Investigating Human Impacts to Coral Reefs in the Republic of the Marshall Islands

by

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Abstract

Both local and global threats are affecting the health of coral reefs worldwide. In addition to endangering the livelihoods and source of food for millions of people, threats to coral reefs may result in flattening reefs, which reduce habitat complexity and the ability of reefs to protect shorelines from erosion. This could be particularly detrimental to low-lying Pacific atolls like those found in the Republic of the Marshall Islands (RMI). I examined the influence of local human disturbance and heat stress on coral and algal community composition in Majuro and Arno Atolls in the RMI to explore how human disturbance affects coral and algal communities, and how to best characterize those communities. With a population of approximately 30,000 people, Majuro is home to the largest population of all of the RMI's 29 atolls and underwent extensive human modifications after American occupation during World War II. By contrast, Arno is home to fewer than 2,000 people and has remained relatively undisturbed. In June of 2016, I conducted benthic surveys at 25 sites along a gradient of human impacts across the two atolls. At each site at 10m depth, I measured percent cover of coral and algae genera and size-frequency of coral. I also utilized limited historical data to explore how reefs had recovered after a thermal stress event in 2014. In order to estimate human disturbance, I used the mean normalized difference vegetation index (NDVI) of the nearby coastline, which measures vegetation intensity. The coral and macroalgae composition of sites differed by atoll, mean NDVI, and wind and wave exposure, but not by sea surface temperature. The most degraded sites had low macroalgae cover and were dominated by turf algae, sponges, and cyanobacteria. One genus of macroalgae, *Halimeda*, was associated with sites that had low disturbance, while another, *Hypnea*, was correlated with higher disturbance. These results suggest that using macroalgae as an indicator of degradation may mask the influence of local human disturbance on reef community composition. Instead, it is important to consider identifying other indicator taxa and to measure coral and macroalgae cover to at least the genus level.

Lay Summary

This project aims to understand how humans influence the coral reefs surrounding two atolls, Arno and Majuro, in the Republic of the Marshall Islands (RMI), by measuring differences in the lifeforms composing and growing on the reefs. Majuro Atoll is the capital of the RMI and home to over half of the country’s approximately 53,000 people, and the coral reefs are subject to a number of human-related threats, such as sediment from construction and overfishing. Arno Atoll, located just 19 km away, has a population of approximately 2,000 and is undisturbed in comparison. The close proximity of the two atolls allowed me to compare the species living on the reefs while controlling for other variables like ocean conditions. Understanding how people affect the reefs will help managers make decisions about how to protect them in the future, especially in the context of climate change.

Preface

I was the lead investigator for this project and was responsible for all major areas of data collection and analysis, as well as the composition of the thesis. I worked closely with my advisor, Dr. Simon Donner of the University of British Columbia's (UBC) Department of Geography, through each step in the research process, including concept formation. I performed all of the data analysis with the guidance of Donner, who also assisted with 2016's data collection in the field (which required at least two people to complete). Both Donner and the other faculty member on my committee, Jennifer Williams of UBC Geography, contributed to edits of the thesis, although I was solely responsible for its composition.

This work makes use of historical data collected by other researchers. Specifically, benthic surveys from Majuro in 2014 were supplied by Maria Beger, Douglas Fenner, Daniela Ceccarelli, and Tyson Martin. Funding for their work was provided by the Winifred Violet Scott Estate Fund, a grant to Don Hess at the College of the Marshall Islands, Maria Beger and Eric Peterson at the University of Queensland, and the Australian Research Council Centre for Excellence for Environmental Decisions. I also utilized data provided by the Marshall Islands Marine Resources Authority from Arno Atoll in 2007, and photos from one site in Majuro were provided by Karl Fellenius of Hawaii Sea Grant and Martin Romain from the College of the Marshall Islands. None of these data have been published.

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List of Acronyms

ANOVA – Analysis of Variance

CCA – Crustose coralline algae

DHW – Degree heating weeks

FSM – Federated States of Micronesia

IPCC – Intergovernmental Panel on Climate Change

MIMRA – Marshall Islands Marine Resources Authority

NDVI – Normalized Difference Vegetation Index

OIFMC – Outer Island Fish Market Center

PerMANOVA – Permutational Multivariate Analysis of Variance

SPC – Secretariat of the Pacific

SST – Sea Surface Temperature

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Huge thanks go to our collaborators Diana Thompson and Emma Reed at Boston University. I am also grateful to our local collaborators, particularly Florence Edwards, Emma Tibon, Kalena deBrum, Benedict Yamamura and the rest of the team at the Marshall Islands Marine Resources Authority in the RMI, and Karl Fellenius of Hawaii Sea Grant and Martin Romain from the College of the Marshall Islands.

I would like to acknowledge Maria Beger, Douglas Fenner, Daniela Ceccarelli, and Tyson Martin for sharing data they collected in Majuro in 2014. Funding for their work was provided by the Winifred Violet Scott Estate Fund, a grant to Don Hess at the College of the Marshall Islands, Maria Beger and Eric Peterson at the University of Queensland, and the Australian Research Council Centre for Excellence for Environmental Decisions.

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I am enormously thankful for the guidance of Tamara Greenstone Alefaio of UBC and the University of the South Pacific Majuro Campus, who provided invaluable assistance with organizing the logistics for this project, her instruction in respecting the *manit* (culture) of the Marshall Islands, and her unwavering support and friendship ever since.

Last but not least, thanks to my mother, Dana Cannon, for the myriad of ways she has supported me, most specifically for providing child care while I was in the Marshall Islands, and to my son, Daniel Lemmon, for his unwavering faith in me, his much-needed distractions, and for constantly making me laugh.

Dedication

This work is dedicated to the memory of my late father, Michael Patrick Cannon (1949 – 2014), who shared his love of the ocean with me when I was a young child and always encouraged me to follow my dreams. His memory and influence are gifts for which I will always be grateful.

Chapter 1: Literature Review

Coral reefs are one of the world's most diverse ecosystems (Connell 1978). More than 100 countries have coastlines with coral reefs (Moberg and Folke 1999), and approximately 10% of the world's population live within 100 km of a reef (Donner and Potere 2007). Coral reefs provide livelihoods to millions of people, the majority of which live in developing countries (Cinner 2014). They also protect vulnerable coastlines from erosion by reducing wave energy an average of 97%, with the reef crest alone responsible for reducing 86% of wave energy (Ferrario et al. 2014). A recent study estimated that coral reefs generate US$35.8 billion annually in tourism expenditures (Spalding et al. 2017).

Decades of research show that the health of coral reefs is declining worldwide (Richmond 1993; Hughes 1994; Aswani et al. 2015; I.D. Williams et al. 2015). They are threatened by both global impacts (such as climate change and ocean acidification) and local impacts (such as overfishing, sedimentation, and eutrophication). In addition to threatening livelihoods and sources of food, many of these threats can kill coral and may result in flattening reefs, which reduce habitat complexity and reduce the ability of reefs to protect shorelines (Alvarez-Filip et al. 2009; Ferrario et al. 2014). Additionally, the potentially additive properties of each impact means that corals may be less able to recover from natural impacts like storms (Scheffer et al. 2015).

1.1 Global Threats

The people who depend most heavily on coral reefs for their livelihoods and sustenance tend to be those in small island nations like the Republic of the Marshall Islands (RMI) (NOAA

1995). Scientists around the world are working urgently to find ways that reefs can be protected from climate change (e.g. Donner et al. 2005; Carpenter et al. 2008; Graham et al. 2013; Scheffer et al. 2015), but it is integral that industrialized nations take action to reduce emissions (Kleypas and Yates 2009; van Woesik et al. 2015). While these efforts may slow the impacts of climate change, researchers are unsure if they will be reversible or if corals will be able to adapt.

1.1.1 Climate Change

When ocean temperatures are higher than the threshold for corals, they will bleach, which is a stress response by which corals expel their zooxanthellae, symbiotic algae that live inside the cytoplasm of a coral polyp (Gates et al. 1992). This makes most corals appear white (hence the term "bleached"). Bleached corals can survive for up to a few weeks without their zooxanthellae, but the symbiotic algae will not return until the source of the stress ends. If the algae is unable to return for several weeks, the coral will die (Glynn 1983). Temperatures only 1-2^{o} C higher than the usual maximum summer temperature are enough to induce coral bleaching (Coles et al. 1976). Sea temperatures have been rising for the past century, and are projected to continue to rise (IPCC 2014). Scientists project that this, coupled with stronger and more regular El Niño events which also produce warmer-than-average sea surface temperatures, will likely cause corals to bleach more often (Donner et al. 2005) and may also reduce their ability to recover from previous bleaching events and other sources of stress (Hughes et al. 2007; Carpenter et al. 2008; Toth et al. 2015).

In Majuro Atoll, historical air temperature data records show that average daily temperatures have increased by approximately 0.15°C per decade beginning in 1956 while sea surface temperature (SST) has increased by approximately 0.07°C per decade. Both mean air temperatures and SST are projected to rise in the future; under the lowest emissions scenario from the Intergovernmental Panel on Climate Change (IPPC), the surface air temperature in the southern Marshalls is projected to rise from 0.4 to 0.9°C between 2020 – 2039, with closely related SST likely increasing a similar amount (PACCSAP 2011). In 2014, the RMI underwent the most extensive thermal stress event in its recorded history. Abnormally high sea surface temperatures from July through December 2014 led to Bleaching Alert Level II warnings (expectations of widespread bleaching and some mortality) from NOAA Coral Reef Watch for the entire country, although heat stress was not as high in the southern Marshalls, including Majuro and Arno Atolls (Coral Reef Watch 2017). A report to NOAA Coral Reef Watch based on limited observations largely from Majuro, but also some observations from Arno, Kwajalein, and Namdrik Atolls, reported that "on average three-quarters of all shallow digitate corals are dead, two-thirds of all table corals, half of all submassives other than *Porites rus*, and maybe one quarter of all massive and encrusting corals" (Fellenius 2014).

Corals in areas with higher annual temperature fluctuations are more resistant to bleaching (Donner 2011), and scientists are currently investigating why this is. Combining this study with work being done by Donner in Kiribati (see: Donner 2007) will help to answer this question. At least in some cases, the zooxanthellae that return to the corals after bleaching are a different, more resilient strain than those living in the coral prior to bleaching (Berkelmans and van Oppen 2006). Other proposed mechanisms include shifting benthic communities, in which some resilient species of corals outcompete other, more sensitive species (Darling et al. 2013), and physiological acclimation (Ateweberhan and McClanahan 2010). Understanding what makes some corals more resilient to bleaching could be critical to finding potential ways that corals could adapt to increasing ocean temperatures. Scientists may also be able to use a new understanding of temperature dynamics in resilient corals to develop new mitigation techniques. In Hawaii, for example, scientists are currently attempting to grow a new genetically engineered species of coral that they hope will be more resilient to high temperatures and acidity (Van Oppen and Gates 2006; Putnam and Gates 2015).

While sea level has been rising since the last ice age (Lambeck and Chappell 2001), increasing atmospheric and oceanic temperatures after the industrial revolution have caused ice sheets to melt, contributing to an unprecedented rate of sea level rise (IPCC 2014). Since the zooxanthellae in coral tissues are photosynthetic, they are dependent on light and are unable to photosynthesize past a certain depth (which depends on water quality and irradiance) (Goldberg 2013). If reefs are unable to grow fast enough to keep up with rising sea levels, they will die. A recent modeling study indicates that *Porites* microatolls, large, massive species that grow in shallow lagoons, may grow fast enough to keep up with current rates of sea level rise in the Pacific, but if atmospheric gas concentrations continue to increase (past 670 ppm by the year 2100), sea level rise will outpace coral growth (van Woesik et al. 2015).

Rising sea levels pose a serious threat to the low-lying islands in the RMI, which have been subject to wave inundation events, ranging from minor to severe (Davenport and Haner 2015). There are a number of governmental agencies and international NGOs working together on outreach and training projects in the RMI in an attempt to warn citizens of the dangers of inundation events and mitigate future risk (White et al. 2015). In 2011, sea level rise in Majuro Atoll was occurring at 3.3 ± 0.4 mm per year, and based on empirical modeling, mean sea level is projected to rise between approximately 7 – 18 cm by 2030, with increases of 23 – 60 cm by 2090 under the lowest IPCC emissions scenario (PACCSAP 2014).

Increasing sea surface temperatures have also been linked to higher intensity extreme weather events, such as hurricanes in the Atlantic and typhoons in the Pacific (Easterling et al. 2000). While storms are natural, they can damage corals, which can allow algae to thrive in the absence of herbivory due to overfishing (Hughes 1994; Stimson et al. 2001; Hughes et al. 2007). When storms occur more often and at stronger intensities, reefs that are already stressed by climate change, diseases, and local factors may be less able to recover. In addition, increasing duration and intensity of storms could contribute to increased erosion, threatening small island nations like the RMI that are already vulnerable to rising sea levels, yet another symptom of climate change.

1.1.2 Ocean Acidification

The pH of the ocean is decreasing as carbon dioxide (CO_2) in the atmosphere rises and becomes sequestered in the oceans. The acidification process has changed the saturation state of the oceans with respect to calcium carbonate ($CaCO_3$) particles (Feely et al. 2004), which comprise the skeletons of corals and the structure of coral reefs. One study predicted that a doubling of pre-industrial atmospheric CO_2 would cause a 40% reduction in coral calcification, leading to less diverse reef communities and weakened reef structures (Hoegh-Guldberg et al. 2008). Field experiments support that ocean acidification has a negative effect on the calcification of most coral species and can therefore lead to slower growth rates (Kroeker et al. 2010; Edmunds et al. 2013). Unfortunately, it is highly unlikely that ocean acidification can be reversed, and currently unknown whether corals have the capacity to adapt (Kleypas and Yates 2009).

Aragonite is the polymorph of $CaCO_3$ that is produced by stony corals and some green algae (Goldberg 2013). Research suggests that an aragonite saturation state above 4.0 is optimal for coral growth and the development of healthy reef systems (Guinotte et al. 2003). In the RMI, the aragonite saturation state declined from about 4.5 in the late 18th century to an observed value of about 3.9 ± 0.1 by 2000. Aragonite saturation rates are projected to decrease through 2100. Climate models predict that by 2035, the annual maximum aragonite saturation state for the RMI will reach values below 3.5, the lowest saturation level considered adequate for coral growth (Guinotte et al. 2003), and will continue to decline, suggesting that coral reefs in the RMI will be vulnerable to dissolution as they will be unable to produce the calcium carbonate necessary to form their skeletons. The effects of ocean acidification on coral reef ecosystems will likely be compounded by other stressors, including climate change and fishing pressure (PACCSAP 2014). Slower coral calcification and reef growth combined with reef dissolution would reduce the ability of reefs to protect islands from erosion, particularly in the context of more intense tropical storms and rising seas.

1.2 Local Threats

Reefs in the RMI, particularly those close to population centers like the Delap-Uliga-Djarrot ("D-U-D") in Majuro, are also affected by local impacts, which are those that can be managed by local resource users and managers. The ways that local impacts affect coral reefs depends on the features of the specific reef in question, including flushing rates and currents, proximity to human settlements, morphometry, bottom topography, and coral species composition. It is therefore vital that plans for the management of coral reefs be specifically tailored to the areas in question. What is detrimental to one reef may have less of an impact to another due to the specific features of each reef. Unlike climate change, each of these impacts could be reversible with local management.

1.2.1 Overfishing

Overfishing is almost uniformly considered the greatest local threat facing coral reefs worldwide, and scientists have found that overfishing herbivorous fishes on reefs may be particularly problematic. A number of studies have shown that when herbivores are removed from a reef, feeding pressure on turf algae is reduced, allowing it to grow unchecked and become larger, leafy macroalgae (Randall 1961; Lewis 1986; Mumby 2006), which can kill coral by a number of mechanisms, both chemical and physical (McCook 1999). Macroalgae also outcompete crustose coralline algae (CCA), a pink encrusting algae that is important for facilitating the settlement of coral larvae (Björk et al. 1995; Arnold et al. 2010). Overfishing or death of herbivores (invertebrates and fishes) has been linked to phase shifts from coral-dominated ecosystems to those dominated by macroalgae, particularly in the Caribbean (Hughes 1994; Hughes et al. 2007). Herbivorous fish populations (coupled with habitat complexity) also play an important role in the ways that coral reefs respond to nutrient influxes (Szmant 1997).

Overfishing of predators may also be deleterious for coral reefs, although its impacts have been less studied. Most coral reef fisheries tend to focus on larger predatory fishes (Myers and Worm 2005), and overfishing of piscivores may lead to trophic cascades (when predators in a food web suppress the abundance of their prey or impact their behavior) (Stallings 2008). In the absence of predators, herbivores may overgraze the turf algae (Randall 1961), which has harmful effects on the resilience of the ecosystem as a whole. If a reef has high densities of herbivores but few piscivores, there may be more coral, but the lack of functional group diversity will make the system less resilient to disturbances (Houk and Musburger 2013).

A number of studies have linked overfishing of predators to widespread outbreaks of the crown-of-thorns starfish, *Acanthaster planci*, in the Indo-Pacific (e.g. Dulvy et al. 2004; Kayal et al. 2012). Crown-of-thorns feed on corals, and in high numbers they can decimate coral reefs. There have been numerous outbreaks of *A. planci* since the early 2000s (Kayal et al. 2012), including in Majuro and Arno Atolls (F. Edwards, personal communication).

1.2.2 Nutrients

Nutrients on coral reefs, along with fishing, have long been considered one of the controlling factors of reef health (Richmond 1993). Indeed, in some cases, high influxes of nutrients from human activities on land have been linked to overgrowth of macroalgae. The most studied example of this was in Kanoehe Bay, Hawaii, where one particular species of algae, *Dictyosphaeria cavernosa*, grew over and replaced corals beginning in the 1960s (Laws and Redalje 1982; Evans et al. 1986). Human sewage had been dumped directly into the bay for approximately 25 years before two of the outfalls were finally diverted in 1978. The last sewage outfall was diverted in 1986 (Hunter and Evans 1995).

After the diversion of the sewage outfalls, the algae decreased significantly (Laws and Redalje 1982; Evans et al. 1986). By 1983, the algae had decreased to one fourth of its previous abundance, indicating that nutrients from the sewage played a major role in its growth (Evans et al. 1986). *D. cavernosa* in Kaneohe Bay have since rebounded at some sites (Hunter and Evans 1995), and blooms have been linked to recent rainfall events, which supports the nutrient hypothesis because rainstorms flush nutrients from farming and other human activities into the bay (Jokiel et al. 1993).

More recent studies have begun to question the nutrient hypothesis and instead suggest that herbivory controls the growth of *D. cavernosa* in Kaneohe Bay, and the blooms were caused by overfishing of herbivores (Stimson et al. 2001). Field studies and laboratory experiments suggest that nutrients play a very small role in the growth of many algae and do little to directly harm the health of corals (McCook 1999; Fabricius et al. 2005; Wolanski and De'ath

2005). Most scientists now agree that while nutrients can contribute to the growth of algae, this is only significant in the absence of herbivores (Szmant 1997; Burkepile and Hay 2006).

Nutrients from land-use practices like farming may harm corals in indirect ways. For example, in Australia, outbreaks of *A. plasti* ("Crown-of-Thorns" starfish) have been linked to nutrients from land-use practices like agriculture, challenging the hypothesis that outbreaks are caused by overfishing of predators (Brodie et al. 2005; Wolanski and De'ath 2005). Land-use practices are less able to explain *A. plasti* outbreaks in the RMI or similar Pacific Islands where there is only enough land for subsistence agriculture (Faechem and Bayliss-Smith 1977), providing evidence that overfishing may contribute to outbreaks in these areas. However, in Majuro, untreated sewage is concentrated and pumped from an outfall pipe that has corroded and leaked sewage directly onto the reef flat (MIMRA 2016).

1.2.3 Sedimentation

Sedimentation can be caused by any human activities that free up sediments that are then washed into the ocean. Major contributors include deforestation, agriculture, development, and dredging. Because mangroves play a major role in trapping sediments from land, coastal developments that remove mangroves also induce sedimentation (Rogers 1990; Richmond 1993). This can smother corals by covering them in soil and preventing them from feeding or preventing the zooxanthellae from photosynthesizing (Weber et al. 2012). Sediments in the water column also increase turbidity, which impacts photosynthesis because light is unable to penetrate as deeply in waters with a lot of suspended sediment (Rogers 1990;

Weber et al. 2012). Sediments can also cover the benthic substrate, preventing coral larvae from settling (Rogers 1990).

Corals have various mechanisms to remove sediments. Some corals produce a surface film of mucous that helps them shed sediments; others use tentacles or cilia to manually remove them (Hubbard and Pocock 1972). These mechanisms allow corals to respond to occasional sedimentation, but they are slow and energetically costly (Hubbard and Pocock 1972; Lasker 1980), and corals exposed to a lot of sediment in a short period of time may be less resilient to other stressors. In Majuro, an artificial channel was built to connect the lagoon and the ocean between Majuro Wharf and the east part of Rairok in the 1980s (Xue 2001). Also, dredging the reef flat to provide aggregate for a controversial expansion of the airport runway began in 2011 (Johnson 2012 Mar 15; RMIPA 2013) and is still under way today. Both of these activities increased sedimentation on nearby reefs. If the land-use practices leading to sedimentation are stopped or if mitigation techniques are put in place to prevent runoff, in many cases, reefs can recover from sedimentation (Brown et al. 1990).

1.3 Coral Reefs in the Marshall Islands

The RMI have been inhabited for approximately 3,000 years (Ratzel 1896). The people who live in the RMI depend heavily on coral reefs for food (fishing is a major source of sustenance), and the reefs protect the low-lying islands from rising sea levels and storm surges (Pinca et al. 2005). Coral reefs in the RMI are threatened by both global and local impacts. Majuro Atoll, the capital of the RMI and home to over half of the country’s approximately 53,000 people (Secretariat of the Pacific Community 2012), was subjected to extensive modifications and population growth after its occupation by the American military during World War II (Spennemann 1996). Reefs in Majuro especially are subject to coastal management challenges brought about by population growth, waste generation, and shoreline construction.

Over the past few decades, immigration from outer atolls and a high birth rate has increased the population density, especially in the eastern population center of the D-U-D, where an American army base was built during World War II (Spennemann 1996; Secretariat of the Pacific Community 2012). In the 1970s, a series of causeways were built to connect the islands of Djarrit and Laura in Majuro, which interrupted water flow from the lagoon to the ocean and contributed to erosion within the lagoon. An artificial channel was built to connect the lagoon and the ocean between Majuro Wharf and the east part of Rairok in the 1980s (Xue 2001). Commercial dredging for aggregate used in construction (particularly of the airport) was common throughout the eastern coast of Majuro through at least the early 2000s, inducing erosion and interrupting sediment supply (Xue 2001). More recently, in 2011 a controversial expansion of the airport runway began, using material dredged from the reef flat (Johnson 2012 Mar 15; RMIPA 2013). In addition to threatening livelihoods and sources of food, sediment pollution, nutrient pollution, reef mining and other local disturbances can kill coral and may result in flattening reefs, which reduce habitat complexity and reduce the ability of reefs to protect shorelines (Alvarez-Filip et al. 2009; Ferrario et al. 2014). Additionally, the potentially additive properties of each impact means that corals may be less able to respond to natural impacts like storms (Scheffer et al. 2015).

Arno Atoll, located only about 19 km east of Majuro, has remained largely undisturbed by population growth and human modifications. The entire atoll, which is larger than Majuro in area, is home to less than 2,000 people, a number that is shrinking annually due to emigration to Majuro (Secretariat of the Pacific Community 2012). Because of the close proximity to Majuro, Arno is home to some fishing pressure by fishers who travel from Majuro, but this is almost entirely pelagic; access to reefs is controlled by the local *iroij* (chief). The Marshall Islands Marine Resources Authority (MIMRA) does sell fish from Arno and other outer island atolls (including reef fish), but reef fisheries are closely monitored for sustainability (Hess 1999).

In the RMI, people depend heavily on the reefs for food, particularly in Majuro, which has a high population density (Pinca et al. 2005; Secretariat of the Pacific Community 2012). While there is some reef fishing pressure in Arno, it is decidedly lower than that in Majuro, and closely monitored by the central government (Hess 1999). MIMRA runs the Outer Island Fish Market Center (OIFMC) on Majuro, which sells fish from Arno and other outer island atolls (including reef fish). The OIFMC is a sustainable development initiative that provides capital to fishers in the outer islands, while also providing sustenance for Majuro's growing population and reducing fishing pressure in Majuro. In 2015, the OIFMC received 33 small boatloads of fish (approximately 2,500 pounds each) from fishers in Arno Atoll (MIMRA 2015).

To date, only a few studies of the coral reefs have been conducted in this region (e.g. Pinca et al. 2005; Houk and Musburger 2013), and this is the first study to compare the health of the reefs between the two adjacent atolls. This study provides information that is essential for the future protection of Majuro's and Arno's coral reefs. Because the two atolls are so close to each other (only 19 km apart), they experience similar oceanographic conditions, including sea surface temperatures. The physical similarities and close proximity of the atolls allowed comparison reef health across a gradient of human impacts, while controlling for some potential confounding factors.

1.4 Research Summary and Objectives

With 10% of the global population living within 100 kilometers or less of coral reefs, their health is intricately linked to the wellbeing of millions of people (Hassan et al. 2005). Reefs are also critical for the protection of vulnerable coastlines from erosion caused by waves (Ferrario et al. 2014), and scientists now estimate that one-third of reef-building corals face an elevated risk of extinction from the combination of climate change and local impacts (Carpenter et al. 2008). Many of the people who depend on coral reefs are in developing countries (Cinner 2007), suggesting that the people who most need the resources reefs provide are those that are contributing the least to global impacts such as climate change and ocean acidification. While it is vital that industrialized nations take swift action to curve emissions to limit these impacts, resource users and managers can take action to limit local threats to coral reefs (such as overfishing, excessive nutrients, and sedimentation). Protecting reefs from local disturbances may increase resilience to global impacts (Micheli et al. 2012; Mellin et al. 2016), essentially buying time for reefs and islands that are being threatened by climate change and rising sea levels. It is therefore of the utmost importance that scientists work closely with managers and resource users to come up with innovative ways to protect reefs on a local scale.

The goal of this thesis was to provide information that would guide future research and conservation efforts, through three main objectives:

- To learn how human activities influenced the benthic composition of coral reefs and the size frequency of coral genera;
- To identify potential new indicators of reef degradation that may be more effective than those commonly used in recent studies (such as macroalgae as a single category);
- And, to understand how local degradation affects coral recovery from thermal stress events.

Arno and Majuro Atolls in the RMI presented an ideal location to investigate these objectives, providing a natural laboratory where the close proximity of the atolls and similarities in oceanographic conditions allowed me to compare reef health across a gradient of human impacts while reducing potential confounding factors. I measured the percent cover of coral and algae taxa and size-frequency distributions of coral genera at 25 sites, using the Normalized Difference Vegetation Index, which measures the intensity of vegetation, as a proxy for human influence. I used historical data from 2007 in Arno Atoll and 2014 in Majuro Atoll to investigate any differences in reef recovery after 2014's thermal stress event.

The fieldwork for this research was undertaken during June and July 2016. The work was conducted in conjunction with Diane Thompson and Emma Reed from Boston University, who collected water samples and identified candidate corals for paleoclimate research. I also worked closely with MIMRA throughout this project, which provided invaluable assistance with logistics and site selection, and helped me to insure the work would provide information useful for marine resource management.

This work will provide information that can help to predict which reef environments are being most impacted by local threats, as well as which are most susceptible to the negative repercussions of climate change and warming ocean temperatures. The results could be extrapolated to other reefs in the region, providing information that could potentially help mitigate both local and global threats to reefs throughout Micronesia, where the high numbers of low-lying atolls makes communities uniquely vulnerable to rising sea levels. Also, identifying new metrics for identifying degraded reefs may change the current scientific paradigm about which reefs are considered ‘healthy.’ This will contribute to the ability of scientists to better identify reefs that would most benefit from protection.

Chapter 2: Body of Thesis

2.1 Introduction

Decades of research have shown that the health of coral reef ecosystems is declining worldwide (Richmond 1993; Hughes 1994; Aswani et al. 2015; G.J. Williams et al. 2015). They are threatened by both global impacts (such as climate change and ocean acidification) and local impacts (such as overfishing, sedimentation, and eutrophication). In addition to threatening the livelihoods and source of food for millions of people (Cinner 2014), many of these threats can kill coral and may result in flattening reefs, which reduces habitat complexity and the ability of reefs to protect shorelines (Alvarez-Filip et al. 2009; Ferrario et al. 2014). Additionally, the potentially additive properties of these impacts may make corals and coral reef ecosystems less resilient to natural disturbances like storms (Scheffer et al. 2015).

Global sea temperatures have been rising for the past century and are projected to continue to rise (IPCC 2014). Scientists predict that this will lead to more frequent and severe heat stress (Donner et al. 2005) leading to coral bleaching, coral mortality, and a reduced resilience to other stressors (Hughes et al. 2007; Carpenter et al. 2008; Toth et al. 2015). As a result, researchers are working hard to identify management actions that could confer coral reef resilience to climate change. Recently, there has been debate within the scientific community about the relative role of local human activities in coral reef degradation as compared to the global threat posed by climate change, with some scientists arguing local impacts play an important role (e.g. Fabricius et al. 2005; Scheffer et al. 2015; Williams et al. 2015; Crane et al. 2017), and others contending their effects are negligible in comparison (e.g. Aronson and Precht 2006; Carpenter et al. 2008; Bruno and Valdivia 2016).

This debate/disagreement may in part stem from disagreements over the metrics of reef health, as well as the very definition of a healthy reef. Macroalgae cover is a commonly used indicator that reefs are ‘unhealthy’ or have a different benthic composition than what was found prior to disturbance (e.g. McCook et al. 1997; Mumby et al. 2005; Hughes et al. 2007). The broad category of macroalgae used in many field studies includes a variety of alga with different sensitivities to disturbance and life history strategies. Using macroalgae cover as an indicator of coral reef health, without considering the forms of algae or the presence of other key reef organisms, could lead to the mischaracterization of reefs as unhealthy versus healthy. Some studies have shown that reefs with high macroalgae cover are not necessarily degraded; in fact, reefs far from people may have high percentages of macroalgae cover (Vroom et al. 2006; Vroom and Braun 2010; Williams et al. 2015).

This disagreement over what constitutes a ‘healthy’ reef may also stem from debate about what reefs may have looked like before the Industrial Revolution. Some scientists argue that some reefs may have naturally high macroalgae cover (Howe 1912; Setchell 1928; Vroom 2011; Finnegan et al. 2015), while others argue that coral cover has decreased and macroalgae has increased even on the most remote reefs due to recent climate change (Aronson and Precht 2006; Carpenter et al. 2008; Bruno and Valdivia 2016). However, while phase shifts from hard coral- to macroalgae-dominated reefs after disturbances are well documented in the Caribbean (Hughes 1994), this may be uncommon in the Indo-Pacific. It is possible that disturbances may instead cause coral reefs to shift to dominance of other taxa, such as sponges (Bell et al. 2013; Powell et al. 2014), or corals with weedy life histories (Darling et al. 2012; Davenport and Haner 2015; Crane et al. 2016).

The atolls of Majuro and Arno in the Republic of the Marshall Islands (RMI) provide a unique opportunity to evaluate ideas about indicators of reef health and the relative threats posed by climate change and human disturbance (Figure 1). The RMI is a nation of 29 atolls and five oceanic islands in the northwest tropical Pacific, just north of the Gilbert Islands in Kiribati and east of the Federated States of Micronesia. The Marshallese people depend heavily on coral reefs for food (fishing is a major source of sustenance) (Gillett 2016), and the reefs protect the low-lying islands from rising sea levels and storm surges (Pinca et al. 2005). Majuro and Arno Atolls, only 19 km apart, have comparable climatic and oceanographic experiences but different histories of human settlement and local coastal disturbance.

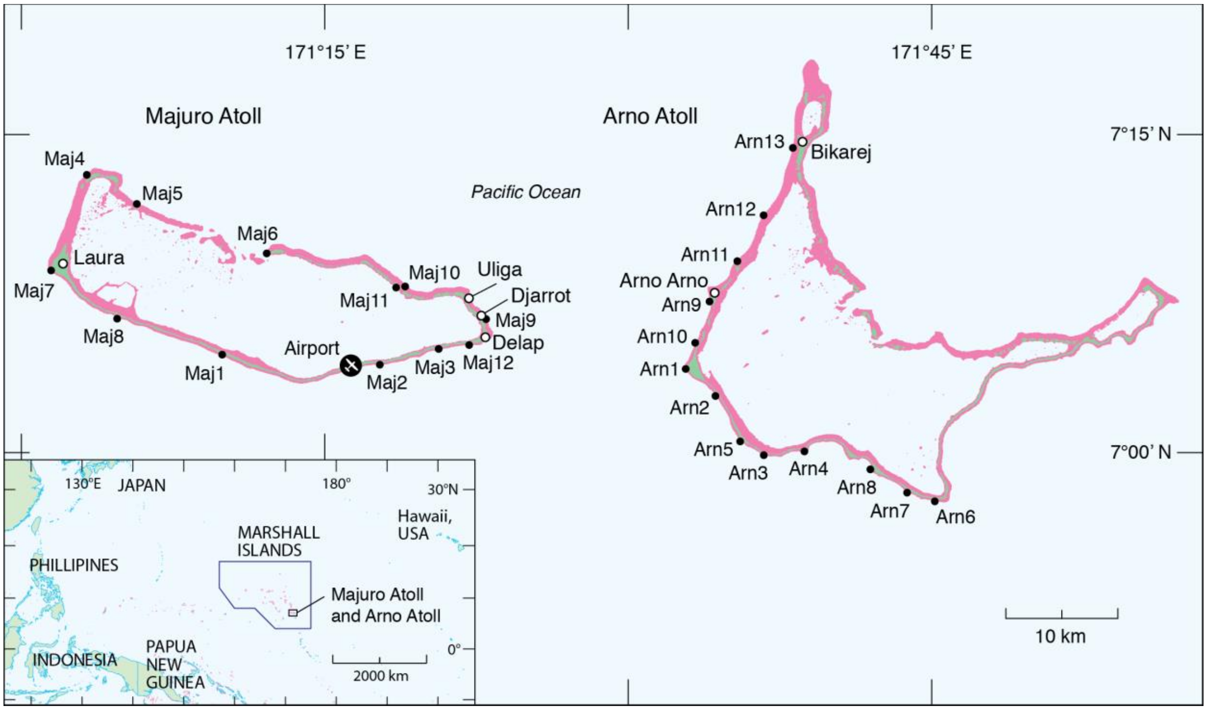

Figure 1: Map of the RMI and study site locations.

In 2014, the RMI underwent the most extensive thermal stress event in its recorded history. Abnormally high sea surface temperatures from July through December 2014 led to Bleaching Alert Level II warnings from NOAA Coral Reef Watch for September through November for the entire country, although heat stress was not as high in the southern Marshalls, including Majuro and Arno (Coral Reef Watch 2017). Although there were some reports of possible shallow water bleaching-related coral mortality based on limited observations in Majuro and Arno (Fellenius 2014), the overall effect of the heat stress event on coral and algal communities is unclear.

In this study, I examine the relationship between human disturbance and the composition of coral and algae communities across Majuro and Arno Atolls to explore the local impact of these disturbances and how they affected the recovery of reefs after the 2014 thermal stress event. This is the first study of Arno's coral reefs and to compare the benthic communities between the two adjacent atolls. I first investigated patterns in percent cover of key coral and alga taxa and their relationship with metrics of human influence across 25 sites in Majuro and Arno. I then examined how size structure of the coral communities varies across sites within each atoll and between the two atolls. Finally, I assessed the recovery from the recent (2014) thermal stress event by comparing percent cover surveys of key benthic life forms from 2007 in Arno and 2014 in Majuro to our data from 2016, at a subset of the original sites. The results provide insight into the limitations of macroalgae as an indicator of reef health and the impacts of human activities on coral communities in the central Pacific.

2.2 Methods

2.2.1 Background

The RMI have been inhabited for approximately 3,000 years (Ratzel 1896). Majuro Atoll, the capital of the RMI and home to over half of the country's approximately 53,000 people (Secretariat of the Pacific Community 2012), was subjected to extensive modifications and population growth after its occupation by the American military during World War II (Spennemann 1996). Over the past few decades, immigration from outer atolls and a high birth rate has increased the population density especially in the eastern population center of Delap-Uliga-Djarrot ("D-U-D"), where an American army base was built during World War II (Spennemann 1996; Secretariat of the Pacific Community 2012). In the 1970s, a series of causeways were built to connect the islands of Djarrot and Laura in Majuro which interrupted water flow between the lagoon and the ocean, and encouraged shoreline development along eastern and southern Majuro. An artificial channel was then built to connect the lagoon and the ocean between Majuro Wharf and the east part of Rairok in the 1980s (Xue 2001).

A controversial expansion of the airport runway, using material dredged from the reef flat, began in 2011 (Johnson 2012 Mar 15; RMIPA 2013) and is still under way as of July, 2017 (RMIPA 2017). Coastal management challenges brought about by population growth, waste generation, and shoreline construction are placing pressure on the local coral reef ecosystems; for example, untreated sewage is concentrated and pumped from an outfall pipe near field site Maj12 that has corroded and leaks sewage directly onto the reef flat (MIMRA 2016), and garbage often accumulates inside the lagoon (Richards and Beger 2011).

Arno Atoll, located only about 19 km east of Majuro, has remained largely undisturbed by population growth and human modifications. Arno is larger than Majuro in area (12.96 km^2 of land, versus 9.72 km^2 in Majuro) but is home to fewer than 2,000 people, a number that is shrinking annually due to emigration to Majuro. The population of Arno is also spread more evenly throughout the atoll; the most populated island, Arno Arno, was home to 281 people as of the most recent census (Secretariat of the Pacific Community 2012). To date, there have only been a few published studies of the RMI's coral reefs (e.g. Pinca et al. 2005; Richards and Beger 2011; Houk and Musburger 2013), none of which have included Arno Atoll. Because of the close proximity to Majuro, Arno is subject to some fishing pressure by fishermen who travel from Majuro, but this is almost entirely pelagic; access to reefs is controlled by the local *iroij* (chief) (Hess 1999). While there is some reef fishing pressure in Arno, it is decidedly lower than in Majuro, and closely monitored by the central government.

The Outer Island Fish Market Center in Majuro, a government sustainable development initiative that provides resource to outer island fishers, reports receiving only 33 boatloads (approximately 2,500 pounds each) of fish (pelagic and reef) from Arno Atoll in 2015 (MIMRA 2015).

2.2.2 Study Sites

A total of 24 outer reef and one lagoon site across Majuro and Arno Atolls (12 in Majuro, 13 in Arno) were sampled between June 25 and July 7, 2016. (Appendix A). Sites were selected to cover the range of habitats, population density, and coastal infrastructure around each atoll. I prioritized sites with previous data (before the 2014 thermal stress event), which included sites Maj03, Maj04, Maj06 through Maj09, and Maj11 in Majuro visited by Beger et al. in 2014, and Arn03 through Arn08 in Arno visited by MIMRA in 2007. Sites in Arno were restricted to the western and southern rim due to difficulties accessing the distant northeast and southeast outer reefs.

In Majuro, sites in Delap-Uliga-Djarrit (DUD) are exposed to the most human influence (Figure 1, Maj09 through Maj01, clockwise); these areas are home to the majority of Majuro's population (Secretariat of the Pacific Community 2012). Maj02 is located just east of a new airport construction site, where dredging of the reef is supplying sediment to extend the runway. Islands in the north of the atoll are either uninhabited or home to fewer than 100 people, and are therefore less affected by human activities. The sites in north Majuro do, however, have the highest exposure to wind and waves (with the exception of Maj11, which is inside the lagoon) from the prevailing northeast trade winds.

In Arno Atoll, sites Arn03 through Arn08 were identified based on previous surveys by MIMRA and the Secretariat of the Pacific Community (SPC). The other sites (Arn01, Arn02, Arn09 through Arn13) were selected based on distance and availability of accessible shallow (<15 m) reef flats. Arn01 was located directly offshore from Arno Arno, the island with the largest population in Arno Atoll, and Arn08 and Arn13 were located offshore of slightly smaller *wetos* (townships). Arn12 was just north of a small boat passage that allowed boats to travel from the outer reefs to the lagoon. Because of Arno's orientation, all of the sites I visited there were relatively unexposed.

Each site was assigned a category of exposure based on the direction perpendicular to the shoreline (north, south, east, west, northeast, southwest, etc.). I later incorporated this into our statistical analysis to account for any potential effects of wind and wave exposure on benthic composition at each site.

2.2.3 Survey Methods

All data were collected between June 25 and July 7, 2016. A 50-m transect tape was laid randomly at 10-m depth at each site. I measured the length (in cm) of corals *in situ* by measuring the length (in cm) along the transect of all coral colonies ≥1 cm that lay at least partially within 25-cm on both sides of the transect. I considered corals with separate patches of living tissue greater than 3-cm apart from each other independent and measured them individually. All corals were identified to the genus level, with the exception of *Porites rus*. I also took 0.33 m^2-sized quadrat photos (50.0 cm width by 66.7 cm length) at 50 cm intervals along the transect, for a total of 100 photos per site.

Maj12 is located at Majuro's sewage outfall; RMI-EPA coliform and enterococci tests consistently exceed safe levels at this site (Doig 1996), and I was therefore unable to sample there because of health concerns. Instead, I obtained 250 quadrat photos taken over an area of 250-m (five transects at 50m each), collected in September 2016 by Karl Fellenius of Hawaii Sea Grant and Martin Romain of the College of the Marshall Islands when the sewage pipe was temporarily turned off. Therefore, Maj12 is included in the benthic cover analysis but not the size frequency analysis.

In order to evaluate the change in benthic composition since before the 2014 thermal stress event, I obtained the limited available data from past benthic surveys in Arno and Majuro. The most recent surveys were a SPC underwater visual census conducted in Arno in summer 2007 at sites Arn03 through Arn08, six sites in total (Marshall Islands Marine Resources Authority, unpublished data). MIMRA's data collection followed underwater visual census methods used by the Secretariat of the Pacific (SPC), described in Clua et al. 2006. Researchers delimited ten 5x5-m quadrats on each side of a 50-m transect, for a total of 20 quadrats per transect per site. The depth of surveys was variable; measured via a dive computer, the average depth at the center of each quadrat was 7.7 m, shallower than the 10 m depth of our 2016 surveys. Sixteen substrate components (including nine abiotic components and seven live coral shapes) were estimated on a semi-quantitative scale (0, 1-10%, 11-30%, 31-50%, 51-75%, and 76-100%), adding up to 100% coverage. These data were then summarized by site and benthic category by the SPC, and provided to us by MIMRA.

In Majuro, past benthic surveys were conducted in July and August 2014 for Maj03, Maj04, Maj06 through Maj09, and Maj11, six sites in total (Beger et al., unpublished data). Here, researchers recorded the percent cover at each site using three point-intercept 50-m transects at 8-10m depth (60-100 points per transect). Each point was categorized within 17 key functional groups. At the same time, coral abundance was recorded (to the species level) within a $10m^2$ (Maj03, Maj04, Maj06) or $25m^2$ (Maj07, Maj09, Maj11) area along the transect tape. These methods are described in Richards 2009.

2.2.4 Human Disturbance

I estimated human influence at each site using the Normalized Difference Vegetation Index (NDVI), calculated using satellite imagery from the United States Geological Survey's Land Satellite 8. NDVI measures the amount of green vegetation within a 60-meter pixel on a scale of -1.0 to +1.0 and is commonly used to represent the extent of human disturbance on terrestrial ecosystems (e.g. Vaidyanathan et al. 2010; Lambert et al. 2015). I used NDVI instead of more traditional measurements such as human population (e.g. Houk and Musburger 2013; Bruno and Valdivia 2016) due to the spatial resolution of the available census data and in order to account for disturbances occurring where there are no permanent residents, such as the construction and dredging at the airport.

Satellite data were obtained from November 26, 2015, selected due to the low cloud cover on that day. Using ArcGIS ArcMap 10.4.1, we cast a circle with a 1-km diameter (chosen to minimize overlap of the circles) around each site and traced the landmass that fell within the circle (Figure 2). We then calculated the average NDVI of the landmass, giving us a proxy to rank human influence at each site (Appendix B). For Arn12, no land was located within a 1-km radius; instead, we used the same NDVI as Arn13, the next closest site, which was uninhabited and therefore similarly undisturbed.

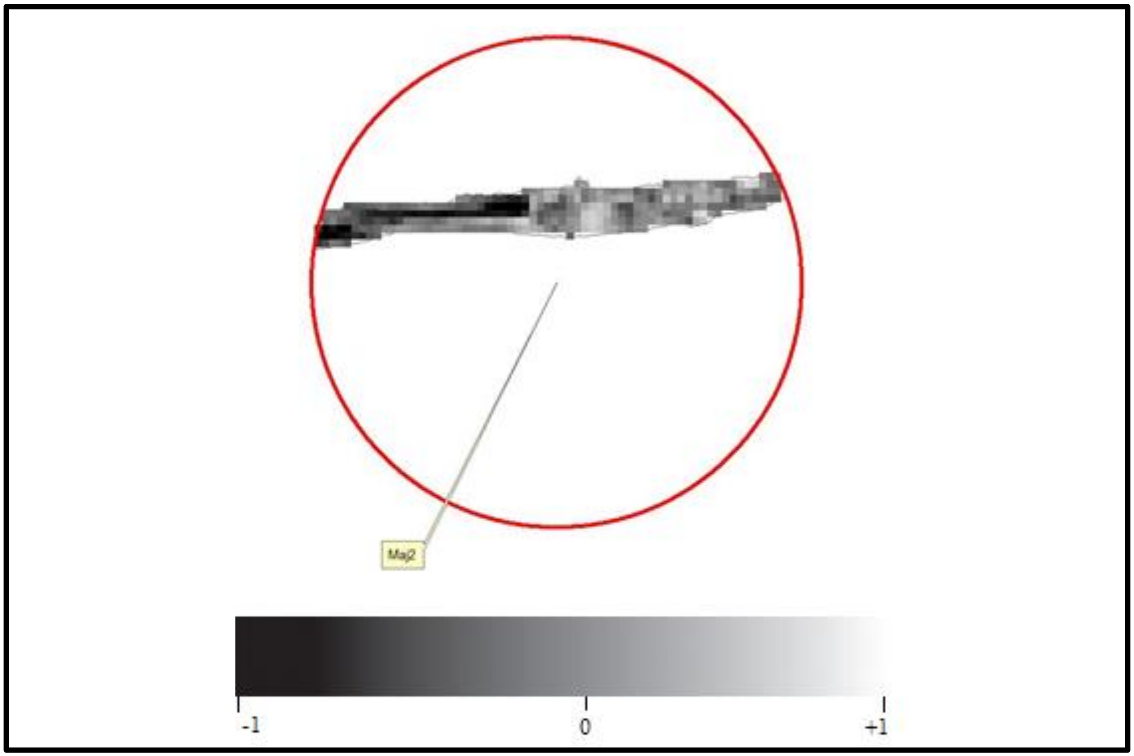

Figure 2: Example of calculating NDVI for site Maj02 using ArcMap 10.4.1.

2.2.5 Oceanographic Data

Sea surface temperatures (SST) and degree heating weeks (DHW) for all sites covering the period June 3, 2013 through April 30, 2017 were obtained from 5km-resolution V3 satellitederived data developed by the NOAA Coral Reef Watch program. I calculated the max DHW for the bleaching year (July 2014 – June 2015) for each site, and these were later incorporated into our statistical analysis to account for any differences in heat stress between sites.

2.2.6 Data Analysis

Photos from the transects were processed in the lab to calculate benthic percent cover using Coral Point Count with Excel Extensions Research Software version 4.1 (Kohler and Gill 2006), which overlaid 20 random points per photo for 100 photos per site (for a total of 2,000 points per site). Each photo covered 0.33 m^2 (50.0 cm width by 66.7 cm length). I identified each point to the genus level for coral and macroalgae and to functional group for sponges, soft corals, turf algae, crustose coralline algae, and cyanobacteria. I also identified the coral *Porites rus* and the sponge *Terpios hoshinota* to the species level.

All statistical analysis was done using R i386 version 3.2.4 (R Core Team 2016). I first ran a series of simple linear regressions to investigate a relationship between NDVI and percent cover of specific benthic categories. Next, I calculated the Shannon-Weaver diversity index (H’) and genera richness per site (Appendix C) using vegan package 2.4-2 (Oksanen et al. 2017) and ran a linear regression of these indices against the NDVI to look for a relationship between diversity and human influence. I also tested if the NDVI and the Shannon-Weaver diversity index or genera richness were significantly different between Majuro and Arno using Welch two-sample t-tests.

I visualized differences in benthic composition by atoll using Principal Component Analysis (PCA) on a subset of the percent-cover data (99% of all observations) of coral and macroalgae taxa. Permutational-based multivariate analysis (PerMANOVA, 99,999 permutations, Anderson 2001) was done using vegan package version 2.4-2 (Oksanen et al. 2017) to test for variation in means of benthic taxa caused by four environmental variables: atoll, NDVI, maximum DHW during the year surrounding the bleaching event (June 2014 through July 2015), and wind and wave exposure (the order of these variables in the test did not affect the results). The prevailing winds in this region come from the northeast, and sites in the north and east of the atoll were most exposed. I used the direction perpendicular to the shoreline at each site as a categorical variable to account for exposure (for example, north, south, east, west, northeast, southwest, etc.). For example, Arn01 and Arn02 were assigned to exposure category "West", while Maj01 was assigned to "Southwest".

To evaluate the differences in size frequency distributions for major coral taxa between sites and atolls, I grouped the size frequency data into eight taxonomic groups representing the most ecologically important and prevalent taxa: *Acropora, Heliopora, Isopora, Montipora, Pavona, Pocillopora* (genera), Favids (family), massive *Porites* (morphology of genus *Porites*), and *Porites rus* (species). For each of these groups, at each site and for each atoll, I calculated demographic statistics on coral abundance and size, including: mean size, standard deviation, coefficient of variation, skewness and skewness standard error, and kurtosis and kurtosis standard error. I considered skewness and kurtosis values greater than two times the standard error significantly different from normal (McClanahan et al. 2008).

Despite log-transformation of the size distribution data for each taxa at each atoll, none of the distributions met the assumptions of normality (Shapiro-Wilk test) or homogeneity of variance (Levene's test), so comparisons of size frequency distributions between sites were conducted using untransformed data. To avoid Type I errors across multiple comparison tests, critical values for all tests were adjusted using the Bonferroni correction. I used the Kolmogorov-Smirnov test to compare size frequency distributions between Arno and Majuro (Adjeroud et al. 2007). I decided to test this across atolls instead of across sites based on our results of the PerMANOVA, which showed that the benthic composition differed more between atolls than by NDVI across sites. I ran Welch's analysis of variance (ANOVA) tests to examine whether the mean size, coefficient of variation, skewness, or kurtosis for each of the nine categories varied between Majuro and Arno (Adjeroud et al. 2007).

Finally, I tested whether percent cover of key benthic taxa had changed after 2014's thermal stress event using a series of Welch's two-sample t-tests for all benthic categories and key coral taxa with Bonferroni corrections. The data were tested for normality using the Shapiro-Wilk test and for homogeneity of variance using Levene's Test, and all assumptions were met. In Majuro, using unpublished data obtained from Beger et al. from 2014, I combined the percent cover (from point-intercept transects) with relative abundance data (from a band around the transect tape) to calculate percent cover of individual coral genera. I tested for changes between 2014 and 2016 in key live coral genera percentage of both total benthic cover and live coral cover. In Arno, I did not have data at the genus level, and was therefore only able to test the overall change in the percent of major benthic categories (comparing 2007 and 2016 surveys).

2.3 Results

2.3.1 Benthic Cover

Macroalgae (including *Halimeda* spp.) cover ranged from 0% to 88% (Figure 3a) across all sites. *Halimeda* spp. was the most common of the observed macroalgae, ranging from 0% to 77% of all benthic cover across all sites. Live coral cover ranged from 1% to 54% across all sites (Figure 3a). In Arno, massive *Porites* were common, while in Majuro, *Acropora* was more prevalent (Figure 3b).

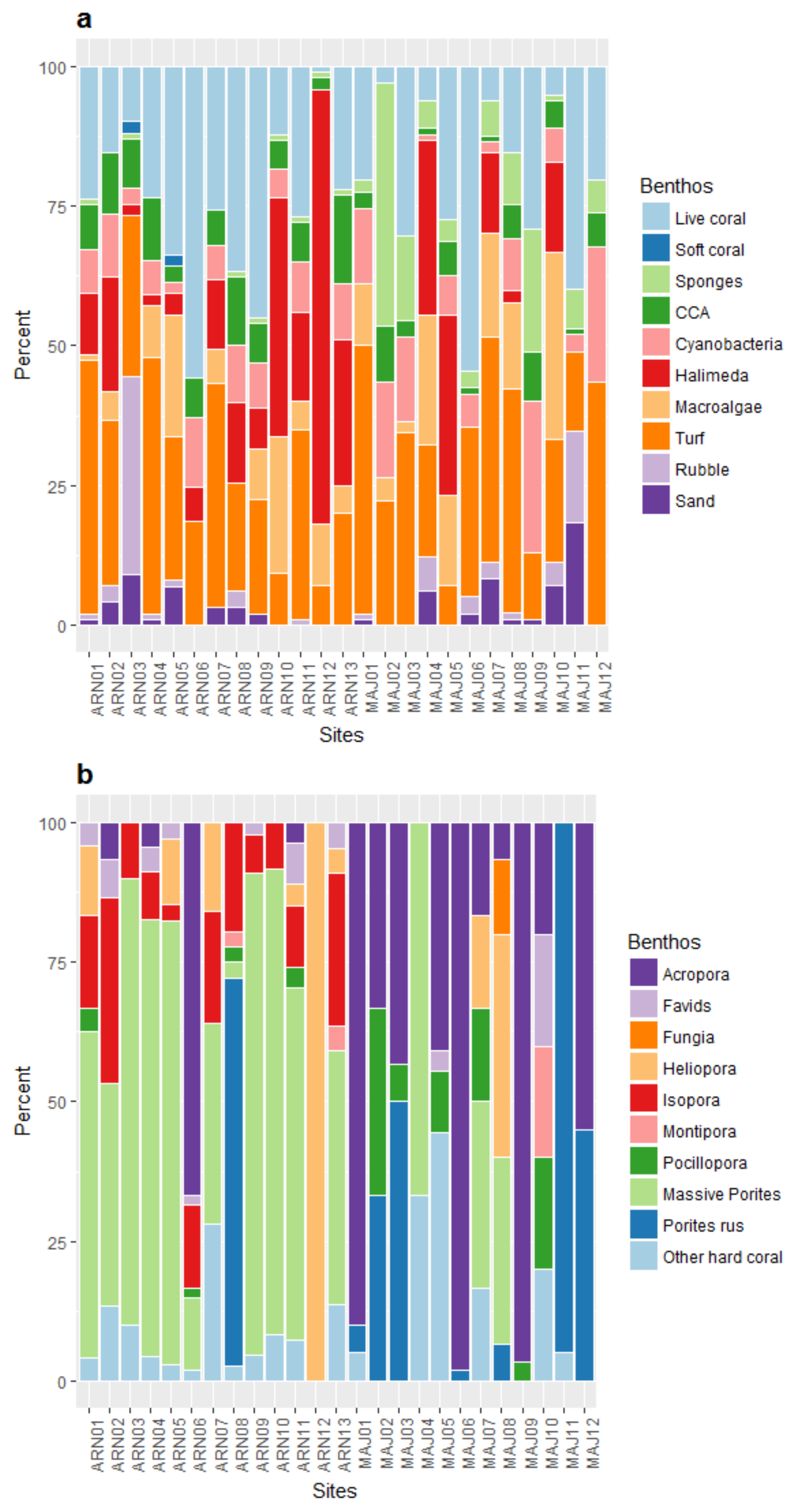

Figure 3: Percent cover of (a) key benthic categories and (b) live coral at each study site.

The PCA of key coral taxa by site suggested some differences in the typical coral community compositions between sites in Majuro and sites in Arno (Figure 3a), with the sum of the first and second principal components in both PCAs greater than 0.50, indicating that these differences are important (Jolliffe 2002). *P. rus* and *Acropora* (in both table and branching morphologies) were more common at sites in Majuro. By contrast, sites in Arno were more likely to be dominated by massive *Porites*.

The PCA of only the macroalgae genera showed that the macroalgae communities were distinct, with very little overlap in the plots between the two atolls, with the exception of sites Maj04 and Maj08 (Figure 3b), which were more similar to the Arno sites than other Majuro sites. These sites are located on the north side of the atoll where there was relatively little human influence. Majuro sites were dominated by the macroalgae genera *Hypnea*, *Dictyota*, *Liagora*, *Lithothamnion*, and *Lobophora*, while Arno sites had higher prevalence of *Halimeda*, *Dictosphaeria*, and *Microdictyon*.

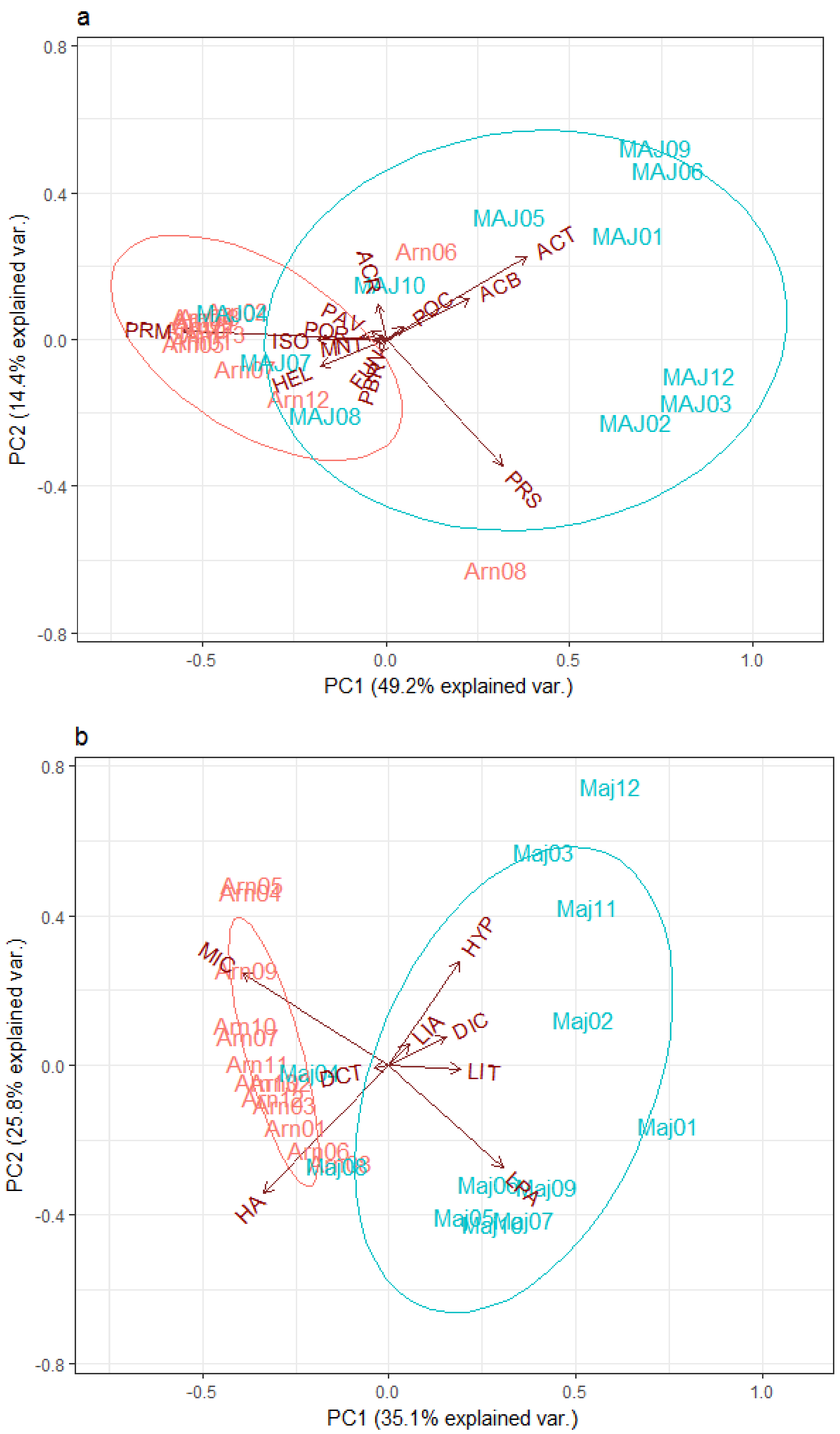

Figure 4: PCA of observed coral taxa by atoll (a) and macroalgae genera by atoll (b), excluding the general that made up less than 1% of observations.

NDVI did not differ significantly between atolls (Welch two-sample t-test, p = 0.114), but benthic composition was statistically distinct (PerMANOVA, p<0.001), and significantly related to mean NDVI (PerMANOVA, p=0.009), and exposure (p=0.016) (Table 1). There was no relationship between benthic composition and maximum DHW in 2014 (PerMANOVA, p=0.519) (Table 1).

Table 1: PERMANOVA of drivers of benthic composition (significant values are underlined).

Source	*df*	Ss	ms	r^2	psuedo-f	p-value
Atoll	1	0.6584	0.6584	0.1756	6.0211	<0.0001
mean NDVI	1	0.3323	0.3323	0.0886	3.0386	0.0090
exposure	6	1.1329	0.1888	0.3021	1.7266	0.0160
max DHW *(bleaching year)*	1	0.0956	0.0956	0.0255	0.8746	0.5191
residuals	14	1.7870	0.1276	0.4746		
Total	**23**	**3.7502**		**1.00**		

Least squares linear regressions showed significant relationships between NDVI and some of the major coral and algal cover categories, but not total live coral cover or total macroalgae cover. *Halimeda* (p=0.0050, r^2=0.2950) and massive *Porites* (p=0.0242, r^2=0.2020) were each significantly positively correlated with NDVI, which means they were more likely to be found in places with less human disturbance (

Table 2). Conversely, *Acropora* ($p=0.0281$, $r^2=0.1928$), cyanobacteria ($p<0.0001$, $r^2=0.5389$), *Hypnea* ($p= 0.0218$, $r^2=0.2084$) and sponges ($p=0.0044$, $r^2=0.3019$) were negatively correlated with NDVI and were therefore more likely to be found in places with higher disturbance (

Table 2). Variation in NDVI across sites explained about 20% or less of the variance across sites for *Acropora*, *Isopora*, massive *Porites*, and *Hypnea*. By contrast, NDVI explained about 54% of the variance of cyanobacteria across sites, and for *Halimeda* and sponges, NDVI explained approximately 30% of the variance of each. I found no relationship between Shannon Weaver Diversity Index (H') for each site (Appendix C) and NDVI (linear regression, $p > 0.80$), or by atoll (Welch two-sample t-test, $p > 0.90$). I similarly did not find a relationship between genera richness (Appendix C) and NDVI (linear regression, $p > 0.70$), or by atoll (Welch two-sample t-test, $p = 0.90$).

Table 2: Results of simple linear regressions of NDVI and relative abundance of benthic taxa across all sites in Majuro and Arno Atolls (values significant at the 0.05 level are underlined).

category	benthic variable	slope	association with people	n	r^2	f-stat	p-value
Live Coral	All live coral	--	--	8968	0.016	0.376	0.546
	Acropora	-435.00	More	3066	0.193	0.568	0.028
	Heliopora	--	--	415	0.036	0.855	0.365
	Isopora	--	--	837	0.156	1.802	0.051
	All Favids	--	--	216	0.074	1.846	0.188
	Montipora	--	--	97	0.008	0.191	0.666
	Pocillopora	--	--	248	0.034	5.823	0.386
	Massive *Porites*	+564.12	Less	3259	0.202	0.195	0.024
	P. rus	--	--	1445	0.000	0.003	0.958
Macroalgae	All macroalgae	--	--	9660	0.088	2.204	0.151
	Dictospheria	--	--	51	0.027	0.627	0.436
	Dictyota	--	--	102	0.008	0.184	0.672
	Halimeda	+1352.10	Less	5873	0.295	3.728	0.005
	Hypnea	-477.42	More	458	0.208	6.056	0.022
	Liagora	--	--	39	0.000	0.006	0.940
	Lithothamnion	--	--	69	0.107	2.750	0.111
	Lobophora	--	--	978	0.028	0.656	0.426
	Microdictyon	--	--	2038	0.038	0.897	0.354
Other	CCA	--	--	2809	0.057	1.393	0.250
	Cyanobacteria	-904.20	More	3731	0.539	26.880	<0.001
	Turf algae	--	--	11,849	0.001	0.023	0.880
	Soft coral	--	--	38	0.001	0.027	0.872
	Sponges	-1032.71	More	2191	0.302	9.944	0.004

Almost half of the sponge cover in Majuro (48.1%) was *Terpios hoshinota*, a cyanobacteria sponge often found in highly degraded areas, which has the ability to overgrow and kill corals. Because this sponge closely resembles cyanobacteria, it is easily misidentified (Rutzler and Muzik 1993). Maj02, a site with high turbidity located close to the airport dredging site, had 29.6% cover of *T. hoshinota* and only 4.2% macroalgae cover (Figure 4). I found no *T. hoshinota* in Arno.

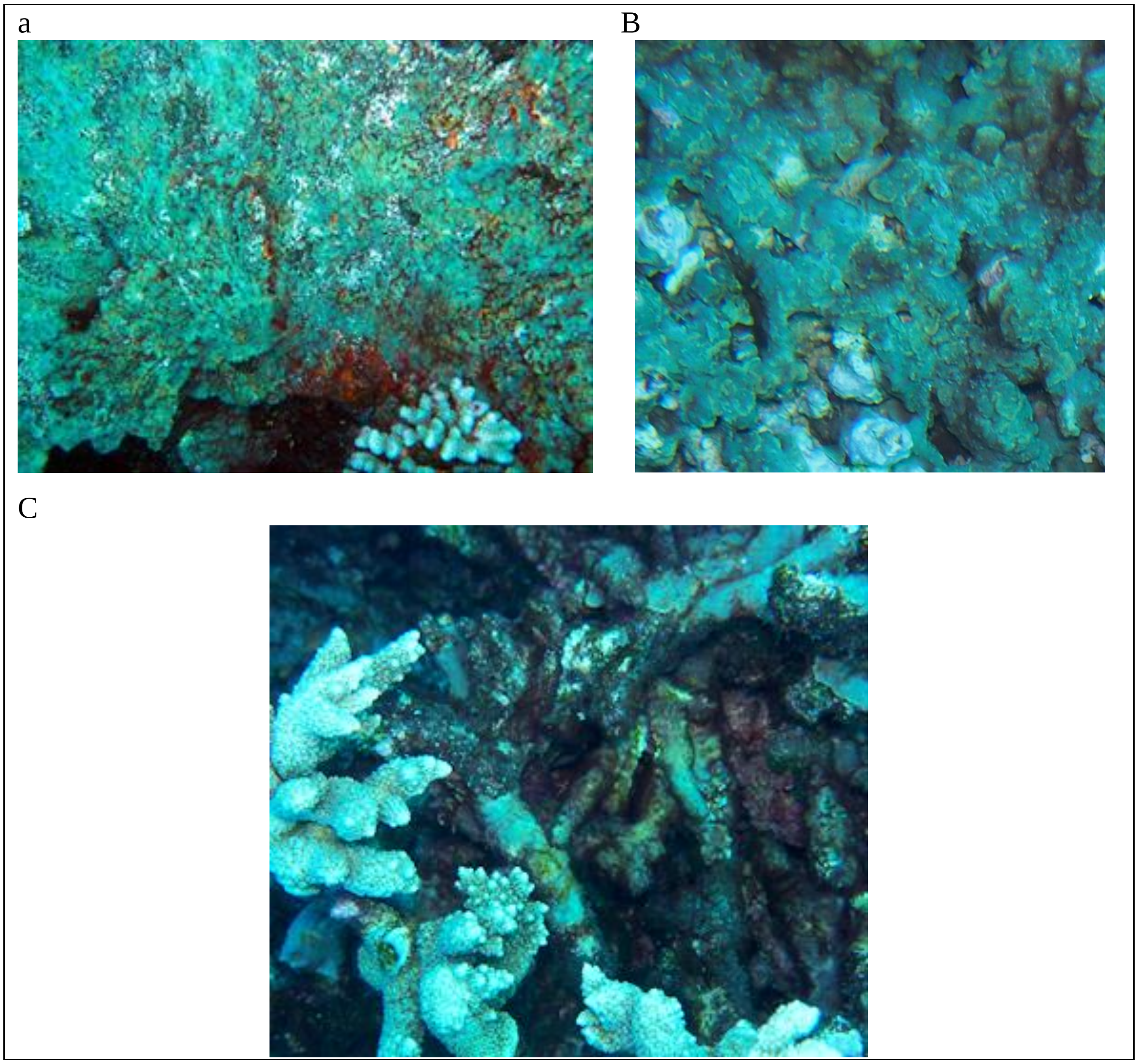

Figure 4: From Maj02, (a) *T. hoshinota* covering a table of *Acropora* sp., (b) Zoomed-in view of *T. hoshinota*, (c) *T. hoshinota* and cyanobacteria growing on a branching *Acropora* sp.

2.3.2 Coral Size Structure

The size-structure data show that corals in Arno were on average smaller than those in Majuro. Across all sites, massive *Porites* were the most common coral in the size-structure data (n = 1887), with an overall mean size of 15.41 cm, the vast majority of these in Arno

(Appendix D). *Acropora* followed closely (n = 1381, mean size = 16.05 cm) followed by Favids (n = 1042, mean size = 8.09 cm) (Figure 5).

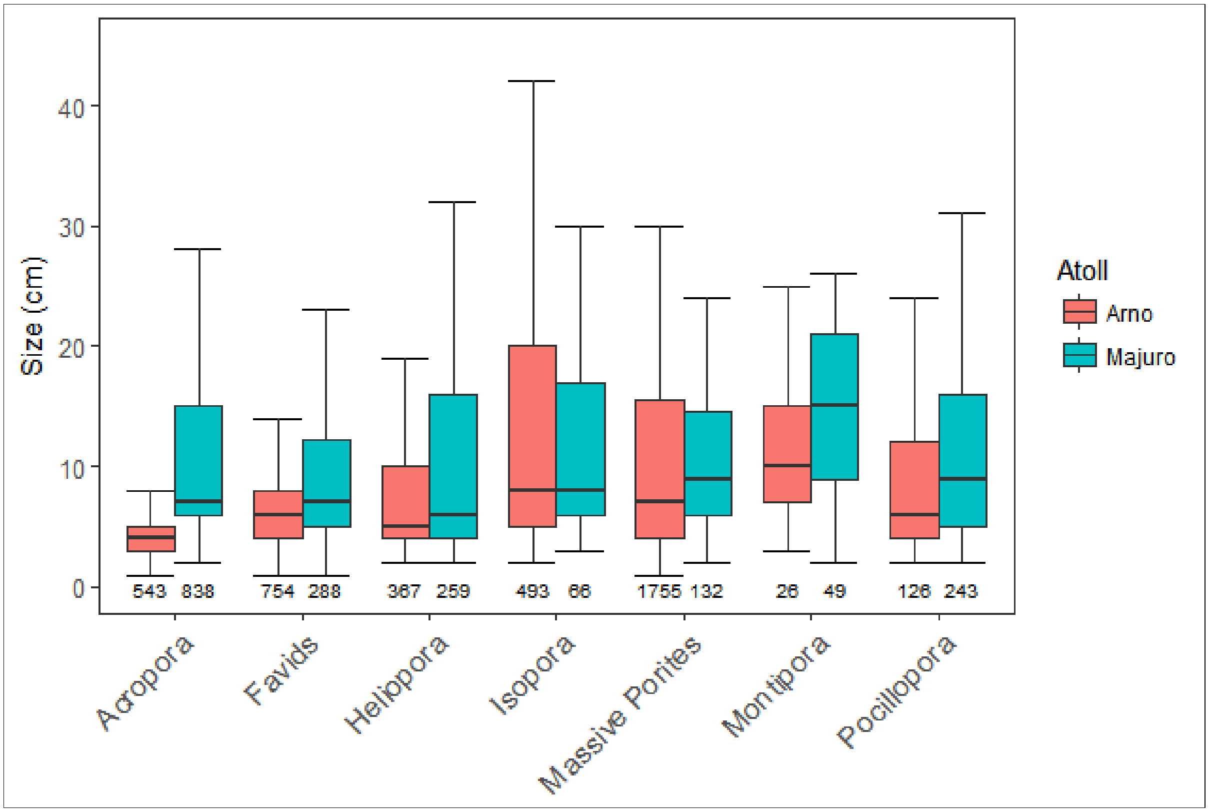

Figure 5: Quartile plots of coral size for major coral categories across both Arno and Majuro Atolls, where the lower and upper hinges correspond with the first and third quartiles, the center line represents the median, and the whiskers indicate 95% confidence intervals. *Porites rus* was omitted due to the low number of observations in Arno.

Within each atoll, skewness and kurtosis were positive and significantly different from normal for all categories, with the exception of *Montipora* in Arno Atoll (Appendix E , example distribution in Figure 6). The positive skewness and kurtosis indicate a peaked distribution dominated by small corals. Skewness was more positive in Arno for all categories except *P. rus*, which was more than twice as common in Majuro as Arno. Greater positive skewness may indicate that there are more juveniles present at sites in Arno, but could also result from partial mortality during the 2014 heat stress event. The shape of the size distributions differed significantly between Majuro and Arno for five of the eight categories (Komogorov-Smirnov test,

Table 3).

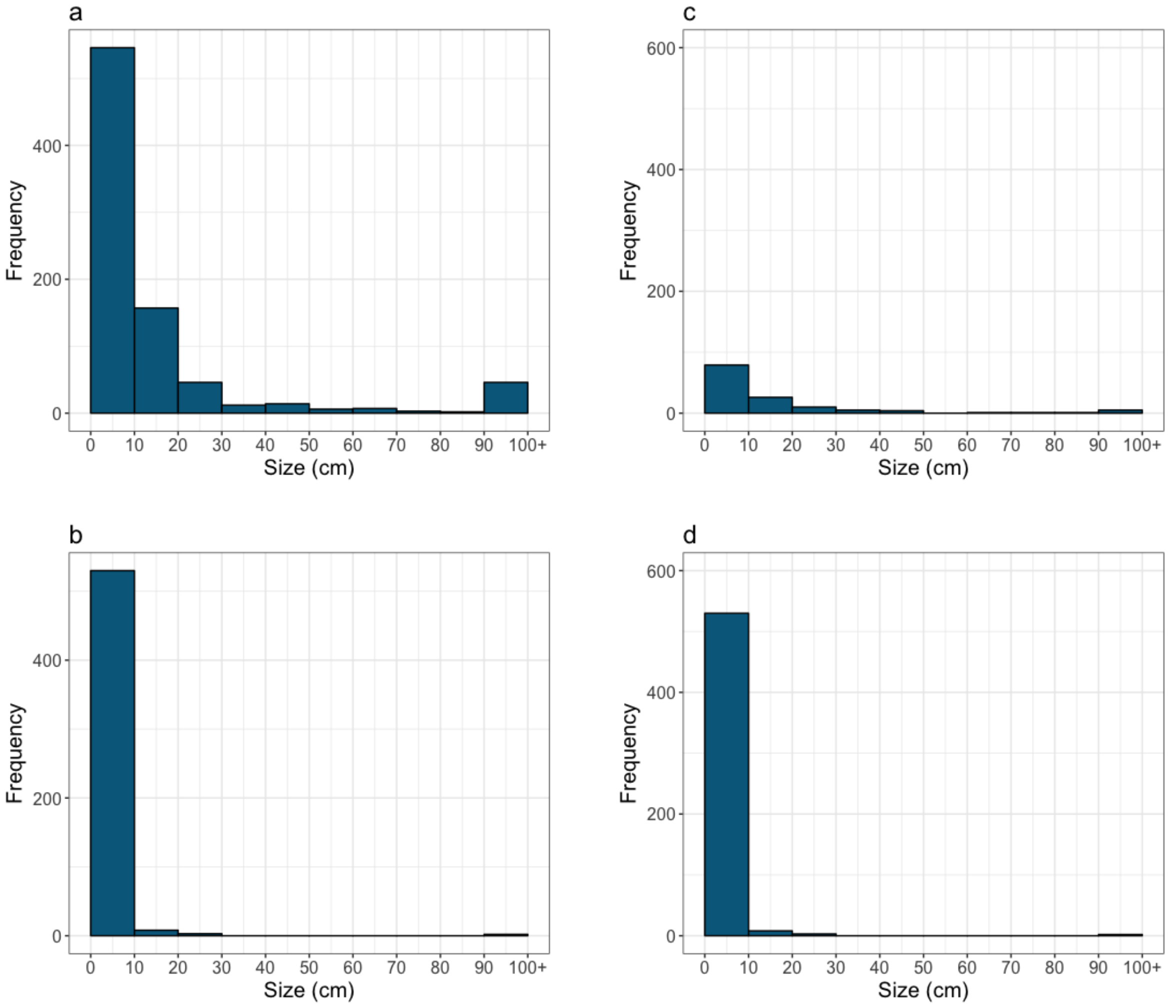

Figure 6: Examples of size frequency distributions in Arno versus Majuro, where (a) is Acropora in Majuro, (b) Acropora in Arno, (c) massive *Porites* in Majuro, and (d) massive *Porites* in Arno.

Table 3: Kolmogorov-Smirnov (ks) test results comparing across atolls, with Bonferroni correction. Significant results are underlined.

Category	ks test statistic (w)	ks p-values	Bonferroni correction
Acropora	0.5385	< 0.0001	<0.0001
Favids	0.2417	< 0.0001	<0.0001
Heliopora	0.1184	0.0284	0.0567
Isopora	0.1807	0.0458	0.0896
Montipora	0.3093	0.0776	0.1552
Pocillopora	0.2187	0.0007	0.0014
Massive *Porites*	0.1727	0.0013	0.0026
P. rus	0.2966	<0.0001	<0.0001

Mean size was greater in Majuro for six of the eight coral categories (Table 4); only *Isopora* and massive *Porites* were larger in Arno. The difference in mean sizes were significant for *Isopora* (Welch's ANOVA, p < 0.01, Table 4), but not for massive *Porites* (Welch's ANOVA, p = 0.80, Table 4) or any other coral categories. Both of these categories also had the largest differentiation in sample sizes between the two atolls; for *Isopora*, 493 were observed in Arno while only 66 were measured in Majuro; for massive *Porites*, 1,755 were observed in Arno and 132 in Majuro.

Table 4: Results of Welch's ANOVA of size-frequency statistics between atolls, where mean is the mean size in centimeters, the numerator degrees of freedom equals 1.00 for all tests, and df is the denominator degrees of freedom. Significant results are underlined. *P. rus* was not included because it was only observed at one site in Arno, so I did not have enough observations for this test.

	mean			coefficient of variation			skewness			kurtosis		
category	f	df	p-value	f	df	p-value	f	df	p-value	f	df	p-value
Acropora	1.76	20.41	0.20	2.18	21.97	0.15	1.01	18.63	0.33	0.65	16.89	0.43
Favids	3.49	11.34	0.09	9.30	20.48	<0.01	12.37	15.91	<0.01	5.45	12.10	0.04
Heliopora	2.16	12.61	0.17	1.85	12.99	0.20	3.51	7.39	0.10	1.50	5.72	0.27
Isopora	14.38	17.12	<0.01	22.78	16.18	<0.01	3.90	13.00	0.07	1.90	15.61	0.19
Montipora	0.56	13.81	0.46	6.41	13.58	0.02	2.52	10.17	0.14	0.20	11.71	0.67
Pocillopora	1.44	17.15	0.25	0.07	19.76	0.79	0.02	16.17	0.90	0.12	13.29	0.74
Massive *Porites*	0.07	10.81	0.80	0.02	7.07	0.90	0.43	8.61	0.53	0.63	17.87	0.44

Favids were the only category to have more than one statistic that differed significantly across the two atolls (CV < 0.01, skewness p < 0.01, kurtosis p = 0.04, Table 4). There were more Favids observed in Arno (n = 754) than in Majuro (n = 288), and the CV, skewness, and kurtosis (all significant) were larger in Arno (CV = 103.4, skewness = 7.3, kurtosis = 87.3) than in Majuro (CV = 65.8, skewness = 1.3, kurtosis = 1.3, Table 4). These results suggest that more of the Favids in Arno were small, and although there was a wider range in sizes observed in Arno, the majority of Favids measured there were close in size to the mean (as opposed to Majuro, where the sizes were more evenly distributed within the range).

The differences in the size distribution of *Acropora* between the two atolls were highly pronounced. The mean size of *Acropora* was smaller in Arno (7.9 cm) than in Majuro (21.3 cm), but this difference was not significant (Welch's ANOVA, p = 0.20, Table 4). In Arno, the coefficient of variation (CV) and the kurtosis were higher than in Majuro (Table 4) both of which suggest a larger range of sizes of *Acropora* in Arno, but with the majority of corals close to the mean size. Neither of these differences were significant (Welch's ANOVA, p = 0.15 for CV, p = 0.43 for kurtosis, Table 4).

By contrast, differences in size distributions of massive *Porites* between the two atolls were less pronounced, even though almost 95% of the massive *Porites* I observed were in Arno. In Majuro, massive *Porites* had a larger mean size than in Arno although the difference was small (17.5 cm in Majuro compared to 15.3 cm in Arno Table 4), and not significant (Welch's ANOVA, p = 0.80, Table 4). The CV for massive *Porites* was similar in both atolls (133.3 in Arno versus 147.7 in Majuro), but kurtosis in Arno (29.4) was more than twice that in Majuro (11.7, Table 4). The range of sizes of massive *Porites* was comparable in both atolls, but in Arno, the majority were similar in size to the mean, although neither of these differences were significant (Welch's ANOVA, CV p= 0.90, kurtosis p=0.44, Table 4).

The size-frequency distribution statistics by atoll (Appendix D) appear to be representative of the statistics within sites (Appendix F), with overwhelmingly positive skewness and kurtosis.

Most coral categories had positive skewness and kurtosis at each individual site (Appendix F), with the exception of *Acropora*, *Isopora*, and *Pocillopora*. Kurtosis was negative for *Acropora* at 4 out of 24 sites, indicating that the *Acropora* at this site tended to be close in size to the mean, but these kurtosis values were all very close to zero, with none equal to or greater than -1.0. Kurtosis was also negative at 4 of the 23 sites where *Isopora* was found, with these values slightly further from zero, ranging from -0.8 to -2.2. The size distribution for *Pocillopora* had negative kurtosis at 7 of the 23 of sites, the most of all coral categories, with values ranging from -0.1 to -2.1. By contrast, only one coral category at one site had a negative skewness value (Favids at Maj05, -0.3, Appendix F).

2.3.3 Comparison with Previous Surveys

Maximum DHW only varied by 1.52 DHW across sites (4.03 at Arn06 and Arn07 to 5.55 DHW at Maj01) during the bleaching year (June 2014 – July 2015), while mean SST varied by less than 0.1 degree (Appendix G). The maximum DHW values surpass the Bleaching Alert Level 1 threshold but not the Alert Level II threshold; this suggests that the heat stress event was less pronounced around the southern RMI than in the rest of the country.

I compared the percent cover of major benthic categories from our 2016 surveys with 2014 data collected just prior to the thermal stress event at the six Majuro sites for which data were available (Maj03, Maj04, Maj06, Maj07, Maj08, Maj09, and Maj11). In Majuro, I saw no significant changes in percent cover of live coral (which ranged from 3.00% to 55.00% in 2014 and 6.44% to 54.48% in 2016), CCA, dead coral, cyanobacteria, or macroalgae from before the 2014 heat stress event to 2016 (

Table 5). Sponges did increase, from 0.19% to 9.55% (Welch two-sample t-test, $p < 0.05$,

Table 5). Of all the coral genera for which I had before and after data, only *Pavona* changed significantly (Welch two-sample t-test, p-value < 0.01,

Table 5), but this was a negligible decrease in terms of percent cover, from 2% to 0.25%. I also tested whether key coral genera percentage of all live coral cover (as opposed to all benthos) had increased or decreased after the thermal stress event, but found no significant changes (

Table 5).

Table 5: Benthic cover in Majuro Atoll in 2014 and 2016 surveys. Significant results are underlined.

	variable	t	df	p-value	Bonferroni correction	mean 2014	mean 2016
key taxa	Live coral	0.50	9.52	0.63	1.00	33.35%	27.32%
	CCA	1.23	7.15	0.26	1.00	6.50%	2.80%
	Dead Coral	1.14	8.31	0.28	1.00	34.80%	24.74%
	Cyanobacteria	-2.11	5.01	0.09	0.81	0.21%	8.56%
	Macroalgae	0.31	9.19	0.76	1.00	11.67%	14.87%
	Sponges	-3.18	5.04	0.02	0.18	0.19%	9.55%
	Sand	0.71	5.79	0.50	1.00	12.37%	5.54%
	Rubble	-1.22	7.46	0.26	1.00	1.37%	4.58%
	Soft coral	-1.41	5.00	0.22	1.00	0.00%	0.08%
coral genera (% all benthos)	*Acropora*	0.08	10.00	0.93	1.00	16.90%	15.88%
	Favids	-0.07	9.96	0.95	1.00	0.08%	0.09%
	Heliopora	0.78	5.45	0.47	1.00	0.60%	0.17%
	Isopora	1.02	5.79	0.35	1.00	0.38%	0.11%
	Pavona	4.84	6.37	<0.01	<0.01	2.01%	0.25%
	Pocillopora	1.14	5.56	0.30	1.00	2.03%	0.71%
	P. rus	0.21	9.65	0.84	1.00	9.92%	8.37%
	Massive *Porites*	-1.54	5.00	0.18	1.00	0.00%	0.64%
coral genera (% live coral)	*Acropora*	-0.38	9.71	0.71	1.00	33.39%	42.49%
	Favids	0.45	7.49	0.67	1.00	1.91%	1.17%
	Heliopora	0.87	5.86	0.42	1.00	7.82%	2.47%
	Isopora	0.44	10.00	0.67	1.00	2.08%	13.63%
	Pavona	1.63	5.46	0.16	1.00	17.90%	3.12%
	Pocillopora	0.46	9.27	0.65	1.00	6.00%	4.63%
	P. rus	-0.00	9.17	1.00	1.00	0.00%	9.46%
	Massive *Porites*	1.03	5.35	0.35	1.00	6.29%	16.05%

In Arno, limited surveys were done in 2007 for sites Arn03 through Arno08 using broader benthic categories. I detected no significant change in mean live coral cover (which ranged from 4.13% to 49.15% in 2007 and 10.25% to 52.47% in 2016), CCA, dead coral, cyanobacteria, or macroalgae in Arno (Table 6). Cyanobacteria increased from 0.00% to 6.31% between 2007 and 2016 (Welch two-sampled t-test, p-value 0.0087, Table 6), but this was no longer significant when I corrected for multiple comparisons using the Bonferroni correction (p = 0.08, Table 6).

Table 6: Change in benthic cover in Arno Atoll since previous available surveys. Significant results are underlined.

variable	t	df	p-value	Bonferroni correction	mean 2007	mean 2016
Live coral	0.07	9.55	0.95	1.00	31.17%	30.54%
CCA	-1.60	9.10	0.14	1.00	4.78%	7.98%
Dead Coral	-1.13	9.03	0.29	1.00	23.54%	29.42%
Cyanobacteria	-4.17	5.00	0.01	0.08	0.00%	6.31%
Macroalgae	-1.85	6.90	0.11	0.99	6.14%	12.97%
Sponges	2.64	5.06	0.04	0.36	0.07%	0.46%
Sand	0.79	6.44	0.46	1.00	1.97%	6.82%
Rubble	-1.22	7.46	0.26	1.00	1.37%	4.58%
Soft coral	2.78	6.09	0.03	0.27	3.46%	0.63%

2.4 Discussion

The results illustrate that the benthic communities at Majuro and Arno Atolls differ in terms of size-frequency distributions of coral and relative cover of coral and algae taxa, both along a gradient of human impacts and between the two atolls. The analysis was conducted using NDVI as a proxy for human influence, potentially a novel (to coral reef studies) way to estimate the level of land-based disturbance near coral reefs. Taken together, the findings imply that more detailed metrics may be necessary to better characterize coral reef degradation and to guide future studies of coral reef resilience across the Pacific.

As expected, the mean NDVI on Majuro was higher than that of Arno, although this was not significant, likely because of the range of disturbance intensity in Majuro where some sites have very little human influence. To my knowledge, this is the first study to use NDVI as a proxy for human influence on coral reefs, although NDVI is commonly used in land-based studies (Vaidyanathan et al. 2010; Leu et al. 2013; Lambert et al. 2015). It was used because human population data is not available in the RMI at a high enough resolution to estimate how human population differed adjacent to each site. However, NDVI may serve as a more accurate predictor of the effects human activities have on reefs, because it accounts for anthropogenic features that may be far away from where people live. For example, one of the most degraded sites, Maj02 (Figure 1), was located near the airport construction site, where the human population is low. NDVI is a way to account for any human activities that could have a detrimental effect on reefs despite low populations living nearby. Roads, bridges, farms, and landfills are other examples of human impacts that could be far from dense population centers.

The key patterns in benthic composition and size-structure across sites and atolls were explained by a combination of local disturbance and exposure to wind and waves, rather than temperature or past heat stress (Table 1). Wind and wave exposure is a known predictor of coral community structure, especially on shallow reef flats where corals may be susceptible to breakage, scouring, and abrasion (Dollar 1982; Grigg 1998; Storlazzi et al. 2005). Because of difficulty accessing the north side of Arno, all of the exposed (north or northeast facing) sites were in Majuro, which could account for some of the differences in benthic composition observed across the two atolls. However, the significance of NDVI as a predictor of benthic communities shows that human influence also played an important role in predicting the community structure of the reefs.

The differences in the benthic community between the two atolls are reflected in the varying sizes and abundances of particular coral taxa. The corals in Majuro were on average larger than those found in Arno, with the exception of *Isopora* and *P. rus*, which had larger mean sizes in Arno (Table 4). Massive *Porites* were more prevalent in Arno than in Majuro and were significantly more likely to be found at sites with lower disturbance, but had a slightly larger mean size in Majuro, although not statistically significant. In addition to smaller mean coral sizes for most categories of corals in Arno, the population size distributions were more positively skewed in Arno than Majuro (with the exception of *P. rus,* Table 4) which also indicates the presence of proportionately more small corals in Arno. Previous research has shown that smaller coral colonies are more vulnerable to mortality (Connell 1973; Hughes and Connell 1987; Wittenberg and Hunte 1992; Bak and Meesters 1998). One potential explanation is that it is rare for small corals to experience partial mortality; because they have less surface area, mortality is more likely to be total (Bak and Meesters 1998). It is possible that higher disturbance in Majuro has contributed to the paucity of small corals found there.

Conversely, there were more *Acropora* in Majuro than in Arno, and an inverse relationship between cover of *Acropora* and NDVI, showing that higher *Acropora* cover was correlated with high levels of disturbance (

Table 2). This was surprising because most species of *Acropora* are competitive corals that tend to be sensitive to environmental fluctuations and local disturbances (Darling et al. 2012). However, some species of *Acropora* are extremely susceptible to predation (Bulleri et al. 2013; Gil et al. 2016); one potential explanation of this pattern may be the higher fishing pressure in Majuro, which could cause a lower density of corallivores. Data on exported reef fishery products from the Marshall Islands are not available (Gillett 2016), although a 2011 report from the Secretariat of the Pacific did conclude that reef fish and invertebrate abundance had decreased in Majuro's lagoon between 2007 and 2011 (Moore et al. 2012). *Acropora* in Majuro were on average larger than those in Arno (21.32 cm in Majuro vs 7.94 cm in Arno), although again, this was not statistically significant. In this case, the differences in mean size could be explained by morphology; I saw very few *Acropora* tables in Arno (instead, *Acropora* in Arno tended to have a branching morphology), but large tables were common in Majuro (tables accounted for 76.70% of all *Acropora* in Majuro compared to 0.01% in Arno).

While there was no relationship between all live coral or macroalgae cover and NDVI, some genera of macroalgae were more likely to be associated with high disturbance, and vice versa (

Table 2). The PCA showed that different macroalgae assemblages could explain much of the variation in benthic communities between atolls. Regression analyses confirmed this, with *Halimeda* more likely to be found at sites with low disturbance and *Hypnea* more prevalent at disturbed sites. This is consistent with studies that have found various taxa of macroalgae respond to disturbance in different ways (Stimson et al. 2001; Mumby et al. 2005; Clausing and Fong 2016). There was not a significant relationship between disturbance and all macroalgae cover, which is important because many researchers group different genera of macroalgae together and use macroalgae as a single category to indicate whether reefs are degraded.

The most disturbed sites (lowest NDVI - Maj09, Maj12, Maj03, Maj02) had low macroalgae cover (ranging from 0.2% to 4.7%), and high cover of other benthic taxa such as turf algae, sponges, and cyanobacteria. Sites in Majuro had higher sponge coral on average than sites in Arno (0.6% average sponge cover in Arno compared to 10.9% in Majuro), and were home to different sponge taxa. Almost half (48.1%) of all sponges in Majuro were *T. hoshinota,* an encrusting cyanobacteria sponge sometimes called “black disease” because of its ability to quickly overgrow and kill corals (Shi et al. 2012). *T. hoshinota* was absent from our surveys from Arno. This sponge is a natural part of coral reef ecosystems, but may be able to outcompete corals in degraded conditions (Rutzler and Muzik 1993). *T. hoshinota* was most prevalent at site Maj02 (covering 29.6% of the substrate, compared to 2.0% live coral and 4.7% macroalgae), which was near the airport expansion project and dredging. This is consistent with previous studies, which have found that *T. hoshinota* tends to be found near areas of coastal development and with high turbidity (Rutzler and Muzik 1993; Reimer, Mizuyama, et al. 2011). *T. hoshinota* may be attracted to sites with high coral cover (Lin and Soong 2009), specifically those with branching corals (Elliott et al. 2016), and is able to persist for long periods of time (Reimer, Nozawa, et al. 2011); therefore, its spread could be devastating to Majuro's already vulnerable reefs. Studies have indicated that outbreaks may be reversible and coral may be able to recover, but data are lacking to estimate the length of outbreaks (Reimer, Mizuyama, et al. 2011).

These results suggest that using cover of macroalgae as a single category to evaluate reef degradation and not considering other potential indicator taxa (such as sponges) could mask the impacts that human activities have on reefs. Percent cover of macroalgae is often used as a proxy for coral reef health (assuming sites with higher cover are more degraded, e.g. McCook et al. 1997; Mumby et al. 2005; Hughes et al. 2007), but other studies have also determined that macroalgae served limited purpose as an indicator of reef health. In Hawaii's uninhabited French Frigate Shoals, for example, Vroom et al. (2005) found that macroalgae cover was higher than that of coral at 46% of their study sites, with considerable heterogeneity across sites, even around the same island. A subsequent study indicated that macroalgae community composition was dependent on latitude (Vroom and Braun 2010). There have also been studies identifying high macroalgae cover at undisturbed sites (e.g. Williams et al. 2013).

The use of macroalgae as an indicator stems from evidence of phase shifts from coral to macroalgae dominance in the Caribbean (Hughes 1994; Hughes et al. 2007), but other studies found little to no evidence of this in the Indo-Pacific (Bruno et al. 2009; Smith et al. 2016).

Instead, degraded reefs in the Pacific may see shifts to other taxa, including sponges (Norström et al. 2009; Bell et al. 2013; Powell et al. 2014) or "weedy" corals (Darling et al. 2013; Crane et al. 2016), with the outcomes varying by oceanographic conditions, local factors, and latitude. In Yap, Federated States of Micronesia (FSM), researchers found that disturbed sites had low macroalgae cover (Crane et al. 2017). This is consistent with the results here, in which degraded sites were not dominated by macroalgae, but instead had high cover of sponges, cyanobacteria, and turf algae. Researchers should consider using metrics other than total macroalgae cover, such as cover of sponges and cyanobacteria, in future studies of reef degradation in the Pacific.

The percent cover of sponges and cyanobacteria in both Majuro and Arno were higher in the2016 surveys than in the previous available survey data, although these data were collected using different sampling methods than those I used, introducing a potential for error. The differences in percent cover were most pronounced in Majuro, where sponges were 0.19% of the benthos in 2014 and 9.55% in 2016 and cyanobacteria increased by 8.35% in just two years. By contrast, nine years had passed since benthic surveys were done in Arno, and during that time period, sponges increased by 0.39% and cyanobacteria increased by 6.31%. It is possible that the increases in cyanobacteria and especially sponge cover were due to mislabeling; the sponge *T. hoshinota* accounted for almost half of the sponges found in Majuro (48.10%), and it is notoriously hard to identify, particularly in photo quadrats, because it resembles cyanobacteria (Rutzler and Muzik 1993). Because sponges were correlated with decreased NDVI (increased disturbance), it is especially important that they are identified consistently. Further study will be needed when another, more severe thermal stress event occurs in order to identify the impacts of thermal stress on the reefs with more certainty, particularly in Arno where more time had passed between surveys.

I may not have detected differences with previous survey data because the effects of the thermal stress event in 2014 on coral cover appears to have been less intense than previously recorded, at least in the southern RMI. Despite a Level II Bleaching Alert from NOAA Coral Reef Watch for the whole of the RMI in 2014 (maximum DHW reached 11.71 °C-week, averaged across the region), Majuro and Arno did not experience severe heat stress (maximum DHW reached 4.03 – 5.55 °C-week at our sites). The comparison of 2014 pre-thermal stress benthic cover data and our 2016 data suggest that any bleaching which may have occurred in 2014 had a limited effect on total coral cover. There was an increase in sponges, particularly in Majuro where the previous surveys were more detailed and more recent, although this change was not significant in Arno after I corrected for multiple comparisons. While bleaching did not appear to alter overall coral cover, it is possible that it may have caused some partial mortality, which would cause the size-frequency distributions to shift towards smaller corals. Unfortunately, this could not be tested because the earlier data did not include size-frequency measurements.

The lack of recent surveys from Arno exemplifies the importance of consistently monitoring reefs, particularly now that coral bleaching is happening more regularly throughout the Indo-Pacific. However, monitoring and managing coral reefs in the Pacific Islands can be challenging, particularly at remote atolls, which are often difficult for researchers and managers to access. The RMI is a good example of a successful locally-managed benthic monitoring program; it is home to the world-renowned Reimaanlok Process, a national conservation plan designed by local marine experts that set conservation targets and objectives, including regular monitoring of natural resources, while encouraging the use of traditional conservation practices (Baker et al. 2011a). Benthic monitoring is done regularly by MIMRA staff at sites throughout Majuro and a number of the outer island atolls (Reimaan National Planning Team 2008).

The success of the Reimaanlok Process highlights the value of locally-managed monitoring programs, which have a number of benefits, including giving tools to remote communities that would allow them to make informed and independent decisions about how best to manage their natural resources in a changing environment. It could also provide valuable information about reef degradation in places that are not easily accessible to scientists, and therefore less studied. Recently, a number of studies have emphasized the effectiveness of citizen science projects to monitor coral reefs globally (Forrester et al. 2015; Loerzel et al. 2017; Schläppy et al. 2017; Stuart-Smith et al. 2017). However, these programs tend to use broad categories such as “hard coral”, “soft coral”, “macroalgae”, or other (e.g. Hill 2006). Our results suggest the results of these programs would be more effective if they included training and identification of common coral and macroalgae genera, as well as more difficult organisms to identify such as *T. hoshinota*. Including these categories would provide managers and researchers alike with a more complete picture of the current state of coral reefs in the Indo-Pacific.

2.5 Conclusion

This study identifies a relationship between local human disturbance, exposure, and the benthic community composition and coral size structure in reefs across Majuro and Arno Atolls. I found no relationship between coral genera diversity and human influence on these reefs. Degraded sites were dominated by turf algae, cyanobacteria, and sponges (particularly *T. hoshinota*) and in general had low cover of macroalgae. Cyanobacteria and sponges may have increased over time in both atolls, although further surveys are needed to confirm this trend in Arno. I also found variation in which genera of macroalgae were found at disturbed sites. *Hypnea* was statistically correlated with high disturbance, while *Halimeda* was more likely to be found at sites with low disturbance. In the context of past studies, which indicated the importance of local and broader geographic conditions in explaining benthic communities, I suggest that broad metrics identifying degraded reefs may not be consistent across different sites and regions, and that using macroalgae alone as an indicator of reef health may serve to mask the influence of local human disturbance on reef community composition. It is important for researchers and monitoring teams to use sampling protocols that identify coral and macroalgae to the genus level, and to consider identifying other indicator taxa that are known to be found on degraded reefs, such as the cyanobacteria sponge *T. hoshinota*.

Chapter 3: Future Implications

For my thesis, I surveyed the benthic cover and coral community at sites across Majuro and Arno atolls to gain an understanding of how the reefs in this region responded to a gradient of human impacts, as well as how sites recovered from a thermal stress event in 2014. This study highlights potential new indicators of reef degradation and provides new evidence in favor of detailed metrics that could guide future studies of resilience across the Pacific. There have been very few studies of the coral reefs in this region (e.g. Pinca et al. 2005; Richards and Beger 2011; Houk and Musburger 2013). None of the previous studies compared the reefs across the two adjacent atolls, which provided a novel opportunity to explore these questions.

The expected outcomes of this research are multifold. MIMRA currently monitors changes in benthic substrate (including coral and algae to the genus level), fish communities, and macroinvertebrates as a part of the Reimaanlok Process (Baker et al. 2011b), and our findings may help to direct their future monitoring plans. For example, the sponge *T. hoshinota* is known to spread and overgrow corals quickly. Training MIMRA staff to recognize *T. hoshinota*, along with regular monitoring at Maj02 where *T. hoshinota* covered almost 30% of the reef, would allow MIMRA to monitor whether the sponge is spreading and how it is affecting reefs.

Our results also show the importance of avoiding broad categories of taxa, such as “macroalgae”, as a proxy for reef degradation. Scientists and community monitoring programs alike often use “macroalgae” as an indicator of degradation, but relying on this category may actually mask the impacts that such studies are attempting to identify. Instead, recording the genera of corals and macroalgae, in addition to other life forms like *T. hoshinota* that do well in impacted reef environments, would provide a more accurate view of how reefs respond to local and global stressors. I hope these results will inform future studies in the Pacific, as well as help to make community-managed monitoring programs more informative and effective.

The central Pacific is an ideal natural laboratory to study the role of past climate experience and local human disturbance on the resilience of coral reefs to climate change. Research has suggested that exposure to higher past temperature variability may make individual corals or coral communities more resistant and/or more resilient to heat stress (McClanahan et al. 2007; Donner 2011; Oliver and Palumbi 2011; Carilli et al. 2012). Eventually, I hope to combine the work from this thesis with data collected by other researchers (see: Donner 2007), which will allow me to compare coral communities across a natural latitudinal gradient of temperature variability that extends through the equatorial Gilbert Islands of Kiribati, south of Majuro and Arno.

The Gilbert and Marshall Islands together provide an uncommon setting for this research. The variability in maximum annual temperatures declines from the more equatorial Gilbert Islands north to the RMI (Figure 7). The data collected from Majuro and Arno Atolls in 2016 followed the same methods used by Donner for a decade in Kiribati (Donner 2007). Eventually, comparing these data to the results of Donner’s work in Kiribati will allow a better understanding of the role of fluctuating temperatures and local human impacts in the resilience of coral reefs to climate change. Specifically, the sites in Arno and Majuro will complete the matrix of sites across temperature variability and different levels of human disturbance (Table 7).

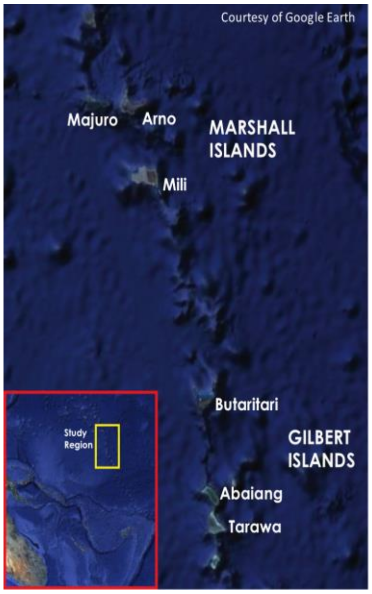

Figure 7: Map of the southern RMI and the northern Gilbert Islands of Kiribati.

Table 7: RMI study sites, together with sites of previous observations in Kiribati, on a matrix of SST variability and human disturbance.

		Sea Surface Temperature Variability		
		Low		High
Human Disturbance	Low	Arno	Butaritari	N. Tarawa/ Abaiang
	High	Majuro		S. Tarawa

Because of the north-south gradient in temperature variability, the central equatorial Pacific from the RMI south to Kiribati’s Gilbert Islands creates a unique opportunity for studying how temperature affects coral reef resilience. By comparing measurements of benthic cover and coral size distribution from the RMI to previous data collected in Kiribati, I will be able to test important hypotheses about the factors which confer resistance and resilience to heat-induced coral bleaching.

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Appendices

Appendix A List of sites with GPS coordinates

site name	latitude	longitude
Arn01n	7.063083	171.545150
Arn02n	7.041067	171.569417
Arn03n	6.992833	171.608900
Arn04n	6.995917	171.642067
Arn05n	7.004033	171.589600
Arn06n	6.955250	171.748517
Arn07n	6.962333	171.725883
Arn08n	6.981267	171.695883
Arn09n	7.117933	171.564600
Arn10n	7.084333	171.552900
Arn11n	7.150800	171.587283
Arn12n	7.188133	171.608750
Arn13n	7.243017	171.632617
Maj01n	7.074700	171.166733
Maj02n	7.066517	171.295450
Maj03n	7.079350	171.343483
Maj04n	7.221050	171.056233
Maj05n	7.197383	171.097083
Maj06n	7.157117	171.203100
Maj07n	7.143250	171.027083
Maj08n	7.103967	171.081000
Maj09n	7.103617	171.382250
Maj10n	7.130200	171.316100
Maj11n	7.129333	171.308750
Maj12n	7.082539	171.368372

Appendix B NDVI by site

site name	average NDVI
Arn01	0.4737
Arn02	0.3473
Arn03	0.3623
Arn04	0.2558
Arn05	0.3829
Arn06	0.4132
Arn07	0.3778
Arn08	0.3984
Arn09	0.4481
Arn10	0.3991
Arn11	0.4646
Arn12	0.4346
Arn13	0.4045
Maj01	0.3761
Maj02	0.2519
Maj03	0.3101
Maj04	0.4446
Maj05	0.3503
Maj06	0.4257
Maj07	0.4520
Maj08	0.3712
Maj09	0.1404
Maj10	0.3867
Maj11	0.4062
Maj12	0.1893

Appendix C Shannon-Weaver diversity indices

site name	shannon-weaver diversity index	genera richness
Arn01	1.8822	17
Arn02	2.3836	18
Arn03	2.0690	14
Arn04	1.5452	18
Arn05	1.5465	16
Arn06	2.0460	14
Arn07	1.8866	17
Arn08	2.0434	17
Arn09	2.1087	24
Arn10	2.1405	19
Arn11	2.5102	23
Arn12	1.9960	14
Arn13	2.3765	23
Maj01	2.0905	25
Maj02	1.6353	15
Maj03	2.3144	13
Maj04	1.5653	20
Maj05	1.9741	17
Maj06	2.2717	11
Maj07	2.0215	20
Maj08	2.4728	20
Maj09	2.7210	25
Maj10	2.7210	23
Maj11	1.2144	6

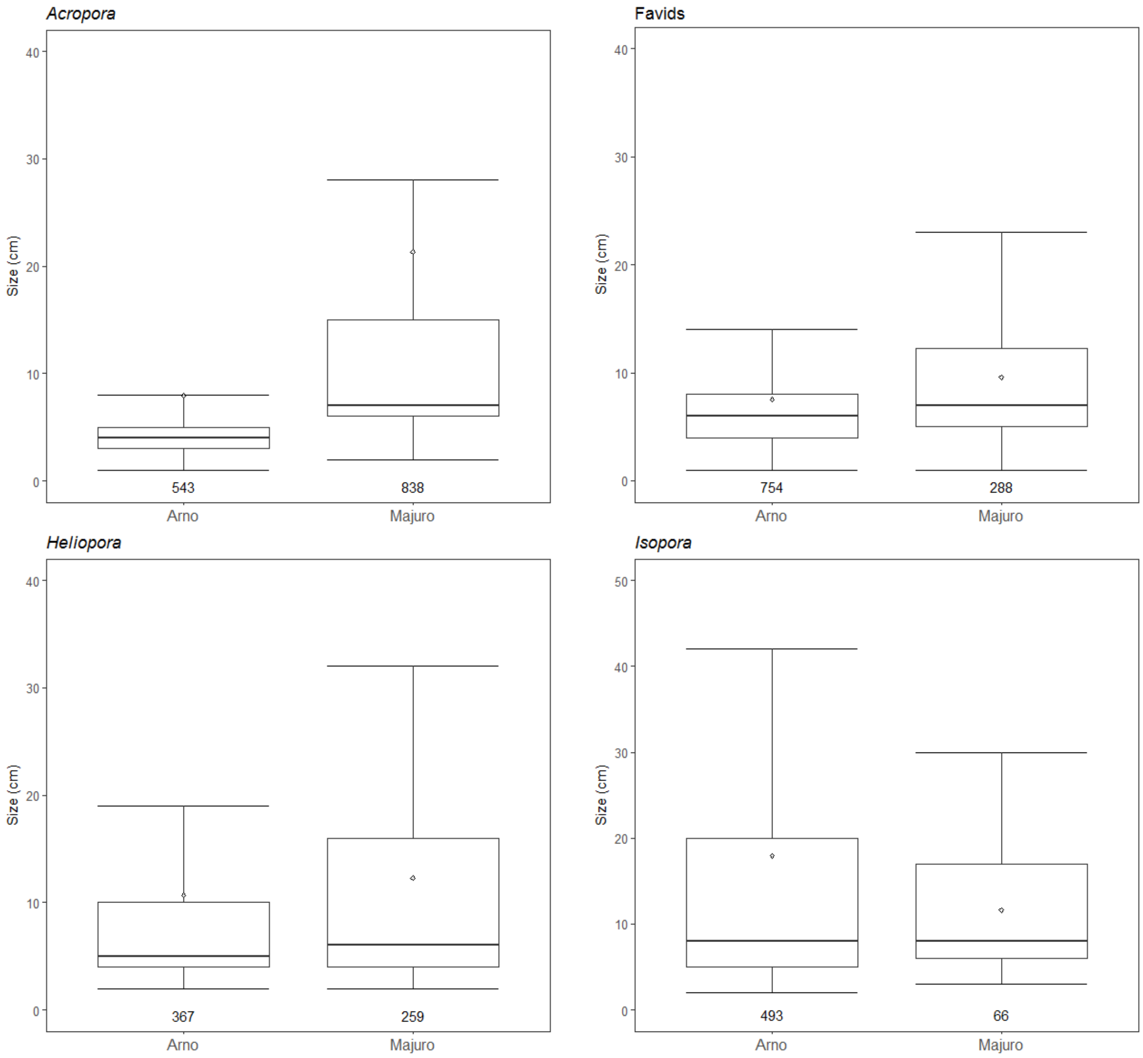
Appendix D Coral size data by coral category for each atoll

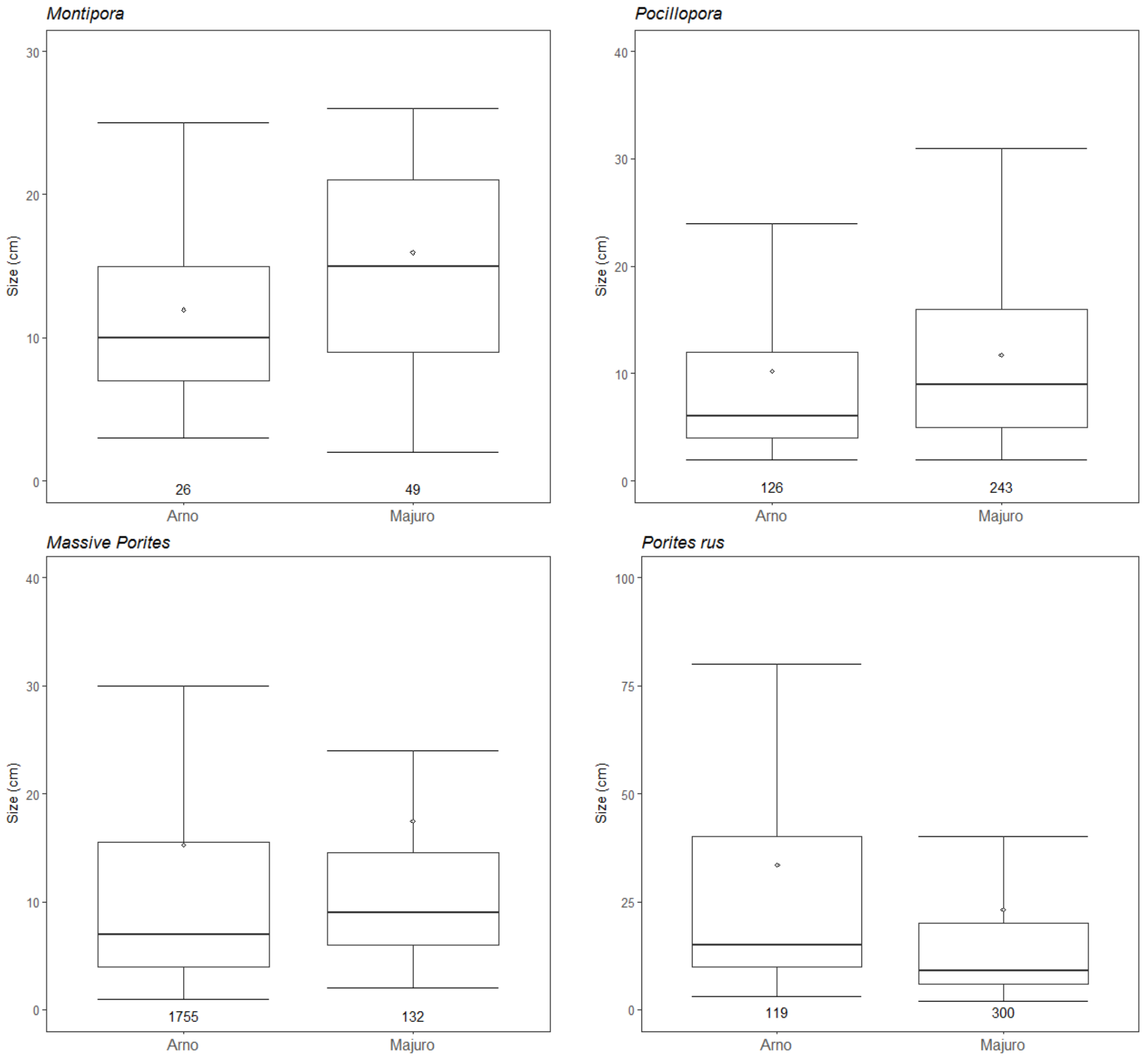
Includes number of colonies (n), mean size in centimeter (μ), standard deviation (sd), coefficient of variation (cv), skewness (sk), and kurtosis (k). The skewness and kurtosis values that are significantly different from normal are underlined.

		Acropora	Favids	*Heliopora*	*Isopora*	*Montipora*	*Pocillopora*	Massive *Porites*	*P. rus*
Arno Atoll	**n**	543	754	367	493	26	126	1755	119
	μ	7.9	7.5	10.7	17.9	11.9	10.2	15.3	33.5
	sd	54.7	7.8	14.0	21.8	6.9	9.5	20.3	43.9
	cv	688.2	103.4	131.0	121.8	58.1	93.0	133.3	131.1
	sk	16.4	7.3	3.2	2.6	1.9	1.9	3.9	2.3
	k	268.0	87.3	12.6	8.2	0.5	3.4	29.4	5.6
Majuro Atoll	**n**	839	288	259	66	49	243	132	300
	μ	21.3	9.6	12.3	11.6	16.0	11.7	17.5	23.1
	sd	46.5	6.3	13.4	7.6	9.4	8.9	25.8	76.2
	cv	218.6	65.8	109.4	54.3	59.1	75.7	147.7	329.3
	sk	5.0	1.3	2.0	1.6	1.4	1.6	3.4	12.1
	k	30.8	1.3	3.9	3.3	3.6	2.8	11.7	170.9
All	**n**	1382	1042	626	559	75	369	1887	419
	μ	16.0	8.1	11.3	17.2	14.6	11.2	15.4	16.1
	sd	50.3	7.5	13.8	20.8	8.8	9.1	20.8	68.7
	cv	313.4	92.1	121.5	120.9	60.5	81.3	134.8	263.4
	sk	10.6	6.1	2.7	2.7	1.5	1.7	3.8	11.8
	k	155.2	73.4	9.0	9.4	3.6	2.9	27.1	182.7

Appendix E Size frequency by atoll

Boxplot and mean colony size (white dots) for the dominant hard coral taxa at each atoll, with n-values specified above the x-axes.




Montipora
Pocillopora
Massive Porites
Porites rus
Size (cm)
0
10
20
30
40
25
50
75
100
26
49
126
243
1755
132
119
300
Arno
Majuro

Appendix F Size frequency values by site

Summary of colony size data collected for each coral genera at each site, including number of colonies (n), mean size in centimeters (mean), standard deviation (sd), coefficient of variation (cv), skewness (sk), and kurtosis (k). The skewness and kurtosis values that are significantly different from normal are underlined.

	category	n	mean	sd	cv	sk	k
Arm01	*Acropora*	19	4.4	1.6	37.5	2.3	7.7
	Favids	34	6.1	5.8	95.6	4.2	19.5
	Heliopora	43	11.3	10	88.3	1.1	-0.1
	Isopora	31	16.4	20.9	127.3	2.7	8.3
	Pocillopora	15	14.4	11.5	79.7	0.9	-0.1
	Massive Porites	246	12.8	16.3	127.6	3.1	12.2
Arm02	category	n	mean	sd	cv	sk	k
	Acropora	29	5.0	2.3	45	0.0	-0.3
	Favids	68	9.0	9.1	101.6	3.5	15.6
	Heliopora	2	25.0	14.1	56.6	0.0	0.0
	Isopora	23	25.0	20.1	80.2	0.7	-0.8
	Montipora	6	7.5	4.4	58.9	1.0	0.7
	Pocillopora	9	13.0	11.6	89.0	1.4	0.4
	Massive Porites	52	20.7	34.2	165.0	3.3	12.2
Arm03	category	n	mean	sd	cv	sk	k
	Acropora	47	3.4	1.2	35.2	0.7	0.2
	Favids	47	10.5	13.8	131.6	3.1	9.1
	Isopora	11	24.1	16.8	69.8	1.1	0.6
	Pocillopora	3	8.3	1.5	18.3	0.9	0.0
	Massive Porites	75	14.5	16.7	115.3	2.5	6.6

Arn04	category	n	mean	sd	cv	sk	k
	Acropora	47	3.4	1.3	38.9	3.2	14.0
	Favids	50	3.7	1.6	44.4	0.8	0.6
	Heliopora	4	6.0	3.4	56.1	0.0	-0.2
	Isopora	10	12.3	12.7	103.3	1.6	1.6
	Montipora	5	8.4	1.7	19.9	-0.5	-0.6
	Pocillopora	5	7.8	3.2	40.9	0.3	-1.3
	Massive Porites	246	11.6	13.1	112.9	2.0	3.6
Arn05	category	n	mean	sd	cv	sk	k
	Acropora	19	6.3	4.8	76.5	2.0	3.5
	Favids	40	7.0	5.2	74.3	2.2	5.1
	Heliopora	48	19.0	19.0	99.9	1.4	1.5
	Isopora	11	26.6	16.9	69.4	0.5	0.2
	Montipora	1	7.0	0.0	0.0	0.0	0.0
	Pocillopora	5	14.2	10.7	75.3	0.9	-0.6
	Massive Porites	252	11.8	15.3	129.2	3.5	17.7
Arn06	category	n	mean	sd	cv	sk	k
	Acropora	32	61.2	221.4	362.1	3.8	13.2
	Favids	21	4.6	5.0	108.4	2.1	4.0
	Isopora	77	15.4	18.0	117.1	2.6	6.6
	Pocillopora	15	11.3	5.9	51.6	0.3	-1.3
	Massive Porites	55	20.1	24.6	122.6	1.5	1.5
Arn07	category	n	mean	sd	cv	sk	k
	Acropora	16	4.0	1.7	42.8	0.8	0.3
	Favids	33	5.8	3.3	56.3	2.8	10.5
	Heliopora	27	24.7	25.9	104.7	1.5	1.7
	Isopora	118	10.5	11.7	111.0	2.8	8.1
	Montipora	2	20.0	14.1	70.7	0.0	0.0
	Pocillopora	5	16.8	20.0	118.9	1.6	2.3
	Branching Porites	202	10.0	11.0	109.6	4.7	29.1
	Massive Porites	95	22.0	24.9	113.4	1.9	3.3

	category	n	mean	sd	cv	sk	k
Arn08	*Acropora*	87	4.5	2.6	57.5	4.7	30.7
	Favids	35	5.7	2.4	42.2	0.7	-0.8
	Isopora	50	34.3	39.2	114.2	1.5	1.5
	Pocillopora	14	15.9	11.9	74.7	0.9	-0.3
	Massive Porites	42	9.9	11.7	118.3	2.4	5.5
	P. rus	119	33.5	43.9	131.1	2.3	5.6
	category	n	mean	sd	cv	sk	k
Arn09	*Acropora*	55	5.4	3.2	59.2	3.3	15.8
	Favids	110	7.6	4.3	56.6	1.9	6.2
	Heliopora	4	16.3	13.2	81.1	0.1	-5.2
	Isopora	29	14.8	14.5	97.9	1.3	0.4
	Montipora	1	11.0	0.0	0.0	0.0	0.0
	Pocillopora	17	4.6	1.3	28.9	0.9	2.1
	Massive Porites	297	16.8	20.3	120.5	2.2	6.1
	category	n	mean	sd	cv	sk	k
Arn10	*Acropora*	65	4.5	1.9	42.4	1.6	3.4
	Favids	46	6.7	3.6	53.4	1.5	2.1
	Heliopora	21	4.2	0.7	17.9	-0.3	4.1
	Isopora	6	23.2	26.7	115.3	2.0	4.0
	Montipora	1	25.0	0.0	0.0	0.0	0.0
	Pocillopora	2	6.0	1.4	23.6	0.0	0.0
	Massive Porites	81	23.8	24.2	101.7	1.2	0.4
	category	n	mean	sd	cv	sk	k
Arn11	*Acropora*	54	5.8	3.5	61.5	3.3	16.0
	Favids	111	10.0	13.2	131.3	6.9	59.5
	Heliopora	67	8.9	9.6	107.8	3.7	17.9
	Isopora	33	19.1	27.3	142.7	2.7	7.6
	Montipora	9	14.6	6.3	43.1	-0.1	-1.9
	Pocillopora	25	8.2	8.4	102.0	2.3	5.0
	Massive Porites	132	21.1	33.3	157.9	5.2	37.8

	category	n	mean	sd	cv	sk	k
Arm12	*Acropora*	34	3.8	1.6	42.0	0.9	-0.3
	Favids	18	4.4	1.9	41.7	0.1	-0.9
	Heliopora	101	4.8	3.0	62.5	2.2	6.9
	Pocillopora	9	4.0	1.0	25.0	1.0	0.8
	Massive Porites	24	5.1	4.2	82.4	4.3	20.1
	category	n	mean	sd	cv	sk	k
Arm13	*Acropora*	39	5.2	2.3	44.3	1.7	4.5
	Favids	141	7.6	5.0	66.1	2.9	12.7
	Heliopora	50	10.9	15.2	140.3	4.0	18.7
	Isopora	94	18.5	18.9	101.9	1.3	0.7
	Montipora	1	9.0	0.0	0.0	0.0	0.0
	Pocillopora	2	5.0	0.0	0.0	0.0	0.0
	Massive Porites	158	13.9	15.6	112.6	2.3	6.1
	category	n	mean	sd	cv	sk	k
Maj01	*Acropora*	64	20.9	50.0	239.6	3.4	10.5
	Favids	33	6.4	3.3	51.3	1.1	1.4
	Heliopora	4	6.3	6.5	104.0	2.0	4.0
	Isopora	2	16.0	12.7	79.5	0.0	0.0
	Montipora	3	8.3	10.1	121.4	1.7	0.0
	Pocillopora	14	8.5	4.3	50.5	0.3	-1.4
	Massive Porites	3	10.0	4.4	43.6	-1.6	0.0
	P. rus	22	12.4	8.7	69.9	0.8	0.5
	category	n	mean	sd	cv	sk	k
Maj02	*Acropora*	29	9.9	13.0	130.9	3.5	12.8
	Favids	3	8.0	0.0	0.0	0.0	0.0
	Pocillopora	13	21.3	15.4	72.2	-0.2	-1.9
	P. rus	27	15.2	15.5	101.9	3.5	14.4
	category	n	mean	sd	cv	sk	k
Maj03	*Acropora*	86	26.7	48.6	181.8	3.3	11.0
	Favids	2	15.5	3.5	22.8	0.0	0.0
	Montipora	3	24.7	22.5	13.0	1.4	0.0
	Pocillopora	31	17.7	11.6	65.4	1.2	0.9
	P. rus	107	19.7	33.9	172.4	4.6	24.6

Maj04	category	n	mean	sd	cv	sk	k
	Acropora	18	6.7	3.7	55.6	1.4	1.2
	Favids	31	7.9	3.7	46.7	1.1	1.2
	Heliopora	38	5.8	7.0	119.5	5.2	29.0
	Isopora	5	9.8	5.4	55.6	0.6	-2.2
	Montipora	6	20.7	13.1	63.2	1.6	2.8
	Pocillopora	18	6.0	3.1	51.1	0.9	0.1
	Massive Porites	27	19.9	32.8	165.4	3.0	8.6
Maj05	category	n	mean	sd	cv	sk	k
	Acropora	213	14.9	18.0	121.1	4.0	20.6
	Favids	10	21.3	8.1	37.8	-0.3	0.7
	Heliopora	21	4.8	3.5	73.3	4.6	21.0
	Isopora	12	15.8	8.6	54.1	-0.1	-1.0
	Montipora	2	13.5	13.4	99.5	0.0	0.0
	Pocillopora	31	15.6	6.9	44.6	0.2	0.0
Maj06	category	n	mean	sd	cv	sk	k
	Acropora	84	66.0	93.5	141.8	2.3	6.1
	Favids	2	2.5	0.7	28.3	0.0	0.0
	Isopora	7	7.7	4.4	56.9	2.0	4.3
	Pocillopora	6	20.2	4.6	22.7	0.3	-2.1
	Massive Porites	7	7.7	6.2	80.5	2.1	4.7
	P. rus	32	12.3	13.4	108.4	2.4	5.5
Maj07	category	n	mean	sd	cv	sk	k
	Acropora	69	7.4	6.1	82.3	6.3	46.9
	Favids	34	9.2	4.6	50.3	1.5	2.9
	Heliopora	37	10.0	10.4	104.1	1.9	3.4
	Isopora	16	12.2	9.4	77.2	2.6	7.9
	Montipora	11	16.0	6.6	41.2	-0.6	-0.8
	Pocillopora	27	9.3	9.2	98.2	2.5	7.2
	Massive Porites	47	13.3	15.1	113.5	2.9	9.4

	category	n	mean	sd	cv	sk	k
Maj08	*Acropora*	79	7.6	4.5	59.6	1.9	4.5
	Favids	22	9.6	5.3	55.3	0.9	0.4
	Heliopora	159	15.5	15.0	97.0	1.6	2.2
	Isopora	2	6.5	0.7	10.9	0.0	0.0
	Montipora	2	7.0	1.4	20.2	0.0	0.0
	Pocillopora	25	9.1	7.5	82.2	2.2	5.5
	Massive Porites	20	26.6	28.0	105.2	2.0	4.2
	P. rus	7	25.3	19.5	77.0	2.1	4.8
Maj09	category	n	mean	sd	cv	sk	k
	Acropora	162	22.9	51.7	225.9	4.6	22.5
	Favids	81	10.0	6.6	66.4	1.1	0.3
	Isopora	13	9.8	6.0	61.9	1.2	0.5
	Montipora	11	15.5	6.6	42.3	0.3	-1.0
	Pocillopora	50	9.5	5.4	56.4	0.9	0.2
	Massive Porites	14	18.8	33.9	180.6	3.6	13.0
	P. rus	1	2.0	0.0	0.0	0.0	0.0
Maj10	category	n	mean	sd	cv	sk	k
	Acropora	28	8.9	4.0	45.3	0.7	-0.6
	Favids	70	10	6.9	68.9	1.1	0.2
	Isopora	9	11.9	6.1	51.2	0.9	-0.7
	Montipora	11	15.5	6.6	42.3	0.3	-1.0
	Pocillopora	28	8.4	4.1	49.5	0.9	0.6
	Massive Porites	14	18.8	33.9	180.6	3.6	13.0
Maj11	category	n	mean	sd	cv	sk	k
	Acropora	7	6.6	2.8	42.9	0.0	-1.0
	Branching Porites	103	8.5	11.8	138.9	4.8	27.4
	P. rus	104	34.4	123.7	359.3	7.9	69.3

Appendix G Sea surface temperature statistics by site for the bleaching year, June 2014 through July 2015 (where SST is in degrees Celsius).

site	mean SST	SST sd	max DHW
Arn01	29.3693	0.5969	4.84
Arn02	29.3746	0.5985	5.14
Arn03	29.3854	0.5977	4.86
Arn04	29.3854	0.5977	4.86
Arn05	29.3746	0.5985	5.14
Arn06	29.3636	0.5886	4.03
Arn07	29.3636	0.5886	4.03
Arn08	29.3751	0.5950	4.52
Arn09	29.3473	0.5984	4.68
Arn10	29.3598	0.6029	5.28
Arn11	29.3385	0.5967	4.39
Arn12	29.3264	0.5956	4.24
Arn13	29.3219	0.5965	4.21
Maj01	29.3983	0.6125	5.55
Maj02	29.3822	0.5970	4.54
Maj03	49.3805	0.5906	4.39
Maj04	29.3834	0.6078	4.16
Maj05	29.3910	0.6113	4.68
Maj06	29.3680	0.6070	4.55
Maj07	29.4124	0.6058	5.37
Maj08	29.4019	0.6114	5.04
Maj09	29.3688	0.5891	4.52
Maj10	29.3678	0.5934	4.23
Maj11	29.3678	0.5934	4.23
Maj12	29.3815	0.5864	4.26