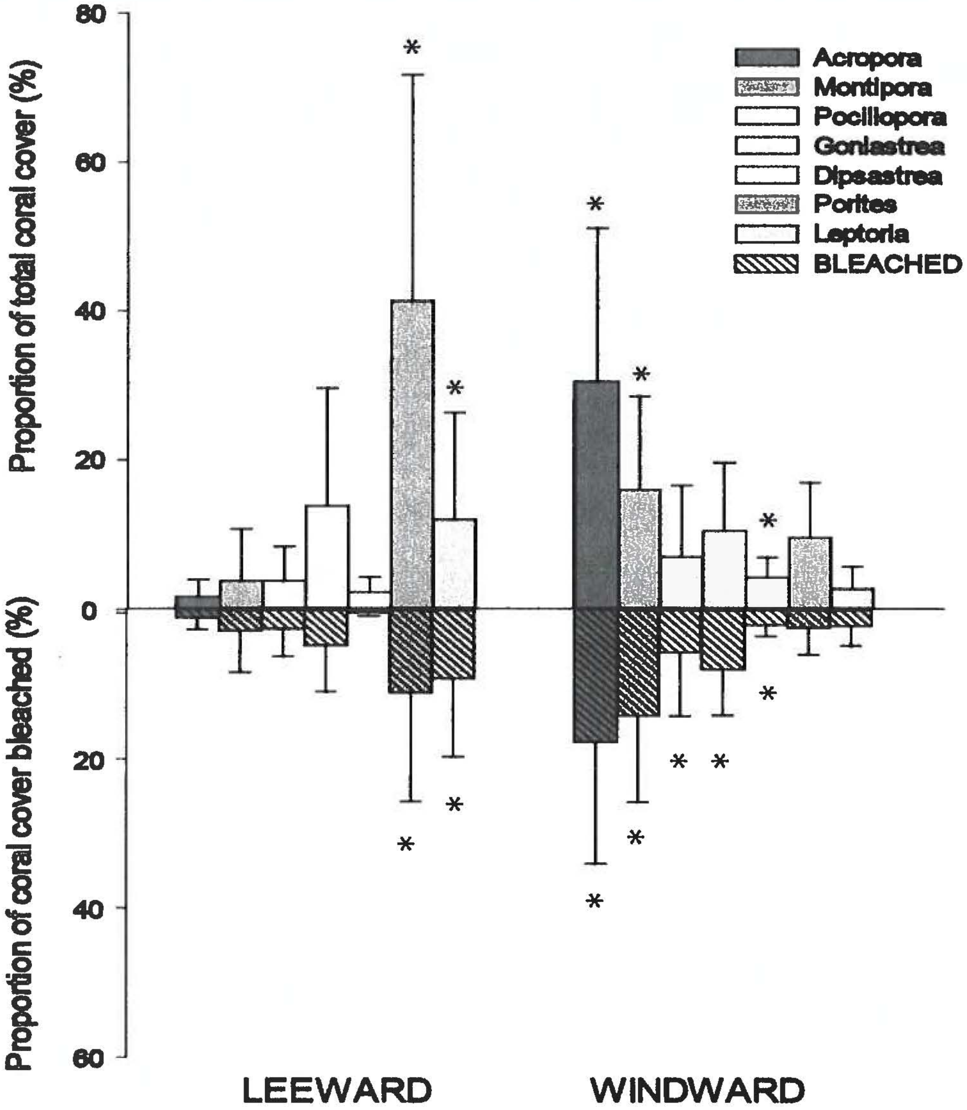


Figure 7. Differences between proportion of total coral cover between leeward and windward Guam are identified above the x-axis and differences between the proportion of coral bleached are found below x-axis. Asterisk (*) represents significant differences identified using Mann-Whitney rank test comparing differences between island side populations. Asterisk also identifies a higher average abundance and error bars reflect standard deviations.

(RELATE analysis, global $r = 0.9$; Figure 8), however, bleaching and abundance patterns became decoupled for corals that had ubiquitous distributions around Guam.

3.3 *Relationships among coral assemblages, the environment, and bleaching prevalence patterns.*

Coral bleaching around Guam was taxon-specific and influenced by the abundance of susceptible species. This relationship shows higher bleaching prevalence occurred along the windward coast where complex, temperature sensitive species existed in high abundance. Correlations between coral demography and environmental gradients revealed species-specific bleaching patterns that was most associated with species richness and wave exposure (Figure 9). Table 5a. and 5b. revealed linear relationships among total coral abundance and proportional bleaching abundances.

Among highly susceptible species, *Acropora* abundance was most influenced by wave exposure ($r^2 = 0.52, p > 0.001$) while *Montipora* was to a less extent ($r^2 = 0.20, p = 0.002$). The negative relationship between *Porites* abundance and wave exposure was also significant ($r^2 = 0.23, p > 0.001$). To a less extent, *Leptoria* was also significantly related to wave exposure gradients with higher abundances in leeward reefs ($r^2 = 0.15, p = 0.008$).

Among bleached corals, a significant positive correlation was associated with species richness ($r = 0.47, p < 0.01$). Regional differences revealed in SIMPER analysis (Table 2a and 2b) indicated varied prevalence's according to the way species assemble in a community (Figure 10). Increased bleaching was correlated with coral taxon along windward reefs as revealed in Figure 9. When testing environmental variables, regression analysis revealed bleaching

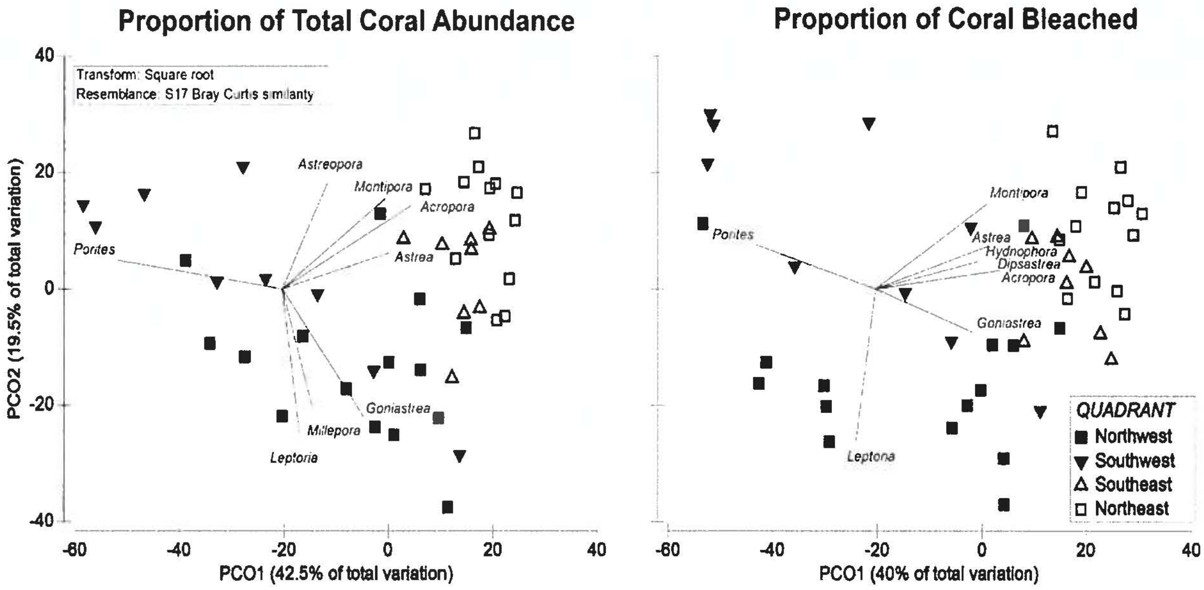


Figure 8. PCO comparisons between two datasets shows similarities in spatial relationships (RELATE, global r = 0.90). Both plots display 0.6 correlation strength for taxon vectors and show differences among taxon driving spatial heterogeneity.

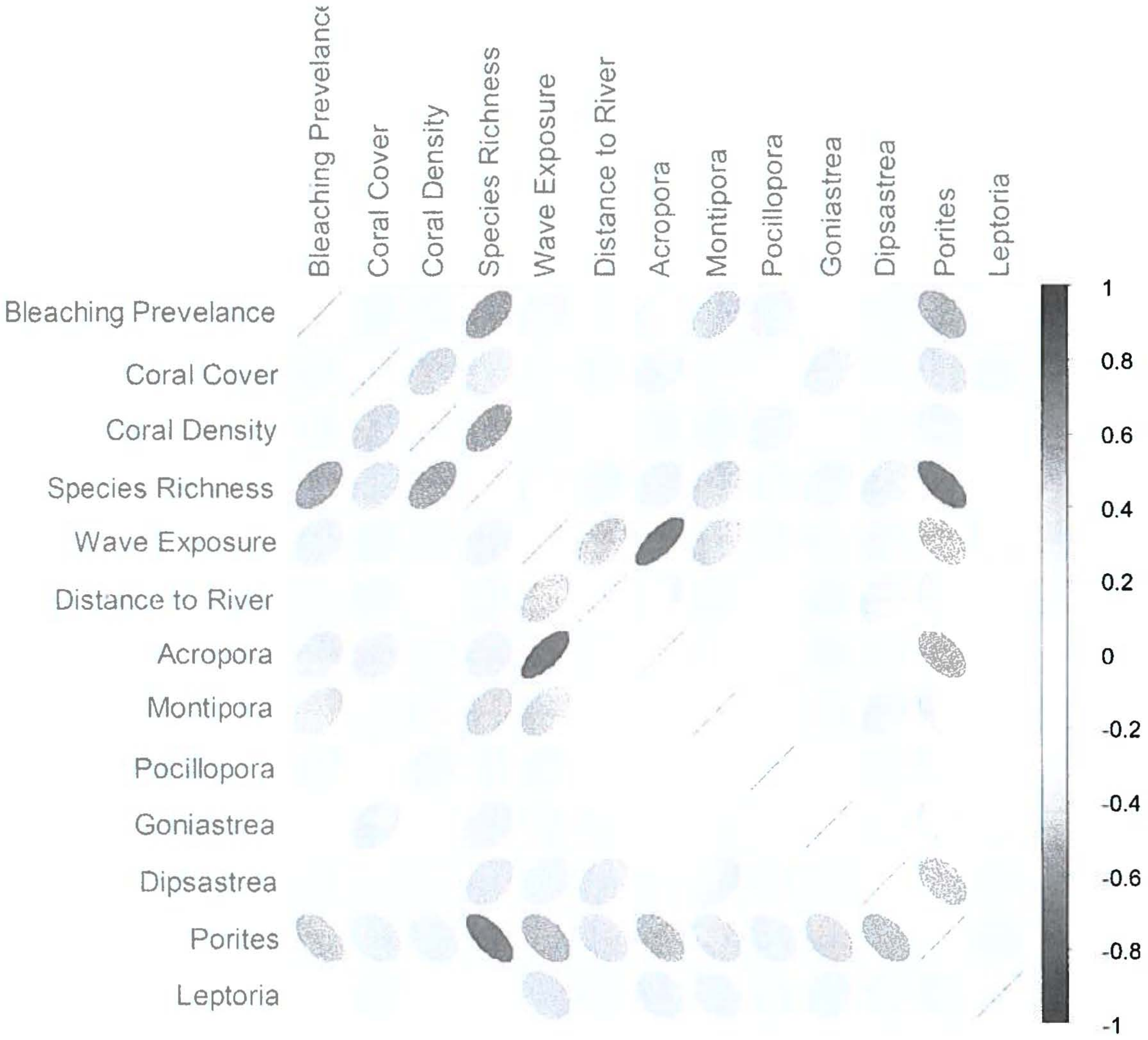


Figure 9. Plot illustrating coral demographic and environmental trait correlations. Color indicates positive (blue) or negative (red) relationships while ellipse shape distinguishes significance with narrowing showing highly significant correlations.

Table 5. Linear models that show relationship between taxon and wave exposure with A) proportional abundance for each taxon, and B) proportion of bleached abundance for each taxon.

A) Proportional Abundance

Genus	**R^2**	**p-value**
Acropora	**0.52**	**> 0.001**
Porites	**0.23**	**> 0.001**
Montipora	**0.20**	**0.002**
Leptoria	**0.15**	**0.008**
Dipsastrea	0.07	0.070
Pocillopora	0.05	0.160
Goniastrea	0.04	0.170

B) Proportion of Bleached Abundance

Genus	**R^2**	**p-value**
Acropora	**0.25**	**>0.001**
Montipora	**0.20**	**0.002**
Leptoria	**0.16**	**0.006**
Dipsastrea	**0.12**	**0.020**
Porites	**0.11**	**0.028**
Pocillopora	0.08	0.060
Goniastrea	< 0.01	0.930

among *Acropora* and *Montipora* was most related to wave exposure ($r^2 = 0.25$ and 0.20, $p > 0.001$ and $p = 0.002$ respectively) (Table 5b). Bleaching among *Dipsastrea* was also significantly effected by exposure gradients ($r^2 = 0.12$, $p = 0.02$), but both *Goniastrea* and *Pocillopora* showed non- significant trends unlike island side comparisons (Figure 7). Bleaching within stress-tolerant *Porites* and *Leptoria* were both significantly related to wave exposure gradients ($r^2 = 0.11$ and $r^2 = 0.16$, $p = 0.028$ and 0.006 respectively), but bleaching among *Leptoria* was more influenced than *Porites*. Distance to river was not related to either total coral abundance or proportional coral bleaching among most taxa and reveals stronger ecological-environmental relationships between coral communities and wave exposure. However, a significant interactive effect occurred between wave exposure and river distance and improves model fit when tested against proportional bleaching abundance of *Acropora* spp. ($r^2 = 0.43$, $p = 0.02$). *Acropora* spp. near river mouths on windward reefs bleached highest in comparison with other Acroporidae habitats around Guam.

IV. Discussion

4.1 Past and present bleaching in the Mariana Islands

Past regional bleaching events are ambiguous and predicted to have occurred less frequently than in central pacific reefs (Thompson and van Woesik 2009). Regardless, several moderate to severe regional events have been recorded locally and nearby in Palau and Japan (van Woesik et al. 2012; Loya et al. 2001; van Woesik et al.; Table 6). In 1994 Paulay and Benyahu (1999) recorded the first quantitative assessment describing Marianas bleaching

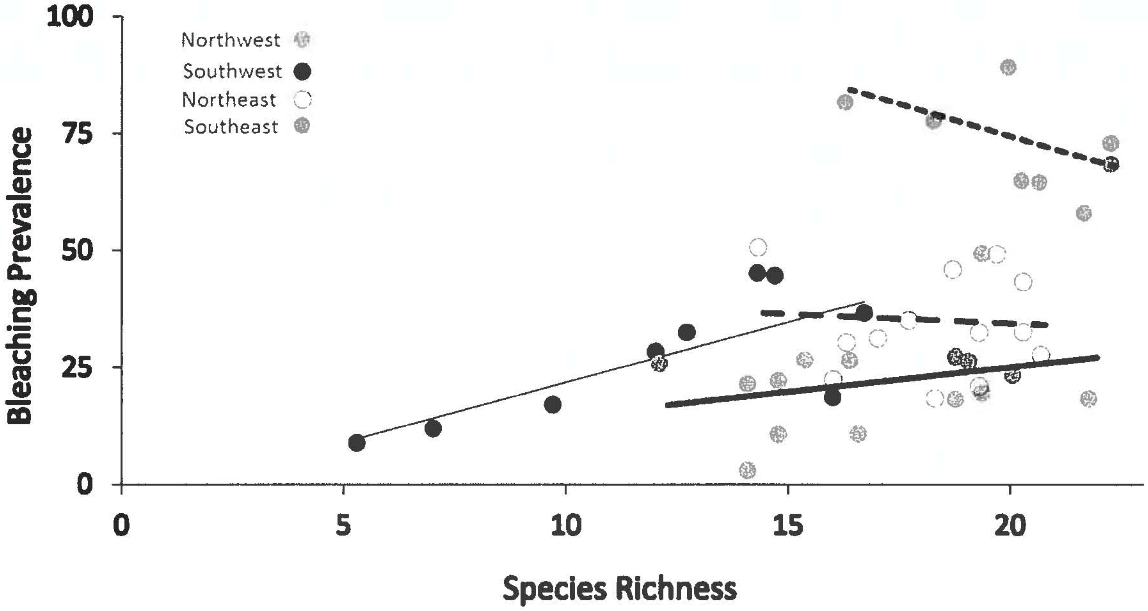


Figure 10. Depiction of the positive relationship between bleaching prevalence and species richness among the four biogeographic regions.

Table 6. Recent bleaching history for Mariana Archipelago. Reefs during 2015 (an El Niño year) SST highs experienced insignificant temperature stress resulting in limited bleaching observations. Tidal extremes during strengthening ENSO resulted in acute bleaching response from exposure in 2015.

Source	Reported Location	Year	Date	ENSO Phase	Severity
Paulay and Benayhu 1999	Guam	1994	October-December	Weak El Nino	low
Paulay and Benayhu 1999	Guam	1996	summer months	Neutral	moderate
Reefbase - unkown, Gourea et al. 2000	CNMI	1998	unknown	Moderate La Nina	low
Reefbase - Lisa Skilang	CNMI	2001	summer months	Neutral	moderate
Reefbase - Peter Houk	CNMI	2003	September	Neutral	low
Reefbase - Lisa Chau, Burdick et al. 2008	Guam	2006	September - October	Weak El Nino	low
Reefbase - Peter Houk, Burdick et al. 2008	Guam/CNMI	2007	August - September	Weak La Nina	low
Laurie Raymundo, pers com	Guam	2010	October	Moderate La Nina	low
Reynolds et al. 2014	Guam/CNMI	2013	June - October	Neutral	severe
Heron et al. 2016	Guam/CNMI	2014	April - June	Neutral	moderate

hierarchy. Although spatially limited to seven leeward sites and one windward site, bleaching occurred during the same months as the 2013 bleaching event (October – December) and impacted a similar species range. Results from 2013 parallel the 1994 event as caespitose *Acropora*, *Millipora*, *Montipora*, and *Astrea* (Pacific *Montastrea*), *Stylophora*, and *Pocillopora* bleached severely and *Porites* and *Leptastrea* showed low bleaching incidence. Interestingly, corymbose *Acropora* bleaching was not observed in 1994 and only moderate to low bleaching incidence during the 2013 event.

Seasonal bleaching is often recorded within the Marianas, but not to the severity or extent of the 2013 event. More recently in the Commonwealth of the Northern Mariana Islands (CNMI), Heron et al. (2016) identified similar relationships between coral community characteristics and bleaching response patterns during a moderate 2014 event. This same event also impacted Guam reefs and occurred 6 months after the 2013 surveys ended. In the CNMI study coral cover, species richness, and DHW were most correlated with bleaching severity. From multiple correlations they constructed linear models to validate 5 km remote sensing products. Because CNMI reefs share a regional species pool, this management tool can be used to accurately describe and predict Guam bleaching severity for this same year. In order of severity, CNMI researchers determined *Stylophora*, *Astreopora*, *Montipora*, and *Acropora* were the most impacted genera in 2014. Like Heron et al. (2016), this thesis also demonstrated the strong correlation between diversity and bleaching prevalence.

In all three bleaching studies, Acroporidae and Pocilloporidae species consistently bleach revealing windward coral communities are most vulnerable in the Marianas Islands. Several species of encrusting *Montipora* and *S. pistallata* severely bleached in 1994, 2013 and 2014. Hawaii *Montipora* can increase heterotrophic feeding to counter zooxanthellae disassociation and quickly recovers following temperature stress (Grotolli *et al.* 2010), but Mariana *Montipora* are physiologically diverse with competitive, weedy, and stress-tolerant life-histories existing within this genus (see Darling *et al.* 2013). Encrusting *Montipora* species will continue exhibiting a wide range of bleaching severities until better taxonomic observations are made (but see Appendix 1). *S. pistallata* has experienced better days. Only 67 individuals were observed in 2013 and a BMI of 88 was recorded. This genus bleached severely in 2014, indicating this locally rare species is highly vulnerable to ocean warming. Paradoxically, *Millipora* species were severely impacted in both 1994 and 2013, but least susceptible to bleaching in 2014 in the CNMI. As suggested in Heron et al. (2016), rapid and extensive mortality during 2013 may have removed susceptible genotypes and led to more resilient populations in 2014.

4.2 *Environmental influence and coral life-histories*

This research found competitive and stress-tolerant life-histories have species distributed in relationship to wave exposure and island geology. Along wave exposed reefs in Guam, competitive life-histories indicated high coral diversity and high bleaching potential – a relationship that increased in moderate wave exposure and adjacent to large watersheds. In SE reefs, caespitose *Acropora*, corymbose *Pocillopora*, and encrusting *Montipora* communities proliferated along sheltered windward environments and contributed to this regions high diversity. Pago Bay (GUA-510) and the backside of Cocos Island (GUA-600) both included these coral genera and experienced the highest recorded bleaching prevalence (81 and 90%, respectively). Using morphological groupings, BMI ranking explicitly revealed a broader range of species-specific bleaching responses (Table 4b). Both Pago Bay and Coco's Island reefs were > 30% caespitose *Acropora* cover – an order of magnitude greater than any other site surveyed

(Figure 11). In contrast, stress-tolerant species groups like arborescent *Porites* (*P. rus*) and massive *Porites* had a negative correlation with bleaching and diversity and were most common within leeward embayments. Sites in Agat Bay (478 and 601) and Tumon Bay (GUA-648) bleached least (< 20%) and were monospecific reefs of *P.rus* (Figure 11). Differences in life history was most related to wave exposure gradients, but geology was a significant indication of which functional groups existed in an area.

4.3 Study improvements and future investigation

Although coral demography and environmental gradients were related to bleaching patterns, high variability in all tested factors was recorded and revealed the complex nature of a reef ecosystem. Improved corollaries may result from testing additional biotic and abiotic factors. Fish, macroinvertebrate, and algal community profiles were not complied in 2013 and may co-influence bleaching relationships at a site-by-site scale. Past research demonstrates that symbiotic algae contribute to intraspecific bleaching patterns (Sampayo *et al.* 2008; Jones *et al.* 2008; Kemp *et al.* 2014), but fish and macroinvertebrate communities are most impacted following extensive reef losses (Berumen and Pratchett 2006). Abiotic variables like SST flux (DHW), anomalous wave exposure, site turbidity and ocean current velocity are all influencing factors and may improve localized ecosystem modeling (Heron *et al.* 2016; Nakamura and van Woesik 2001, Williams *et al.* 2010). During the 2014 CNMI bleaching event, abiotic relationships and observed bleaching patterns better explained spatial variation among taxa, sites, and regions. Regardless, biogeographic regions in this study represented generalized relationships between taxonomy and the environment. Bleached *Goniastrea* and *Pocillopora* had significantly higher abundances along windward reefs, but linear modeling revealed weak

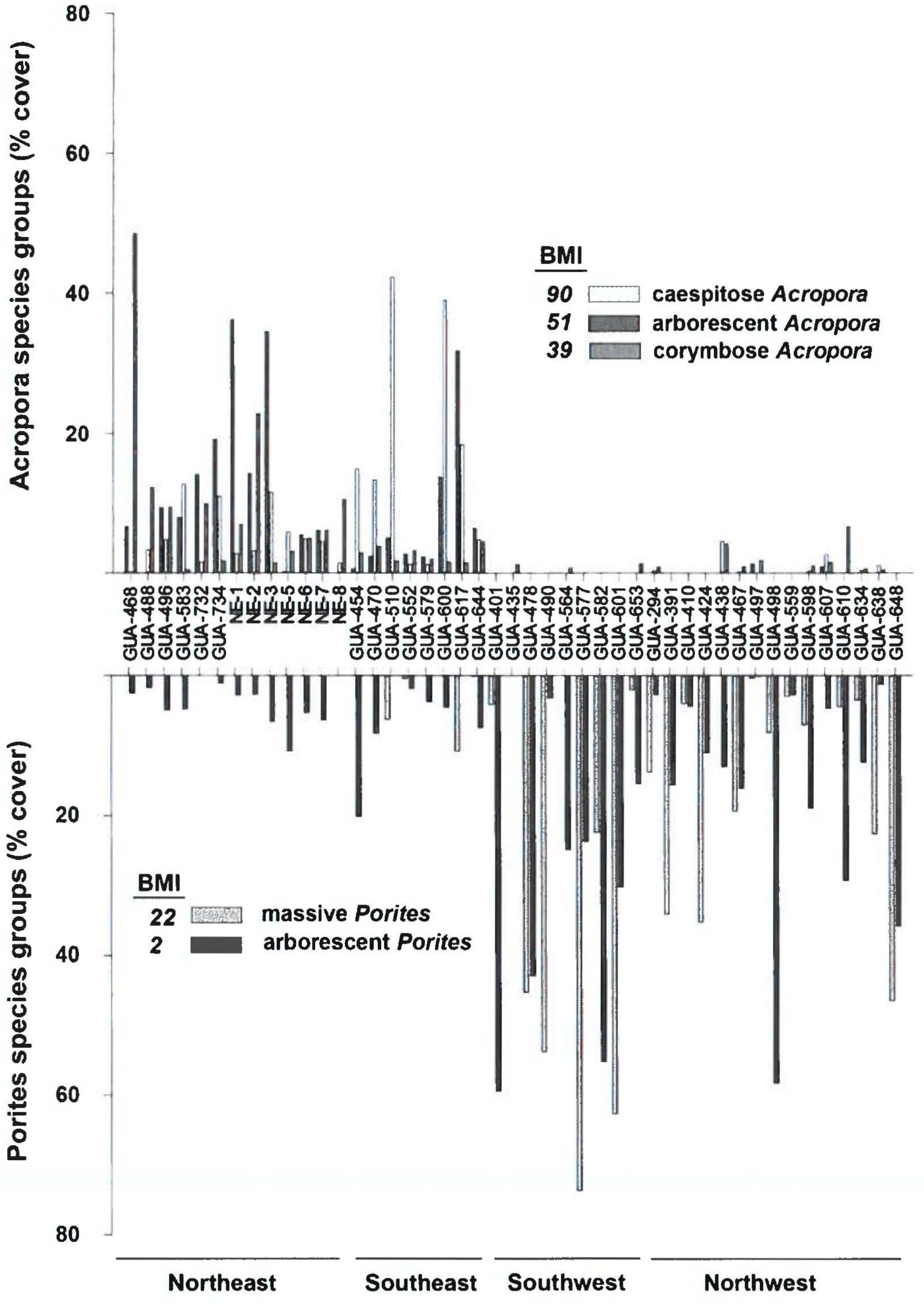


Figure 11. Proportional abundance of 3 major morphological groups in Acropora and the 2 major functional groups in Porites.

relationships with wave exposure. In contrast, higher windward *Dipsastrea* abundance and bleaching abundances demonstrated that bleaching was amplified along this coastline across more species than on leeward reefs. Weak linear relationships between most taxa and environmental gradients suggested weak interdependencies with the environment exist around Guam. However, this may have resulted from inadequate representation of wave exposure as westerly and storm driven swell events were unaccounted for. Still, complex and massive species groups clearly differentiated between life-history modes according to Guam's island geology and wave exposure regimes.

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VI. Appendices

Appendix 1. Bleaching species list compiled during qualitative spot checks along site depth gradients.

Species Recorded	(%) Impacted	(%) Normal	n	Count of Normal	Count of Pale	Count of Bleached	Count of Dead
Acanthastrea echinata	44	56	39	22	10	7	0
Acropora abrotanoides	61	39	69	27	12	22	8
Acropora aculeus	100	0	1	0	0	1	0
Acropora azurea	79	21	47	10	9	13	15
Acropora cerealis	88	12	42	5	13	15	9
Acropora cophodactyla	41	59	17	10	4	3	0
Acropora digitifera	25	75	12	9	2	1	0
Acropora gemmifera	25	75	12	9	2	1	0
Acropora globiceps	55	45	38	17	6	9	6
Acropora granulosa	25	75	4	3	0	1	0
Acropora humilis	69	31	65	20	11	21	13
Acropora lutkeni	0	100	1	1	0	0	0
Acropora monticulosa	75	25	32	8	4	12	8
Acropora multiacuta	0	100	2	2	0	0	0
Acropora nasuta	50	50	14	7	2	4	1
Acropora obtusicaulis	88	13	24	3	4	12	5
Acropora palmerae	72	28	29	8	7	7	7
Acropora polystoma	0	100	1	1	0	0	0
Acropora quelchi	58	42	12	5	4	3	0
Acropora secale	75	25	4	1	3	0	0
Acropora selago	40	60	5	3	2	0	0
Acropora surculosa	54	46	79	36	16	16	11
Acropora tenuis	60	40	20	8	7	4	1
Acropora valida	63	38	8	3	2	2	1
Acropora verweyi	76	24	51	12	10	16	13
Acropora wardii	50	50	2	1	1	0	0
Astreopora listeri	40	60	15	9	2	4	0
Astreopora myriophthalma	42	58	33	19	5	8	1
Astreopora ocellata	100	0	1	0	0	1	0
Astreopora randalli	0	100	1	1	0	0	0
Cyphastrea agassizi	50	50	2	1	1	0	0
Cyphastrea chalcidicum	38	63	16	10	3	3	0
Cyphastrea serailia	0	100	2	2	0	0	0
Diploastrea heliopora	33	67	6	4	2	0	0
Dipsastrea danae	50	50	6	3	0	3	0
Dipsastrea favus	38	62	13	8	1	4	0
Dipsastrea granulosa	0	100	2	2	0	0	0
Dipsastrea helianthoides	73	27	11	3	2	6	0
Dipsastrea maritima	0	100	1	1	0	0	0
Dipsastrea matthaii	29	71	17	12	3	2	0
Dipsastrea pallida	59	41	71	29	26	16	0
Echinophyllia echinata	50	50	2	1	1	0	0

(Continued)

Species Recorded	(%) Impacted	(%) Normal	n	Count of Normal	Count of Pale	Count of Bleached	Count of Dead
Echinopora pacificus	56	44	9	4	1	3	1
Euphyllia glabrescens	0	100	1	1	0	0	0
Favites abdita	83	17	6	1	2	3	0
Favites flexuosa	57	43	21	9	4	8	0
Favites russelli	57	43	7	3	2	2	0
Fungia fungites	50	50	2	1	0	1	0
Galaxea fascicularis	3	97	31	30	0	1	0
Gardineroseris planulata	100	0	4	0	0	4	0
Goniastrea edwardsi	78	22	50	11	10	24	5
Goniastrea pectinata	77	23	13	3	2	7	1
Goniastrea retiformis	63	37	78	29	15	31	3
Goniastrea stelligera	69	31	55	17	14	22	2
Goniopora fruticosa	0	100	6	6	0	0	0
Heliopora coerulea	38	62	13	8	4	0	1
Hydnophora expansa	0	100	1	1	0	0	0
Hydnophora microconos	67	33	48	16	10	22	0
Isopora palifera	67	33	3	1	0	2	0
Leptastrea immersa	9	91	11	10	0	1	0
Leptastrea pruinosa	0	100	2	2	0	0	0
Leptastrea purpurea	17	83	6	5	0	1	0
Leptastrea transversa	0	100	7	7	0	0	0
Leptoria phrygia	74	26	90	23	26	33	8
Leptoseris incrustans	100	0	1	0	0	1	0
Lobophyllia corymbosa	100	0	1	0	1	0	0
Lobophyllia flabelliformis	50	50	2	1	0	1	0
Lobophyllia hemprichii	64	36	22	8	8	6	0
Merulina ampliata	100	0	2	0	0	1	1
Millepora dichotoma	86	14	7	1	1	4	1
Millepora latifolia	75	25	16	4	3	6	3
Millepora platyphylla	62	38	84	32	14	22	16
Montipora acanthella	100	0	3	0	1	1	1
Montipora caliculata	0	100	1	1	0	0	0
Montipora efflorescens	100	0	2	0	0	1	1
Montipora floweri	0	100	4	4	0	0	0
Montipora foveolata	89	11	18	2	2	12	2
Montipora grisea	55	45	11	5	1	4	1
Montipora hoffmeisteri	50	50	2	1	1	0	0
Montipora lobulata	100	0	2	0	0	2	0
Montipora monasteriata	33	67	3	2	0	1	0
Montipora myriophthalma	100	0	1	0	0	1	0
Montipora nodosa	75	25	4	1	1	1	1
Montipora planiuscula	0	100	2	2	0	0	0
Montipora socialis	100	0	3	0	1	1	1
Montipora venosa	0	100	1	1	0	0	0

(Continued)

Species Recorded	(%) Impacted	(%) Normal	n	Count of Normal	Count of Pale	Count of Bleached	Count of Dead
Montipora verrucosa	91	9	11	1	1	6	3
Oulophyllia crispa	0	100	2	2	0	0	0
Pachyeris speciosa	67	33	3	1	1	1	0
Pavona albamarginata	0	100	1	1	0	0	0
Pavona albomarginata	0	100	3	3	0	0	0
Pavona chiriquiensis	6	94	16	15	0	1	0
Pavona decussata	0	100	1	1	0	0	0
Pavona divaricata	0	100	2	2	0	0	0
Pavona duerdini	67	33	12	4	1	7	0
Pavona explanulata	100	0	1	0	0	1	0
Pavona maldivensis	67	33	3	1	1	1	0
Pavona meandrina	30	70	10	7	0	3	0
Pavona minuta	0	100	1	1	0	0	0
Pavona varians	40	60	20	12	5	3	0
Pavona venosa	54	46	13	6	4	2	1
Phymastrea colemani	100	0	1	0	0	1	0
Phymastrea curta	68	32	53	17	13	20	3
Phymastrea magnistellata	52	48	25	12	6	7	0
Platgyra daedalea	79	21	48	10	13	21	4
Platygyra pini	76	24	75	18	18	32	7
Pocillopora ankeli	55	45	22	10	7	4	1
Pocillopora coniculus	100	0	1	0	1	0	0
Pocillopora damicornis	25	75	8	6	1	1	0
Pocillopora danae	20	80	5	4	0	1	0
Pocillopora elegans	50	50	14	7	2	4	1
Pocillopora eydouxi	58	42	64	27	13	20	4
Pocillopora ligulata	40	60	10	6	4	0	0
Pocillopora meandrina	78	22	63	14	11	25	13
Pocillopora setchelli	59	41	29	12	5	6	6
Pocillopora verrucosa	64	36	47	17	10	18	2
Pocillopora woodjonesi	100	0	2	0	0	1	1
Porites australiensis	20	80	15	12	0	2	1
Porites cylindrica	33	67	3	2	0	1	0
Porites deformis	0	100	9	9	0	0	0
Porites horizontalata	50	50	2	1	0	1	0
Porites lichen	74	26	19	5	5	6	3
Porites lobata	33	67	9	6	1	2	0
Porites lutea	37	63	27	17	3	7	0
Porites mammalata	20	80	5	4	0	1	0
Porites mayeri	0	100	1	1	0	0	0
Porites monticulosa	0	100	1	1	0	0	0
Porites murrayensis	0	100	1	1	0	0	0
Porites myrmidonensis	50	50	2	1	0	1	0
Porites rus	0	100	19	19	0	0	0

(Continued)

Species Recorded	(%) Impacted	(%) Normal	n	Count of Normal	Count of Pale	Count of Bleached	Count of Dead
Porites sp. - massive	**16**	**84**	31	26	4	1	0
Porites sp. - submassive	**25**	**75**	8	6	0	2	0
Porites vaughani	**0**	**100**	1	1	0	0	0
Psammocora contigua	**67**	**33**	3	1	1	1	0
Psammocora digitata	**62**	**38**	13	5	0	8	0
Psammocora haimeana	**33**	**67**	3	2	0	1	0
Psammocora loculata	**0**	**100**	1	1	0	0	0
Psammocora nierstraszi	**43**	**57**	7	4	1	2	0
Psammocora superficialis	**0**	**100**	4	4	0	0	0
Scapophyllia cylindrica	**100**	**0**	5	0	0	4	1
Stylocoeniella armata	**50**	**50**	4	2	1	1	0
Stylophora mordax	**83**	**17**	23	4	4	12	3
Turbinaria stellulata	**0**	**100**	1	1	0	0	0