

**CORAL REEF ECOLOGY AND CONSERVATION
IN THE TROPICAL PACIFIC OCEAN**

by

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Abstract

Both local and global stressors threaten coral reefs, putting the food security, cultural continuity, and livelihoods of millions of reef-dependent people at risk. Still, scientists lack an understanding of how climate-driven heat stress interacts with local stressors such as fishing and pollution to influence reef health. Coral reef communities in the Marshall Islands and Kiribati, both low-lying atoll nations in the central Pacific, offer an opportunity to examine these interactions. The Gilbert Islands of Kiribati, which straddle the equator, experience highly variable sea surface temperatures (SSTs) inter-annually due to El Niño / Southern Oscillation, driving coral bleaching events in 2004/2005 and 2009/2010, while the Marshall Islands further north of the equator experience more stable SSTs. Both nations are home to degraded reefs near their capitol atolls, which host over half of each country's populations. I first analyzed the benthic trajectories of coral reefs in the Gilbert Islands from 2012, 2014, 2016, and 2018, across a gradient of local human disturbance after multiple stressors, including two heat stress events and an outbreak of the corallivorous Crown-of-Thorns (CoTs) starfish, finding that locally degraded reefs were more resistant to heat stress than less trafficked reefs because the former were home to hardier taxa. Next, comparing locally disturbed and undisturbed reefs in Kiribati to those in the Marshalls demonstrated that the interactions between local and global stressors were context-dependent; the taxa that were present dictated the interactions. Then, via a meta-analysis of 1,205 sites in the Indian and Pacific Oceans, I demonstrated that a proxy often used to assess the effects of local human disturbance on reef health, the percent cover of macroalgae, does not correlate with local human disturbance. Instead, different genera of macroalgae exhibited diverse and often opposing responses to various sources of local human disturbance. Finally, I used public archives from an email listserv popular among the coral conservation community to

analyze the policy narratives used by participants when discussing local threats to reefs, the actors involved in the local threat, their distal drivers, and the proposed solutions, revealing underlying assumptions about reefs and local people, which could inadvertently undermine conservation.

Lay Summary

I evaluated open questions in coral reef conservation science and practice in the context of climate change. First, via benthic surveys from the Gilbert Islands, Kiribati, I found that degraded reefs were less affected by heat stress. Next, I compared Kiribati reefs, which experience variable ocean temperatures from year to year, to those in the Marshall Islands where temperatures are less variable, finding that interactions between stressors depended on the taxa present. Then, via an analysis of macroalgae cover and its relationship to local human disturbance across the Indian and Pacific Oceans, I demonstrate that macroalgae cover did not correlate with local disturbance, undermining its utility as a proxy for reef health. Finally, I analyzed conversations on a public coral reef conservation listserv, finding that embedded racism and colonialism in conservation science affected discussions about local threats facing reefs today, and provide suggestions for ways forward.

Preface

This dissertation contains my original research and findings. I am responsible for the design, data curation, analyses, and writing for all the content, with the guidance and advice of my advisor, Dr. Simon D. Donner. Each of the research chapters (Chapters 2, 3, 4, and 5) are self-containing. Because Chapters 2 and 3 use some of the same data and methods (described below), there are some redundancies from chapter to chapter. The introductions within each chapter provide more detailed background information and context for each study.

A version of Chapter 2 was published as: Cannon, SE, Aram E, Beiateuea T, Kiarati A, Peter M, Donner SD (2021) Coral reefs in the Gilbert Islands of Kiribati: Resistance, resilience, and recovery after more than a decade of multiple stressors. PLoS One 16(8): e0255304.

<https://doi.org/10.1371/journal.pone.0255304>. I conducted the data collection with assistance from SD Donner and collaborators at the Kiribati Ministry of Fisheries and Marine Resources Development, Erietera Aram, Toaea Beiateuea, Aranteiti Kiareti, and Max Peter, in 2018. This chapter and the resulting publication also made use of data collected prior to the start of my PhD program by SD Donner, Erietera Aram, Toaea Beiateuea, Aranteiti Kiareti, Tuake Teema, Iobe Arabua and Timon Ribanti in 2012, 2014, and 2016. I processed all data from these surveys, conducted the analysis, and authored the manuscript, with assistance and editing from SD Donner. E Aram, T Beiateuea, A Kiareti, and M Peter also offered edits on the manuscript prior to its publication.

I am the lead author of a version of Chapter 3 that is currently undergoing peer review. Angela Lui and SD Donner coauthored this manuscript. This chapter makes use of the data I collected

with SD Donner and our collaborators in Kiribati from 2018 (described above). It also used data that I collected with SD Donner from the Republic of the Marshall Islands in 2016, which I published previously as: Cannon, SE, Donner SD, Fenner D, Beger M (2019) The relationship between macroalgae taxa and human disturbance on central Pacific coral reefs. *Marine Pollution Bulletin* 145:161-173. <https://doi.org/10.1016/j.marpolbul.2019.05.024>. Other than the description of the methods in Chapter 3, this publication is unrelated to the chapter. I conducted all data analysis and drafted Chapter 3 with the assistance of SD Donner, while A Lui assisted with collecting and processing satellite data that I incorporated into the statistical analysis (described further in the chapter). A Lui also provided feedback on the manuscript prior to submission.

I have prepared a formatted version of Chapter 4 for submission to a peer-reviewed journal. This chapter made use of benthic survey data collected by 46 individuals from 1,205 sites across the Indian and Pacific Oceans, between 2004 and 2020: Andrew Baird, Julia Baum, Andrew Bauman, Maria Beger, Cassandra Benkwitt, Matthew Birt, Yannick Chancerelle, Joshua Cinner, Nicole Crane, Vianney Denis, Martial Depczynski, Nur Fadli, Douglas Fenner, Christopher Fulton, Yimnang Golbuu, Nick Graham, James Guest, Hugo Harrison, Jean-Paul Hobbs, Andrew Hoey, Thomas Holmes, Peter Houk, Fraser Januchowski-Hartley, Jamaluddin Jompa, Chao-Yang Kuo, Gino Limmon, Yuting Vicky Lin, Timothy McClanahan, Dominic Muenzel, Michelle Paddack, Serge Planes, Morgan Pratchett, Ben Radford, James Reimer, Zoe Richards, Claire Ross, John Rulmal Jr., Brigitte Sommer, Gareth Williams, and Shaun Wilson. I collected and reconciled the data from these individuals, conducted the statistical analysis, and drafted the manuscript, with the guidance of SD Donner. Angela Liu and Pedro González Espinosa

downloaded and assisted with processing the satellite data that I used to calculate the independent variables used in this analysis. The 46 contributors provided feedback and comments on an early draft of the chapter.

Finally, I was responsible for conceptualizing the research questions in Chapter 5, analyzing all data, and drafting the chapter, with guidance from SD Donner and Terre Satterfield. Because this chapter uses records that are publicly available, the UBC Behavioural Research Ethics Board indicated that it did not require ethics approval.

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List of Abbreviations

BIPOC – Black, Indigenous, and people of color

CoTS – Crown of Thorns starfish

DHW – Degree Heating Weeks

GHG – Greenhouse gases

IPLC – Indigenous peoples and local communities

LMM – Linear mixed effects models

MFMRD – Government of Kiribati Ministry of Fisheries and Marine Resources Development

MIMRA – Marshall Islands Marine Resources Authority

MMM – Maximum Monthly Mean

NDVI – Normalized Difference Vegetation Index

NOAA – United States National Oceanic and Atmospheric Association

RDM – Relative Dominance Model

RMI – Republic of the Marshall Islands

SST – Sea surface temperature

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Dedication

*I dedicate this dissertation to
my son,
Daniel Lee Lemmon,*

And to the memories of

*Michael P. Cannon,
December 9, 1949 – June 24, 2015*

*Jeffrey P. Cannon
May 21, 1988 – May 2, 2020*

and

*Kristy Keller-Burley
January 23, 1985 – February 4, 2020*

Chapter 1: Introduction

Both local and global stressors have threatened the health and functioning of coral reefs around the world for decades (Richmond, 1993; Hughes, 1994), putting the food security, livelihoods, and cultural continuity of millions of people who live near and depend upon reefs at risk, the majority of whom are in the Global South (Cinner, 2014). Climate change, which drives increasing sea surface temperatures (SSTs), threatens even reefs that are far from people (Baumann *et al.*, 2022). Heat stress triggered by higher-than-normal SSTs can cause corals to bleach, a physiological response to environmental stress in which the coral animal ejects the microscopic, symbiotic algae living within its tissue. Because these photosynthetic algae, called zooxanthellae, provide energy to their coral hosts, prolonged bleaching can result in widespread coral mortality (Brown, 1997; Hughes, Kerry, *et al.*, 2017). Global SSTs have been rising for the past century and are projected to continue to rise (IPCC, 2021). This, coupled with stronger El Niño events which also produce warmer-than-average SSTs (Wang *et al.*, 2016), is causing corals to bleach more frequently (Hughes, Kerry, *et al.*, 2017), which means that there may not be time between events for benthic communities to recover. Repeated bleaching events might also increase coral reef's vulnerability to other sources of stress, such as local anthropogenic stressors (Hughes *et al.*, 2007; Toth *et al.*, 2015).

Marine scientists are racing to find ways to increase coral reef resilience to multiple stressors and to conserve coral reef ecosystems but disagree about what actions to prioritize. For example, there is considerable debate over whether attempts to address local anthropogenic stressors such as pollution and overfishing are effective and justified, given the universal threat climate change poses to all reefs (Hughes *et al.*, 2007; Bruno and Valdivia, 2016). While coral reef scientists

generally agree that climate change is the most pressing threat facing reefs today (Hughes, Barnes, *et al.*, 2017), many argue that addressing local stressors should remain a priority alongside global efforts to reduce greenhouse gas emissions (Abelson, 2020).

However, settling this debate and prioritizing the most effective conservation interventions requires an understanding of how global and local threats interact to influence coral reefs.

Currently, scientists and managers have limited ability to make strategic, informed decisions about the most effective coral reef conservation. As climate change continues to intensify, the ability to make these tactical choices will become increasingly vital (Darling *et al.*, 2019).

Making decisions without this understanding puts scientists and managers at risk of inadvertently supporting maladaptive solutions that could undermine conservation goals and/or waste limited conservation resources.

Unfortunately, the challenges in isolating the effects of global and local stressors makes studying interactions between climate change and the local stressors facing coral reefs difficult. Given that climate change has driven increasing SSTs in some parts of the world for more than a hundred years (Bove, Mudge and Bruno, 2022), scientists lack a baseline for comparing coral reef benthic communities today to the communities that existed prior to anthropogenically-driven heat stress. While remote reefs with few local human influences are often used to isolate signatures of local human disturbance on reefs (Sandin *et al.*, 2008; Smith *et al.*, 2016), even the reefs that are farthest from people are threatened by rising SSTs (Hughes, Kerry, *et al.*, 2017; Baumann *et al.*, 2022).

One approach to addressing this challenge has been to compare the recovery of coral reefs inside and outside of marine protected areas (MPAs) after a bleaching event, but these studies have produced mixed results. While some have found that reducing local stressors through establishing MPAs can increase coral reef resilience to heat stress (Anthony *et al.*, 2015; Davies *et al.*, 2016; Mellin *et al.*, 2016; Mcleod *et al.*, 2019), others have shown that the opposite may be true; at least in some cases, reducing local stressors may increase vulnerability to heat stress and bleaching (Darling, McClanahan and Côté, 2010; Bates *et al.*, 2019; Bruno, Côté and Toth, 2019). Studies also suggest that low diversity reefs that have been highly impacted by local human activities are more resilient to bleaching than those that are less degraded and host more biodiversity (Carilli *et al.*, 2014; Baumann *et al.*, 2022), potentially because the more sensitive coral species are weeded out by local threats, leaving behind a community of hardy corals that are less affected by heat stress (Côté and Darling, 2010; Bates *et al.*, 2019). In addition, reefs in places with highly variable SSTs or that have experienced bleaching in the past have greater resilience to future bleaching (Thompson and Van Woesik, 2009; Carilli, Donner and Hartmann, 2012; Coles *et al.*, 2018; Donner and Carilli, 2019). This part of the world may provide insight into how coral communities respond to frequent heat stress, as is project to happen with continued ocean warming (Donner and Carilli, 2019). Understanding how heat stress interacts with local human-driven degradation, and how these interactions will influence ecosystem functioning, is vital to finding ways to mitigate the effects of climate change for reef-dependent people around the world.

1.1 Threats to reefs in Micronesia

Nowhere are these questions more important than for atolls in the Micronesia region of the tropical Pacific Ocean. Atoll countries such as the Republic of the Marshall Islands (RMI) and the Republic of Kiribati are especially susceptible to rising sea levels driven by climate change because of their low elevations (Storlazzi *et al.*, 2018); there are few places in either nation with an elevation higher than 5 meters above sea level (Woodroffe, 2008). The Marshallese and i-Kiribati (Gilbertese people) rely on coral reef fisheries for sustenance, especially in atolls that are far from population centers (Eme *et al.*, 2020; MIMRA, 2020), and depend upon reefs to protect the islands from rising sea levels and storm surges (Ford, Merrifield and Becker, 2018; Summers and Donner, 2022). Low-lying atolls like those found in Kiribati and the RMI are already experiencing wave-driven flooding, which threatens supplies of drinking water via saltwater inundation (Woodroffe, 2008; Terry and Chui, 2012; Ketabchi *et al.*, 2014; Ford, Merrifield and Becker, 2018; Storlazzi *et al.*, 2018). Supporting local efforts to conserve coral reef ecosystems in these nations is therefore especially crucial.

While conserving these reefs is vital to preserve the services they provide to local people, reefs in the Micronesia region may also help scientists to untangle the complex interactions between local and global anthropogenic stressors. Reefs in the RMI and Kiribati experience a gradient of local human stressors, from undisturbed to highly affected. While both countries are home to many atolls with small or absent populations, each also has areas with extremely dense populations (Secretariat of the Pacific Community, 2012; Republic of Kiribati National Statistics Office, 2021), which can place intense pressure on reefs through fishing and pollution (Kirata *et al.*, 2005; Beger *et al.*, 2010; Pinca *et al.*, 2012; Campbell and Hanich, 2014; MIMRA, 2016).

The urban areas of two atolls in particular, Tarawa in the Gilbert Islands, Kiribati and Majuro in the RMI, have large populations living on small land masses, resulting in some of the highest population densities in the world (United Nations Population Fund, 2014). Because of their geographies, the reefs in these nations also have different histories of exposure to past heat stress. The Gilbert Islands are located on the equator in the central Pacific and thus experience highly variable SST inter-annually due to the El Niño / Southern Oscillation, and reefs here have undergone two mass bleaching events (in 2004/2005 and 2009/2010, Donner and Carilli, 2019), while reefs in the RMI are further away and have less inter-annual variability in SSTs, and have not experienced widespread bleaching (Figure 2.2). The gradient of SST variability, where inter-annual variability decreases as distance from the equator increases, coupled with a gradient of human influence, provide an ideal opportunity for investigating interactions between global and local stressors (Table 1.1).

Table 1.1 Atolls in Kiribati (Tarawa and Abaiang) and the RMI (Majuro and Arno) by local human disturbance and SST variability.

		SST Variability	
		High	Low
Local Human Disturbance	High	S. Tarawa	Majuro
	Low	N. Tarawa & Abaiang	Arno

1.2 Distal drivers of reef degradation

Importantly, while the local threats facing coral reefs around urbanized atolls in Kiribati and the RMI are related to high local population densities, the distal driver of these local threats—processes that are physically removed from the reef, but underlie direct, proximate stressors (Forster *et al.*, 2017)—was the histories of colonial occupation within these atolls. As discussed further in Chapters 2 and 3, the actions of colonial powers, the USA and UK respectively, led to the dense populations on Majuro and Tarawa today. Both the USA and UK instituted policies encouraging migration to the capital atoll atolls by centralizing resources and economic opportunities in the capitals (Connell and Lea, 1998; Cannon, 2020). In the RMI, the US also forced people from the northernmost atolls and relocated them in Majuro and other atolls to make way for nuclear testing (Johnston and Barker, 2008). The USA, UK, and Japan (which occupied parts of Kiribati and the RMI before the second World War) also contributed to local degradation through direct alteration of the environment, for example by constructing causeways that altered waterflow between the open ocean and lagoons (Johannes *et al.*, 1979; Spennemann, 1996). Further, people in the RMI and Kiribati contribute almost nothing to the greenhouse gas emissions (GHGs) that are driving climate threats to coral reefs. Despite this, they are among the first people in the world to face the consequences of global climate change (Wolff *et al.*, 2015; Dean, Green and Nunn, 2017; Bordner, Ferguson and Ortolano, 2020).

I suggest that without being aware of the histories underlying the drivers of degradation, and how conservation can perpetuate these inequalities today, coral reef scientists, most of whom come from the Global North (Ahmadia *et al.*, 2021), may assume that local people are to blame for reef degradation and are unable to effectively manage their resources. These misconceptions may

cause scientists and conservationists to encourage interventions and policies that further marginalize Indigenous peoples and local communities (IPLC) such as the Marshallese and i-Kiribati. Given that community involvement and equitable governance are important aspects of successful marine conservation, such misconceptions among coral reef conservationists could potentially undermine conservation outcomes (Fidler *et al.*, 2022). An understanding of how coral reef conservationists conceptualize the drivers of local threats facing coral reefs and the actors involved would therefore be valuable and may highlight ways to improve the efficacy of coral reef conservation efforts.

1.3 Research questions and contribution

Here, I address open questions in coral reef conservation science and practice in the context of climate change across four distinct research chapters. My first two chapters seek to advance coral reef science by improving our understanding of interactions between local and global anthropogenic stressors and their effects on coral reef benthic communities, using sites in the central Pacific Islands as a case study. My third research chapter assesses the utility of a common proxy for reef health used by coral reef scientists to inform conservation practice. Finally, in my fourth research chapter, I use a mixed qualitative and quantitative approach to investigate how perceptions of local threats to reefs influences conservation practice. I sought to answer the following research questions:

- How do local human threats to reefs in the Gilbert Islands of Kiribati influence their recovery trajectories in the years after multiple heat stress events (in 2004/2005 and

2009/2010) and an outbreak of the predatory Crown-of-Thorns (CoTs) starfish in 2014, and what does this tell us about coral reef resilience to multiple stressors?

- How does the past frequency of climate-driven heat stress through exposure to variable SSTs influence coral reef recovery after multiple stressors, and do responses differ across a gradient of local human degradation?
- How do coral reef scientists talk about the local stressors threatening coral reefs, their drivers, the actors involved, and their potential solutions, and what does this reveal about assumptions or blind spots that may influence coral reef conservation?

I used multiple quantitative and qualitative analyses to answer these questions, via in situ quantitative benthic surveys of coral reefs, a suite of metrics to represent different stressors from satellite data, and qualitative mixed methods analyses of communications among scientists (described further below). To investigate how reefs in Kiribati have changed over time following exposure to multiple stressors (including two major bleaching events that occurred prior to the study), and whether the trajectories of benthic communities differed across a gradient of local human disturbance, my first chapter uses data collected by my advisor, Simon Donner, in 2012, 2014, and 2016 from Abaiang and Tarawa Atolls, alongside data I collected in situ with SD Donner in 2018. These data included size-frequency transects of coral reef taxa identified to the genus level, and photo quadrats. I processed all photo quadrats, including those collected by SD Donner, using the online software CoralNet to estimate the percent cover of key benthic taxa, and manually identified all coral and macroalgae to the genus level. I then compared the percent cover of these key taxa across atolls and years to identify similarities and/or differences in

benthic trajectories in sites with low human disturbance (Abaiang and North Tarawa) versus those with high local degradation (S. Tarawa).

In my second chapter, to investigate how the history of climate-driven heat stress influences benthic communities, I compared benthic surveys from Tarawa and Abaiang in 2018 to surveys from Arno and Majuro Atolls in the RMI in 2016. I collected the data from the RMI in 2016 alongside Dr. Donner as a part of a previously published research project, again using the same methods to ensure comparison across surveys (Cannon *et al.*, 2019). I planned to return to both the RMI and Kiribati in 2020 to repeat these surveys and to collect additional data (for example, to conduct fish surveys). These additional surveys would have provided more information about whether degraded reefs can continue to provide the services that are important to people (for example, if they support local small-scale subsistence fisheries) across these gradients of local human impacts and past exposure to variable SSTs. Unfortunately, I was unable to return to the RMI or Kiribati because of travel restrictions imposed during the COVID-19 pandemic (from March 2020 through spring 2022).

My third research chapter tested the utility of a common metric used by coral reef scientists to estimate the health of coral reefs. Survey methods for assessing the current state (or “health”) of a coral reef are still controversial and there is no agreed-upon definition of reef health in the literature. In the absence of an absolute measure of reef health, it is common for researchers to use proxy metrics of health to track how coral reef communities have changed over time, and/or to inform management (for example, by identifying reefs that are most in need of conservation intervention). One of the most common proxies for estimating the state of a coral reef is the

percent cover of fleshy macroalgae, which assumes that high macroalgae percent cover represents reefs that are degraded (Littler, Littler and Brooks, 2006; Littler and Littler, 2007). While reef degradation may be caused by natural stressors (such as storms), the idea that fleshy macroalgae cover is driven by anthropogenic stressors acting through top-down or bottom-up processes (e.g. the Relative Dominance Model, or RDM (Littler, Littler and Brooks, 2006; Littler and Littler, 2007) has led to the common assumption that reefs disturbed by local anthropogenic stressors are likely to have high cover of fleshy macroalgae (Pandolfi *et al.*, 2005; Hoegh-Guldberg *et al.*, 2007; e.g. Bruno and Valdivia, 2016; Smith *et al.*, 2016). Several studies have found that this is oversimplified (McCook, 1999; McClanahan *et al.*, 2004; Bruno *et al.*, 2009; Vroom, 2011; Fulton *et al.*, 2019); not only is fleshy macroalgae influenced by multiple environmental factors (such as wind and wave exposure, SSTs, and photosynthetically-available radiation) (Keith, Kerswell and Connolly, 2014), but different species or genera of fleshy macroalgae respond to local disturbance in diverse ways (Cannon *et al.*, 2019). Still, scientists continue to use fleshy macroalgae cover to identify signatures of local human-driven degradation on coral reefs (Bruno and Valdivia, 2016; Smith *et al.*, 2016). To investigate the utility of fleshy macroalgae percent cover as an indication of how local people affect the health of coral reefs, I conducted a meta-analysis using pre-existing survey data collected from 45 scientists who conducted surveys that identified fleshy macroalgae to at least the genus level. These data contained the percent cover of fleshy macroalgae from 1,205 sites across the Indian and Pacific Oceans, collected between 2004 and 2015.

Finally, to investigate how coral reef scientists talk about local reef degradation and its drivers with the goal of identifying ways to improve conservation efficacy, I used a mixed-methods

approach to process conversational emails sent via a listserv hosted by the United States National Ocean and Atmospheric Administration (NOAA) for the coral reef conservation community (NOAA CHAMP, 2019). The listserv archives are publicly available online, and I used mixed quantitative statistical methods alongside a qualitative discourse analysis to compare emails from the first five years of its existence (1995 through 2000) and to emails in a more recent five-year period (2015 through 2020) to look for changes in the most discussed threats to reefs and their drivers. Specifically, I used qualitative iterative coding to track discussions of local threats facing reefs, their distal drivers, the actors involved, and their solutions. By identifying different policy narratives and how they were employed by Coral List participants (for example, crisis narratives or resilience narratives, described further in Chapter 5), I identified underlying assumptions held by some influential members of the coral reef conservation community that could influence their views of reef degradation and its drivers. Research has repeatedly found that conservation efforts are most effective when IPLC engage in management (Fidler *et al.*, 2022), and assumptions that IPLC are unable to effectively manage their resources and/or that the rights to access marine resources are at odds with conservation efforts may therefore undermine conservation outcomes. Because coral reefs are often considered “the canary in the coalmine” for ecosystems that are threatened by climate change (Riegl and Dodge, 2008), these findings have implications for conservation more broadly, especially for locations that are not yet experiencing frequent climate-driven heat stress but may in the future.

1.4 Structure of dissertation

Each of the following four research chapters addresses the questions described above. I

structured each chapter as an independent, self-contained manuscript, and therefore each contains sections describing the relevant background, concepts, research questions, and methods. Because Chapter 3 makes use of data that I also used in Chapter 2, there is some overlap in the methods and repetition or similarities across chapters.

I describe how local anthropogenic stressors affect coral reef recovery after multiple stressors (including two heat stress events occurring prior to the study period and an outbreak of CoTs), the influence of past SST variation on benthic communities, methods for estimating local human influences on coral reefs, and how the coral reef conservation community discusses local drivers of threats facing coral reefs through the following chapters and hypotheses:

- **Chapter 2** describes the recovery trajectories of benthic communities after more than a decade of multiple stressors, including two coral bleaching events prior to the start of the study and a subsequent CoTs outbreak, across a gradient of human disturbance using data collected in 2012, 2014, 2016, and 2018 from Tarawa and Abaiang Atolls. I hypothesized that coral reefs with highly variable inter-annual SSTs (in Kiribati) would host less diverse but hardier benthic communities (as predicted by Darling *et al.*, 2012), and would be more resilient to bleaching. I also predicted that sites that were already degraded by local human impacts would be more resistant to heat stress and would be less likely to bleach (as suggested by Carilli *et al.*, 2014).
- **Chapter 3** investigates how the history of SST variation at a given coral reef influences the responses of benthic communities to local and global stressors. I compared the percent cover of key benthic taxa in the Gilbert Islands (Abaiang and Tarawa Atolls)

from 2018 to those in the RMI (Arno and Majuro Atolls) from 2016 to test the hypothesis that local human-driven reef degradation does not compound the impacts of climate change on living coral cover, but can pre-condition benthic communities to withstand frequent heat stress by weeding out the more sensitive coral taxa (discussed further in Chapter 3). I expected sites within the Gilbert Islands (all of which have experienced repeated bleaching-level heat stress) to host more hardy, heat-resistant taxa than the atolls in the RMI, which experience less variable SSTs. However, I also expected this to be mediated by local human disturbance, such that sites exposed to chronic, ongoing local human disturbance (Majuro and Tarawa) hosted coral communities with higher percent cover of opportunistic or hardy taxa than the less populated atolls (Arno and Abaiang).

- In **Chapter 4**, I conducted a meta-analysis of benthic community composition data from the Indian and Pacific Oceans, to investigate the association of different macroalgae genera with varying levels of local human disturbance. The percent cover of fleshy macroalgae is a widely used proxy for reef health and degradation, but my past research showed that in the RMI, some genera of macroalgae were negatively correlated with local human disturbance (Cannon *et al.*, 2019). I gathered benthic survey data identifying fleshy macroalgae to the genus level from 44 researchers spanning 1,205 sites in the Indian and Pacific Oceans (described in more detail in Chapter 4). I hypothesized that fleshy macroalgae cover would not correlate with local human disturbance, but that classifying macroalgae by genus would reveal that some taxa were positively correlated with disturbance, while others were negatively correlated.
- **Chapter 5** analyzes how the coral reef conservation community discussed local threats to coral reefs, using a mixed-methods approach to process conversational emails sent via the

NOAA Coral-List (NOAA CHAMP, 2019). I anticipated finding that coral reef scientists most frequently discussed direct, proximate drivers of reef degradation while overlooking the underlying root causes, as distal drivers of reef health or degradation are rarely considered in the scientific literature (Forster *et al.*, 2017). I expected this to lead scientists to attribute blame for reef degradation to local people, reinforcing colonial ideas that IPLC are incapable of managing local resources. However, I also expected that calls to address inequality in reef conservation and conservation more broadly (Alcorn and Royo, 2007; Büscher *et al.*, 2016; Bennett *et al.*, 2017) might have led to greater recognition of how conservation interventions can inadvertently perpetuate colonial attitudes that harm IPLC and undermine the effectiveness in the more recent Coral-List period (2015-2020). Given that conservation efforts are most effective when they recognize and support IPLC leadership and autonomy (Artelle *et al.*, 2019; Hessami *et al.*, 2021), the lingering effects of colonialism on perceptions held by coral reef scientists may undermine conservation.

Chapter 2: Coral reefs in the Gilbert Islands of Kiribati

2.1 Introduction

Phase shifts or regime shifts, changes in the community in response to a persistent change in environmental conditions (Dudgeon *et al.*, 2010), are well-documented responses to disturbance on coral reefs. Phase shifts can happen over broad spatial scales, ranging from local (a few kilometers) to regional (thousands of kilometers), and wide time scales (from a period of 1-2 years to decades or longer) (McManus and Polsenberg, 2004; deYoung *et al.*, 2008). There may also be time lags of several years or more between the disturbance and the resulting change in community composition. Together, these characteristics may make identifying the drivers of phase shifts challenging, but doing so can have important implications for resource management (deYoung *et al.*, 2008).

Once an ecosystem has undergone a phase shift, it can remain in the new state even after drivers are relieved due to hysteresis (Scheffer *et al.*, 2001). However, there is evidence that this is not always the case: coral reefs that have undergone phase shifts to stable communities after long-term, ongoing, chronic disturbances may recover when the responsible stressors are relieved, or the perturbed aspect of the system is restored (Precht and Aronson, 2006; Dudgeon *et al.*, 2010). One well-known example of this is the case of reefs in Kane'ohe Bay, Hawai'i, where diversion of sewage outflow led to a reversal of a previous phase shift to macroalgae dominance (Hunter and Evans, 1995). This example illustrates that identifying and reversing a phase shift requires establishing a link between the drivers and the ecosystem response (deYoung *et al.*, 2008).

On coral reefs, the potential drivers of phase shifts have been well-documented, and may include acute (short-term) disturbances such as climate-driven events (e.g., marine heat waves or tropical cyclones) or chronic (long-term) disturbances (e.g., fishing pressure, nutrient enrichment, sedimentation, or a combination of these) (Connell, 1997). The most well-known examples of phase shifts on coral reefs are from coral-dominated to macroalgae-dominated states (Done, 1992; Knowlton, 1992; Mumby, 2006), but this type of phase shift may occur more often in the Caribbean than in the Indian and Pacific Oceans (Bruno *et al.*, 2009; Smith *et al.*, 2016; Cannon *et al.*, 2019). Instead, phase shifts to other dominant organisms may be more common in the Indian and Pacific Oceans. For example, phase shifts to coral taxa with ‘weedy’ life history strategies (Darling *et al.*, 2012) have been documented in parts of the Pacific (Crane *et al.*, 2016), as well as shifts to sponges (Bell *et al.*, 2013; Powell *et al.*, 2014) or corallimorphs (Work, Aeby and Maragos, 2008; Crane *et al.*, 2016).

The coral reefs of Tarawa Atoll and its less populated neighbour Abaiang Atoll in the Republic of Kiribati provide a unique opportunity to investigate the role of chronic human disturbances on coral reef recovery from acute disturbances. These reefs have been exposed to repeated bleaching-level heat stress events in the past 30 years due to the El Niño/Southern Oscillation (ENSO) (Carilli, Donner and Hartmann, 2012; Donner and Carilli, 2019); heat stress affecting coral reefs in this region occurs during El Niño events, during which the slowdown or reversal of easterly trade winds and the South Equatorial Current (SEC) bring anomalously warm conditions to the equatorial Pacific (Wang *et al.*, 2016). Eastern Pacific (EP) El Niño events, during which the easterly trade winds and SEC reverse, drive warm water anomalies that spread across the equatorial Pacific from west to east (Kao and Yu, 2009; Kug, Jin and An, 2009). By contrast,

during central Pacific (CP) El Niño events, the shutdown or reversal of easterly trade winds and the SEC is limited to the western Pacific, concentrating warm water anomalies in the central Pacific (including Kiribati), while eastern Pacific waters remain cool (Kao and Yu, 2009; Kug, Jin and An, 2009). CP events have most consistently caused bleaching-level heat stress in the Gilbert Islands (Donner and Carilli, 2019), but both types of El Niño events can bring heat stress to reefs in the region (Cole and Fairbanks, 1990; Cole, Fairbanks and Shen, 1993; Donner, 2011). Although EP El Niño are historically stronger than CP El Niño, CP El Niño have occurred more frequently over the past several decades and may also be increasing in intensity (but the reasons for this are still not well understood) (Lee and McPhaden, 2010; Zheng *et al.*, 2014; Wang *et al.*, 2016).

The two atolls, however, experience different levels of local human disturbance. Tarawa is home to roughly 60% of the 110,136 people in Kiribati according to the 2015 census (National Statistics Office, 2016). About 90% of the Tarawa's population is concentrated in communities spread across the southern rim of the atoll (referred to administratively as South Tarawa). By contrast, neighboring Abaiang Atoll, about seven miles north of Tarawa's northern-most point, has less than a tenth of Tarawa's population, about 5,500 people (National Statistics Office, 2016). This difference in human population translates to a difference in chronic human-related pressures like fishing, nutrient loading, and sedimentation. For example, reefs in S. Tarawa experience much higher fishing pressure than those in N. Tarawa and Abaiang. Although fishers in Abaiang export much of their catch to S. Tarawa, a report from 2004 indicates that fish populations in Abaiang were healthy and showed no signs of overexploitation (Awira *et al.*,

2008), and research suggests that such small-scale subsistence fisheries are unlikely to substantially affect reef fish assemblages (Martin *et al.*, 2017).

The gradient in human pressures on the reefs emerged from the colonial history of Kiribati, more so than from recent governance. The Gilbert Islands, known as *Tungaru* by the i-Kiribati prior to colonization, were first settled 2,000 – 3,000 years ago (Macdonald, 1982). The British seized control in 1892, and retained colonial oversight of the Gilberts until Kiribati's independence in 1979, with the exception of a six-year period during and after World War II (Macdonald, 1982; Connell and Lea, 2002). During British colonial occupation, which lasted almost 80 years, causeways were built that altered natural water flow and sedimentation patterns in S. Tarawa and, to a lesser extent in other atolls like Abaiang, also blocked fish populations from reaching their traditional spawning and nursery grounds within the lagoon (Johannes *et al.*, 1979; Thomas, 2009; Biribo and Woodroffe, 2013). The British also centralized and expanded government activity in S. Tarawa, creating a draw for people looking for education, employment, and access to goods and services, and spurring the high population density seen in Tarawa today (Johannes *et al.*, 1979; Macdonald, 1982; Connell and Lea, 2002). The population of S. Tarawa is growing at about 4.5% per year and is expected to double by 2030 (Asia Development Bank, 2014). The Kiribati government has attempted to meet the needs of this growing population through major infrastructure projects in S. Tarawa, including many that are underway today (Babinard *et al.*, 2014). Conversely, there have been few major infrastructure projects in N. Tarawa, Abaiang, and other “outer” atolls, with the exception of causeways, all of which were built prior to Kiribati's independence in 1979 (Macdonald, 1982). Most outer atolls have experienced steady or

declining human populations as people migrate to S. Tarawa (National Statistics Office, 2016).

South Tarawa's growing population meant that sewage pollution was also increasing and becoming a growing threat to the health of both people and coral reefs. In 1985, the British completed the first sewage scheme in S. Tarawa (Macdonald, 1982), which aimed to improve water quality by pumping raw sewage out of three outflows at seven meters depth along the reef crest, via pipes crossing the reef flat. Until recently, the outfalls had not been regularly maintained and leaked untreated sewage onto the reef flats (Kirata *et al.*, 2005). Notably, these sewage pipes only served a portion of the population on S. Tarawa; as of 2013, about 60% of residents use the ocean, beaches, or lagoon instead of toilets (Asia Development Bank, 2014).

The local government is concerned about the impacts of sewage pollution on reef health (Kirata *et al.*, 2005; Ministry of Public Works and Utilities, 2019). In 2019, Kiribati's Ministry of Public Works and Utilities completed a project to improve access to toilets (reducing the number of residents not using toilets from 60% to 20%) and to update the sewage system, which included fixing the leaking pipes and moving the outflows from the reef crests to 30m depth (Ministry of Public Works and Utilities, 2019). Some coral taxa are unable to tolerate high concentration of nutrients, which can contribute to reef degradation by allowing fleshy macroalgae (as in the case of Kane'ohe Bay, Hawai'i) (Hunter and Evans, 1995), or weedy coral species like *Porites rus* to outcompete the more sensitive corals (Dizon and Yap, 2005).

These distinct histories of local, anthropogenic disturbance influenced how reefs in Tarawa and Abaiang responded to recent acute disturbances, discussed further below, including mass coral

bleaching events, other recurrent bleaching-level heat stress events and an outbreak of the corallivorous Crown-of-Thorns (CoT) sea star, *Acanthaster cf solaris* (Donner, Kirata and Vieux, 2010; Carilli, Donner and Hartmann, 2012; Donner and Carilli, 2019). The first reported bleaching event at Tarawa and Abaiang occurred in 2004-2005, due to prolonged exposure to higher-than-average SSTs during an El Niño event (Donner, Kirata and Vieux, 2010). There were no prior reports of bleaching on the outer reefs (in the published literature, grey literature, or via local experts) (Donner, Kirata and Vieux, 2010) and cores from massive *Porites* spp., confirmed that reefs across both atolls bleached in response to heat stress in 2004/2005 and 2009/2010, but did not find evidence of bleaching events prior to 2004 (Carilli, Donner and Hartmann, 2012). It is possible that mass bleaching occurred during past El Niño events that went unreported and undetected in the subsample of *Porites* spp. colonies. After the first heat stress event, coral genera that are more tolerant of heat stress became more dominant, although the specific taxa differed across a gradient of local human disturbance (discussed below); researchers observed a similar pattern after a subsequent bleaching event in 2009-2010 (Donner, Kirata and Vieux, 2010; Donner and Carilli, 2019). Then, in 2013-2014, a CoTs outbreak occurred in both Tarawa and Abaiang (Kiareti *et al.*, 2013). A CoTs outbreak also occurred in the 1970s (Johannes *et al.*, 1979; Lovell, 2000), and other unreported events may have occurred in the intervening years (Biribo and Woodroffe, 2013). Outbreaks of CoTs can cause widespread damage and coral loss on reefs (Pratchett *et al.*, 2017), particularly after coral bleaching, when predation may target the thermally-tolerant surviving corals such as massive *Porites* spp. (Haywood *et al.*, 2019; Keesing *et al.*, 2019).

The weedy coral species *Porites rus* is thermally tolerant, and previous studies document its spread over time in S. Tarawa that likely contributed to these highly disturbed reefs' greater resistance to the 2004-2005 and 2009-2010 bleaching events than those experiencing lower human influence (Donner and Carilli, 2019). Prior to bleaching in 2004, the coral community in S. Tarawa was also home to larger populations of both fast-growing, thermally sensitive genera like *Acropora* and *Pocillopora*, and slower-growing, more thermally tolerant genera like massive *Porites* (Donner, Kirata and Vieux, 2010; Donner and Carilli, 2019). After the first bleaching event ended in 2005, researchers documented a rapid increase in *P. rus* at a single site in Tarawa; subsequent surveys showed that *P. rus* continued to survive or even proliferate across sites in S. Tarawa despite the subsequent heat stress event (Donner and Carilli, 2019). By 2012, *P. rus* accounted for the majority of coral cover across all sites in S. Tarawa (Donner and Carilli, 2019). It is possible that the rapid change in the benthic communities of S. Tarawa — where benthic taxa were already facing ongoing local stressors related to high local population densities, unlike in Abaiang— underwent a phase shift triggered by the 2004/2005 bleaching event, which might have enabled the spread of *P. rus* by killing the more sensitive coral taxa and reducing competition over space. Detecting when a community is in the process of shifting is important because a single perturbation could push that community into a catastrophic shift to a degraded state (Beisner, Haydon and Cuddington, 2003). If a phase shift has already occurred, identifying it, for example through an analysis of benthic communities across multiple survey years to confirm whether a perturbed ecosystem state is persistent, identifying the parameters that may have caused it, and how the phase shift may affect ecosystem services could inform next steps for management.

Here, I assess how benthic communities, including coral, algae, and other key taxa, have responded to multiple stressors across two atolls with the same historical exposure to heat stress, but different levels of local anthropogenic stressors, Abaiang and Tarawa. I examine benthic cover and size frequency data collected in surveys from 2012 through 2018 to test a series of hypotheses about the trajectories of coral reef communities after disturbance. First, I test whether post-bleaching benthic community composition differed by year. Second, I test whether the shift to *P. rus* in S. Tarawa, documented in previous studies, has been persistent, stable, and represents a phase shift. Third, I test whether the taxon-level response to the CoTs outbreak differs from that of bleaching, with massive *Porites* sensitive to CoTs but more resistant to bleaching. Finally, I examine whether the trajectories of post-bleaching communities differ based on local human disturbance while accounting for environmental variables that could also influence the benthic communities, within and across atolls.

2.2 Materials & Methods

2.2.1 Study Sites

We sampled 19 sites on the outer reefs across Abaiang and Tarawa Atolls between 2012 and 2018 (Figure 2.1; Appendix A.1). These outer reefs feature spur and groove formations from the reef crest seaward to approximately 10 to 15m depth. The southeastern and eastern reefs are more exposed to prevailing easterly wind directions and swells, and thus have narrower reef terraces than those on the western outer reefs.

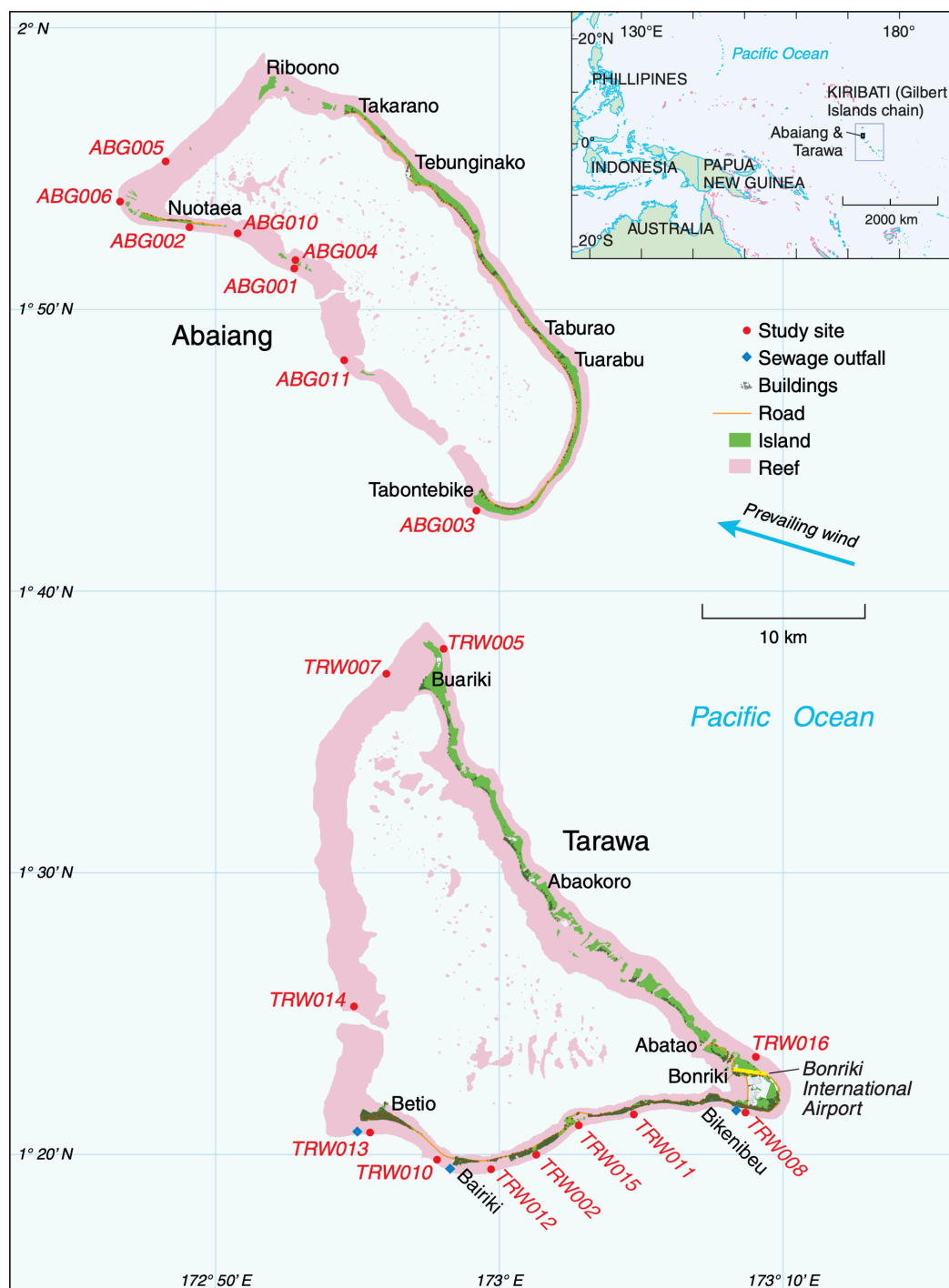


Figure 2.1. Study sites in Tarawa and Abaiang.

Because of the complexity of conducting fieldwork under varied ocean conditions in such a remote location, I was unable to use data from a consistent set of sites during each of visit,

resulting in an uneven sampling effort across sites and atolls. Sites were unevenly sampled every two years from 2012 to 2016 (Appendix A.1), and were selected to cover a range of habitats, population density, and coastal infrastructure. In 2018, we sampled a wide array of the intended sites (17 out of 20), which provides the most recent and complete snapshot of benthic communities in both atolls. We obtained permission to access field sites and conduct scientific research from the Kiribati Ministry of Environment, Lands, and Agricultural Development for the 2018 surveys, and through an established research partnership with the Ministry of Fisheries and Marine Resource Development (MFMRD) for all previous surveys. Repeats of the 2018 surveys planned for 2020 had to be postponed indefinitely because of the COVID-19 pandemic.

All sites are on the ocean side of the atolls (i.e., we did not survey sites within the lagoons). Most sites are limited to the south and west rims of each atoll due to unsafe diving conditions and difficulties accessing the northern and northeastern reefs. As in previous work, sites located in the northern tip of North Tarawa (TRW005, TRW007) are grouped with sites from Abaiang because they are physically closer to Abaiang and have similar levels of human disturbance (Donner, Kirata and Vieux, 2010; Donner and Carilli, 2019). Going forward, I refer to sites in North Tarawa and Abaiang as ‘Abaiang’, and sites in South Tarawa as ‘Tarawa.’ This figure uses data extracted from the Millennium Coral Reef Mapping Project Version 4.0 (UNEP-WCMC *et al.*, 2018), and the OpenStreetMap Foundation, available under a CC BY-SA 2.0 license with permission from © OpenStreetMap contributors, original copyright 2012 (Open Street Map Foundation, 2021).

2.2.2 Survey methods

All data were collected between April and May in 2012, 2014, 2016, and 2018. Benthic community composition and size-frequency of coral communities were measured using the methods we described in a previous study (Cannon *et al.*, 2019). We collected data from a single 50-m transect at each site, laying the tape at a haphazardly-selected (unplanned) starting point at 10-m depth. We took 0.33m²-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. These photos were later analyzed to calculate the percent cover of macroalgae and coral genera, with other key benthic taxa, at each site (see Statistical analysis).

I also measured the length (in cm) of corals in situ along the transect, including all coral colonies ≥ 1 cm that lay at least partially within 25-cm on both sides of the tape. I considered corals with separate patches of living tissue > 3 -cm apart from each other independent and measured them individually. All corals were identified to the genus level, with the exception of *P. rus*, which I identified to the species level.

All identification relied on taxonomy from Veron (2000). Since this resource was published, the taxonomy of the Faviidae family has undergone several changes (Huang *et al.*, 2011). I was unable to reflect those changes in these analyses because the size-frequency data were collected in situ and the genera thus cannot be corrected to account for the most up-to-date taxonomy. I have included a list of species observed in Tarawa and Abaiang (Lovell, 2000) in the supplementary materials for reference (Appendix A.2).

I used photos from the transects to calculate benthic percent cover using the open-source web tool CoralNet (Beijbom *et al.*, 2012), which overlaid 20 random points per photo for 100 photos per site (for a total of 2000 points per site). I manually identified each point to the genus level for coral and macroalgae, and to functional group for sponges, soft corals, turf algae, crustose coralline algae (CCA), and cyanobacteria. I also identified the coral species *P. rus* to the species level. To estimate the impacts of 2014's CoTs outbreak, I manually counted the number of recent feeding scars visible in our photo quadrats at the sites we visited that year and identified the genera of the coral with the feeding scars. I considered scars recent if the dead coral patch was still white, and other organisms had not yet colonized the coral skeleton (e.g., algal turf). In this way, I avoided counting scars from bleaching or other causes of mortality, although this method likely underestimates the number of CoTs feeding scars as a result.

2.2.3 Human disturbance

I used two metrics to estimate different aspects of human disturbance. First, I used 2015 census data from Kiribati, which provides the population for each village in the nation (National Statistics Office, 2016), to calculate a population metric. Using ArcGIS ArcMap 10.6.1, I measured the distance from each reef site to the center of the nearest village and then divided the population of that village by the distance to the reef. This metric incorporates localised human disturbance that is related to population size and proximity to the reef (such as nutrification and fishing pressure).

I calculated the second human disturbance metric using the Normalized Difference Vegetation Index (NDVI), obtained from the United States Geological Survey's Land Satellite 8 imagery

following a method developed in a previous analysis of the neighbouring Republic of the Marshall Islands (Cannon *et al.*, 2019). NDVI measures the amount of green terrestrial vegetation within a 60-m pixel on a scale of -1.0 to +1.0 and is commonly used to represent the extent of human disturbance on terrestrial ecosystems. This metric captures human alterations of the landscape that are not necessarily related to local population size. I used NDVI in addition to the population metric described above to account for land-based disturbances where there are few permanent residents (e.g., Tarawa's Bonriki airport). NDVI has an inverse relationship with disturbance; a high NDVI value (i.e., a more green pixel) indicates a low level of disturbance.

To calculate the NDVI metric, I obtained satellite data from November 11, 2017 and February 8, 2018, selected for coverage of all sites and for the low cloud cover on those days. Because the Gilbert Islands are close to the equator, they do not experience seasonal changes in climate that could influence vegetation density, and the months selected are unlikely to impact the results. Using ArcGIS ArcMap 10.6.1, I mosaicked the satellite data into a single data layer, and then 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. I then calculated the average NDVI of the landmass, giving us a proxy to rank human influence at each site. For TRW014, the one site that was not within 1-km of land, I used the highest NDVI value from the sites closer to land (indicating the lowest level of disturbance, Appendix A.1).

2.2.4 Oceanographic data

To characterize the temperature and heat stress experience at each of the sites, I obtained time series of daily SST for all sites for the years 1985 through 2018 from 0.05° x 0.05° resolution

CoralTemp SST Version 3.1 satellite-derived data (Skirving *et al.*, 2020). I used the daily SSTs to calculate the Maximum Monthly Mean (MMM), the mean temperature of the warmest month in a 1985-1994 climatology, to represent the local climatological maximum SST prior to the first bleaching observations in the region and following NOAA Coral Reef Watch methods (Liu *et al.*, 2018). The MMM is used rather than the MMM_{max} —an alternative baseline developed to account for inter-annual variability in the timing of maximum monthly SST—because although the latter can lead to be more accurate bleaching predictions in regions with high inter-annual variability such as the Gilbert Islands, it produces higher rates of Type I errors and overestimates bleaching frequency (Donner, 2011). I also calculated the coefficient of variation of SST (CV_{SST}) for each site using the entire available dataset of SSTs from CoralTemp version 3.1 (1985 – 2018) to represent variation in SSTs (Liu *et al.*, 2018; Skirving *et al.*, 2020). Previous research has demonstrated that the CV_{SST} is highly correlated with metrics representing the latitudinal gradient in inter-annual climate variability in the region (e.g., frequency of annual heat stress, Donner and Carilli, 2019).

I also obtained the Degree Heating Weeks (DHW) for all sites for the years 1985 through 2018 from CoralTemp SST Version 3.1 satellite-derived data (Skirving *et al.*, 2020). The DHW (in $^{\circ}C \cdot weeks$) is a metric of accumulated heat stress that is widely used in real-time bleaching prediction. DHW values are the sum of weekly HotSpots—the difference between weekly SST and a local climatological maximum (the MMM)—over the previous 12 weeks. The Coral Reef Watch program releases a Bleaching Alert Level I when $DHW > 4^{\circ}C \cdot weeks$, and a Bleaching Alert Level II when $DHW > 8^{\circ}C \cdot weeks$ (Liu *et al.*, 2018; Skirving *et al.*, 2020).

Finally, I obtained the satellite-derived monthly chlorophyll-a (chl-a) concentration (in mg m³) via NASA's Moderate Resolution Imaging Spectroradiometer, from July 2002 – May 2019 (NASA, 2014), and applied a nearest value interpolation in order to fill missing values. I used this full dataset to calculate a mean chl-a value at each site to account for differences in net primary productivity across sites that might influence benthic community composition.

2.2.5 Wind and wave exposure

To account for differences in benthic community composition across sites and atolls that might be caused by wind and wave exposure and not human disturbance, I used a proxy for wind and wave exposure utilising the angle of each of the sites to the prevailing wind (following Cannon *et al.*, 2019). I first calculated the average prevailing wind direction ($p = 111^\circ$, roughly East-Southeast) for 2000 – 2008 using wind vector data recorded by the Kiribati Meteorological Service at the station in Betio, Tarawa. I used Google Earth Pro to draw lines at each site perpendicular to the reef crest, and then used the advanced ruler tool to measure the compass heading of that line at each site (C). Using the prevailing wind direction (p) and the compass heading (C), I calculated a normalized exposure metric, where 1 is maximum exposure (when the reef crest is exactly perpendicular to the prevailing wind) and 0 is minimum exposure to the prevailing winds:

$$\text{Exposure Metric} = 1 - (|(p - C)|)/180$$

2.2.6 Statistical analysis

I investigated change over time at available sites from 2012 – 2018 to test a series of hypothesis about the trajectories of coral reef communities after disturbance. All statistical analysis was done using R version 4.0.2 (R Core Team, 2021) and RStudio version 1.3.959 (RStudio Team, 2020). Plots were created with the R packages ggplot2 (Wickham, 2016) and ggbiplot (Vu, 2011).

I grouped the observed coral abundances and size-frequency analyses into seven categories comprising the taxa that collectively composed 99% or more of the benthic communities across all sites, referred to as “key taxa” in the remainder of the chapter. The hard coral taxa included the genera *Acropora*, *Heliopora*, *Montipora*, *Pocillopora* (genera), Favids (genera of the former family Faviidae), and massive *Porites* (morphology of genus *Porites*, including the species *Porites lutea* and *Porites lobata*), and the species *P. rus*. The octocoral *Heliopora* spp. is included in the coral taxa analysis because of its prevalence throughout the Gilbert Islands. Other frequent benthic taxa and substrate types included in the top 99% of observations were *Halimeda* and *Lobophora* (macroalgae genera), crustose coralline algae (CCA), corallimorphs, cyanobacteria, rubble, sand, soft corals, sponges, and turf algae.

I began by testing my first hypothesis that communities were dominated by bleaching-resistant coral taxa and macroalgae, and the second hypothesis that the shift in *P. rus* in Tarawa was persistent. To do so, I investigated the change in percent cover for each key taxon and substrate type over time using linear mixed effects models (LMM) with the R package lme4 (Bates *et al.*, 2015). I visually confirmed that the assumptions of normality were met using QQ plots for each

of the key taxa, followed by scatter plots to confirm that error terms met the assumption of equal variance when accounting for repeated measurements (described in next paragraph). I followed the LMM with chi-square tests and Tukey's post hoc tests.

I conducted post hoc analyses to in response to observed irregularities in how the data were distributed across reef morphologies, and to evaluate whether I needed to control for these irregularities *a priori*. Some sites had less common features than others and may have resulted in higher percent cover of sand in years when we visited these sites; for example, TRW010 is a reef with a spur-and-groove system that has deep and sometimes wide grooves consisting largely of sand, while sites TRW013 and TRW014 had lower live hard coral cover than other sites in Tarawa but were not visited for the first time until 2014, which might have given the impression that there was a large decline in coral cover across Tarawa between 2012 and 2014. To evaluate the effects of the uneven sampling, I omitted TRW013 and TRW014 and corrected the total live coral and *P. rus* cover at TRW010 in 2014 by removing sand from the total percent cover, which reduced the decline from 2012 to 2014 is reduced by two-thirds. Including TRW013 and TRW014 sites in the statistical analyses did not, however, affect the model results, and I therefore present the unadjusted values going forward.

The LMM allowed me to account for the uneven and repeated sampling of sites across years, using the equation: $\text{Percent} \sim \text{Year} + (1|\text{Site})$, where 'Percent' is the response variable, 'Year' is a fixed effect, and 'Site' is a random effect. I calculated conditional and marginal R^2 values using the Nakagawa method (Nakagawa, Johnson and Schielzeth, 2017), and tested the significance of 'Year' by comparing a null model (without 'Year' as a fixed effect) to a full model (which

included the fixed effect) using chi-square tests. I was unable to conduct a time series analysis with year an ordered variable and with autocorrelation because of the different number of sites within each of the years. Finally, I conducted Tukey's post hoc tests for each of the full LMM using the R package multcomp (Hothorn, Bretz and Westfall, 2008) to investigate the magnitude and direction of change in the percent cover of each taxa between years. I ran the models on three different datasets to ensure that the results were consistent despite the uneven sampling of sites: (1) the full dataset containing all sites, (2), from only the sites we visited each year from 2012 through 2018 (ABG001, ABG002, ABG003, TRW002, and TRW010, Appendix A.1); and finally (3) the sites where we found evidence of CoTs (Appendix A.1). Because of small sample sizes of some of the key taxa within each of the atolls (for example, *P. rus* was common in Tarawa but mostly absent in Abaiang) and the uneven sampling across years, I did not have enough observations for each of the key taxa both within atolls and across years to run the LMM separately for each atoll (the models were overfitted). I also conducted a similarity percentages analysis (SIMPER) using the full percent-cover dataset (999 permutations) (Clarke, 1993) in the vegan package in R (Oksanen *et al.*, 2020), to identify the key taxa driving differences in benthic communities across atolls and years.

To test the third hypothesis that massive *Porites* was more sensitive to CoTs but resistant to past heat stress, I ran an additional LMM, chi-square test, and Tukey's post hoc tests for massive *Porites* within Abaiang, where I had observed greater prevalence of CoTs scars (discussed further below).

I further tested the first hypothesis, along with the third hypothesis about the taxon-level response to the CoTs outbreak (and its disproportionate impact on massive *Porites* spp.) by investigating changes in the size-frequency distributions of key coral taxa over the study period. I did not include *P. rus* in the size frequency analysis, despite its prevalence in Tarawa, because this species grows in extensive mats covering wide areas, and we were unable to distinguish individual colonies. Size-frequency data were log-transformed to meet assumptions of normality, and critical values for all tests were adjusted using the Bonferroni correction to avoid Type I errors across multiple comparison tests. I first calculated demographic statistics on coral abundance and size for each of the key coral taxa (except for *P. rus*), including mean size, standard error, 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 than normal (McClanahan, Ateweberhan and Omukoto, 2008). I used the Kolmogorov-Smirnov test to compare size frequency distributions across years and atolls (Adjeroud *et al.*, 2007), and Welch's analysis of variance (ANOVA) tests to examine whether the mean size, coefficient of variation, skewness, or kurtosis for each of the six key taxa (excluding *P. rus*) varied over time (Adjeroud *et al.*, 2007). Again, I did not have enough observations of some of the key taxa within each atoll to separate the results of the Welch's ANOVA for sites within Abaiang and Tarawa individually.

I then used permutational-based multivariate analysis (PERMANOVA), to test the final hypothesis that the trajectories of benthic communities differed based on the magnitude of local human disturbance. The analysis, conducted with 99,999 permutations, (Anderson, 2001) using the vegan package (Oksanen *et al.*, 2020), tested for variation in site-level means of all benthic

taxa as explained by five environmental variables: mean NDVI, the population metric, wind-and-wave exposure, the coefficient of variation of SST, and mean chl-a. To test for the effects of drivers that changed across years, I also considered ‘Year’ as a grouping factor, with each of these explanatory factors nested within ‘Year’:

$$\text{Percent} \sim (\text{mean NDVI} + \text{population metric} + \text{wind and wave exposure} + CV_{SST} + \text{mean chl-a}) : \text{Year}$$

In the equation above, ‘Percent’ is the response variable while the explanatory variables within parentheses are nested within the grouping factor, ‘Year’. Although PERMANOVA is not sensitive to collinearity, we excluded atoll as a factor because a factor analysis conducted using the R package psych (Revelle, 2020) found that atoll and the population metric were closely correlated (F-statistic = 76.17, $p < 0.001$) and because it did not add to the fit or explanatory power of the model. Instead, in addition to the PERMANOVA that included all sites from both atolls, I also ran the PERMANOVA separately for each atoll to investigate whether there were differences in how each of these factors influenced the benthic compositions within atolls.

2.3 Results

2.3.1 Disturbance history

I quantified the disturbances affecting reefs during our study period, to test our specific hypotheses about coral reef community trajectories post-disturbance. NOAA’s Coral Reef Watch historical SST data indicates that reefs in Abaiang and Tarawa experienced bleaching-level heat stress twice between 2012 and 2018. DHWs were greater than $8^{\circ}\text{C}\cdot\text{week}$ in 2012-2013 and 2014-2015, and again six months after the last surveys were conducted in 2018 (Figure 2.2). The

2013-14 CoTs outbreak is described in a later section.

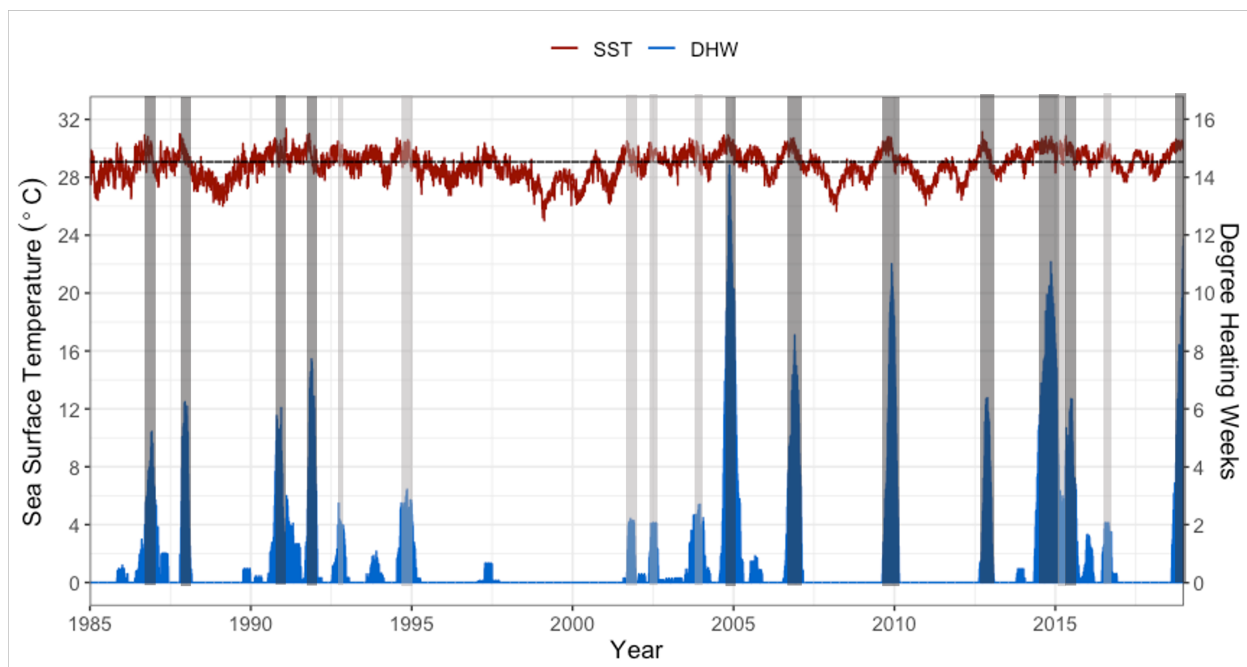


Figure 2.2. Daily sea surface temperature (red), Degree Heating Weeks (blue) averaged across study sites from 1985 through 2018, with the Maximum Monthly Mean (black). Light grey bars represent DHWs > 4 and dark grey bars represent DHWs > 8.

Two-way ANOVAs confirmed that the premise of this study – that the two atolls differ in the intensity of local human activities – is supported using current estimates of human population density and NDVI. I found that sites within the two atolls experienced different levels of local human disturbance, as represented by the population metric and mean NDVI. The means of the site-specific population metric was significantly different across atolls, and the NDVI and population metric are highly correlated (F-statistic = 76.17, $p < 0.001$, adjusted $R^2 = 0.81$). The means of the site-specific NDVI values were also significantly different across atolls, but the correlation between atoll (as an explanatory factor) and NDVI is less strong (F-statistic = 13.304,

$p < 0.001$, adjusted $R^2 = 0.23$).

2.3.2 Benthic community trajectories between 2012 and 2018

The percent cover data by site and year for each of the key taxon are presented in Figure 2.3. In Abaiang, both the average percent hard coral cover and the average percent macroalgae cover across all sites declined from 2012 to 2016, and then increased from 2016 to 2018. In Tarawa, hard coral cover and macroalgae cover followed slightly different trajectories (Figure 2.3). Hard coral cover declined from 2012 to 2014, increased from 2014 to 2016, and then remained steady from 2016 to 2018; macroalgae cover declined from 2012 to 2014, and then increased from 2014 to 2018.

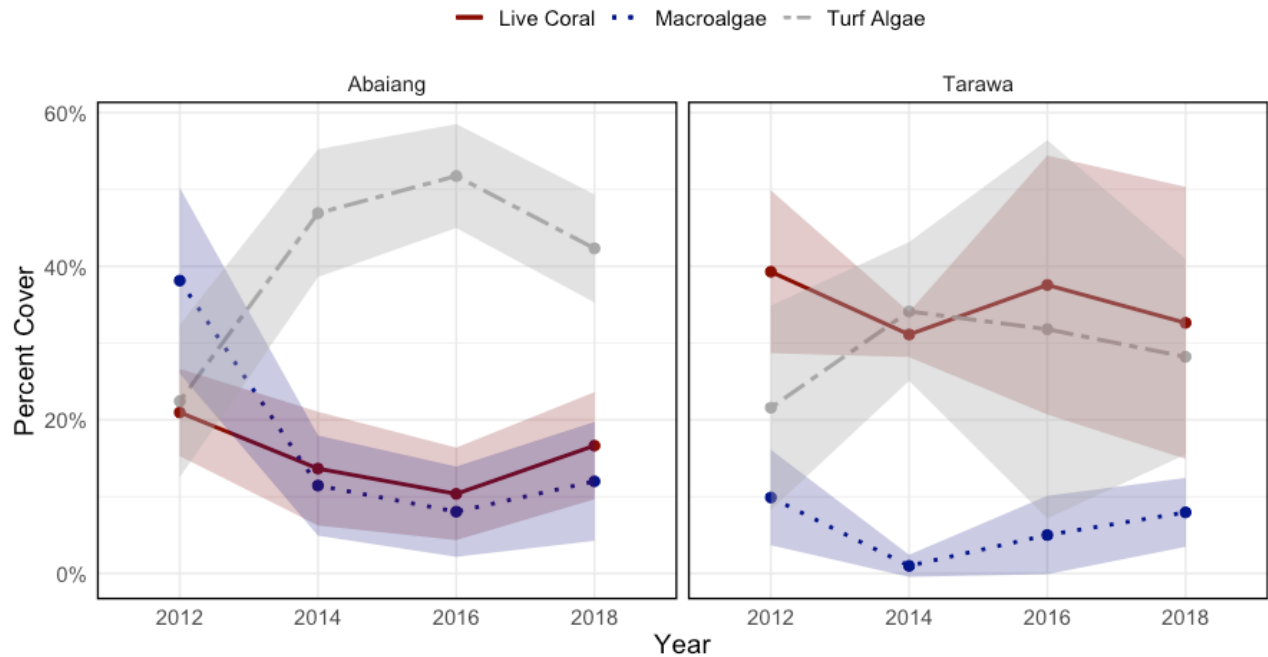


Figure 2.3. Time series of mean percent cover of live coral, macroalgae, and turf algae by atoll.

The results for the LMMs, including all sites across both atolls, suggest that the percent cover of several key taxa changed significantly from 2012 – 2018 (Table 2.2). The change in percent cover of all live coral varied significantly across years ($\chi^2 = 8.36$, $p = 0.04$), as well as changes in Favids ($\chi^2 = 15.00$, $p < 0.01$), *Heliopora* ($\chi^2 = 8.59$, $p = 0.04$), *Montipora* ($\chi^2 = 16.41$, $p < 0.01$), and *Pocillopora* ($\chi^2 = 14.77$, $p < 0.01$) genera, and massive *Porites* ($\chi^2 = 9.62$, $p = 0.02$) morphology. The percent cover of macroalgae genera also varied significantly across years ($\chi^2 = 19.68$, $p < 0.01$) and for *Halimeda* specifically ($\chi^2 = 14.27$, $p < 0.01$), as well as for CCA ($\chi^2 = 7.95$, $p = 0.05$), rubble ($\chi^2 = 9.81$, $p = 0.02$), sponges ($\chi^2 = 14.09$, $p < 0.01$), and turf algae ($\chi^2 = 14.34$, $p < 0.01$). While I was unable to separate these results by atoll, some of the taxa were only present in one atoll or the other, which allows me to extrapolate which atolls were most affected; *P. rus* and corallimorphs were rare in Abaiang, while massive *Porites* were rare in Tarawa. A

repeat of the LMM using only those sites that we visited every year found similar results (Appendix A.3), so all sites for which we gathered data are used in the following analyses.

Table 2.1. Mean and standard deviations of the percent cover of key benthic category, for each survey year by atoll.

Category	Atoll	2012	2014	2016	2018
Hard Coral Taxa					
All Live Coral	Abaiang	20.97 ± 5.68	16.37 ± 7.75	11.47 ± 6.86	18.26 ± 7.45
	Tarawa	39.28 ± 10.60	14.16 ± 9.83	27.84 ± 19.17	28.26 ± 16.87
<i>Acropora</i>	Abaiang	0.20 ± 0.20	0.17 ± 0.17	0.02 ± 0.04	0.21 ± 0.13
	Tarawa	0.33 ± 0.41	1.09 ± 1.26	0.09 ± 0.04	0.11 ± 0.13
Favids	Abaiang	2.41 ± 0.57	0.28 ± 0.27	0.34 ± 0.46	2.35 ± 1.25
	Tarawa	0.41 ± 0.48	0.24 ± 0.40	0.07 ± 0.06	0.99 ± 1.24
<i>Heliopora</i>	Abaiang	6.00 ± 4.25	8.59 ± 5.28	3.03 ± 2.31	6.52 ± 4.40
	Tarawa	3.89 ± 3.09	2.40 ± 1.50	1.91 ± 1.43	1.81 ± 1.56
<i>Montipora</i>	Abaiang	0.33 ± 0.01	0.09 ± 0.11	0.00	0.58 ± 0.27
	Tarawa	0.18 ± 0.17	0.23 ± 0.26	0.08 ± 0.09	0.37 ± 0.42
<i>Pocillopora</i>	Abaiang	1.20 ± 0.21	1.09 ± 0.88	0.57 ± 0.33	2.90 ± 1.65
	Tarawa	1.56 ± 1.14	1.04 ± 1.10	1.29 ± 1.14	2.07 ± 1.14
Massive <i>Porites</i>	Abaiang	6.17 ± 1.98	4.92 ± 4.93	3.09 ± 4.85	3.23 ± 2.25
	Tarawa	0.71 ± 0.26	0.94 ± 1.20	0.23 ± 0.16	0.65 ± 0.72
<i>P. rus</i>	Abaiang	0.11 ± 0.03	0.06 ± 0.05	0.26 ± 0.42	0.07 ± 0.04
	Tarawa	28.31 ± 13.97	5.05 ± 4.19	22.19 ± 19.83	23.49 ± 19.84
Macroalgae Taxa					
All Macroalgae	Abaiang	38.13 ± 12.09	13.86 ± 5.96	7.93 ± 7.19	13.29 ± 8.70
	Tarawa	9.90 ± 6.21	2.61 ± 3.88	5.40 ± 4.91	7.99 ± 3.96
<i>Halimeda</i>	Abaiang	38.10 ± 12.04	13.74 ± 5.92	2.68 ± 0.40	13.04 ± 8.71
	Tarawa	2.40 ± 3.47	2.27 ± 4.30	1.88 ± 3.44	3.09 ± 4.03
<i>Lobophora</i>	Abaiang	0.00	0.10 ± 0.14	5.17 ± 6.80	0.12 ± 0.11
	Tarawa	8.00 ± 4.06	0.86 ± 1.37	4.21 ± 5.06	6.70 ± 4.64
Other Benthic Taxa					
CCA	Abaiang	6.99 ± 0.52	10.38 ± 3.31	12.27 ± 2.31	9.83 ± 4.72
	Tarawa	4.48 ± 2.04	9.34 ± 4.95	9.54 ± 4.42	9.02 ± 3.74
Corallimorphs	Abaiang	0.00	0.05 ± 0.00	0.00	0.07 ± 0.03
	Tarawa	8.85 ± 15.12	2.79 ± 2.38	2.64 ± 4.32	4.30 ± 5.74
Cyanobacteria	Abaiang	2.76 ± 1.87	2.33 ± 0.66	1.96 ± 1.67	2.43 ± 2.42
	Tarawa	4.50 ± 1.65	3.09 ± 5.22	4.69 ± 4.43	8.67 ± 4.86
Rubble	Abaiang	2.49 ± 2.07	6.43 ± 4.45	8.90 ± 5.30	4.32 ± 3.10
	Tarawa	2.07 ± 1.20	7.69 ± 4.45	3.29 ± 3.46	2.67 ± 3.02
Sand	Abaiang	4.06 ± 3.21	6.70 ± 5.07	4.65 ± 2.85	8.31 ± 5.80
	Tarawa	9.48 ± 12.20	17.46 ± 14.19	8.74 ± 9.25	5.20 ± 7.78
Soft Coral	Abaiang	0.02 ± 0.04	0.27 ± 0.25	0.25 ± 0.44	0.13 ± 0.16
	Tarawa	0.13 ± 0.19	0.00	0.04 ± 0.05	0.14 ± 0.12
Sponges	Abaiang	1.95 ± 0.41	1.34 ± 0.48	3.59 ± 1.19	2.05 ± 0.91
	Tarawa	6.59 ± 3.33	1.58 ± 1.03	4.05 ± 1.69	4.52 ± 1.76
Turf Algae	Abaiang	22.45 ± 9.92	42.25 ± 4.25	48.73 ± 3.76	41.22 ± 6.96
	Tarawa	21.58 ± 13.28	41.49 ± 13.61	35.52 ± 24.98	31.69 ± 13.71

The difference between marginal and conditional R^2 values in the LMM indicates the extent of the variance explained by the sites surveyed (the random effect) and the year (the fixed effect). For example, the cover of some taxa, such as *Montipora* spp., varied more with the year of the survey (conditional $R^2 = 0.35$, or 35% of the variance) than the sites surveyed (marginal R^2 - conditional $R^2 = 0.10$, or 10%) (Table 2.2). For all live coral cover, the entire model explained 89% of the variance, with the majority of that (86%) explained by differences across sites, and only 3% explained by the difference across years. Similarly, the entire model explained most of the variance in massive *Porites* spp. (79%), with sites surveyed explaining 72% of the variance and the year of the survey explaining 7% (Table 2.2). This is not surprising, given that I found most massive *Porites* spp. colonies at sites in Abaiang.

Table 2.2. Results of linear mixed effects models for each key benthic category. Statistically significant results at $\alpha = 0.05$ are in bold, while those that are significant at $\alpha = 0.10$ are underlined.

Categories	χ^2	p	Marg R ²	Cond R ²
Hard Coral Taxa				
All Live Coral	8.36	0.04	0.03	0.89
<i>Acropora</i>	<u>7.74</u>	<u>0.05</u>	<u>0.18</u>	<u>0.19</u>
Favids	15.00	<0.01	0.32	0.49
<i>Heliopora</i>	8.59	0.04	0.05	0.79
<i>Montipora</i>	16.41	<0.01	0.35	0.45
<i>Pocillopora</i>	14.77	<0.01	0.14	0.68
<i>Porites</i> (Massive)	9.62	0.02	0.07	0.79
<i>P. rus</i>	<u>6.75</u>	<u>0.08</u>	<u>0.02</u>	<u>0.91</u>
Macroalgae Taxa				
All Macroalgae	19.68	<0.01	0.29	0.53
<i>Halimeda</i>	14.27	<0.01	0.26	0.55
<i>Lobophora</i>	5.15	0.16	0.09	0.33
Other Benthic Categories				
CCA*	7.95	0.05	0.14	0.38
Corallimorphs	4.06	0.26	0.12	0.51
Cyanobacteria	5.21	0.16	0.08	0.41
Rubble	9.81	0.02	0.14	0.53
Sand	<u>6.33</u>	<u>0.10</u>	<u>0.06</u>	<u>0.71</u>
Soft Coral	1.48	0.69	0.04	0.40
Sponges	14.09	<0.01	0.16	0.64
Turf algae	14.34	<0.01	0.17	0.66

*CCA = crustose coralline algae

The statistically significant results of the Tukey analyses are shown in Table 2.3 (full results in Appendix A.4). The mean live coral percent cover declined by an estimated 7.59% across all sites from 2012 to 2014 ($z = -2.74$, $p = 0.03$). The percent cover of Favids, *Montipora* spp., and *Pocillopora* spp. all increased modestly between 2014 and 2018 and between 2016 and 2018 (Table 2.3), while massive *Porites* spp. was the only key coral taxon to decline significantly at $\alpha = 0.05$ (by 1.92% between 2012 – 2016, $z = -3.00$, $p = 0.01$). While the percent change of the total benthic taxa across both atolls was small, massive *Porites* spp. in Abaiang declined in half (from $6.17 \pm 1.98\%$ in 2012 to $3.09 \pm 4.85\%$ in 2016, Table 2.1). The Tukey results show that

the percent cover of macroalgae declined significantly, while the percent cover of turf algae increased during the same periods. In Abaiang, there was roughly a two-thirds decline of *Halimeda* over our study period (from $38.10 \pm 12.04\%$ in 2012 to $13.04 \pm 8.71\%$ in 2018, Table 2.1), and an almost doubling of turf algae (from 22.45 ± 9.92 in 2012 to 41.22 ± 6.96 in 2018, Table 2.1). All other key taxa changed by less than 5% over the given time periods (Table 2.3).

Table 2.3. Significant results of Tukey Contrasts Multiple Comparisons of Means for changes in percent cover, using $\alpha = 0.05$.

Categories	Years	Estimate	St. Error	z-value	p-value
<i>Hard Coral Taxa</i>					
All Live Coral	2012 – 2014	-7.59	2.77	-2.74	0.03
Favids	2014 – 2018	1.40	0.42	3.32	<0.01
	2016 – 2018	1.40	0.42	3.38	<0.01
Montipora	2014 – 2018	0.30	0.11	2.70	0.03
	2016 – 2018	0.42	0.10	4.18	<0.01
Pocillopora	2014 – 2018	1.06	0.33	3.25	<0.01
	2016 – 2018	1.05	0.31	3.43	<0.01
Massive Porites	2012 – 2016	-1.92	0.64	-3.00	0.01
<i>Macroalgae Taxa</i>					
All Macroalgae	2012 – 2014	-14.70	3.47	-4.24	<0.01
	2012 – 2016	-14.46	3.42	-4.23	<0.01
	2012 – 2018	-11.61	3.26	-3.57	<0.01
Halimeda	2012 – 2014	-13.99	4.47	-3.13	<0.01
	2012 – 2016	-19.13	4.61	-4.15	<0.01
	2012 – 2018	-12.95	4.44	-2.92	0.02
<i>Other Benthic Categories</i>					
CCA	2012 – 2016	4.53	1.65	2.74	0.03
Rubble	2012 – 2014	3.92	1.41	2.79	0.03
	2014 – 2018	-3.02	1.16	-2.60	0.04
Sponges	2012 – 2014	-2.41	0.71	-3.40	<0.01
	2014 – 2016	1.96	0.61	3.19	<0.01
	2014 – 2018	1.70	0.59	2.89	0.02
Turf Algae	2012 – 2014	16.88	5.04	3.35	<0.01
	2012 – 2016	18.67	4.85	3.89	<0.01
	2012 – 2018	13.38	4.61	2.90	0.02

In addition to changes in the percent cover of these taxa, I found that the average size (in cm) of key coral taxa declined between 2012 and 2018. The only exception is *Acropora* spp. in Tarawa, which increased from a mean size of 10.3 cm in 2012 to 12.3 cm in 2018 (Table 2.3.2.4) but remained rare (average of two colonies per site in 2018). With some exceptions (Favids and

Acropora spp. in Tarawa), skewness increased for most of the key taxa, showing an overall shift to smaller sizes. Kurtosis, a measure of the steepness of the size-distribution curve, also increased for most coral taxa, suggesting that the size-frequency of each taxon has become more concentrated among a smaller range of values. By 2018, the size of most key coral taxa decreased, the range of sizes also decreased, and smaller corals dominated most of the benthic communities in each atoll compared to 2012. None of the changes in mean size (in cm) and skewness among the key taxa between 2012 and 2018 were significant according to Welch's two-way ANOVA tests, although the kurtosis and coefficient of variation did change significantly for *Montipora* spp. and massive *Porites* spp. (Appendix A.5).

Table 2.4. Size-frequency statistics for key coral taxa. Skewness and kurtosis values that are significantly different from normal (greater than two times the standard error) are in bold.

	Year	Abaiang							Tarawa						
		n*	Mean Size (cm)	Standard Error (SE)	Skewness	Skewness SE	Kurtosis	Kurtosis SE	n*	Mean Size (cm)	Standard Error (SE)	Skewness	Skewness SE	Kurtosis	Kurtosis SE
<i>Acropora</i>	2012	3	22.0	4.8	1.0	1.5	-0.1	3.1	4	10.3	1.5	1.6	1.3	2.4	2.5
	2014	1	24.3	7.5	-1.8	2.4	3.6	4.9	10	15.0	6.3	6.0	0.8	36.4	1.6
	2016	1	5.0	0.0	NA	2.8	NA	5.7	1	9.9	2.2	0.5	1.9	-1.3	3.7
	2018	6	12.9	0.9	1.4	0.7	2.2	1.5	2	12.3	1.9	1.6	1.3	2.4	2.6
<i>Favids</i>	2012	22	22.6	1.7	1.0	0.6	0.1	1.2	7	10.5	1.4	1.7	0.9	3.2	1.9
	2014	10	5.2	0.3	1.4	0.6	2.0	1.1	19	9.0	0.8	1.5	0.6	2.8	1.1
	2016	11	6.8	0.4	1.2	0.8	0.9	1.5	10	5.1	0.3	1.7	0.6	3.2	1.2
	2018	142	8.2	0.1	4.7	0.1	48.5	0.3	16	8.8	0.4	1.3	0.4	1.9	0.8
<i>Heliopora</i>	2012	16	56.1	5.4	1.4	0.7	2.5	1.4	15	22.6	2.9	2.9	0.6	9.9	1.3
	2014	18	22.0	1.5	1.6	0.4	2.3	0.8	18	15.4	1.2	0.9	0.6	0.2	1.2
	2016	7	10.3	1.4	1.6	0.9	1.7	1.8	43	9.7	0.8	4.9	0.3	30.6	0.6
	2018	69	13.5	0.7	4.1	0.2	23.9	0.4	32	10.2	0.6	3.6	0.3	18.0	0.6
<i>Montipora</i>	2012	1	18.3	8.8	0.9	2.8	NA	5.7	2	28.5	5.3	0.8	2.0	0.3	4.0
	2014	2	6.7	1.4	2.0	1.4	4.4	2.8	2	22.8	5.7	0.4	2.0	0.9	4.0
	2016	3	8.8	0.8	0.8	1.5	1.9	3.0	1	7.4	0.9	-1.3	1.9	1.9	3.7
	2018	17	12.9	0.6	1.6	0.4	3.8	0.8	2	16.0	2.1	1.0	1.3	0.8	2.5
<i>Pocillopora</i>	2012	11	25.4	2.0	0.3	0.8	-0.3	1.7	14	21.0	1.5	1.0	0.6	0.5	1.3
	2014	3	21.9	1.9	-0.6	1.0	-0.3	2.0	9	21.4	2.1	1.1	0.8	3.2	1.7
	2016	4	16.3	3.5	1.2	1.3	0.5	2.5	13	21.9	1.3	0.8	0.6	1.6	1.1
	2018	69	10.2	0.4	2.3	0.2	5.4	0.4	121	16.1	1.0	1.9	0.4	5.4	0.7
Massive <i>Porites</i>	2012	18	45.5	4.9	1.8	0.7	3.7	1.3	2	31.7	7.5	0.5	2.0	-0.6	4.0
	2014	16	20.7	2.0	2.0	0.4	3.5	0.9	2	15.9	6.1	2.1	1.6	4.6	3.3
	2016	5	8.1	0.9	1.8	1.2	4.8	2.3	5	6.5	0.5	0.2	0.9	-0.9	1.9
	2018	72	10.7	0.5	5.5	0.2	40.6	0.4	4	19.1	3.2	2.1	0.9	5.5	1.7

n* = n-values normalized to the number of sites we visited each year in each atoll.

Two-sample Kolmogorov-Smirnov (KS) tests found that the size distribution of Favids (D = 0.82, p-adjusted < 0.01), *Heliopora* genus (D = 0.51, p-adjusted < 0.01), and the massive morphology of the *Porites* genus (D = 0.53, p-adjusted < 0.01) had significantly changed in

Abaiang, but not Tarawa, among all years of the dataset. The results are similar comparing 2012 and 2018, with Favids ($D = 0.69$, p -adjusted < 0.01) and massive *Porites* spp. ($D = 0.76$, p -adjusted < 0.01), which are uncommon in Tarawa, size distributions differing only in Abaiang.

Finally, I used the SIMPER analysis to identify and rank the taxa that had contributed the most to changes in the percent cover over time. In Abaiang, the changes in percent cover of *Halimeda* spp. (macroalgae) and turf algae were significant components of the variation of benthic taxa (Table 2.5). In Tarawa, *P. rus*, turf algae, corallimorphs, sand, and *Lobophora* spp. (macroalgae) contributed the most to changes in percent cover across time, although none of these taxa were statistically significant components of variation across time.

Table 2.5. Most influential taxa in benthic community difference between 2012-2018, as identified by SIMPER analysis. Statistically significant results are in bold.

2012 – 2018					
Abaiang			Tarawa		
Taxa	%*	p	Taxa	%*	p
<i>Halimeda</i>	33.38	0.01	<i>P. rus</i>	23.50	0.61
Turf algae	24.97	0.02	Turf algae	19.55	0.90
Sand	8.01	0.23	Corallimorphs	0.14	0.10
CCA**	4.84	0.36	Sand	8.26	0.97
--	--	--	<i>Lobophora</i>	6.16	0.52
--	--	--	Cyanobacteria	6.08	0.66
Total (%)	72.21	--	Total (%)	72.69	--

* Percent contribution

** Crustose coralline algae

At the end of the observation period, five of the seven sites in Tarawa had higher percent cover of live coral than any sites in Abaiang, despite experiencing greater localized human disturbance (Figure 2.4A). The live coral cover in Tarawa was almost entirely composed of the weedy coral *P. rus* (81.48% of all coral cover) while sites in Abaiang were composed of comparatively more

diverse coral assemblages, including higher cover of the *Pocillopora* spp. and the octocoral genera *Heliopora* spp. (Figure 2.4B).

2.3.3 The effect of the CoTS outbreak

To test the hypothesis that the taxon-level responses to the CoTs outbreak in 2014 differed from that those to the bleaching that occurred prior to the study, I counted the number of recent CoTs scars by taxon at all sites in 2014. Almost all the sites where CoTs scars were observed in the surveys were in Abaiang; only one (TRW010) was in Tarawa (Appendix A.1). CoTs scars were most frequently noted on massive *Porites* spp., which accounted for 130 of the 146 observed scars (89%). The remaining 11% of scars were observed on *P. rus* (n = 6), the Favid family (n = 4), and the genera *Platygyra* (n = 2) and *Turbinaria* (n = 2), the table morphology of the *Acropora* genus (n = 1), and the encrusting morphology of the genus *Porites* (n = 1).

I also conducted a LMM using only those sites with evidence of CoTs but found similar results to LMM using all sites (Appendix A.3). I found that the year of the survey was a significant factor in the model ($\chi^2 = 8.27$, $p = 0.04$). The Tukey analysis also showed that within Abaiang, the percent cover of massive *Porites* spp. declined significantly between 2012 and 2016, by 3.00% (St. Err = 1.11, $z = -2.72$, $p = 0.03$), as suggested by analysis of the CoTs scars observational data.

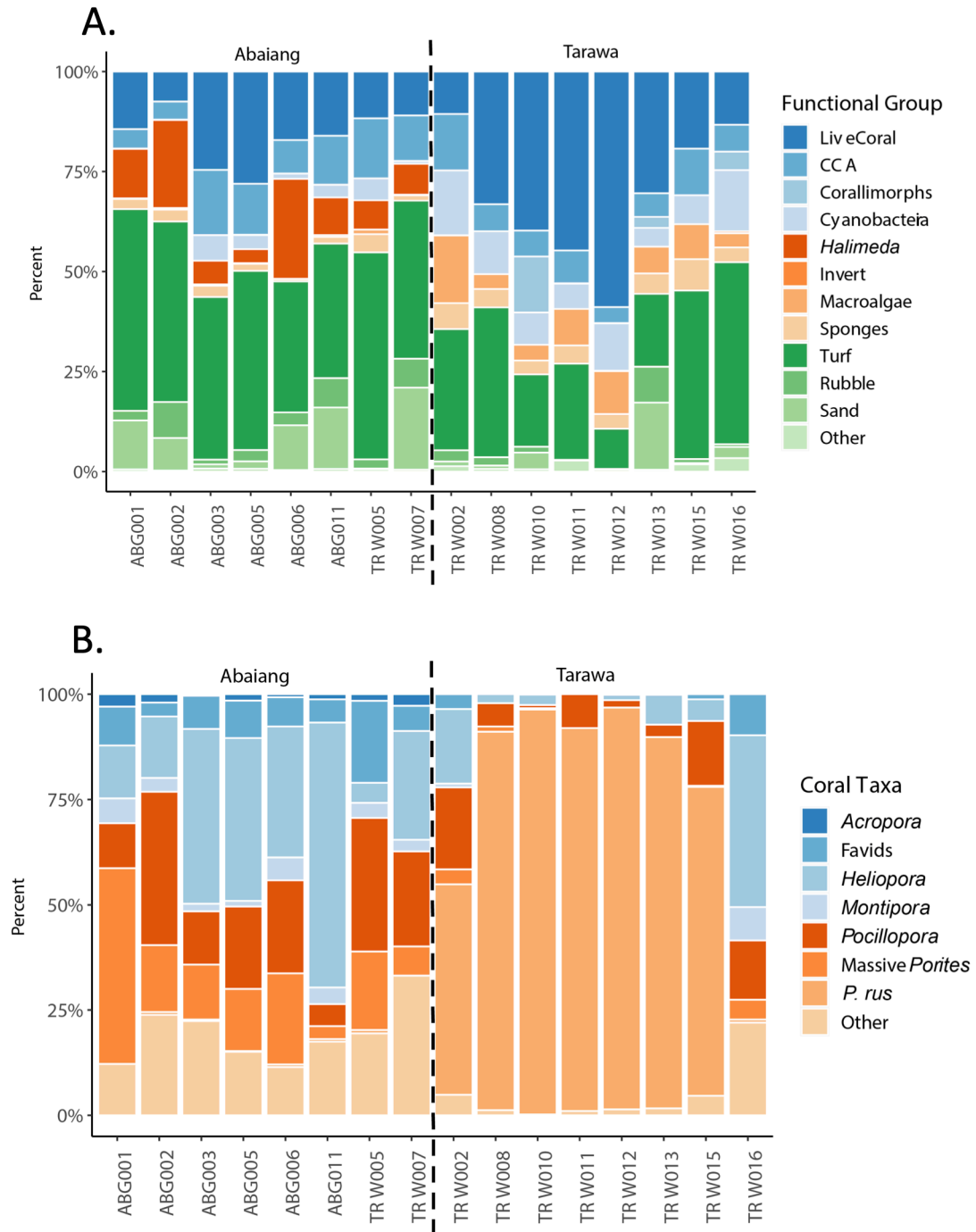


Figure 2.4. Percent cover of benthic taxa in 2018.

(A) Percent cover of key functional groups. (B) Percent cover of key reef-building coral taxa.

The cover of massive *Porites* spp. declined by over 20% between 2012 and 2014 in Abaiang (from 6.17% cover in 2012 to 4.92% in 2014) and by 50% between 2012 and 2016 (3.09% in 2016), and the latter decline was statistically significant (Tukey post-hoc test, $z = -2.72$, $p = 0.03$) while the former was not (Appendix A.4). The average size of massive *Porites* also declined in Abaiang, from 45.5 cm in 2012 to 10.7 cm in 2018. While this change was not statistically significant, the KS test confirms that the size distribution of massive *Porites* spp. shifted significantly to smaller sizes over time in Abaiang (Appendix A.3).

2.3.4 The role of human disturbance

I used a PERMANOVA to test the final hypothesis, that local human disturbance was a significant factor driving changes in community composition over time (Table 2.6). Overall, the model containing data from all sites accounted for 44.74% of the variation in the benthic communities (Pseudo-F = 4.86, p -value < 0.01). The model results show that time alone ('year') explained little of the variation in percent cover across the benthic communities (3% of the variation) and was not statistically significant (Pseudo-F = 1.74, p -value = 0.14). The interaction between year and mean NDVI contributed most to the variation in the percent cover, and collectively explained 25% of the variation in community composition across sites ($p < 0.01$). The other statistically significant interactions were between year and CV_{SST} (7% of the variance, $p < 0.01$) and the population metric (6% of the variance, ($p < 0.01$).

I also ran the PERMANOVA separately for each atoll (Table 2.6) to test for change over time and its potential attribution to local human disturbance. In Abaiang, the full model (Table 2.6) accounted for 51.14% of the variation in benthic community composition across sites (Pseudo-F

= 2.27, $p = 0.01$), while in Tarawa it accounted for 62.87% of the variation (Pseudo-F = 4.52, $p < 0.01$). In Abaiang, 'Year' was the only significant factor in the model at $\alpha = 0.05$ ($F = 3.53$, $p = 0.02$), explaining 13% of the difference in benthic composition across sites. By contrast, in Tarawa, the percent cover changed differently across years based on the mean NDVI (Pseudo-F = 10.55, $p < 0.01$) and the population metric (Pseudo-F = 3.21, $p = 0.03$). The interactions between Year and the two metrics of human influence collectively accounted for 31% of the variation across sites in Tarawa (Year and Mean NDVI accounted for 24% of the variation, and Year and the population metric accounted for 7%). The interaction between Year and Chl-a was also significant in Tarawa (Pseudo-F = 7.99, $p < 0.01$), accounting for 19% of the variation across sites.

Table 2.6. PERMANOVA of predictors of benthic composition across sites. Statistically significant values are in bold.

	All Sites				Abaiang				Tarawa			
Factor	SS ¹	R ²	F	p	SS ¹	R ²	F	P	SS ¹	R ²	F	p
Year	0.14	0.03	1.74	0.14	0.14	0.13	3.52	0.02	0.10	0.04	1.82	0.14
Year: Mean NDVI	1.27	0.25	16.16	<0.01	0.11	0.10	2.67	0.05	0.58	0.24	10.55	<0.01
Year: Mean Chl- a	0.11	0.02	1.43	0.21	0.05	0.05	1.27	0.26	0.44	0.19	7.99	<0.01
Year: CV _{SST}	0.37	0.07	4.71	<0.01	0.09	0.08	2.25	0.08	0.09	0.04	1.65	0.18
Year: Population Metric	0.32	0.06	4.11	<0.01	0.05	0.05	1.27	0.26	0.18	0.07	3.21	0.03
Year: Exposure	0.08	0.02	1.01	0.37	0.10	0.10	2.62	0.05	0.10	0.04	1.87	0.13
Residual	2.83	0.55	--	--	0.52	0.49	--	--	0.88	0.37	--	--

¹Sum of Squares

2.4 Discussion

This study investigated how the benthic communities at sites experiencing different levels of localized human-related degradation responded to a series of acute environmental stressors, and also identified and documented the coral reef community trajectories after those stressors. In addition to the coral bleaching events in the Gilberts that preceded the study period (2004-2005 and 2009-2010), which were described and evaluated in detail by Donner and Carilli (2019), there was a CoTs outbreak in 2014 and bleaching-level heat stress from 2014 through 2016, although the MFMRD did not report any bleaching and evidence was not apparent in the data. While it is possible that bleaching occurred between 2014 and 2016 and went unobserved, corals may not have bleached because the community composition in both atolls has shifted towards dominance by more heat-resistant coral taxa, such as *P. rus* in Tarawa and *Heliopora* spp. and massive *Porites* spp. in Abaiang (Donner and Carilli, 2019). Also, while the heat stress in 2014 through 2016 was long-lasting, the magnitude never reached the levels of the 2004-05 and 2009-10 events ($>12^{\circ}\text{C}\cdot\text{week}$) (Figure 2.2).

The analysis broadly confirmed four hypotheses about the trajectories of these coral reef communities, with some caveats (discussed further below). First, the LMM analyses suggest that after the bleaching events in 2004/2005 and 2009/2010, these communities shifted towards dominance by taxa that are less affected by heat stress over the study period. Second, those results also suggest the shift to *P. rus* in Tarawa, documented in previous studies (Donner, Kirata and Vieux, 2010; Donner and Carilli, 2019), were persistent and could represent a phase shift. Third, the scar observations and coral cover data indicate that the taxon-level response to the CoTs outbreak differed from that of bleaching (with massive *Porites* spp. more sensitive to CoTs

but resistant to bleaching). Finally, the analysis of the 2018 data indicates that the benthic communities after the sequence of acute disturbances (heat stress and the CoTs outbreak) differed based on the level of local human disturbance.

These results show that most sites in Tarawa and Abaiang have followed the trajectories shown in Figure 2.5, discussed further below. While ‘site’ explained more of the variation in percent cover than ‘year’ for some taxa, these were all found in one atoll or the other (for example, *P. rus* was almost entirely limited to sites in Tarawa while massive *Porites* spp. were limited mostly to Abaiang). As indicated by the PERMANOVA, these distinct trajectories were correlated with different levels of human disturbance across Tarawa and Abaiang (as mentioned above, the variability of SST did not vary much across sites). Before the bleaching event in 2004-2005, previous studies reported that outer reefs in Abaiang had high (>50%) coral cover, and communities were dominated by massive *Porites* spp., *Pocillopora* spp., *Heliopora* spp., Favids, the macroalgae *Halimeda* spp., and to a lesser extent, *Acropora* spp. In Tarawa, outer reef communities tended to have low coral cover, and were dominated by *Pocillopora* spp., *P. rus*, and *Heliopora* spp. (Lovell, 2000; Donner, Kirata and Vieux, 2010). After the 2004-2005 and 2009-2010 bleaching events, reefs in Abaiang shifted to lower coral cover dominated by hardier, slower-growing corals (like massive *Porites* spp.), and *Heliopora* sp., a branching thermally-tolerant octocoral, while reefs in Tarawa adjacent to growing human communities shifted to higher coral cover that was almost entirely composed of *P. rus* (Donner, Kirata and Vieux, 2010; Donner and Carilli, 2019). While I found that Abaiang’s reefs were more impacted by bleaching and CoTs, they may still be able to recover to a similar coral-dominated state as what was there prior to these acute disturbances, due to the relative lack of localized human influence (discussed

below). These results suggest that sites in Tarawa, by contrast, may have undergone a phase shift and settled into their current state, with sites that are dominated by *P. rus*. Below I discuss the trajectories of the coral reefs in Tarawa and Abaiang, respectively, the impact of CoTs relative to bleaching, and finally the implications of these results for future resource management in the Gilbert Islands.

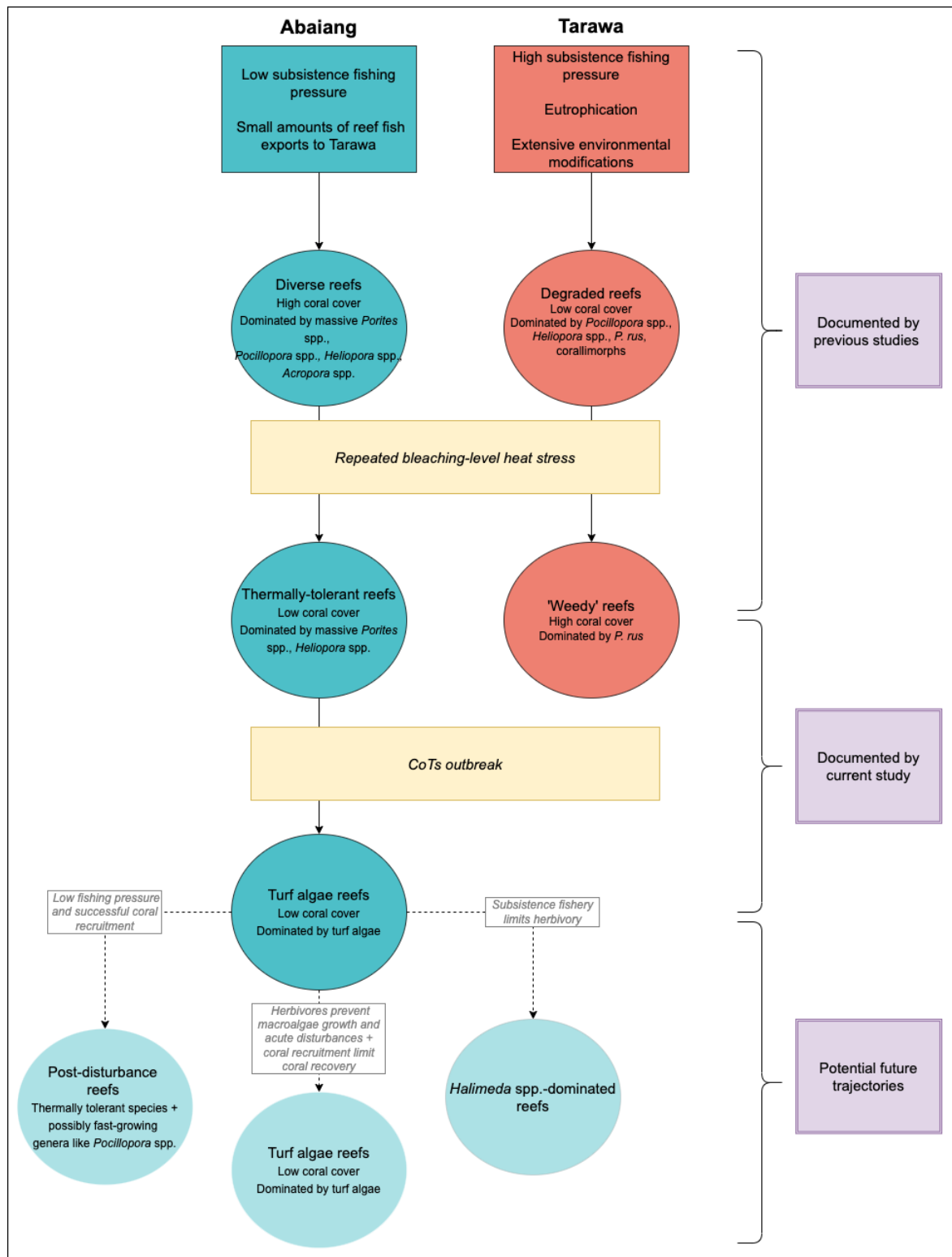


Figure 2.5. Proposed drivers of community composition on reefs in Tarawa and Abaiang.

2.4.1 Tarawa

The results of this and past studies support the first and second hypotheses, that the outer reefs in Tarawa adjacent to dense human communities (which were well represented in the sites we surveyed, and are spaced along the southern rim of urbanized Tarawa Atoll, Figure 2.1) have shifted to dominance by disturbance-tolerant taxa, and that the coral reef communities adjacent to dense human populations in S. Tarawa have undergone a phase shift to communities dominated by a single coral species, *P. rus*. Here, when I say ‘dominated’, I mean that *P. rus* is the most common single taxon found on those reefs, not necessarily that it accounts for more than 50% cover. While reports of phase shifts from coral to macroalgae-dominated reefs are more common, studies from Micronesia and the Pacific region have observed phase shifts to weedy coral species (Crane *et al.*, 2016), sponges (Bell *et al.*, 2013; Powell *et al.*, 2014) and corallimorphs (Work, Aeby and Maragos, 2008; Crane *et al.*, 2016).

A report on the state of the sewage system in Tarawa suggests that the benthic community’s shift to *P. rus*-dominance could have been begun as early as the mid-1980s, when installation of the sewage pipes damaged corals along the reef flats and crests (Kirata *et al.*, 2005). Unlike many other corals, *P. rus* is tolerant of nutrient loading, turbidity, and heat stress (Loya *et al.*, 2001; McClanahan, 2004; Putnam *et al.*, 2012). The percent cover of *P. rus* remained relatively stable between 2012 and 2018 (representing on average between $28.31 \pm 13.97\%$ in 2012 to $26.51 \pm 19.03\%$ in 2018 across sites in Tarawa), although there was a decline from 2012 to 2014 due in part to previously mentioned sampling issues (see Methods). This decline in *P. rus* between 2012 and 2014 could have also been in part the result of CoTs predation, although I did not find much evidence to support this. I only observed one example of CoTs feeding in Tarawa (and recorded

only six CoTs scars, all from a single site), although this may have been the result of the sampling method, because scars are easier to identify on massive *Porites* spp. than *P. rus*.

Research discussing phase shifts on coral reefs often consider recovery to the ‘original’ state, or phase shift reversals, as a goal for conservation efforts, while noting that the nature of phase shifts makes this difficult (Bellwood, Hughes and Hoey, 2006; Graham *et al.*, 2013). Reversing a phase shift requires addressing the underlying drivers of change, which may ultimately create conditions that facilitate the natural recovery of reefs (Graham *et al.*, 2013). One of the most pressing and long-standing issues for reefs in Tarawa is the effects of sewage on the local water quality. In other places, when sanitation systems were improved, local reefs were able to recover from local degradation, although it took several decades before the effects were realized. For example, in Kāne’ohe Bay, Oahu, Hawai’i, reefs shifted from coral dominance to communities dominated by the macroalgae *Dictosphaeria cavernosa* after sewage was discharged into the bay. Like Tarawa, reefs in Kāne’ohe Bay also experienced other stressors, including dredging and siltation. In 1977, the sewage was diverted out of the bay, and by 2006, *D. cavernosa* had virtually disappeared. Since then, coral cover has increased, and after 44 years of research, researchers have declared that this a successful example of a phase shift reversal (Lamare *et al.*, 2014; Caballes, 2017; Stimson, 2018).

While this example shows that removing sources of nutrient pollution can allow reefs to recover from degradation over long time scales, if the relatively stable benthic communities found in Tarawa have entered an alternative stable state, long-term recovery may be more challenging than simply removing the source. However, the definition of an alternative stable state is still

being debated. Dudgeon et al (2010) define them as occurring when ecosystems exhibit hysteresis (i.e. more than one state can exist under the same environmental conditions at different times). Per this definition, ecosystems with multiple stable states cannot be restored by simply reversing the stressor causing the system to shift into an alternative stable state (Scheffer *et al.*, 2001; Norström *et al.*, 2009). Others define alternative stable states as community changes resulting from trends of environmental change (Beisner, Haydon and Cuddington, 2003); by this definition, there is no difference between an alternative stable state and a phase shift. There is also debate over whether alternative stable states exist at all in nature (Petraitis and Dudgeon, 2004).

Regardless of how alternative stable states are defined (and whether they exist), as Fung et al. (2011) point out, tackling multiple human stressors simultaneously can maximize coral reef resilience to phase shifts. Because I had no way of empirically testing whether sites in Tarawa have undergone phase shifts or entered an alternative stable state, I do not speculate further here. Reversing all the threats facing coral reefs in Tarawa will not be possible; coral reef resources are integral for local food and economic security, and while the water quality will likely improve after the sewage system updates, some nutrient pollution is unavoidable. Because of the ‘wicked’ nature (Head and Alford, 2013) of human-related coral reef degradation in Tarawa, direct human intervention (via coral transplantation projects, for example) will likely be required to change the state of local reefs regardless of whether they entered an alternative stable state and/or have undergone a phase shift. However, tracking whether water quality improves with the new sewage system would be prudent prior to investing limited management resources in active coral restoration in S. Tarawa. Restoration projects that transplant corals onto degraded reefs without

addressing the underlying stressors are unfortunately often unsuccessful (Boström-Einarsson *et al.*, 2020). A pilot coral restoration project is currently underway in S. Tarawa and will provide more information on whether coral restoration is a viable strategy for increasing reef resilience in this location (Fellenius, 2019).

Understanding the trade-offs associated with the shift to *P. rus*-dominant reefs will therefore be integral for local decision makers who are tasked with conserving reefs and the ecosystem services that they provide in S. Tarawa. For example, a reef dominated by a single species like *P. rus* may be less able to protect shorelines from wave activity than reefs that are more diverse and are home to a wider range of coral morphologies, although confirming this requires further study. That said, recent work from these sites found that there was not a significant difference in the rugosity (or structural complexity) of reefs between Abaiang and Tarawa (Summers and Donner, 2022), and complexity is key to reefs' ability to protect shorelines (Ferrario *et al.*, 2014). This difference in structural complexity across atolls is likely because of the low coral cover in Abaiang (Summers and Donner, 2022), and if reefs in Abaiang are able to regain coral cover and larger colonies, we may see that reefs in Abaiang become more structurally complex than those in Tarawa in the future.

2.4.2 Abaiang

In Abaiang, where the population is smaller compared to the urban communities found along the southern rim of Tarawa, *P. rus* is rare or absent at all sites (Table 2.1). Sites in Abaiang do not experience the same influx of nutrients and sediments that are found in Tarawa, nor do they experience high fishing pressure. The results supported the first hypothesis, that post-disturbance

communities shifted to dominance by disturbance-resistant benthic taxa. After the 2004-2005 bleaching event, coral reef communities in Abaiang were dominated by relatively thermally tolerant coral taxon such as massive *Porites* spp. They may have remained in this state after the 2004-2005 bleaching event had they not experienced further disturbance, but the 2013-2014 CoTs outbreak, along with 2009-2010 bleaching event, likely drove the shift in benthic communities toward a turf-dominated state. As a result, coral cover dropped to the lowest measured since the 2004-2005 bleaching event $11.47 \pm 6.86\%$, with half the sites below the proposed 10% cover threshold necessary for reefs to grow fast enough to keep up with rising sea levels (Perry *et al.*, 2015). Although coral cover increased to 18.26 ± 7.45 percent in 2018, one of the sites (ABG002) remained below the 10% threshold.

As hypothesized, the CoTs outbreak disproportionately affected massive *Porites* spp. in Abaiang, one of the ‘winners’ after the 2004-2005 and 2009-2010 bleaching events. The results show that massive *Porites* spp. has declined in terms of the percent of the benthos it covers, and the size-structure of the community has shifted towards smaller size classes, which may indicate fragmentation due to partial mortality from the CoTs outbreak. This explanation is consistent with other studies, which found that CoTs outbreaks commonly cause partial mortality of coral colonies (Cameron, Endean and DeVantier, 1991). The fragmentation of massive *Porites* spp. could have long-term implications for coral communities in Abaiang. For example, smaller corals of reproductive age release less gametes, which will likely slow recovery of massive *Porites* populations (Baird, Guest and Willis, 2009). Massive *Porites* spp. are also slow-growing, stress-tolerant corals, and recovery from disturbance therefore takes longer than it might for faster-growing genera like *Acropora* spp. (although fast-growing, competitive corals also tend to

be less resilient to environmental perturbations; this could explain why *Acropora* spp. were rare in Abaiang) (Darling *et al.*, 2012).

Previous analyses found that the percent cover of *Pocillopora* spp. declined significantly between 2004 and 2012 (Donner and Carilli, 2019), which may have made massive *Porites* spp. more vulnerable to CoTs predation in 2014. *Pocillopora* spp. is often one of the ‘losers’ of coral bleaching events, while massive *Porites* spp. are more tolerant of heat stress and are more likely to be ‘winners’; this is consistent with what Donner and Carilli (2019) observed when investigating the impacts of the 2004-2005 and 2009-2010 bleaching events. *Pocillopora* spp., a branching genus of coral, also may indirectly protect massive *Porites* spp. from predation by CoTs. Both *Acropora* and *Pocillopora* spp. are preferred food of CoTs, and thus CoTs will consume those genera over massive *Porites* spp. when there is plenty of prey available (Pratchett *et al.*, 2017; Haywood *et al.*, 2019). CoTs will actively avoid feeding on massive *Porites* spp. unless its preferred foods are scarce (De’ath and Moran, 1998).

I found some evidence that reefs in Abaiang could be beginning to recover from coral loss after bleaching in 2004/2005 and 2009/2010, and the CoTs outbreak. Although the cover of the many common taxa remained low (as a percent) in all years, the mean percent cover of *Pocillopora* spp. in Abaiang increased by over 60% between 2014 and 2018 (from $1.09 \pm 0.88\%$ in 2014 to $2.90 \pm 1.65\%$ in 2018), while the mean cover of Favids increased by 88% (from $0.28 \pm 0.27\%$ in 2014 to $2.35 \pm 1.25\%$ in 2018), and *Montipora* spp. increased by 85% (from $0.09 \pm 0.11\%$ in 2014 to $0.58 \pm 0.27\%$ in 2018). Overall, the mean live coral cover in Abaiang in 2018 increased by almost 40% between 2016 ($11.47 \pm 6.86\%$) and 2018 ($18.26 \pm 7.45\%$). I had originally

planned to repeat our benthic surveys in 2020, but these plans were delayed indefinitely because of COVID; future surveys will hopefully help to further untangle the current and future trajectories of reefs in Abaiang.

I have suggested three potential recovery scenarios for reefs in Abaiang, which are currently dominated by turf algae. In one scenario, the reefs follow a trajectory similar to that experienced by a reef in Moorea, where researchers were able to observe the entire trajectory of a CoTs outbreak (Adjeroud *et al.*, 2009). Like what we observed from Abaiang, turf algae were the first taxa to colonize the empty spaces left after CoTs had decimated coral populations, but coral dominance returned about a decade post-disturbance, and the communities went from coral-dominant to turf algae-dominant, and then back to coral-dominant. Under this scenario, Abaiang's communities recover to become dominated by thermally-tolerant species such as massive *Porites* spp. and *Heliopora* spp., along with some fast-growing species, such as *Pocillopora* spp. but likely not *Acropora* spp. Because *Pocillopora* spp. reproduce via brooding, its recovery is not density-dependent like most *Acropora* spp., which are vulnerable to Allele effects (Baird, Guest and Willis, 2009; Teo and Todd, 2018; Hughes *et al.*, 2019). Corals of the *Acropora* genera were rare in Abaiang prior to the study period (Donner and Carilli, 2019), and bleaching and CoTs both disproportionately negatively affect *Acropora* spp. (Keesing *et al.*, 2019).

Alternatively, it is possible that reefs in Abaiang will experience a shift towards dominance by *Halimeda* spp. the future (with *Halimeda* spp. cover exceeding that of turf algae), if the local reef fishery sufficiently limits herbivory on reefs; *Halimeda* spp. is vulnerable to predation from

common herbivorous reef fish, in particular *Acanthuridae* spp. and *Scaridae* spp. (Brown *et al.*, 2018). The data suggest this is unlikely, given that *Halimeda* spp. has declined significantly over the current study period (Table 2.2). Indeed, the case study from Moorea suggests that a phase shift to macroalgae dominance would require an additional disturbance post-CoTs, such as a reduction in grazing due to fishing pressure or poor water quality (Adjeroud *et al.*, 2009). We have no evidence that either of these two conditions currently exist in Abaiang.

The third potential scenario we propose for reefs in Abaiang is that they remain in their current turf-dominated state. If future acute disturbances occur in Abaiang, they may prevent coral communities from recovering. However, I also find it unlikely that benthic communities in Abaiang will remain dominated by turf algae given that the percent cover and size frequency of corals have both changed after disturbance in Abaiang. A previous study found that massive *Porites* spp. in the Gilberts that survived bleaching in 2004-2005 were less susceptible to bleaching in 2009-2010 (Carilli, Donner and Hartmann, 2012). This suggests that the corals remaining in Abaiang that survived both bleaching (in 2004/2005 and 2009/2010) and CoTs are less likely to bleach during future heat stress events.

2.4.3 CoTs outbreak

Previous research suggested that low-latitude coral reefs might be less susceptible to CoTs outbreaks because CoTs are not tolerant of SSTs that are higher than 30°C (Lamare *et al.*, 2014; Caballes *et al.*, 2017). Survivorship, particularly of larvae and juveniles, declines above 30°C, and temperatures above 29°C can negatively impact embryonic and larvae development (Pratchett *et al.*, 2017). Extended La Niña conditions lowered SSTs in the Gilberts from 2010 –

2013, during which SST at our sites averaged 28.62°C, just below the 29°C temperature threshold for negative impacts on CoTs larvae development (for comparison, the mean SST for 2010-2018 was 29.08°C). These slightly cooler-than-average conditions could have facilitated the survival of CoTs larvae, contributing to the outbreak in 2013-2014. However, CoTs may be able to adapt to increasing SSTs (Sparks *et al.*, 2017), in which case Tarawa and Abaiang may be vulnerable to more CoTs outbreaks in the future. I recommend that future studies investigate the potential links between ENSO events and CoTs outbreaks in the central Pacific (for example, see Houk and Raubani, 2010; Houk *et al.*, 2020).

The CoTs affected sites in Abaiang disproportionately, and I am unable to account for the different severities of the outbreak across atolls. CoTs larvae may have been more likely to settle and survive at some sites than others. Their survival and impact at specific reefs may have varied by local conditions, including oceanography, water quality, and the amount and type of coral prey available and quality. Further, many of the dynamics of CoTs larvae settlement and their survival post-settlement are largely unresolved (Pratchett *et al.*, 2017). While larvae may have reached Tarawa at the same time as Abaiang, they may not have been as successful at settling and/or reaching maturity in Tarawa, but it is unlikely that this differential survivorship would be due to excess nutrients in Tarawa; on the Great Barrier Reef, researchers have found that CoTs outbreaks are positively correlated with high levels of nutrients (Brodie *et al.*, 2005; Brodie, Devlin and Lewis, 2017). CoTs will actively avoid feeding on *P. rus* in favor of other corals, but they will feed on less-preferred prey when their preferred food items are scarce (Done, 1992; Sonoda and Paul, 1993; Caballes, 2017).

Because I was not able to conduct reef surveys at beginning of the outbreak, these data represent a limited snapshot of the event at one point in time. Reports by MFMRD from the outer atolls suggest the outbreak was widespread, stretching from Butaritari Atoll (3°N) to at least Abemama Atoll (~0°), where a related team observed a CoTs outbreak during fieldwork in October – November, 2013 (Kiareti *et al.*, 2013). Synchronous outbreaks of CoTs over wide distances has occurred before (Moran, 1986); still, even I assumed that all sites in Abaiang were affected by CoTs, I am unable to say whether all sites experienced the same levels of predation and/or outbreak duration. In addition, the CoTs scars I counted in Abaiang are likely underestimated because we only counted scars that were recent (as indicated by the visibility of the coral skeleton); any scars that had already been colonized by turf algae or other taxa were excluded because I could not say positively how old they were or that they were not caused by other factors.

2.4.4 Disturbance, reef health, and resilience

The sites at both atolls exhibit characteristics that are the opposite of what would be expected based on the most common metrics of disturbance on coral reefs, for example, the percent of all macroalgae or the percent of all live coral cover. For example, high macroalgae cover is often used by coral reef researchers to quantify degradation or to distinguish between ‘healthy’ and ‘unhealthy’ reefs (Cannon *et al.*, 2019). However, macroalgae was most common on reefs in Abaiang (and had very low cover in Tarawa). The percent cover of the macroalgae genera *Halimeda* has declined over time in Abaiang, while turf algae has increased. Sites in Abaiang had lower coral cover than sites in Tarawa; if I had chosen to consider the percent cover of all live coral a metric for reef health, I may have mistakenly concluded that sites in Tarawa are

healthier and less degraded than those in Abaiang. That said, while reefs in Abaiang are arguably less impacted by local human disturbance than reefs in Tarawa (that is, less impacted by local human disturbance), I also would not necessarily consider them ‘healthy,’ given that the community composition in Abaiang at the end of our study period is the result of repeated acute disturbances from which they have yet to recover. Past work in the Marshall Islands similarly found that using broad categories of taxa like macroalgae and live coral to classify the health of coral reefs could be misleading and lead to incorrect conclusions (Cannon *et al.*, 2019). Here, I echo that call to use more concise metrics and language when discussing the state of coral reefs facing multiple stressors at different scales.

This work may support the hypothesis proposed by other reef scientists that more degraded reefs may be more resistant to the impacts of climate change (Côté and Darling, 2010; Bruno, Côté and Toth, 2019), which is contrary to the argument that controlling local stressors could improve resistance to and recovery from temperature stress and other acute disturbances (Bruno, Côté and Toth, 2019). For example, sites in Tarawa were more impacted by local stressors than sites in Abaiang, but the coral cover has remained higher in Tarawa. The percent cover of *P. rus* did not change significantly over time in Tarawa, indicating that *P. rus* was largely unaffected by both heat stress and the CoTs event. There is evidence that *P. rus* is indeed insensitive to heat stress (Loya *et al.*, 2001; McClanahan, 2004; Putnam *et al.*, 2012), and is also not significantly affected by short-term exposure to high pCO₂ (Comeau, Carpenter and Edmunds, 2013). Combined with the evidence that *P. rus* is also resilient to localized human impacts such as nutrient loading and turbidity, I find it likely that *P. rus* will be able to outcompete other species that are more sensitive to multiple stressors in the future, particularly if local impacts continue unabated

(although the sewage upgrades will likely reduce nutrient loading). Unlike other corals that are sensitive to high pCO₂, increased acidification does not appear to negatively impact calcification rates of *P. rus*, and researchers do not expect that the calcification of this species will be affected strongly by the projected increase in pCO₂ that is expected to occur by the end of the century (Comeau, Carpenter and Edmunds, 2013).

However, for a coral reef to be considered resilient, it must be both resistant to disturbance and be able to recover to the original community structure post-disturbance, without an associated loss in function and services (Côté and Darling, 2010). I have provided further evidence that the *P. rus*-dominated reefs in Tarawa are more resistant to heat stress than those in Abaiang, which is in agreement with previous studies (Donner and Carilli, 2019). Sites in Abaiang may become more resistant to heat stress in the future, depending on their recovery trajectory (if, for example, coral cover increases and is composed of more thermally tolerant genera). Also, because sites in Tarawa were dominated by a single coral species (*P. rus*), they are potentially vulnerable to future ‘ecological surprises’ (Berumen and Pratchett, 2006); any disturbance that has a disproportionate impact on *P. rus* could have a severe impact on the ecosystem as a whole. There may have been a loss in function and services associated with the phase shift to *P. rus* at sites in Tarawa, but this requires further research. If the shift to *P. rus* did cause a decline in ecosystem services, it would indicate that while these reefs are resistant to heat stress, they may not be resilient. Surveys of fish and invertebrate assemblages in Tarawa and Abaiang, as well as repeating the monitoring of reef structural complexity done by Summers and Donner (2022) to monitor changes over time, would provide useful information about how the phase shift to *P. rus*

is influencing the ecosystem services that are valuable to people residing in Tarawa and whether these are different from the services reefs provide in Abaiang.

Coral reefs in the Gilbert Islands have experienced years with prolonged heat stress more frequently than 99% of the world's coral reefs (Donner and Carilli, 2019), but this may change in the future; other reefs will likely experience more heat stress going forward, given that climate change-driven global coral bleaching events have increased in frequency and are expected to continue increasing in the due to climate change (Hughes *et al.*, 2018). Reefs in the Gilbert Islands could therefore provide a rare glimpse into what reefs may look like in the future while also accounting for a gradient of local human impacts. I hope this work will provide novel information that is important for the future management of coral reef resources. Because coral reefs in the Gilbert Islands could provide a glimpse of what reefs in other parts of the world may look like as heat stress becomes more frequent and widespread (Donner and Carilli, 2019), these findings may be useful for predicting the ways that climate change will affect reefs, and the millions of people around the world who depend on them, so that they may prepare for the future.

Chapter 3: Interactions between local disturbance and climate-driven heat stress on central Pacific coral reefs

3.1 Introduction

Coral reefs have come to epitomize the effects of climate change after several global bleaching events, driven by increasing sea surface temperatures (SSTs), occurred over the last three decades. While scientists widely agree that climate change is the greatest existential threat to coral reefs today, perspectives are more divided on the relative impact of local anthropogenic threats like fishing and pollution, especially when trying to understand how these local threats interact with climate impacts and what to do in response. As the climate continues to warm, there is a pressing need to identify the most effective ways to protect these threatened ecosystems and to support the millions of people depending on them, for example by increasing coral reef resilience to climate-related stressors.

Researchers have conventionally assumed that local human stressors reduce the resilience – defined as the resistance to and recovery from the effects of a given stressor – of coral reefs to climate change (Darling and Côté, 2013) and there is some evidence to support this assumption. For example, improving water quality (Wooldridge and Done, 2009; Carilli *et al.*, 2010) and management actions that limit macroalgae cover– such as preventing nutrient pollution and the overfishing of herbivores (Donovan *et al.*, 2021)– may increase coral resilience to heat stress. This has led many scientists to argue that strategies to reduce local stressors, such as creating marine protected areas, are crucial tools for ensuring that coral reefs persist into the future

(Hoegh-Guldberg *et al.*, 2007; Mellin *et al.*, 2016). However, some research finds that reducing local impacts does not influence coral reefs resistance to heat stress, and may actually make reefs more susceptible to bleaching through the “protection paradox”, in which reducing one set of stressors selects for species that are more sensitive to other stressors (Bates *et al.*, 2019). Still other research finds that protected areas can play a role in protecting coral reef ecosystems and reef fish populations under climate change, but that the species and functional groups benefiting from this protection has shifted to benefit low trophic level herbivores (Graham *et al.*, 2020).

One way to untangle the complex interactions between local and global stressors on coral reefs is to categorize them by interaction type, for example as additive (where the combined effects of two or more stressors are equal to the sum of the individual effects) or multiplicative, which includes synergistic effects (those with cumulative effects that are greater than an additive interaction), and antagonistic effects (those with cumulative effects that are less than an additive interaction; Folt *et al.*, 1999). Antagonistic interactions may increase coral reef resilience to multiple stressors, and in some cases, can even diminish the effects of the worst single stressor (Folt *et al.*, 1999). By contrast, by amplifying the effects of each independent stressor, negative synergistic interactions can decrease coral reef resilience, leading to ‘ecological surprises’ (Paine, Tegner and Johnson, 1998). The conventional view that local human disturbance decreases coral reef resilience to climate change presumes that both stressors interact to have an overall negative effect on coral reefs, and are synergistic; one stressor (local human disturbance) reduces the ability of reefs to respond to a second stressor (climate-driven heat stress) (Darling and Côté, 2013; Bruno and Valdivia, 2016; Cabral *et al.*, 2019). By contrast, the Protection Paradox presumes that heat stress and local human disturbance interact antagonistically, in which

the negative effects of local human disturbance preconditions coral reefs to withstand heat stress (Bates *et al.*, 2019).

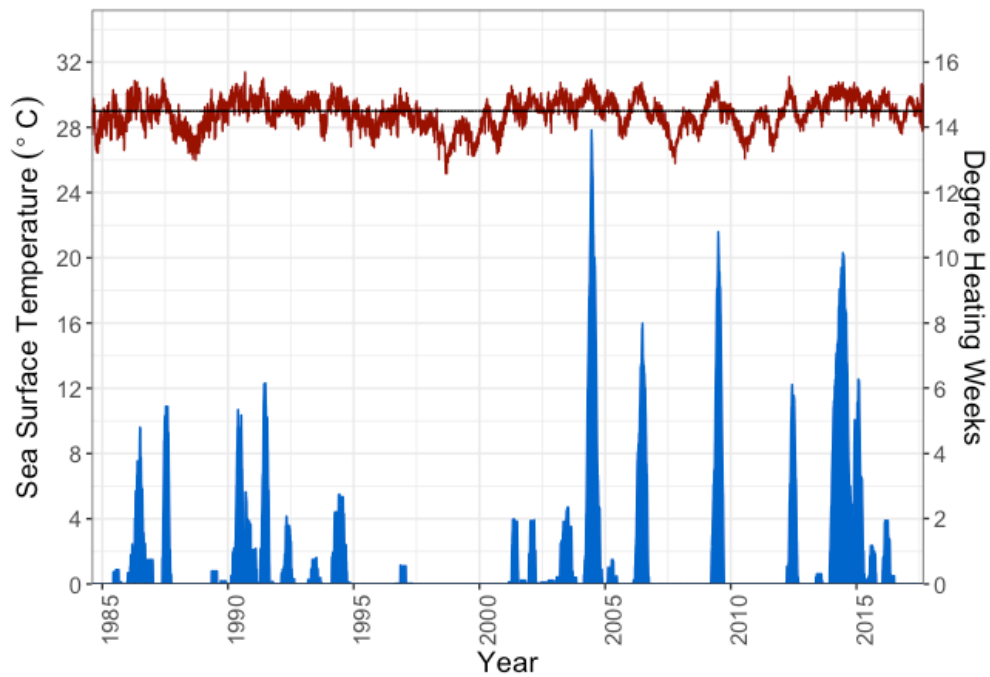
Because negative synergistic interactions are seen as the worst case scenario for ecosystems facing multiple stressors, there is a broad body of research seeking to quantify synergistic interactions and identify where interventions are possible to prevent the most extreme outcomes (Crain, Kroeker and Halpern, 2008; Gunderson, Armstrong and Stillman, 2016; Cabral *et al.*, 2019; Ellis and Mehrabi, 2019; Pancrazi *et al.*, 2020). However, scientists are increasingly recognizing that synergisms are less common than once thought, resulting in an overemphasis on synergistic interactions in research about multiple stressors, with potentially harmful implications for conservation (Côté, Darling and Brown, 2016). Management efforts often assume that stressors will interact additively (Sorte and Bracken, 2015), because local interventions will theoretically produce greater than expected results if interaction between stressors are synergistic (Crotty, Angelini and Bertness, 2017). However, at best, assuming that stressors are synergistic may result in managers prioritizing less effective conservation actions. At worst, if the interaction is antagonistic, management actions could backfire and be detrimental to the ecosystems that managers are working to conserve (Côté and Darling, 2010; Brown *et al.*, 2013). Past studies confirm that synergisms are common (Crain, Kroeker and Halpern, 2008; Darling and Côté, 2008; Cabral *et al.*, 2019), but these may not represent realistic interactions *in situ* because they were mostly based on laboratory research that often applied stressors simultaneously and constantly (Gunderson, Armstrong and Stillman, 2016; Cabral *et al.*, 2019). In addition, the focus on identifying synergisms may have led to underreporting of other interaction types. A review found that only 15% of 616 papers in the ecological literature

investigating multiple stressors mentioned antagonisms (Côté, Darling and Brown, 2016), even though Darling and Côté (2008) reported that antagonistic interactions were most common among experimental studies.

While field studies are necessary to confirm the relationships identified *ex situ*, in marine ecosystems, *in situ* studies are geographically biased, and most publications researching interactions between global and local stressors in marine environments are from the temperate Atlantic and Pacific Oceans (Gissi *et al.*, 2021). Surprisingly, there have been no studies investigating relationships between global and local stressors affecting coral reefs in the central or eastern tropical Pacific, despite the presence of unique gradients in environmental conditions caused by El Niño / Southern Oscillation (ENSO). In the central Pacific, the frequency of bleaching-level heat stress decreases sharply away from the equator. During El Niño events, the trade winds and the South Equatorial Current (SEC), which travels along the equator, weaken, bringing warmer-than-average SSTs from the Western Pacific Warm Pool to the central and eastern equatorial Pacific. During Central Pacific (CP, also called Modoki-type) El Niño events, the weakening or reversal does not extend as far east, causing warm water to pool near Kiribati's equatorial Gilbert Islands (from 2°S to 2°N) until CP El Niño conditions dissipate (Liu *et al.*, 2017). As a result, the coral reefs in the Gilbert Islands experience frequent bleaching-level heat stress (e.g., Degree Heating Week [DHW] > 4 °C·week or NOAA Bleaching Alert Level 1 occurred in 10 different years from 1985-2019). By contrast, coral reefs in the southern Republic of the Marshall Islands (RMI) just to the north lie in a different current regime (the eastward Pacific North Equatorial Countercurrent) and experience more uniform year-to-year SSTs and weaker SST anomalies from ENSO; these reefs have yet to experience DHW > 4°C·week in the

satellite record. The capital atolls of the RMI (Majuro) and Kiribati (Tarawa) are about 665 kilometers apart, a distance less than 1/3 of the length of the Great Barrier Reef, but experience sharply contrasting ocean climates (Figure 3.1).

A.



B.

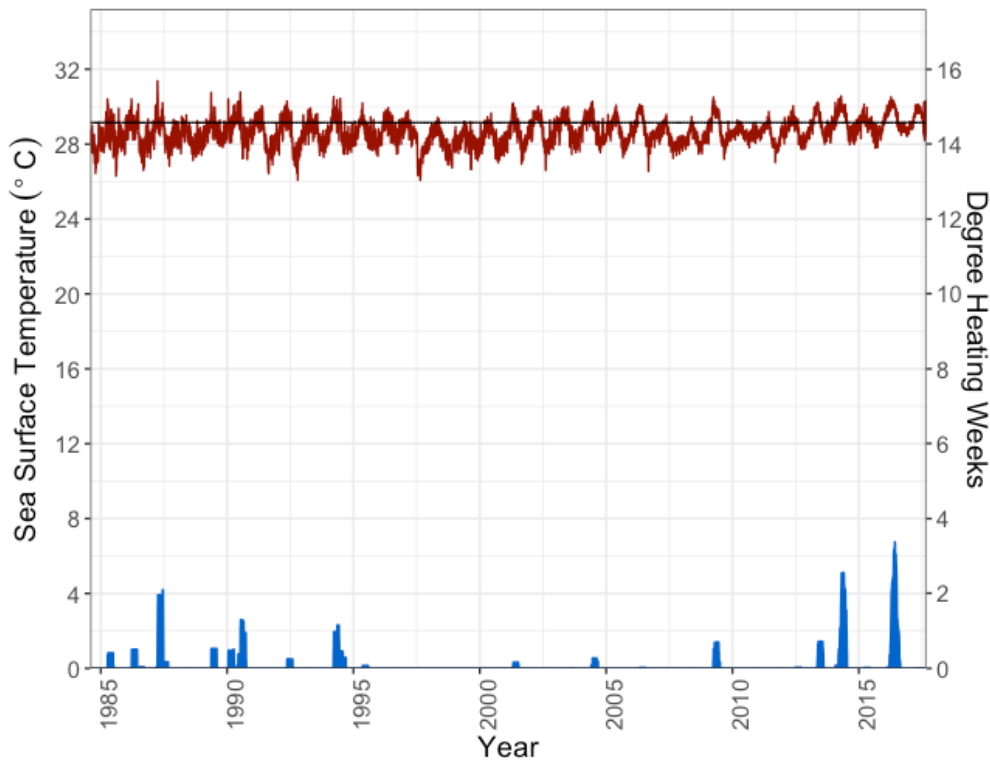


Figure 3.1. Daily sea surface temperature (red), degree heating weeks (blue), averaged across study sites in (A) Kiribati and (B) the RMI from 1985 – 2018, with the maximum monthly mean (black). This figure uses historical temperature data from NOAA Coral Reef Watch.

There are also strong gradients in local human disturbance within the northern Gilbert Islands and the neighboring southern RMI. Comparing sites in the Gilbert Islands to those in the RMI allows us to investigate how gradients in heat stress and in local human stressors interact to influence coral reef communities. Like Tarawa, Majuro is also a densely populated atoll (home to about 28,000 people as of the 2011 census) and is neighbored by a less populated atoll, Arno, where the population is about 1,800 people (Secretariat of the Pacific Community, 2012). In both Tarawa and Majuro, reef degradation began with colonial legacies that drove increased population densities and the construction of infrastructure such as international airports and causeways (Cannon, 2020; Cannon *et al.*, 2021). These high population densities continue to place pressure on reefs today through high local fishing rates, sedimentation, and nutrient loading. By contrast, in both Arno and Abaiang local threats to reef are fewer and less extreme. Subsistence fisheries are important for local people in both of the less populated atolls, but the smaller population size means that there is less pressure on reefs; while fishers from Tarawa or Majuro do travel to Abaiang or Arno, they tend to target pelagic species and reports indicate that these fisheries have minimal effects on the reefs (Awira *et al.*, 2008; MIMRA, 2015).

Long-term coral reefs surveys in the Gilbert Islands found support for the inverse of the protection paradox: that exposure to chronic local human disturbances selected for coral species that were more resistant to heat stress (Cannon *et al.*, 2021). After repeated bleaching-level heat stress, benthic communities in South Tarawa, subject to high local human disturbance, became increasingly dominated by bleaching-resistant coral and disturbance-resistant macroalgae taxa (Donner, Kirata and Vieux, 2010; Darling and Côté, 2013; Cannon *et al.*, 2021). By contrast, the benthic communities of North Tarawa and neighboring Abaiang Atoll, with a tenth of the human

population and lower local disturbance, were more diverse but less resistant to heat stress. This supports an alternative view of resilience: local disturbance may increase, not decrease, coral reef resilience to climate change (Côté and Darling, 2010; Darling and Côté, 2013).

Here, I add to our understanding of how local and global threats interact to affect coral reef communities via an *in-situ* study that takes advantage of unique gradients in local human disturbance and past interannual SST variability. I hypothesize that local human-driven degradation does not compound the impacts of climate-driven heat stress on living coral cover, but instead pre-conditions benthic communities in Tarawa and Majuro to withstand frequent heat stress by weeding out the more sensitive taxa, and heat stress and local human disturbance interact antagonistically. I expect that sites in the Gilbert Islands to host more hardy, heat-resistant benthic taxa than atolls in the RMI, while sites exposed to chronic, ongoing local human-driven degradation (Majuro and Tarawa) hosted benthic communities with greater abundances of opportunistic or hardy taxa than the reefs in the less populated atolls (Arno and Abaiang). In Arno, where reefs experience low levels of both human disturbance and heat stress, I expect to find sites hosting diverse communities with higher abundances of sensitive coral genera than in Abaiang, Tarawa, or Majuro. I find that the interactions between local human disturbance and variability in past interannual SSTs were context-dependent, and provide evidence for antagonistic interactions between local and global stressors in places where local human disturbance has preconditioned coral reef benthic communities to withstand heat stress.

3.2 Methods

3.2.1 Survey Methods

I visited 24 sites in the RMI in June-July 2016 (13 in Arno and 11 in Majuro), and 16 sites in Kiribati in April 2018 (eight sites in North Tarawa and Abaiang and eight in South Tarawa) (Figure 3.2, Appendix B.1). As in previous work (Donner and Carilli, 2019; Cannon *et al.*, 2021), I grouped sites within Abaiang and North Tarawa together because they experience similar levels of local disturbance, are administered separately from South Tarawa, and are located nearer to each other than sites in South Tarawa are to North Tarawa; throughout the remainder of the manuscript, I refer to North Tarawa and Abaiang as ‘Abaiang’, and South Tarawa as ‘Tarawa’. As demonstrated in Chapter 2, the coral reefs in N. Tarawa and Abaiang experienced significantly different levels of local human disturbance (Cannon *et al.*, 2021). I measured the benthic community composition of coral communities using the methods we described further below and in previous studies (Cannon *et al.*, 2019, 2021).

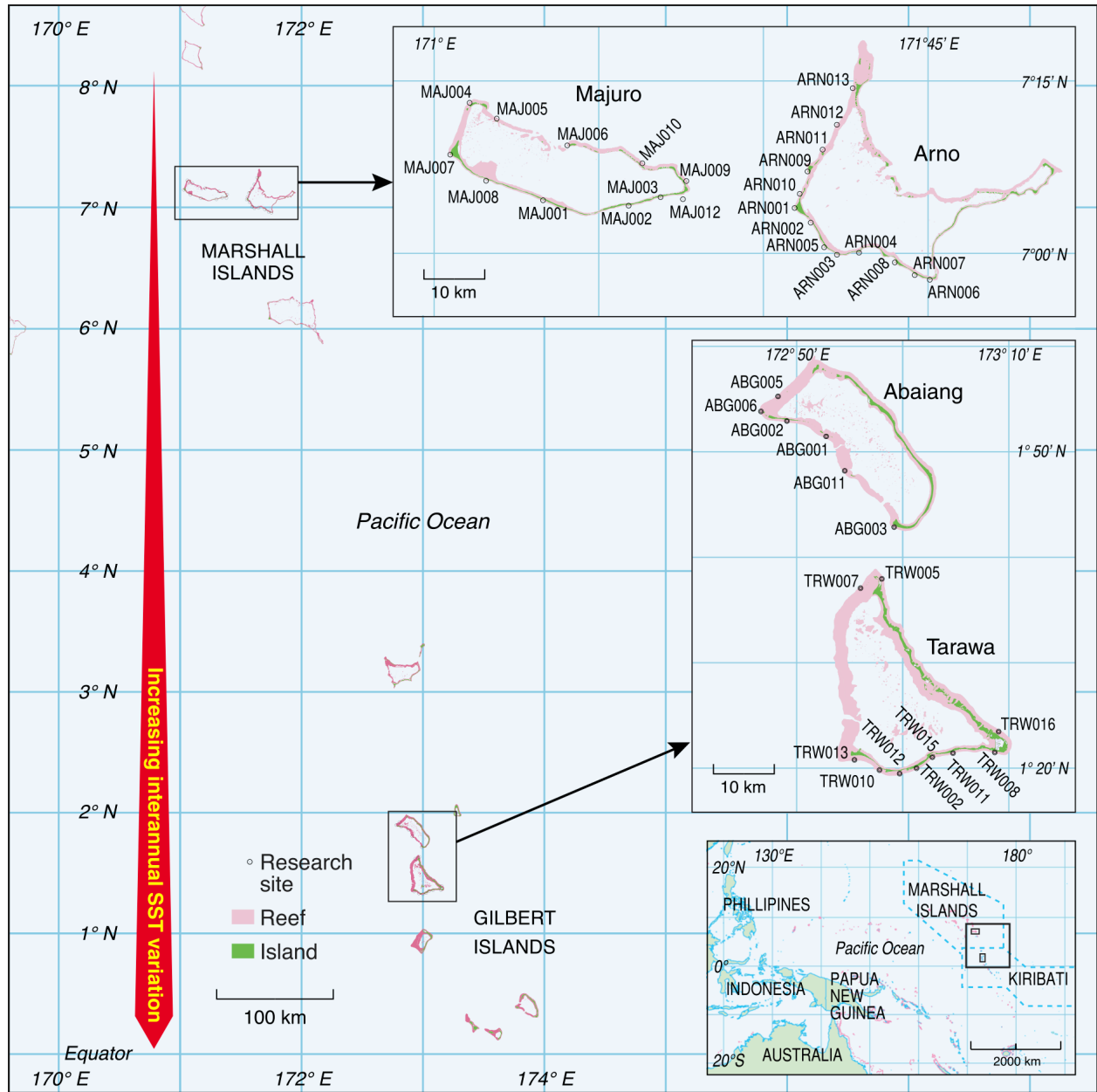


Figure 3.2. Study sites in Tarawa and Abaiang, Gilbert Islands, Kiribati and Majuro and Arno, RMI. This figure uses data extracted from the Millennium Coral Reef Mapping Project Version 4.0 (UNEP-WCMC et al., 2018), and the OpenStreetMap Foundation, available under a Open Database License “ODbL” 1.0 with permission from © OpenStreetMap contributors, original copyright 2012 (Open Street Map Foundation, 2012).

I laid one 50-m transect tape haphazardly at 10-m depth at each site and took 0.33m²-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. I later analyzed these photos to calculate the percent cover of macroalgae and coral genera, with other common benthic taxa, at each site (see *Statistical Analysis*). Site MAJ012 is the only exception; because this site was located at Majuro's sewage outfall, where RMI-EPA coliform and enterococci tests regularly exceeded safe levels (Doig, 1996; MIMRA, 2016), I was unable to dive there because of health concerns. Instead, I obtained 250 quadrat photos taken over an area of 250-m (five transects laid haphazardly at 50 m each), collected eight weeks later than data from our other sites by Karl Fellenius (Hawaii Sea Grant) and Martin Romain (College of the RMI) when the sewage pipe was temporarily turned off.

I used photos from the transects to calculate benthic percent cover using the open-source web tool CoralNet (Beijbom *et al.*, 2012), 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 m² (50.0 cm width by 66.7 cm length). I manually classified each point to the genus level for coral and macroalgae, and to functional group for sponges, soft corals, turf algae, crustose coralline algae (CCA), and cyanobacteria. I also identified the coral species *Porites rus*, which is abundant in Tarawa and has an opportunistic life-history strategy (Darling *et al.*, 2012), to the species level.

All identification relied on taxonomy from Veron (2000). Since this resource was published, the taxonomy of the Favidae family has undergone several changes (Huang *et al.*, 2011). I use the older taxonomy here to remain consistent with the past research and with reports for the Kiribati

government that were based on data from these surveys and earlier surveys which I do not include here.

3.2.2 Human Disturbance

I calculated a metric representing human disturbance using the Normalized Difference Vegetation Index (NDVI), obtained from satellite imagery from the United States Geological Survey's Land Satellite 8 following a method developed in a previous analysis of the RMI sites (Cannon *et al.*, 2019) and used in the analysis described in Chapter 2 from Kiribati, where NDVI was correlated with local population size (Cannon *et al.*, 2021). NDVI measures the amount of green terrestrial vegetation within a 60-m 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. Lambert *et al.*, 2015). This metric captures human alterations of the landscape and is not necessarily affected by local population size. I was unable to use a population metric to estimate human-related disturbance because the RMI census data are not available in sufficiently high resolution (population is reported for groups of islands, but not individual islands or villages).

The methods for calculating the mean NDVI are described in detail in Cannon *et al.* (2019, 2021). While this past work used NDVI in analyses of human disturbances on coral reefs, this is the first analysis to compare NDVI across sites experiencing different climates. The RMI experiences higher rainfall than Kiribati, and therefore sites in the RMI had higher mean NDVI values on average due to the greater density of vegetation. To create a metric that was comparable across regions, I scaled the mean NDVI values for each country to be between zero and one, with one indicating the least local human disturbance and zero the highest disturbance.

For ease of interpretation, because NDVI has an inverse relationship with disturbance, I use the absolute value of one minus the scaled mean NDVI such that a low value indicates low disturbance and vice versa using the following equation:

$$NDVI_{-1} = \left| 1 - \frac{(NDVI_{orig} - \min(NDVI))}{(\max(NDVI) - \min(NDVI))} \right|$$

3.2.3 Oceanographic Data

Time series of daily SST and Degree Heating Weeks (DHW) for all sites for the years 1985 through 2018 were obtained from 0.05° x 0.05° lat-long resolution CoralTemp SST Version 3.1 satellite-derived data (Skirving *et al.*, 2020). I obtained the 0.04° x 0.04° lat-long resolution satellite-derived monthly chlorophyll-a (chl-a) concentration (in mg m⁻³) from July 2002 – May 2019 and the monthly climatology of PAR (Einstein m⁻² day⁻¹) from July 2002 – December 2020 via NASA’s Moderate Resolution Imaging Spectroradiometer (NASA, 2014). For chl-a concentration, I applied a temporal nearest value interpolation to fill missing values. While there are well-known limitations to using chl-a as a proxy for net primary productivity (Chen *et al.*, 2013), including that satellite measurements only capture near-surface chl-a concentration (in the top 5 meters of the ocean), it is still the only remote sensing product available that does not require further modeling to compute and is therefore a common metric used in coral reef studies (e.g. Walsh, 2011; Donner and Carilli, 2019).

I used these data to calculate a series of metrics representing the variation of past SST at each site, including: the standard deviation (SD_{SST}), coefficient of variation of SST (CV_{SST}), skewness, and kurtosis of SST. I also calculated metrics representing the history of heat stress at each site, including the maximum DHW, years since the maximum DHW, and maximum annual mean DHW using the entire available dataset of SSTs and DHWs (1985 – 2018); mean annual PAR and mean PAR during the warmest months of the year (when peak heat stress typically occurs: September-November; August-October) using the entire available dataset (July 2002 – December 2020); and finally, the annual range of chl-a and the mean chl-a to represent net primary productivity (between 2002 and 2019). Notably, the climatological periods are different for each of these datasets. However, this should not affect the results or interpretation given that the recent El Niño events driving bleaching in 2004/2005 and 2009/2010, and heat stress in 2014 through 2016 in the Gilbert Islands, were captured in all datasets.

In addition to the metrics representing exposure to past heat stress, I also calculated additional metrics to account for factors that might confound the effects of past heat stress exposure and local human disturbance: wind and wave exposure (WWE), photosynthetically-available radiation (PAR), and net primary productivity (represented by chlorophyll-a concentration). Finally, I calculated a metric for wind and wave exposure (WWE) following the methods described by Rohweder et al. (2012) and Chollett and Mumby (2012), considering wave exposure a function of fetch, wind speed, and wave height. First, I calculated the fetch at each site via a fetch model from Finlayson (2005) that I employed in Python using land polygons obtained from UNEP World Conservation Monitoring Centre Global Distribution of Coral Reefs dataset (UNEP-WCMC *et al.*, 2018). Then, I calculated wind speed and direction using an 11-

year 0.25° x 0.25° lat-long resolution monthly climatology of blended sea wind vectors obtained from the National Centers for Environmental Information (Zhang, Reynolds and Bates, 2006; Peng *et al.*, 2013). I averaged the monthly wind speed and direction values for Abaiang and Tarawa (1.325° to 1.920° N and 172.777 to 173.151°E) and then for Majuro and Arno (7.243° to 6.955°N and 171.021 to 171.749°E) to calculate the average annual wind direction for each region (the Gilbert Islands versus the RMI). I used the fetch model to produce an individual fetch raster for each possible wind direction for the two regions, producing fetch estimates for each gridcell within each region (see Rohweder *et al.*, 2012 for details). Finally, I mosaiced and averaged the fetch rasters by gridcell in ArcGIS ArcMap 10.6.1 (see Rohweder *et al.*, 2012), and then used the fetch rasters and average annual wind direction rasters to calculate the wave exposure values for each site using the equations described by Ekebom *et al.* (2003).

3.2.4 Statistical Analyses

I used R version 4.0.2 (R Core Team, 2021) and Rstudio version 1.3.959 (RStudio Team, 2020) for all statistical analysis, and created plots with the R packages ggplot2 (Wickham, 2016) and ggbiplot (Vu, 2011).

As described above, I calculated a series of environmental metrics that could account for differences in benthic community composition across the sites, atolls, and countries, for use in the statistical analyses alongside the NDVI₁, which represents the local human disturbance (Appendix B.1). I chose the metrics to include in the statistical analyses based on a correlation analysis (Appendix B.2), which found that the metrics representing each of the environmental phenomena were highly correlated. Specifically, the three metrics for PAR were all highly

correlated, as were the two metrics we calculated to represent chl-a concentration and the seven metrics I considered to represent heat stress frequency or interannual variation in SSTs. Given the correlation within each set of environmental metrics, I selected CV_{SST} to represent the variability of past heat stress. The CV_{SST} is a more appropriate metric for comparing values in the Kiribati versus the Marshall Islands than SD_{SST} , because CV_{SST} normalizes the SST values by the mean of each group and is therefore more informative when comparing variability across groups with different means. Using CV_{SST} as a proxy representing past exposure to heat stress is also consistent with previous studies (Donner and Carilli, 2019). The CV_{SST} values did not vary much within each country (in the RMI CV_{SST} varied by 0.04 while in the Gilberts it varied by 0.10) but were different when comparing sites in Kiribati to sites in the RMI (mean CV_{SST} in the Gilberts was 3.25, compared to a mean of 2.38 in the RMI), confirming that country also serves as a proxy for high versus low CV_{SST} . I also selected the variables with the lowest correlation score to represent the potential environmental or oceanographic factors that could influence benthic communities (mean PAR and mean chl-a).

I followed Clarke (1993) to identify similarities or differences in benthic communities across the four atolls. First, I visualised differences across sites and atolls as explained by the genera of the two main functional groups, live coral and macroalgae, through unscaled principal component analyses (PCAs) of the percent-cover data covariance matrix. I then conducted an additional PCA that included all of the taxa and benthic categories collectively accounting for more than 99% of observations, this time scaling the percent cover data for unit variance in order to account for the potential disproportionate influence of common taxa (Clarke, 1993). To examine whether the communities clustered by atoll, I used the first three principal components of this PCA to run

an agglomerative hierarchical clustering analysis with the R package FactoMineR (Sebastien Le and Husson, 2008). This analysis produced groups of sites based on differences and similarities in the community composition and mean percent cover data. Next, I used the vegan package in R (Oksanen *et al.*, 2020) to conduct a series of analyses of similarities (ANOSIMs, 999 permutations) that compared Bray-Curtis dissimilarities of (1) total benthic community composition, (2) live coral percent cover, and (3) macroalgae cover, first between atolls and then between countries (for a total of six independent models).

To evaluate how the explanatory variables affected the benthic communities at each site, I followed the ANOSIMs with BIO-ENV procedures (999 permutations) as described by Clarke (1993), to identify which of the five explanatory variables (NDVI_L, WWE, mean chl-a, mean PAR, and CV_{SST}) best predicted the community structure by testing all possible combinations with the percent cover of benthic communities (Appendix B.1). I repeated the analyses three times to investigate how the environmental variables correlated with the full benthic community composition versus just live coral cover and macroalgae cover independently. I then conducted permutational multiple analysis of variance (PERMANOVA) with 9,999 permutations (Anderson, 2001) with each of the three data subsets to estimate the amount of variation in benthic taxa across our sites that can be explained by human disturbance (NDVI_L), the variation in SST (CV_{SST}), or the combination between the two variables on all benthic taxa across our sites. I ran these three models with an additional factor, atoll, to account for potential differences in the benthic communities by atoll. However, because the four atolls were each correlated with distinct levels of CV_{SST} and NDVI_L, considering atoll a factor did not improve model fit, and I have not included those results here.

Finally, to identify the interaction types between local human disturbance ($NDVI_{-1}$) and exposure to past heat stress (CV_{SST}) on live coral, macroalgae, and specific key taxa (hard coral or macroalgae taxa that represented more than 1% of the total benthic cover within Kiribati or the RMI) and to estimate the effect sizes, I ran a series of multiple linear regression models using the equation:

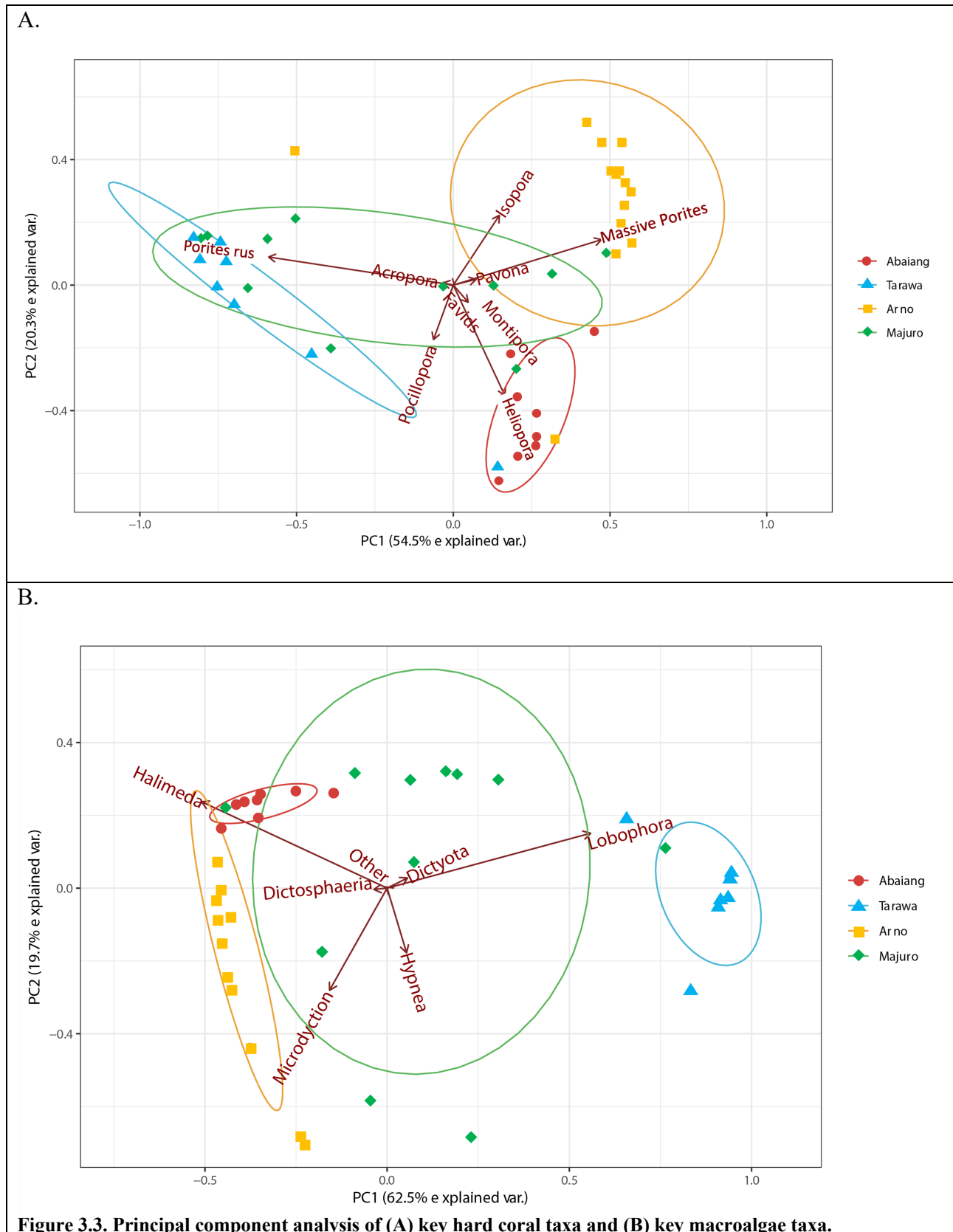
$$Percent\ Cover = \beta_0 + \beta_1 NDVI_{-1} + \beta_2 CV_{SST} + \beta_{12}(NDVI_{-1} * CV_{SST})$$

I standardized the $NDVI_{-1}$ and CV_{SST} metrics by subtracting the mean of the variable and dividing the result by the variable's standard deviation, for ease of interpreting and comparing the model coefficients. I ran standard tobit regression models with the CensReg package in R (Henningsen, 2020) for any taxa with zero values in the dataset, which censor the dependent variable (percent cover) at zero to account for over-inflation of zero values, and simple linear regressions for taxa or groups that were present at all sites. Following Schäfer and Piggott (2018), I classified each interaction as additive ($[\beta_1 + \beta_2 - \beta_1 \cdot \beta_2] = \beta_{12}$), or multiplicative, which includes synergistic ($[\beta_1 + \beta_2 - \beta_1 \cdot \beta_2] < \beta_{12}$), or antagonistic ($[\beta_1 + \beta_2 - \beta_1 \cdot \beta_2] > \beta_{12}$) interactions (here, β represents the regression coefficients).

3.3 Results

In this analysis, I quantified differences in benthic communities across four atolls (Abaiang and Tarawa in the Gilbert Islands of Kiribati and Arno and Majuro in the RMI), estimated the potential drivers affecting these benthic communities and their effects on the benthic community

structures, and then finally, quantified interactions between local and global stressors to estimate their effects on live coral, macroalgae, and the most common coral and macroalgae genera. I first confirmed the differences in the benthos across atolls by visualizing the differences in key coral and macroalgae taxa via unscaled PCAs (Figure 3.3). Collectively, the first two principal components of the hard coral percent cover explained 74.80% of the difference in live coral cover between sites and atolls (Figure 3.3A) while the first two principal components of the macroalgae percent cover explained 75.70% of the difference in macroalgae cover between sites and atolls (Figure 3.3B). The clear grouping of sites by atoll shows that each atoll is home to distinct benthic communities when considering hard coral and macroalgae communities independently.



Specifically, sites in Tarawa, which experienced high NDVI_L and high CV_{SST} (Appendix B.1), were all similar and communities were home to high percent cover of *P. rus* and the macroalgae *Lobophora* spp. In Abaiang, where CV_{SST} was similarly high but human disturbance was low, the hard corals *Montipora* spp. and *Heliopora* spp. were more common than at other sites, as was the macroalgae *Halimeda* spp., whereas *P. rus* was absent. The sites in Arno, which experienced both low human disturbance and low CV_{SST}, had communities dominated by the hard corals *Isopora* spp. and massive *Porites* spp., while *Halimeda* spp., *Dictyosphaeria* spp., and *Microdictyon* spp. dominated the macroalgae communities. Finally, the spread of sites in Majuro (Figure 3.3), where most but not all sites were exposed to high NDVI_L but low CV_{SST}, shows that benthic communities at sites in Majuro were less distinct than sites in the other atolls. For example, some sites had coral communities that were more like those in Tarawa because of the presence of *P. rus*, while others more like sites in Arno with *Pavona* spp. and massive *Porites* spp. Macroalgae communities were also least distinct in Majuro when compared to the other three atolls, with some sites home to *Microdictyon* spp. and *Halimeda* spp., similar to sites in Arno and Abaiang, while others had high cover of *Lobophora*, similar to sites in S. Tarawa. The macroalgae *Hypnea* was also a distinct part of some macroalgae communities in Majuro (Figure 3.3B).

The first three principal components from a third PCA that included all taxa and categories accounting for $\geq 99\%$ of the benthic percent cover explained 52.54% of the variation across sites and atolls. The clustering analysis grouped sites into three clearly defined clusters defined by similarities in their benthic community compositions (Figure 3.4, Table 3.1). Unlike the PCA (Figure 3.3), one cluster included sites with high NDVI_L (i.e. high local human disturbance)

regardless of their past exposure to heat stress, resulting in sites from both Majuro and Tarawa within a single cluster (Group 2, Table 3.1). The cluster analysis also grouped two of Majuro's sites (MAJ010 and MAJ007) and one site from Arno (ARN003) within Group 3, a cluster that otherwise included only sites with high CV_{SST} and low human influence.

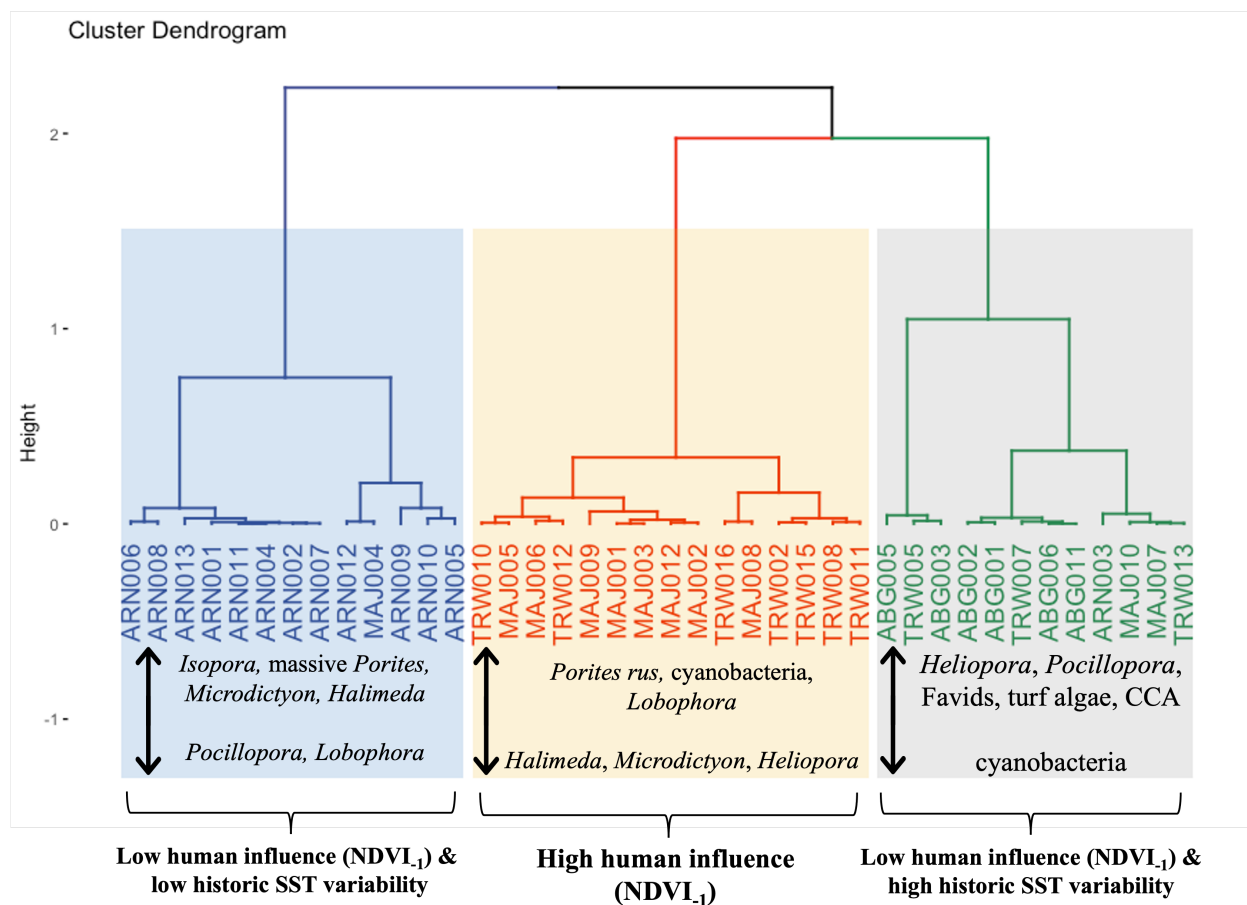


Figure 3.4. Hierarchical clustering analysis of the first three principal components incorporating 99% of all benthic cover. The arrows in each cluster indicate high or low relative abundance of the taxa driving differences across clusters.

Table 3.1. Explanatory taxa by cluster. All results are statistically significant at $\alpha = 0.05$.

Group	Definitive Taxa	More/ Less than overall	Mean % (group)	Mean % (overall)	SD % (group)	SD % (overall)	Test stat	P- value
1	<i>Isopora</i>	+	3.33	1.14	2.63	2.15	4.42	<0.01
	<i>Microdictyon</i>	+	8.54	2.79	7.69	5.93	4.20	<0.01
	Massive <i>Porites</i>	+	12.42	5.06	10.43	8.06	3.96	<0.01
	<i>Halimeda</i>	+	20.71	10.80	19.78	15.09	2.85	<0.01
	<i>Lobophora</i>	-	0.38	3.03	1.30	5.07	-2.27	0.02
	<i>Pocillopora</i>	-	0.24	1.32	0.27	1.29	-3.29	<0.01
2	<i>Lobophora</i>	+	6.94	3.03	6.05	5.07	3.94	<0.01
	<i>P. rus</i>	+	14.74	6.58	1.75	1.35	3.08	<0.01
	Cyanobacteria	+	10.68	7.69	5.96	1.59	2.73	<0.01
	<i>Acropora</i>	+	0.03	0.01	0.05	0.03	2.59	<0.01
	<i>Halimeda</i>	-	4.18	10.80	9.06	15.09	-2.23	0.03
	<i>Microdictyon</i>	-	0.02	2.80	0.02	5.92	-2.39	0.02
	<i>Heliopora</i>	-	0.51	2.02	0.68	3.03	-2.54	0.01
	<i>Isopora</i>	-	0.07	1.14	0.13	2.15	-2.55	0.01
	Massive <i>Porites</i>	-	0.22	5.06	0.55	8.06	-3.06	<0.01
3	<i>Heliopora</i>	+	5.19	2.02	3.99	3.03	4.03	<0.01
	Favids	+	0.01	<0.01	0.01	<0.01	3.99	<0.01
	Turf algae	+	42.60	30.85	8.10	112.97	3.48	<0.01
	<i>Pocillopora</i>	+	2.40	1.32	1.50	1.29	3.22	<0.01
	Sand	+	7.45	3.82	6.55	5.17	2.70	<0.01
	Rubble	+	6.58	2.90	9.83	5.90	2.40	0.02
	Crustose- coralline algae	+	9.90	7.71	3.74	4.05	2.08	0.04
	Cyanobacteria	-	4.64	7.69	4.75	5.59	-2.09	0.04

ANOSIMS indicated that all three subsets of the data (all coral cover, all macroalgae cover, and all benthic cover combined) were significantly different across the four atolls (all taxa: $R = 0.37$, $p < 0.01$; live coral only: $R = 0.55$; $p < 0.01$; macroalgae only: $R = 0.50$, $p < 0.01$) and two countries (all taxa: $R = 0.12$, $p = 0.02$; live coral only: $R = 0.17$, $p < 0.01$; macroalgae only: $R = 0.17$, $p < 0.01$). The variables best correlating with the community data per the BIO-ENV

procedures for all of the benthic taxa and categories across all sites included four parameters, with a Spearman's correlation value of 0.43: NDVI_{L1}, wind and wave exposure, mean chl-a, and CV_{SST}. The most parsimonious model for the live coral and macroalgae subsets included three of these parameters – NDVI_{L1}, wind and wave exposure, and CV_{SST} – with Spearman's correlation values of 0.43 for live coral and 0.40 for macroalgae.

Overall, PERMANOVAs estimated that the model (NDVI_{L1} + CV_{SST} + NDVI_{L1}* CV_{SST}) explained 31.09% of the variation in benthic community composition across sites. The NDVI_{L1} had a greater explanatory affect, accounting for 15.84% of the total variation (F-statistic = 8.27, $p < 0.01$), while CV_{SST} explained 8.27% of the variation (F-statistic = 4.32, $p < 0.01$), and the interaction between the NDVI_{L1} and CV_{SST} explained 6.99% of the overall variation (F-statistic = 3.64, $p < 0.01$).

Finally, I used multiple linear regressions for taxa present at all sites (6 of 18 categories) and left-censored tobit models with logistic distributions for taxa not found at all sites (12 of 18 categories, Table 3.2) to estimate how NDVI_{L1} and CV_{SST} effected the total cover of hard coral, macroalgae, and key independent taxa (those representing more than 99% of the cover across sites). A negative coefficient (β_1) means that the percent cover of the taxa in question decreased while the disturbance in question increased. The full regression equations explained 25% of the variation in total live coral ($p < 0.01$) and 13% of the variation in macroalgae cover ($p < 0.01$, Table 3.2, Appendix B.3). While neither NDVI_{L1} nor CV_{SST} explained the variation in live coral cover ($p = 0.48$ and $p = 0.41$, respectively), both had positive effects, and the interaction between NDVI_{L1} and CV_{SST} was positive, synergistic, and statistically significant (6.62, $p < 0.01$). Total

macroalgae cover did not depend on NDVI₋₁, CV_{SST}, or their interaction (2.68, $p = 0.37$). Neither stressor had a significant effect on macroalgae at $\alpha = 0.05$, but NDVI₋₁ was significant at $\alpha = 0.10$ (-5.32, $p = 0.08$) suggesting that the trend observed between NDVI₋₁ and macroalgae abundance was 90% likely to be a real trend, rather than spurious, given the data.

Table 3.2. Results of regressions of scaled NDVI_L and CV_{SST} versus the percent cover of key groups and taxa. CI = confidence intervals (shown with upper and lower limits).

Taxa/ Category	Model Type	# Cens- ored	R ²	NDVI _L			CV _{SST}			NDVI _L * CV _{SST}			Type*
				β_1	P	CI (95%)	β_2	P	CI (95%)	β_{12}	P	CI (95%)	
All Live Coral	Linear	--	0.25	1.44	0.48	(-2.62, 5.50)	1.68	0.41	(-2.44, 5.80)	6.62	<0.01	(2.66, 10.58)	Syn
<i>Acropora</i>	Tobit	8	-0.13	0.00	0.78	(-0.01, 0.02)	-0.02	0.01	(-0.03, -0.01)	-0.02	0.04	(-0.03, 0.00)	Add
Favids	Tobit	8	-0.03	-0.00	0.02	(0.00, 0.00)	0.00	<0.01	(0.00, 0.00)	-0.00	0.17	(0.00, 0.00)	--
<i>Heliopora</i>	Tobit	12	0.09	-1.68	0.01	(-2.97, -0.38)	2.41	<0.01	(1.22, 3.60)	-0.47	0.43	(-1.65, 0.71)	--
<i>Isopora</i>	Tobit	22	-0.20	-19.34	0.58	(-89.99, 50.71)	-73.04	0.05	(-144.8, -1.29)	-20.86	0.63	(-106.4, 65.69)	--
<i>Pocillopora</i>	Tobit	3	0.21	-0.13	0.44	(-0.44, 0.19)	1.01	<0.01	(0.68, 1.33)	-0.36	0.03	(-0.67, -0.05)	Ant
Massive <i>Porites</i>	Tobit	9	0.05	-4.45	0.01	(-7.90, -1.01)	-1.51	0.34	(-4.60, 1.58)	2.14	0.18	(-1.01, 5.28)	--
<i>P. rus</i>	Tobit	17	0.13	8.58	<0.01	(4.01, 13.14)	4.65	0.05	(-0.06, 9.37)	5.74	0.01	(1.37, 10.11)	Syn
All Macro- algae	Linear	--	0.13	-5.32	0.08	(-11.40, 0.77)	-4.63	0.14	(-10.81, 1.54)	2.68	0.37	(-3.26, 8.61)	--
<i>Halimeda</i>	Tobit	7	0.06	-9.35	<0.01	(-15.04, -3.65)	-4.17	0.12	(-9.44, 1.11)	-2.47	0.42	(-8.48, 3.55)	--
<i>Hypnea</i>	Tobit	36	0.14	10.48	0.04	(0.34, 20.64)	0.06	0.99	(-10.21, 10.34)	-3.67	0.38	(-11.94, 4.59)	--
<i>Lobophora</i>	Tobit	16	0.03	0.63	0.63	(-1.92, 3.18)	1.87	0.16	(-0.74, 4.47)	1.58	0.20	(-0.85, 4.02)	--
<i>Micro-dictyon</i>	Tobit	18	0.05	-2.03	0.20	(-5.16, 1.09)	-3.38	0.03	(-6.46, -0.31)	1.23	0.44	(-1.87, 4.33)	--
CCA	Linear	--	0.09	0.15	0.82	(-1.20, 1.51)	1.42	0.04	(0.05, 2.80)	-1.07	0.11	(-2.39, 0.26)	--
Coralli- morphs	Tobit	31	0.21	1.10	0.45	(1.77, 3.97)	2.54	0.05	(-0.03, 5.12)	1.47	0.23	(-0.94, 3.87)	--
Cyano- bacteria	Linear	--	0.40	3.81	<0.01	(2.30, 5.33)	-2.24	<0.01	(-3.78, -0.71)	-0.93	0.21	(-2.41, 0.55)	--
Sponges	Linear	--	0.32	0.01	<0.01	(0.00, 0.01)	-0.01	0.03	(-0.01, 0.00)	-0.01	0.01	(-0.01, 0.00)	Ant
Turf algae	Linear	--	0.09	-2.96	0.17	(-7.29, 1.37)	5.00	0.03	(0.60, 9.39)	-3.01	0.16	(-7.23, 1.21)	--

* I defined the interactions as additive ($[\beta_1 + \beta_2 - \beta_1 \cdot \beta_2] = \beta_{12}$), or multiplicative, which includes synergistic ($[\beta_1 + \beta_2 - \beta_1 \cdot \beta_2] < \beta_{12}$), or antagonistic ($[\beta_1 + \beta_2 - \beta_1 \cdot \beta_2] > \beta_{12}$) interactions (see Methods).

Among individual taxa present at all sites, the full models were statistically significant at $\alpha = 0.05$ for all of the live coral taxa except *Acropora* spp, for the macroalgae *Halimeda* spp. and *Hypnea* spp., and for corallimorphs, cyanobacteria, and sponges (Appendix B.3). The full equation for cyanobacteria has the highest explanatory power ($R^2 = 0.40$), indicating that cyanobacteria cover increased with increasing NDVI_{L1} ($p < 0.01$) and decreased with increasing CV_{SST} ($p < 0.01$). As with the linear regressions, the tobit regressions showed that the variables had different effects depending on the taxa. The CV_{SST} had a significant and positive effect on *Pocillopora* spp. (1.01, $p < 0.01$), while the interaction between CV_{SST} and NDVI_{L1} was negative (-0.36, $p = 0.02$). CV_{SST} also had a positive effect on *P. rus*, although this was marginally significant (4.54, $p = 0.05$); the percent cover of *P. rus* also increased with increasing NDVI_{L1} (8.58, $p < 0.01$) and with the interaction between NDVI_{L1} and CV_{SST} (5.74, $p = 0.01$); the equation explained 13% of the variation in the percent cover of *P. rus* across sites. Among the macroalgae taxa, NDVI_{L1} had a significant, negative effect on the percent cover of *Halimeda* spp. (-9.35, $p = 0.01$), but a positive effect on the percent cover of *Hypnea* spp. Of the other benthic categories, the CV_{SST} had a positive, marginally significant impact on the percent cover of corallimorphs (2.54, $p = 0.05$), but neither NDVI_{L1} nor the interaction between NDVI_{L1} and CV_{SST} had a significant impact, although the full equation explained about 21% of the percent cover. While *Isopora* spp. was negatively affected by CV_{SST} and these results were marginally significant ($p = 0.05$), the negative R^2 value shows that the model was a poor fit.

The interactions between the variation of past heat stress (CV_{SST}) and local human disturbance ($NDVI_{-1}$) were multiplicative (non-additive) for four out of the five significant interactions (Table 3.2). Two were synergistic and two were antagonistic. The hard coral genus *Acropora* experienced the interactions between $NDVI_{-1}$ and CV_{SST} as additive, but the R^2 value was negative indicating the model fit poorly, indicating that for this category the results are not dependable.

3.4 Discussion

This analysis of coral reefs across gradients of human disturbance and the variation in past exposure to heat stress in the Central Pacific identified distinctive clusters of benthic communities. The differential exposure to interacting stressors influenced the community compositions, which in turn influenced the overall interaction types between stressors, as I explain further below. The hierarchical analysis divided the sites into three clusters based on similarities in the benthic community compositions: two of these clusters were composed of sites with low human influence but different heat stress frequency (represented by high or low CV_{SST}), while the third contained sites with high human influence (represented by high $NDVI_{-1}$). While the BIO-ENV analysis and the PERMANOVA together show that the frequency of heat stress was a significant factor explaining benthic community compositions across all sites (along with wind and wave exposure and chl-a concentrations), the clustering analysis showed that the frequency of heat stress was less influential at sites with high local anthropogenic stressors and where hardy or weedy coral and macroalgae taxa were most prevalent (specifically, in Tarawa and Majuro).

The sites in Tarawa, which are dominated by the weedy coral *P. rus* and experienced multiple stressors consecutively (human disturbance is ongoing and has been chronic for decades, while bleaching-level heat stress has occurred intermittently over the past 25 years), may provide an example of what Crain et al. (Crain, Kroeker and Halpern, 2008) called conditioning. In this case, a positive response from some taxa to the first stressor (local human disturbance) resulted in a community that was pre-conditioned to responses from the second stressor (frequency of past heat stress). Here, as past research has shown, tolerance caused by stress led to synergistic interactions because tolerance to a single stressor can improve tolerance to a second stressor (Crain, Kroeker and Halpern, 2008). By contrast, the Majuro sites have not experienced severe heat stress during the satellite record (Figure 3.1), but because many of those sites have already adjusted to localized disturbance through shifting community compositions, they may be more pre-conditioned to future heat stress than other undisturbed locations. As occurred in when reefs in Tarawa experienced higher-than-average SSTs, future heat stress may have less effect on overall coral and macroalgae cover in Majuro than at sites in a nearby atoll, Arno, which have not been pre-conditioned by exposure to local disturbance. Future heat stress in Arno may impact benthic communities in similar ways as in Abaiang after bleaching in 2009/2010, resulting in dominance by heat-resistant taxa like massive *Porites* spp. and *Halimeda* spp. (Cannon *et al.*, 2021).

Collectively, these results demonstrate that coral reef management will be increasingly complex as the climate warms and coral bleaching becomes more frequent. The potential to address or prevent synergistic interactions, along with the conventional understanding of resilience (that

local stressors may reduce resilience to climate impacts), has driven a focus on synergisms in the literature. Multiple stressor synergies are widely viewed as the worst-case scenario for ecosystems (Paine, Tegner and Johnson, 1998; Folt *et al.*, 1999; Piggott, Townsend and Matthaei, 2015), although antagonistic interactions– which I found were equally common among the individual taxa– may be more difficult to address unless there is a clear ‘dominant stressor’. By contrast, stressors that interact synergistically may respond favorably to removing a single stressor (Crain, Kroeker and Halpern, 2008; Brown *et al.*, 2013), but this assumes the combined effects have a negative impact. For massive *Porites*, for example, both local human disturbance and the frequency of heat stress negatively impacted the percent cover (although only human disturbance was significant) but the combined effects were positive, which complicates management decisions. Reducing local human degradation may therefore have unpredictable effects on the cover of massive *Porites* spp. in places where local degradation and high frequency of heat stress co-occur (such as Abaiang).

While our results suggest that reducing or removing local stressors might confer some resistance to climate change, as noted by Piggott *et al.* (2015), what is stressful for one species or taxa in an ecosystem may be beneficial for others. Management actions to reduce local stressors will have the greatest benefit for those taxa that experience climate and local stressors synergistically and negatively, but possibly at the expense of taxa that experience positive synergies or antagonistic interactions. Conservation interventions may result in clear winning and losing taxa, depending on which taxa are present, the stressors acting upon them, and the way those stressors interact (McClanahan *et al.*, 2020). Therefore, managers and scientists must inform their choices about actions to conserve local reefs by considering the taxa that are present, their role in ecosystem

functioning (e.g., contribution to reef building), and how they are affected by interactions between local and global climate stressors (Darling *et al.*, 2019; Anthony *et al.*, 2020; McClanahan *et al.*, 2020). For example, at these sites, *P. rus* experienced interactions between local and global stressors positively and synergistically, and the independent stressors also had a positive effect on its overall cover. Because of its high prevalence, *P. rus* composed a high percentage of all live coral, and the combined effects of NDVI_{L1} and CV_{SST} were also positive and synergistic. This indicates that management action to reduce either stressor would not benefit the overall hard coral cover. In contrast, addressing local human disturbance could help increase the percent cover of *Pocillopora* spp. because the combined stressors had a negative, antagonistic effect. However, the effectiveness of taxa-driven management decisions would be limited by interactions between taxa due to competition for space and other factors that limit the ability to reverse phase shifts on reefs (Cannon *et al.*, 2021).

Before scientists and managers can make a fully informed decision about management, they must first understand the potential risks associated with management actions. In our case, decisions or lack of decisions that benefit *P. rus* at the expense of other established reef-builders like *Pocillopora* spp. could come with trade-offs in terms of the ecosystem services provided by altered, low diversity reefs such as those found in Tarawa and Majuro. Recent work has estimated that ecosystem services provided by reefs have declined by about half globally, and that protecting social-ecological systems that provide local seafood from reefs will be integral in the Micronesia region especially, where people have the highest global per-capita consumption of coral reef fish (Eddy *et al.*, 2021). Changes in coral communities due to mass bleaching can cause declines in reef structural complexity (Fordyce *et al.*, 2019; Magel *et al.*, 2019) and reef

carbonate production (Perry and Alvarez-Filip, 2018; Courtney *et al.*, 2020), which together influence shoreline protection as well as fish habitat. Scientists expect that as the climate continues to warm, coral reef communities around the world will become less diverse, and communities will shift towards dominance by more stress-resistant taxa (Hoegh-Guldberg *et al.*, 2007; Logan *et al.*, 2021). The effect of shifts to communities dominated by taxa like *P. rus* on reef structure and growth is an integral concern for people in low-lying atoll countries like Kiribati and the RMI that are threatened by sea-level rise (Summers and Donner, 2022). We had hoped to research broader ecosystem responses to heat stress and human disturbance through benthic, fish and geological surveys in 2020; unfortunately, we were unable to do so because of COVID-19. Understanding potential trade-offs associated with managing these reefs in the Gilbert Islands, where heat stress is already more frequent than in other parts of the Pacific, would provide essential insights that could inform adaptation and mitigation efforts in places where heat stress is not yet common but may be in the future, such as in the RMI.

It is also essential that any management approaches to conserve coral reefs be adaptive, which would help to address any unpredictable outcomes that might occur when managers act to reduce local human-caused degradation, as described above for massive *Porites* spp. In this study, we employed linear models to estimate the interactions among stressors, but there is no guarantee that the stressors will interact in a linear fashion in nature; interactions may be entirely non-linear or they could be linear for some taxa and not others (Brown *et al.*, 2013). Interaction types may also change in the future depending on several factors including the taxa that are present, interactions between taxa, and the time between stressors (Orr *et al.*, 2020). The effect of past interactions may also limit management options; for example, if the system has undergone a

phase shift, as is suspected for Tarawa (Cannon *et al.*, 2021), removal of a previously synergistic or additive stressors like local fishing pressure or nutrient pollution may not lead to a change in the coral community. There may also be factors affecting community composition that are unknown or difficult to account for in models. Therefore, ongoing monitoring is vital so that managers can ensure that actions are having the intended effect and can adjust if they are not. This approach to management also allows decision-makers to respond quickly if the circumstances change, for example should species shift their tolerance of one stressor in response to another stressor (Brown *et al.*, 2013).

Analysis of changes in coral reef communities across environmental gradients, as conducted in this and previous studies, provide important real-world ground truthing of results from manipulation experiments. The limitation of this approach is the inability to completely account for or control environmental variables. In this case, all sites experienced some level of human influence, and within Majuro, some sites experienced greater human disturbance than others, which explains why the third cluster from the hierarchical clustering analysis included some sites from Majuro alongside sites from Arno. I was also unable to account for stressors happening prior to this study that influenced benthic community compositions. For example, sites in the RMI and in Abaiang were all previously affected by outbreaks of the predatory Crown-of-Thorns (CoTs) starfish. I documented the impact of the CoTs outbreak on reefs in Abaiang in the previous chapter. Given the research indicating that competition among species can increase the negative impacts of multiple stressors (Orr *et al.*, 2020), one avenue for future research might be to consider the interactions among coral reef taxa and how those intraspecific interactions influence the community response to the frequency of heat stress and local human degradation.

Finally, the community structures at each atoll could be path dependent and caused by random biogeographic factors, rather than the differences in exposure to past heat stress and local human disturbance. Fully accounting for this possibility would require data from additional coral reefs that experience similar environmental conditions, which may be another opportunity for future research.

There are also a few caveats when interpreting the results of the regression analyses. First, I found no *Isopora* spp. in Kiribati where CV_{SST} was high, which explains the large, estimated effect size (73.04, $p = 0.05$) for CV_{SST} in the model, but it is unlikely that this absence was driven by the frequency of heat stress. Past studies conducted in 2000 (Lovell, 2000) and between 2012 and 2016 (Cannon *et al.*, 2021) also did not find any *Isopora* spp., suggesting that Tarawa and Abaiang may be outside of the geographic range where *Isopora* spp. exist in sufficient abundance to be detected in surveys. In addition, some of the regression results may not be representative because of the small percent cover of certain taxa (specifically, for *Acropora* spp., sponges, and corals in the Favid family) and the low or negative R^2 values.

Mitigating greenhouse gas emissions globally remains the most wide-reaching, effective, achievable, and beneficial way to conserve coral reefs overall and decision-makers must pursue reducing emissions alongside local and regional actions (Kleypas *et al.*, 2021). Local management actions are not enough to mitigate climate change and may have little long-term effect countering its impacts on benthic communities, even when there are negative synergistic interactions or co-tolerance relationships, although local management may buy more time in the short-term in the presence of negative synergies (Brown *et al.*, 2013). While MPAs remain a

popular strategy for conserving coral reefs, managers must also consider that MPAs may decrease resilience to climate stressors (Bates *et al.*, 2019); considering the taxa that are present at a given site and the ways multiple stressors might interact to affect benthic communities is therefore integral to successful reef management.

It is becoming increasingly common for researchers to promote active coral reef restoration efforts that not only protect reefs from local threats such as fishing and pollution, but also increase resilience and adaptation to climate-driven stressors like warming SSTs. For example, coral reef scientists have suggested establishing protected areas alongside assisted evolution and coral gardening or seeding projects that aim to increase the prevalence of heat-resistant reef building corals (Abelson, 2020). In addition to considering the taxa present and their relative responses to interacting stressors – which I show is crucial – decision-makers must also consider both socioeconomic and environmental drivers that can influence reef resilience (Darling *et al.*, 2019). Collectively, these factors can help identify where protected areas and restoration efforts might be effective for increasing resilience to climate-driven impacts. While coral reef scientists may still undervalue the utility of restoring reefs (Gorton *et al.*, 2020), more researchers and managers are recognizing that some aspects of both protection and restoration will likely become inevitable components of coral reef conservation as the climate continues to warm (Possingham, Bode and Klein, 2015; Abelson, 2020).

Chapter 4: Macroalgae exhibit diverse responses to human disturbances on coral reefs

4.1 Introduction

Changes in the relative abundance of indicator taxa are used to evaluate the effects of disturbances on coral reefs, an exercise that is vital as human-driven stressors intensify (Williams *et al.*, 2019). Two common indicators for evaluating coral reef health are macroalgae cover and coral cover, reflecting the understanding that high percentages of macroalgae indicate degraded reefs while high cover of hard corals is evidence of healthy reefs (McCook, Price and Klumpp, 1997; Littler and Littler, 2007; Bruno *et al.*, 2009, 2014; Mumby *et al.*, 2013).

However, despite its widespread use, there is mixed evidence supporting that macroalgae is a useful indicator of reef health. Macroalgae-dominated reefs have always existed and are not necessarily indicative of degradation (Vroom *et al.*, 2006; Vroom, 2011). While macroalgae and corals compete for space (Mumby *et al.*, 2006), and some algae taxa harm corals through shading, abrasion, or chemical defenses (Littler, Littler and Brooks, 2006; Mumby *et al.*, 2006; Littler and Littler, 2007), there are also positive interactions between corals and fleshy macroalgae; for example, macroalgae can protect corals from bleaching (Jompa and McCook, 1998) and predation (Clements and Hay, 2015). The belief that macroalgal-dominated reefs are always less desirable than coral-dominated reefs (Littler and Littler, 2007) also obscures the roles that macroalgae reefs play in ecosystem functioning, for example by providing nursery habitat that supports fish populations (Sievers *et al.*, 2020) and tropical reef fisheries (Wilson *et al.*, 2022).

The idea that the percent cover of macroalgae can indicate whether a reef is healthy or degraded, combined with the theory that macroalgae cover is driven by local anthropogenic stressors acting through top-down or bottom-up processes (e.g. the Relative Dominance Model, or RDM, (Littler and Littler, 1984, 2007) has led to the common assumption that reefs disturbed by local anthropogenic stressors are likely to have high cover of macroalgae. For example, one reported a significant relationship between populated islands and macroalgae cover across the central Pacific, concluding that human populations negatively affect reef health (Smith *et al.*, 2016). Another study did not find a relationship between population and macroalgae cover on reefs, which they interpreted as evidence that local signatures of degradation are being obscured by climate-driven stressors (Bruno and Valdivia, 2016). However, each study defined macroalgae differently, highlighting the challenges in identifying consistent relationships between macroalgae and local human disturbance, and may explain their different conclusions; what scientists consider macroalgae is not consistent across studies. Smith *et al.* (2016) included turf algae and excluded erect, calcifying macroalgae such as *Halimeda* spp., while Bruno and Valdivia (2016) excluded turf algae but included *Halimeda* spp. and other erect, calcifying species. In addition, studies using macroalgae to indicate local human disturbance may be misleading because they overlook that several environmental factors influence the percent cover of macroalgae, for example exposure to wind and waves (Page-Albins *et al.*, 2012), seasonality (Fulton *et al.*, 2014; Brown *et al.*, 2018), and sea surface temperature (SST) (Tanaka *et al.*, 2012; Graba-Landry *et al.*, 2020), all of which confound relationships between local human disturbance and macroalgae cover. Macroalgae taxa also exhibit considerable variability in their responses to local human stressors, including fishing pressure (Gilby *et al.*, 2015), water

pollution (McCook, 1999; McClanahan *et al.*, 2004; Fabricius, 2005) and sedimentation (Fabricius, 2005; Harris, 2021). Still, research investigating these taxon-specific responses to local stressors are lacking for all but the most common macroalgae.

Here, I re-examine the relationship between macroalgae cover and local human disturbance via monitoring data from 1,205 sites in the Indian and Pacific Oceans collected between 2004 and 2020 (Figure 4.1). Specifically, I test the hypothesis that macroalgae percent cover is correlated with local human disturbance when accounting for additional factors that might have confounded the findings in two previous studies (Bruno and Valdivia, 2016; Smith *et al.*, 2016). I calculated 15 variables representing local human disturbance, and considered an additional 45 covariates across seven categories to identify and account for factors potentially obscuring relationships between local human stressors and macroalgae cover: survey methodologies and biogeography, reef connectivity, net primary productivity, seasonality, storms, temperature stress, and wind and wave exposure (Appendix C.1). Then, for all sites and within six biogeographic realms (Costello *et al.*, 2017, see Methods), I selected variables best explaining the genera-specific macroalgae communities via canonical correspondence analysis (CCA) and stepwise ordination, and fit permutational analysis of variance (PERMANOVA) to estimate the effects of each variable. I used Similarity Percentage Analysis (SIMPER) to identify the taxa driving differences across biogeographic realms. Finally, I identified the 24 most common macroalgae genera across all sites and realms, and fit linear mixed effects models (LMMs) for each genus, division (brown, green, or red macroalgae), and for all macroalgae combined, using five variables representing local human disturbance (see Methods).

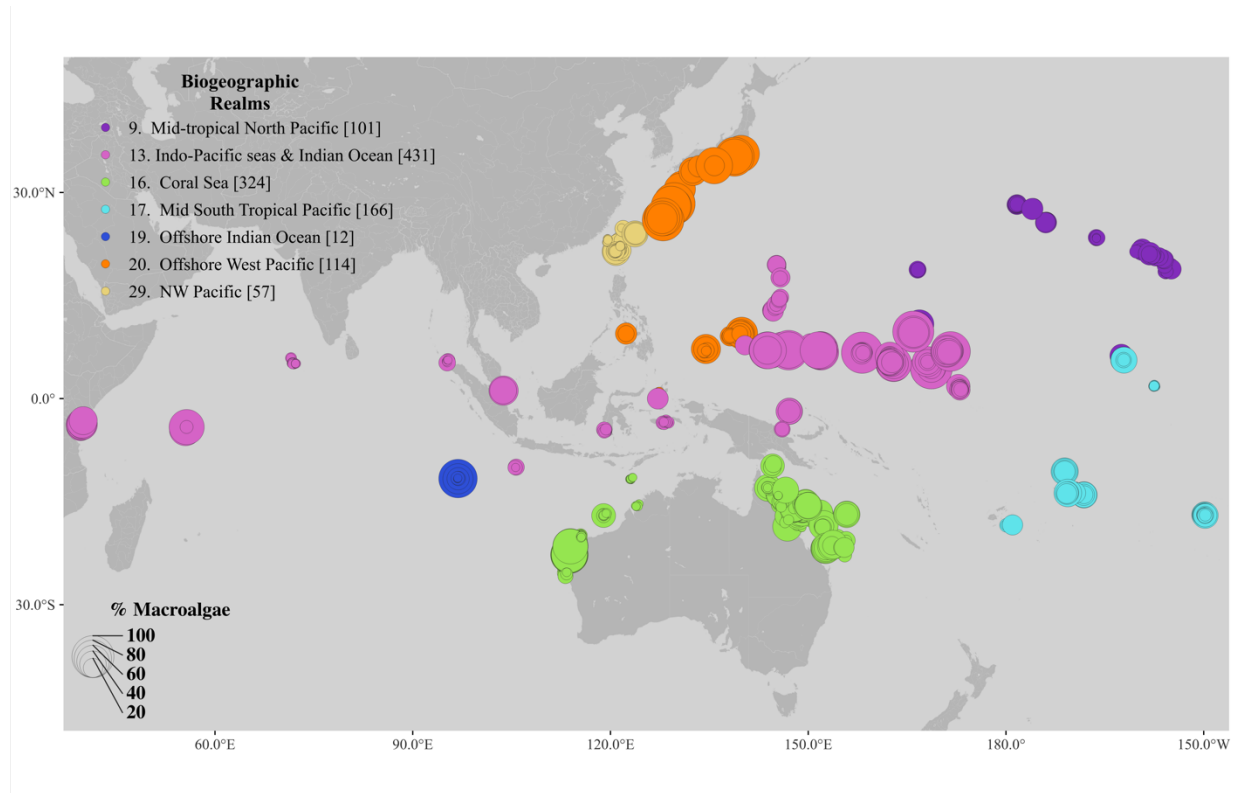


Figure 4.1. *Map of 1,205 study sites across the Indian and Pacific Oceans.*

4.2 Methods

I collected data from genus-level alga benthic surveys conducted from 1,205 individual coral reef study sites across the Indian and Pacific Oceans between 2004 and 2020. Because it was not feasible to collect this volume of data covering such broad geographic regions individually, I relied on data collected from other scientists and collated these data into a meta-analysis.

However, it is uncommon to identify macroalgae to the genus level in coral reef surveys, and the dataset I amassed contains an unequal number of sites within each region (Figure 4.1). To gather these data, I contacted scientists and researchers who had co-authored or contributed data to previously published large-scale meta-analyses employing the benthic percent cover collected

via coral reef surveys in the Pacific and Indian Oceans (e.g. Darling *et al.*, 2019), and I inquired whether they had identified macroalgae to the genus level. If they had, I asked if they would share those data for this analysis. I collated benthic survey data collected from 1,205 sites by 46 researchers across the Indian and Pacific Oceans between 2004 and 2020, covering a period of 16 years. Of the 1,205 sites, 1,145 identified all macroalgae to the genus level, while 60 surveys only identified macroalgae of the genus *Halimeda* spp. I did not include these *Halimeda*-only surveys in the investigation of community drivers of macroalgae, but I included them in the genus-specific analysis described below. The surveys identified 96 genera of macroalgae (Appendix C.2). All statistical modeling, figures, and plots were done using R Statistical Software version 4.4.1 (R Core Team, 2021), R Studio version 2021.09.0 Build 351 (RStudio Team, 2020), and the R packages ggplot2 (Wickham, 2016), and pheatmap (Kolde, 2019). I created the map in QGIS version 3.24 (QGIS Development Team, 2022) using a base map from OpenStreetMap (Open Street Map Foundation, 2021).

To limit the ability of confounding factors to obscure potential relationships between macroalgae and local human disturbance, I identified and calculated 45 site-specific variables (in addition to the 15 variables representing human disturbance) representing drivers known to influence macroalgae growth and distribution at multiple resolutions. These variables encompassed eight categories: connectivity with other reefs, heat stress, human disturbance, methodological and site descriptive variables, net primary productivity, seasonality, storms, and wind and wave exposure. Because the estimates of these variables cover a wide geographic area, I conducted the analysis for the entire dataset, and also separated the sites into seven marine biogeographic realms (Costello *et al.*, 2017) to test whether the macroalgae communities within realms were explained

by different variables. I also considered each data contributor and the survey methodologies as explanatory variables to account for differences in site selection and/or sampling methodologies. A table describing each variable, including its definition, source, spatial resolution, and justification for inclusion in the analysis, is included in Appendix C.1. This Table had to be placed in the appendix rather than the chapter, due to its length.

I assessed multicollinearity during variable selection at two steps in the analysis. First, I used the R package Hmisc (Harrell, Jr., 2021) to calculate the Pearson's r correlation coefficients for all possible pairs of variables and eliminated any with r correlation values of greater than 0.7 within each of the eight covariate categories. When multiple variables were correlated within a given category, I chose those with the lowest summed Pearson's r coefficient, eliminating 33 variables (Appendix C.3). Then, to select variables that best explained the macroalgae community compositions, I conducted CCA and stepwise variable selection via the R package vegan (Oksanen *et al.*, 2020) for all sites combined and independently for each of the six realms (not including sites in realm 19, the offshore Indian Ocean, because it contained too few sites). I addressed multicollinearity in this second step by eliminating any variables with a variable inflation factor (VIF) > 10 (Table 4.1) (Borcard, Gillet and Legendre, 2011). The variables selected by the CCAs and their VIF are detailed in Appendix C.4.

Using the R package vegan,²² I ran SIMPER (999 permutations) to identify the macroalgae taxa driving differences across biogeographic realms. I also analyzed the drivers of macroalgal community composition by fitting seven PERMANOVAs: one for all the data combined and for each of the six realms independently (excluding offshore Indian Ocean sites). Each

PERMANOVA included the variables selected by the CCA, excluding those with VIFs > 10 (Appendix C.4).

Last, I evaluated how local human disturbance specifically influenced the distribution of the most common genera of macroalgae, which I defined as genera comprising more than 1% of the total macroalgae cover, either across the entire dataset or within one of the seven realms. I then repeated this analysis for each division and for all macroalgae cover combined to evaluate whether relationships with human disturbance were different when considering specific taxa, and to assess whether total macroalgae cover was significantly correlated with any of the human disturbance metrics. To estimate the effects of human disturbance on each of the most common macroalgae taxa and their divisions, and for all macroalgae combined, I fit linear mixed effects models (LMMs) with the R package lme4 (Bates *et al.*, 2015) using the following equation, where the symbol ‘~’ represents the relationship between the dependent variable (‘Percent’) and the independent variables. I considered the interaction between latitude and longitude a random effect as represented by the notation (1|Latitude:Longitude) and described below.

$$\text{Percent} \sim \text{cumulative human impact score} + \log(\text{population}) + \text{NDVI} + \text{nutrients} + \text{market gravity} + (1|\text{Latitude:Longitude})$$

I also fitted two alternative linear mixed effects equations to evaluate whether to include additional covariates. Both alternative equations considered all the biogeographic and methodological variables fixed effects (Appendix C.1); the first included all the variables selected via the CCA and VIF scores as random effects, and the second included only the human

disturbance metrics. Because the alternative equations were overfitted, I did not include them here. Percent cover data were re-standardized in R to have a mean of zero and standard deviation of one, using the standardized package (Eager, 2017). I considered each of the five human disturbance variables fixed effects, and the interaction between latitude and longitude a random effect to account for spatial autocorrelation across sites. I evaluated the model assumptions (that independent variables are independent, and that the model's error terms have equal variance and are normally distributed) using the performance package (Lüdecke *et al.*, 2021) in R, and log-transformed the population variable to meet the model assumptions. Finally, I calculated the R^2 values (marginal R^2 , which represents only the fixed effects, and conditional R^2 , which measures the fit of the entire model) using the Nakagawaka method (Nakagawa, Johnson and Schielzeth, 2017).

4.3 Results

Across these 1,205 sites, total macroalgae cover varied from zero to 88.20% per site, with a mean of 12.80% and a median of 6.79%. The genus occurring at the most sites was *Halimeda*, which was identified in 68.24% of all sites.

Macroalgal community compositions differed across realms (Figure 4.2). The genus *Halimeda* was common in all realms except for the offshore Indian Ocean, where *Lobophora* was the most common taxa; *Lobophora* was also most common in the northwest Pacific (realm 29). We describe the most common taxa within each realm in detail in Appendix C.5, and the full SIMPER results comparing all realms to each other are supplied in Appendix C.6.

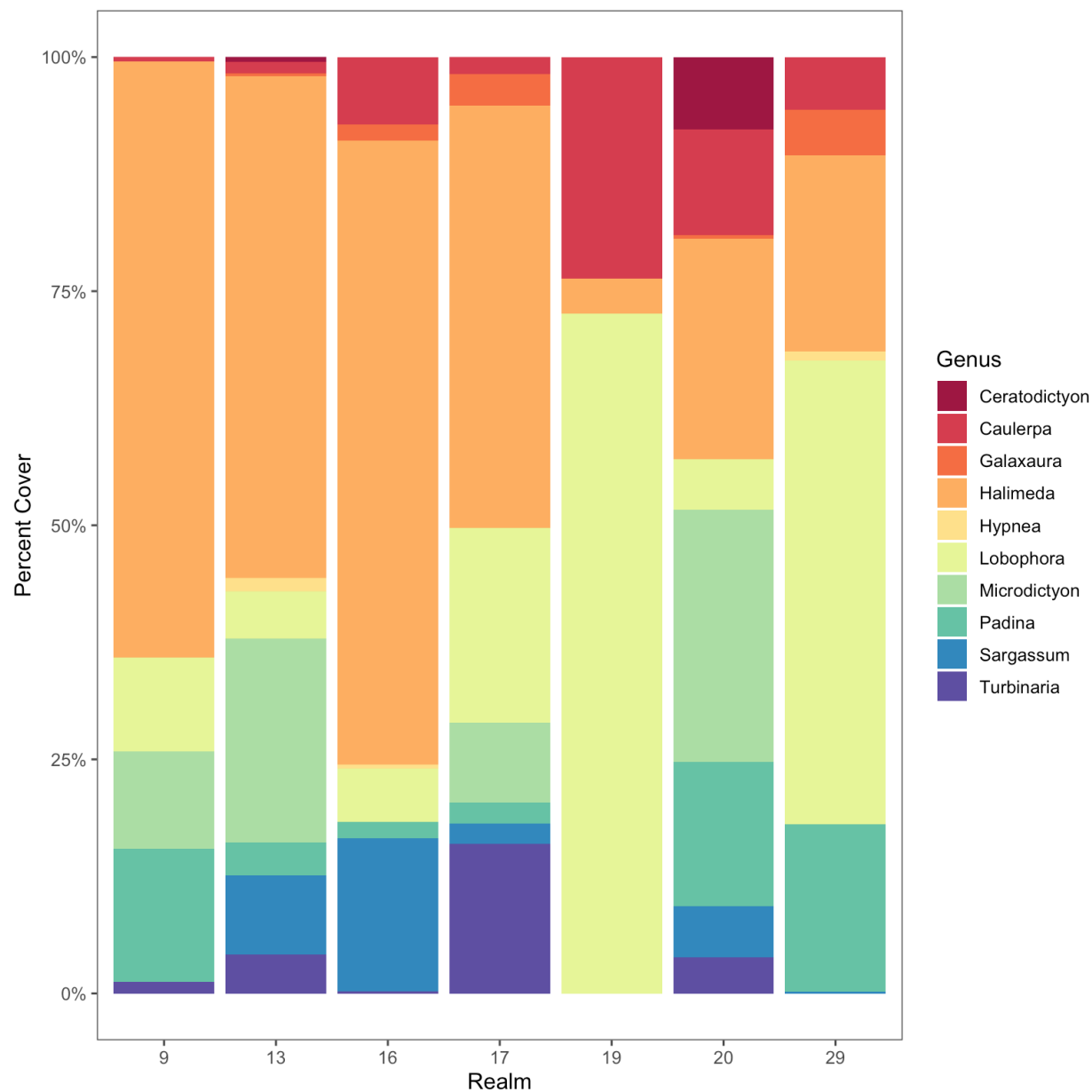


Figure 4.2. Top ten most frequent macroalgae taxa by biogeographic realm.

The drivers of macroalgal community compositions differed when considering the full model (containing all sites) or within each of the realms (Table 4.1, Appendix C.7). The full equations for all the PERMANOVAs were statistically significant with p -values < 0.01 for the model

containing all sites, and models for each of the realms except the mid-tropical North Pacific, which was marginally significant at $p = 0.08$. The explanatory power of each model varied, and each of the independent variables had R^2 values less than 0.10. For all macroalgae combined, the PERMANOVA accounted for 10% of the variation in macroalgae percent cover across sites. The model for Realm 9 had the least explanatory power for variation in macroalgal community composition ($R^2 = 0.05$), while the model for sites in Realm 17 had the greatest ($R^2 = 0.21$). The human disturbance metrics had the largest effect of all drivers contributing to the variation in macroalgal communities in all realms. Of these human disturbance indicators, NDVI and nutrients from agriculture had the greatest presence in the models, although nutrients were only significant in two of seven models, while NDVI was significant in four of the seven. Three of the models also included a categorical variable representing fisheries management (open-access, restricted, or closed / no access), which had greater explanatory power than the other human disturbance metrics, which all had R^2 values less than 0.05. Of the biophysical indicators, mean wave energy was another common driver of macroalgae community composition and was significant in four out of seven models. Except for management, all the variables had R^2 values that were less than or equal to 0.05.

Table 4.1. Variables that best explained macroalgal communities (CCA results) and had variable inflation factors of less than 10, shown with their pseudo- R^2 values (PERMANOVA results).

Variable Type	Variable	All Data	9. Mid-tropical N. Pacific	13. Indo-Pacific seas & Indian	16. Coral Sea	17. Mid South Tropical Pacific	20. Offshore West Pacific	29. NW Pacific
R^2 (full equation)		0.10	0.05	0.12	0.21	0.18	0.07	0.16
Connectivity	Reef Area (15km)			0.05				
	Reef Area (200km)	0.00		0.01				
Human Disturbance	Cum. Human Impact	0.01						
	NDVI	0.00		0.02		0.02	0.03	
	Nutrients (Agriculture)	0.00	0.03		0.04			0.04
	Management	0.01				0.08		0.09
Methodology & Sampling	Depth	0.00		0.02		0.04		
	Habitat	0.02						
	Latitude							
Net Primary Productivity	Chl-a (kurtosis)	0.00		0.01	0.02			0.02
	NPP (sd)	0.00			0.05			
Seasonality	Month of survey (by SST)	0.03						
	PAR average (survey mo.)	0.00				0.04		
	SST mean (survey mo.)			0.01				
Storms	# Storms \geq Type 3	0.00	0.02		0.01			
	Cyclone Score				0.02			
Heat stress	MaxDHW	0.00						
	MMM	0.00						
	SST _{SD}	0.00						
Wind and Wave Exposure	Aspect	0.00				0.00	0.01	
	Wave energy (mean)	0.00		0.00	0.04		0.02	
	Wind and Wave Exposure						0.01	0.01

The relationships between the percent cover and each of the human disturbance metrics varied for different macroalgae genera (Figure 4.4, Appendix C.8). Four out of five human disturbance variables had a negative influence on the percent cover of all macroalgae, although again, the effect sizes were small. Some disturbance variables had negative relationships with specific taxa.

For example, all the green macroalgae were positively affected by nutrients from agriculture, with the exception *Udotea* spp.; however, the cumulative human impacts metric had a consistently negative affect on all green macroalgae except for *Dictosphaeria* spp. For example, logged human population was negatively correlated with *Dictyota* spp., but NDVI had an almost equal, positive effect. The log of population had a positive impact on *Padina* spp., while market gravity had a negative effect. By contrast, market gravity had a positive effect on *Turbinaria* spp.

Human disturbance also had an overall positive relationship with the percent cover of red algae. This was uniformly true for all red macroalgae taxa, although again, the type of human disturbance mattered, and some genera had stronger relationships with disturbance than others. The genus *Halymenia* spp. was the most positively correlated with human disturbance overall, with nutrients and log of the human population having strong, positive relationships with total cover, but both NDVI and the cumulative human impact score having negative relationships. By contrast, for the red macroalgae, the human disturbance metrics collectively had the weakest overall effect on *Laurencia* spp. Cumulative human impact drove an increase in percent cover of this taxa while the log of population, market distance, and market gravity all had negative effects.

By contrast, green macroalgae were more negatively correlated with human disturbance metrics than the other divisions. The cumulative human impact score was negatively correlated with five of nine green macroalgae taxa, while NDVI had negative relationships with seven of nine. NDVI had particularly strong negative associations with *Halimeda* spp. and *Microdictyon* spp.

Nutrients had a positive effect on the percent cover of all green macroalgae taxa, but the negative

effects of human disturbance outweighed the positive for *Halimeda* spp., *Microdictyon* spp., and *Udotea* spp. (and for all green macroalgae combined).

-0.02	0.03	-0.01	0.00	0.01	All Macroalgae
0.01	0.07	0.05	0.12	0.01	All Brown Macroalgae
0.14	-0.17	0.05	0.09	0.10	Dictyota
-0.04	0.09	-0.08	0.09	0.09	Dictyopteris
-0.06	0.02	0.03	0.03	-0.02	Lobophora
0.00	0.15	-0.01	0.03	0.08	Padina
-0.02	0.02	0.12	0.03	-0.07	Spatoglossum
0.05	0.07	0.03	0.12	-0.05	Sargassum
0.06	-0.02	0.11	-0.02	0.01	Turbinaria
-0.31	0.15	-0.01	-0.06	0.06	All Green Macroalgae
-0.12	0.14	0.09	0.01	0.12	Bryopsis
-0.12	-0.01	0.06	-0.02	0.14	Chlorodesmis
-0.12	0.05	-0.02	-0.04	0.11	Caulerpa
-0.01	0.00	0.02	-0.02	0.27	Cladophoropsis
0.01	0.18	-0.12	-0.01	0.06	Dictosphaeria
-0.17	0.03	0.07	-0.07	0.06	Halimeda
-0.17	0.14	-0.09	0.06	0.02	Microdictyon
-0.06	0.06	0.00	0.01	0.08	Neomeris
-0.03	-0.06	0.06	-0.05	0.00	Udotea
-0.13	0.19	0.03	0.07	0.19	All Red Macroalgae
-0.04	0.07	0.03	0.00	0.14	Amansia
-0.02	-0.09	0.11	0.13	-0.02	Asparagopsis
-0.21	0.00	0.04	0.02	0.23	Ceratodictyon
-0.08	-0.01	0.04	-0.07	0.12	Galaxaura
-0.05	0.15	0.00	-0.02	0.21	Halymenia
0.01	0.08	0.10	0.04	0.01	Hypnea
0.01	-0.02	-0.04	0.08	0.02	Laurencia
-0.03	0.04	0.08	0.00	0.08	Neurymenia
-0.05	0.05	0.03	0.02	0.08	Mean
Cumulative Human Impacts	log(Population)	Market Gravity	NDVI	Nutrients (agriculture)	

Figure 4.3. Coefficient estimates for fixed effects from linear mixed effects models. *Coefficient estimates for NDVI and Market Distance have been multiplied by -1 to account for these variables' inverse relationship with disturbance.

4.4 Discussion and Conclusions

The percent cover of macroalgae is not a robust indicator metric for local anthropogenic disturbance, for two main reasons that I explain further below: (1) the drivers of macroalgae communities are unclear, challenging to estimate, and differ across realms, and (2) different macroalgae genera have distinct and often opposite responses to diverse types of human disturbance.

First, I find that multiple factors, most of which were not related to local anthropogenic degradation, influenced macroalgae community compositions (connectivity, wind and wave exposure, storms, net primary productivity, and seasonality), and these factors differed within each of the realms. This creates a quandary in that accounting for these factors is necessary before total macroalgae cover can serve as an indicator of reef health. Otherwise, a researcher risks attributing observed patterns in macroalgae community composition to the wrong drivers and potentially misidentifying the sites most in need of conservation and management, wasting valuable time and resources. Despite assessing 60 variables that could influence macroalgae communities, the most parsimonious models still included few variables, and the PERMANOVAs all had R^2 values of less than 0.25, indicating that the models were still unable to account for the majority of drivers of macroalgae community distribution (discussed further below).

Second, the macroalgae genera we assessed exhibited diverse relationships with human disturbance but combining all macroalgae into a single category concealed these relationships;

the total macroalgae cover metric was uniformly weakly explained by each of the human disturbance variables (Figure 4.4). The cumulative human impacts score, which includes fishing pressure, sedimentation, nutrients from agriculture, and industrial activities, was negatively correlated with most of the genera, although it was strongly positively associated with *Dictyota* spp. All taxa exhibited different and oppositional relationships with human disturbance that depended on the specific variable; none of the taxa had uniformly positive or negative relationships across all human disturbance variables. This suggests that signatures of human disturbance are difficult to distinguish from the additional factors driving macroalgae percent cover and demonstrates that they cannot be relied upon to accurately represent the effects of local human disturbance on coral reefs.

The individual traits of the macroalgae genera may explain their relationships with the various disturbance metrics, each of which represent a different form of localized disturbance. For example, for all green macroalgae combined, cumulative human impacts, NDVI, and market gravity were all negatively correlated with the percent cover, while log of the population and nutrients were positively correlated; on average, human disturbance had a negative overall effect on green macroalgae. The genus *Halimeda* was present at almost 70% of the sites and was the most common macroalga in our dataset. As a calcifying algae that is one of the most common on tropical reefs globally, *Halimeda* spp. are an important sediment producer on coral reefs (Hillis-Colinvaux, 1980). Because of its ubiquity, the percent cover of *Halimeda* had strong influence over the relationships between disturbance and all green macroalgae combined. The one exception was market gravity, which was positively correlated with the percent cover of *Halimeda* but had a weak and negative correlation with the percent of green macroalgae

combined. While market gravity was designed as a metric for fishing pressure (Cinner *et al.*, 2018), it incorporates population size; market gravity and the log of the population may therefore also reflect nutrient loading present in realms with high human populations. This, and the positive relationship with nutrients from agriculture, aligns with past findings showing that *Halimeda* spp. growth is stimulated by nutrients (Delgado, 1994; Teichberg, Fricke and Bischof, 2013). However, coral reef herbivores show low preferences for *Halimeda* spp. (Hay *et al.*, 1988) and increasing fishing pressure might increase competition with other macroalgae taxa that would otherwise be kept in check by herbivory, which could explain the negative correlation with the cumulative human impact score. Collectively, these results reveal a complex relationship between *Halimeda* spp. and human disturbance; it is more likely to grow where nutrients are high, but not necessarily where there is high fishing pressure.

The results suggest that similarly complex relationships exist with other macroalgae taxa, although confirming these relationships will require further research. For example, I found that among canopy-forming brown algae, which provide important habitat for fish and support small-scale fisheries (Sievers *et al.*, 2020; Wilson *et al.*, 2022), exhibit diverse responses to disturbance. *Turbinaria* spp. has a positive relationship with disturbance (represented by the inverse NDVI) which may be explained by its high tolerance for sedimentation (Sura *et al.*, 2021). *Sargassum* was one of the few taxa exhibiting a negative correlation with nutrients from agriculture (along with *Lobophora* spp., *Spatoglossom* spp., and *Asparagopsis* spp.), which aligns with past research but is in direct opposition of the RDM, an influential theory positing that macroalgae cover on coral reefs is dictated by nutrients acting through top-down (e.g.,

fishing pressure) or bottom-up (e.g., nutrients) processes (McClanahan *et al.*, 2004).

While past research helps explain many of the relationships between specific macroalgae taxa and our human disturbance variables, I also found relationships that were unexpected. The morphology of *Turbinaria* spp., along with their chemical defenses, make it unpalatable to many herbivores (Bittick *et al.*, 2010) and I would not anticipate an increase in percent cover with increasing fishing pressure. However, I found a positive correlation with market gravity. Blooms of *Turbinaria* spp. have been linked to high nutrient concentrations (McCook, 1999) but our results found that this relationship was weak, and the percent cover of *Turbinaria* spp. was also negatively correlated with the log of human population. Other studies have also reported that macroalgae taxa often do not respond as predicted to stressors (McCook, 1999), again, underscoring how little scientists understand about these interactions. Unfortunately, studies investigating taxa-specific interactions with human disturbance for tropical macroalgae are lacking for all but the most common reef taxa and often report conflicting results (Ramseyer *et al.*, 2021). The studies that do exist have primarily been motivated by negative interactions between corals and macroalgae (Fulton *et al.*, 2019), and because of the RDM's predictions, studies are usually limited to investigating the effects of fishing pressure or nutrients (Fong and Paul, 2011).

Without closer attention to the relationships between macroalgae, local human disturbance, and reef health or degradation more broadly, scientists risk reaching misleading conclusions about the effects of locally driven anthropogenic coral reef degradation, as two influential studies demonstrate. The first compared the percent cover of macroalgae around inhabited and

uninhabited islands in the central Pacific, finding that macroalgae cover was correlated with human population, and the authors concluded that people negatively affect reef health (Smith *et al.*, 2016). In this study, the authors included turf algae in their definition of macroalgae, and excluded *Halimeda* spp. and other erect, calcifying macroalgae taxa. However, again, high percent cover of macroalgae does not necessarily indicate a degraded reef (Vroom, 2011), nor does it reflect local human disturbance according to this analysis. Although I did not include turf algae in this analysis, the genera and division-specific analyses described above demonstrates that the non-calcifying macroalgae taxa responded to local human disturbance in diverse ways; defining macroalgae to exclude *Halimeda* and other erect, calcifying genera is unlikely to make macroalgae as a category a more robust proxy for human disturbance. Smith *et al.* (2016) aimed to create a baseline that would inform management decisions, but without accounting for the specific macroalgae taxa that are present, including the non-calcifying taxa, and the environmental processes affecting macroalgae cover, the authors may have erroneously attributed high macroalgae cover to human population.

By contrast, the second study using macroalgae cover to investigate the effects of local stressors on coral reefs did not find a relationship between local human disturbance and the percent cover of macroalgae on reefs. Bruno and Valdivia (2016) excluded turf algae from their definition of macroalgae, but included erect, calcifying species such as *Halimeda* spp. They concluded that signatures of human-driven degradation on coral reefs were undetectable because climate-driven heat stress overwhelmed the effects of local human impacts (Bruno and Valdivia, 2016). By employing genus-level data, the results support the finding that total macroalgae cover does not correlate with human disturbance. However, we also show that this lack of correlation may be

because of the varied interactions between disturbance and an individual macroalgae taxa. Signatures of human disturbance that were undetectable using total macroalgae cover may still be evident when identifying macroalgae at the genus level. In these cases, relying on the assumption that macroalgae percent cover correlates with local disturbance may lead to maladaptive interventions. For example, if managers assume that all macroalgae will respond the same way to enhanced herbivory or misidentify undisturbed reefs as degraded, this approach could lead to ineffective management interventions that waste scarce conservation resources.

For reef-building corals, significant efforts have greatly improved our understanding of diverse and complex responses to disturbance; we recognize differences in how corals respond to bleaching, for example, because of their morphology, heterotrophic feeding ability, physiology, and several other factors (Darling *et al.*, 2012). Yet, the focus on coral in the literature (Vroom, 2011; Fulton *et al.*, 2019) demonstrates that scientists have failed to consider how the large diversity of macroalgae may also respond to disturbance in diverse ways. We have also failed to consider the negative effects that disturbance might have for macroalgae taxa, and what this means for ecosystem function overall (Vroom, 2011). Like reef-building coral communities, macroalgae communities are becoming less diverse and complex as the oceans warm and acidify (Fulton *et al.*, 2019). Our limited understanding of the relationships between both human and climate disturbance and macroalgae taxa, and their importance in reef ecosystem functioning, impedes our ability to respond to the many threats facing coral reef ecosystems as a whole (Vroom, 2011).

Further, the idea that coral-dominated reefs are more desirable than reefs dominated by other taxa may also be misleading. For example, some degraded reefs host high percent cover of a single opportunistic coral species and low macroalgae cover (Crane *et al.*, 2017; Cannon *et al.*, 2021). These reefs would be considered healthy or even a ‘bright spot’, where coral cover is higher than expected based on estimates of local disturbances (Sully, Hodgson and van Woesik, 2022), by anyone assuming that high coral cover indicates reef health. In addition, the focus on corals in the literature has led to a dearth of research on other taxa that can dominate reefs, for example sponges (Pawlik and McMurray, 2020; Reverter *et al.*, 2022). Like macroalgae, the dynamics driving the distributions of many of these taxa are poorly understood and are often investigated only in the context of their influence on corals.

This study builds on previous research that has called the RDM and the subsequent assumptions that macroalgae is correlated with local human disturbance an oversimplification (McCook, 1999; McClanahan *et al.*, 2004; Vroom, 2011) potentially negative implications for management (McCook, 1999; Vroom, 2011) and that has criticized the widespread reliance on macroalgae as an indicator of reef health or degradation (Bruno *et al.*, 2009; Vroom, 2011). Still, researchers and managers continue to use total macroalgae cover to provide proxy estimates on the health of coral reefs and how they are affected by people (Bruno and Valdivia, 2016; Smith *et al.*, 2016). A key limitation to this study is the lack of available survey data identifying macroalgae at the taxon level; in addition, we know little about the global drivers of macroalgae distributions (but see Keith, Kerswell and Connolly, 2014). Most of the survey data I use here were designed to investigate coral reef health and site selection may have excluded parts of the reef with higher macroalgae cover. In addition, the sampling was uneven across realms, and the reliance on large-

scale, low-resolution global databases to calculate site-specific independent variables may have affected my ability to account for drivers of macroalgal communities because of differences in scale. Finally, the stepwise variable selection methods may have excluded explanatory variables that drive differences in the benthic community composition, resulting in a model that fits these data well but does not perform well when adding additional data (Smith 2018). Despite these limitations, this study demonstrates how the links between macroalgae percent cover and human disturbance are uncertain, which undermines the usefulness of total macroalgae cover as a way of estimating local, human-driven degradation.

Scientists have repeatedly found that coral reef communities exhibit varied responses to disturbance, warning that attempts to find universal metrics to allow tracking reef health or degradation across broad scales are unlikely to be successful (Gouezo *et al.*, 2019; De Valck and Rolfe, 2022). Our results support this assertion for macroalgae; the taxa that are present will drive different responses to local anthropogenic stressors. We urge researchers and managers conducting benthic monitoring on coral reefs to identify macroalgae to lower taxonomic levels, so that they may consider the responses of distinct taxa to diverse types of disturbance and what this might indicate for overall reef health within their unique localities.

Strategic management of coral reefs will be increasingly vital as the climate continues to warm (Darling *et al.*, 2019). Evaluating how coral reefs are being affected by disturbance is an indispensable part of research and management, but the most common metrics used in that work are based on an outdated and oversimplified paradigm. I have shown here that total macroalgae cover does not correlate well with local human disturbance but that evaluating macroalgae cover

at the genus level shows more promise as a management and assessment tool. Genus-level data might also provide greater understanding of the drivers of macroalgae and how they influence overall ecosystem functioning. Science, management, and policy aiming to protect reefs all rely on quantitative estimates of reef health and using an inaccurate or misleading relationship could, and possibly already has, undermined those endeavors. Investments in further research on macroalgae at higher taxonomic resolutions, including genus-specific interactions with human-driven stressors, may prove to be an important future coral reef conservation tool. As others have argued, testing long-standing paradigms in coral reef ecology will be increasingly necessary as climate change intensifies (Williams *et al.*, 2019). I hope that by demonstrating that total macroalgae cover is not correlated with human disturbance or an effective way to estimate coral reef health in the Indian and Pacific Oceans, this work catalyze much-needed consideration of how we define reef health and the effects of local human disturbance, especially under rapidly changing environmental conditions.

Chapter 5: The Call Is Coming From Inside The House: legacies of racism and colonialism persist in coral reef conservation.

“It’s a simple calculus. This universe is finite, its resources, finite. If life is left unchecked, life will cease to exist. It needs correcting.”- Thanos.¹

‘If you set aside emotional and cultural biases, the math is straightforward. Reducing population is just basic math.’ – Coral List participant.

5.1 Introduction

Conservation has an enduring racism problem (Kashwan *et al.*, 2021; Rudd *et al.*, 2021) that dates back to its origins in colonialism (Hendlin, 2014; Murdock, 2021). While calls for conservationists and natural scientists more broadly to address this racism have existed for as long as the field itself (Godet and Devictor, 2018), these calls have remained largely siloed within the social sciences and humanities (Baker, Eichhorn and Griffiths, 2019). As a result, conservationists are only beginning to recognize the problematic beginnings of contemporary mainstream conservation and their effects today. While this is an important first step, conservationists must also reckon with the ways that enduring racism within our ranks has not only hindered efforts to enhance diversity among biologists and conservation practitioners, but has also impeded our ability to fulfil conservation’s mandate to protect biodiversity (Kashwan *et al.*, 2021; Rudd *et al.*, 2021; Fidler *et al.*, 2022).

Understanding the history of the field helps to contextualize the persistence of racism and discrimination in conservation today. Conservation consists of two ‘twin spheres’: the first, conservation practice, includes applied conservation policy and programs (Rudd *et al.*, 2021),

¹ See Love (2018).

while the second, conservation biology, is branch of ecology and evolutionary biology (EEB) that applies science-based decision-making to conservation problems (Soulé, 1985; Rudd *et al.*, 2021). What we today call conservation practice is a set of conservation principles put in place in the United States to halt the rapid overexploitation of wildlife during colonial expansion in the 19th and 20th centuries (Hessami *et al.*, 2021). This approach dates back to European imperialism and colonialism, during which European governments invaded, divided, and annexed parts of Africa, India, and South America to assert control over nature, natural resources, and people (Neumann, 1996; Kashwan, 2017; Gissibl, 2019). Today, conservation practice has been dubbed the North American model of wildlife conservation because it became globally ubiquitous after westward expansion in the United States (Dowie, 2009; Hessami *et al.*, 2021). A defining feature of the North American model was its definition of wilderness as separate and apart from humanity, and early American conservationists wielded this definition to assert that protecting nature required removing Indigenous peoples (Dowie, 2009). Conservation practice was thus a product of settler colonialism, the system that drives displacement of Indigenous peoples in a colonized region and replaces them with settlers building a permanent society in their stead (Wolfe, 2006). Because Europeans typically justified settler colonialism through their assertions of racial superiority, settler colonialism has and continues to perpetuate racism today (Wolfe, 2006).

The concept of wilderness as separate from people is also at odds with many Indigenous worldviews, which are diverse but united by a shared view of humans as a part of and in relationship with ecosystems (Gómez-Pompa and Kaus, 1992; Cronon, 1995; Fletcher *et al.*, 2021; Hessami *et al.*, 2021). The North American definition of wilderness is also limited in its

failure to recognize that people have altered the environments they live in for at least 12,000 years (Ellis *et al.*, 2021). Despite this, the definition was codified into law in the U.S. Wilderness Act of 1964 (Dowie, 2009), leading conservationists to create spatially delineated and guarded protected areas that aimed to protect wildlife by keeping people out (West *et al.*, 2018; Murdock, 2021). Fortress conservation spread gradually across the world until it became synonymous with mainstream conservation practice (Dowie, 2009). Fortress conservation continues to reinforce settler colonialism through further displacement of (Dowie, 2009; Murdock, 2021) and violence against Indigenous peoples and local communities (IPLC). Although there have been great strides in recent decades to recognize and ameliorate the ways that conservation mistreats IPLC, fortress conservation is still widely practiced, particularly in the Global South (Dowie, 2009; West *et al.*, 2018; Kashwan *et al.*, 2021). Estimates of the number of people displaced by conservation globally range from five million to tens of millions; one scholar estimated that tens of millions of people may have been displaced by conservation in Africa alone (Dowie, 2009). Today, Indigenous peoples manage or have tenure rights over more than a quarter of global terrestrial areas, which overlap with 40% of all terrestrial protected areas and intact ecosystems (Garnett *et al.*, 2018).

In the late 1800's and early 1900's, when conservation practice was in its infancy, Western science was exclusively the purview of upper-class white men, who viewed their faith in the scientific process and rationality as evidence of their own superiority and justification for their racism.² Many of the founding figures of conservation were openly eugenicists who believed in

² For examples, see the rich literature on race and science in the Enlightenment (Eze, 1997).

Malthusian ideas about resource scarcity (Brecht, 1996; Allen, 2013). In 1798, Malthus famously predicted that human populations would continue to increase exponentially as long as the resources existed to support them, but because resources are finite, unconstrained population growth would lead to resource depletion, and ultimately, mass starvation (Malthus, 1798). He was also an early proponent of biological determinism, arguing that food shortages and poverty were natural ‘checks’ to population growth (Rao, 1994; Seidl and Tisdell, 1999; Robertson, 2012). Malthusianism had far-reaching implications; in addition to directly motivating some of the most foundational theories and statistical methods in EEB, Malthusian concepts remain influential today, despite the lack of empirical evidence (Rao, 1994; Seidl and Tisdell, 1999). For example, both Charles Darwin and Alfred Russell Wallace, whom independently authored similar theories of evolution, were inspired by Malthus’s notions of resource scarcity, competition, and natural selection (Rao, 1994; Gould, 1996; Robertson, 2012). Garrett Hardin, the scientist and environmentalist who wrote the famous article about the ‘tragedy of the commons’ (Hardin, 1968) and a white nationalist extremist (Amend, 2019; Mildenberger, 2019), applied the concept of carrying capacity to people to argue against providing aid to the poor (Hardin, 1976). Carrying capacity, the maximum population a given region can support given the resources available, remains hugely influential in ecology today; for example, the field of population ecology is built upon the concept (Odum, 1971). This may prime ecologists to see population growth as inherently threatening (Robertson, 2012).

Conservation practice continued operating separately but tangentially to scientific research until 1985, when Michael E. Soulé introduced the field of conservation biology, a new branch of EEB, in response to a perceived need for science-based decision making to protect biodiversity (1985).

Soulé differentiated conservation biology from EEB by categorizing the former as a crisis discipline, describing conservation biology's relationship with biology as 'analogous to that of surgery to physiology and war to political science' (1985, p. 727). Conservation biology was also distinct from EEB in that it was meant to be multidisciplinary and holistic, specifically through its consideration of social science and population genetics, the latter of which was applied to identifying viable population sizes given an environment's carrying capacity (Soulé, 1985; Godet and Devictor, 2018).

Notably, in describing the necessity for a scientific approach to conservation problems, Soulé cited Paul and Anne Ehrlich³ (Soulé, 1985), who famously used Malthusian ideas to describe population growth as an existential threat to humanity in their 1968 bestseller, *The Population Bomb* (Robertson, 2012). Overpopulation has remained a popular scapegoat for environmental degradation and biodiversity loss, and more recently, environmentalists have linked population to climate change, alongside other forms of environmental degradation (Barra and Zotti, 2018; Schultz, 2021). However, these narratives ignore the huge disparities in consumption between people in the Global North and South (Liu *et al.*, 2003; Machovina, Feeley and Ripple, 2015; Wilting *et al.*, 2017; IPCC, 2022). Scholars have also heavily criticized overpopulation narratives for their role in encouraging population control programs, driving human rights abuses that disproportionately affected the most vulnerable people in society, especially Black and

³ Anne Ehrlich co-authored *The Population Bomb* with her husband Paul, but was not given credit at the time (Ehrlich and Ehrlich, 2009).

Indigenous peoples and people of color (Hartmann, 1994; Rao, 1994; Robertson, 2012; Hendrixson and Hartmann, 2019).

Without an understanding of this history, we risk perpetuating it, and this is especially critical as the climate threats to ecosystems intensify. An illustrative example of this relevance today is the debate surrounding the legacy of recently-deceased biologist E.O. Wilson, founder of sociobiology: the idea that genetics and natural selection explain social behavior (Wilson, 1975). While his book by the same name was widely praised (Salzman, 1979; Kaye, 1986), several of Wilson's colleagues spoke out to criticize his application of the theory to humans (Allen *et al.*, 1975; Lewontin, 1979; Salzman, 1979), likening it to social Darwinism and eugenics (Salzman, 1979; Gould, 1996). Among conservation biologists, Wilson was also well-known for his 2016 book, *Half Earth*, which called for protecting 50% of the Earth's surface through a series of depopulated, interconnected protected areas (Wilson, 2016). Critics to this proposal pointed out that not only are there ethical concerns about removing people from so much of the Earth, which could lead to a global land grab (Ellis and Mehrabi, 2019; Schleicher *et al.*, 2019; Kashwan *et al.*, 2021), but the proposal did nothing to address what they argued were the root cause of environmental degradation, the chronic overconsumption of limited resources in industrialized countries, instead placing the burden of conservation on IPLC (Büscher *et al.*, 2016; Kashwan *et al.*, 2021). Protecting half of the Earth would directly affect over a billion people, and this estimate is on the conservative side (Schleicher *et al.*, 2019). Still, the Convention on Biological Diversity (CBD) instituted similar approaches, such as the 30 x 30 initiative, which calls for protecting 30% of the Earth's surface by 2030 (Dinerstein *et al.*, 2019; Kashwan *et al.*, 2021), and has discussed whether to extend this goal to 50% by 2050 (Pimm, Jenkins and Li, 2018; Ellis

and Mehrabi, 2019; Kashwan *et al.*, 2021). Recently, U.S. President Joe Biden committed the United States to meeting the 30 x 30 goal as a part of the ‘America the Beautiful’ Initiative (U.S. Department of the Interior, 2021).

While the colonial legacies of conservation persist, there have also been significant efforts to resist these legacies and to change them, to address past and ongoing wrongs imposed on IPLC and to increase conservation’s efficacy. These efforts are not new, but until recently, they remained siloed within the social sciences and humanities and have had limited impacts on conservation biology and practice (Baker, Eichhorn and Griffiths, 2019). This may have begun to change in recent decades, as efforts to democratize science are gaining traction (Salomon *et al.*, 2018). Conservationists are also increasingly recognizing that colonial approaches to conservation are not only unethical; they are also less effective at protecting biodiversity than participatory, egalitarian approaches (Fidler *et al.*, 2022).

There have also been significant efforts to recognize and revitalize the role of IPLC in conservation, for example through calls to decolonize or Indigenize conservation that include co-creating knowledge to inform conservation, recognition of and greater deference to Indigenous leadership and knowledge, repatriation of lands and waters, and supporting Indigenous sovereignty (Eckert *et al.*, 2018; Artelle *et al.*, 2019, 2021; Cohen *et al.*, 2021; Collins *et al.*, 2021; Fletcher *et al.*, 2021; Hessami *et al.*, 2021; Jacobs *et al.*, 2022). These efforts have highlighted the importance of democratizing and/or decolonizing or Indigenizing conservation globally, and to ensure that voices from the Global South are represented and heard (Collins *et al.*, 2021; Stefanoudis *et al.*, 2021; Asase *et al.*, 2022; Genda *et al.*, 2022; Patel, 2022). Still, to

date, material changes in system-wide conservation approaches have disproportionately occurred in the Global North, where most academic, research institutions, and conservation non-governmental organizations (NGOs) are based (Pyšek *et al.*, 2008; Tydecks *et al.*, 2018; Hazlett *et al.*, 2020) and where Indigenous peoples have some access to monetary resources and legal avenues to advocate for exercising their rights. While colonial dynamics continue to limit IPLC access to these resources within the Global North, particularly in older national parks (e.g. Woo, 2011; Cohen *et al.*, 2021), newer initiatives offer some paths for self-advocacy that may be less accessible for IPLC in the Global South (Lanjouw, 2021).

As a unique community within conservation science and practice, coral reef conservation provides an interesting subject for exploring how conservation biologists and practitioners talk about degradation, conservation efforts, and the roles of IPLC. Coral reef scientists call coral reefs Earth's 'canaries in the coal mine' for climate change, in that they provide a glimpse of what could happen to other ecosystems if humans are unable to halt greenhouse gas emissions (e.g. Riegl and Dodge, 2008; Andradi-Brown *et al.*, 2020). They are also unique among globally threatened ecosystems in that they exist in both densely populated areas and in remote areas of the tropical oceans that are not frequently visited by people, providing invaluable ecosystem functions in both (Williams *et al.*, 2019); they provide livelihoods, subsistence, and hold immense cultural importance for millions of people (Cinner, 2014). Still, climate change and ocean acidification threaten even reefs that are far from people (Baumann *et al.*, 2022), and coral reef scientists are still investigating the ways that local human impacts like fishing and water pollution interact with these global stressors to influence the function of coral reef ecological communities (Bruno and Valdivia, 2016; Smith *et al.*, 2016). Because human-driven stressors

threaten all coral reefs (Baumann *et al.*, 2022), coral reef scientists who may or may not have training as conservation biologists have nonetheless found themselves thrust into conservation by necessity.

Coral reef conservation also faces unique issues of geography in terms of both location and scale; for example, most coral reefs are in the Global South, but people in the Global North, where there are few reefs, disproportionately drive climate change, which scientists widely agree is the greatest threat to reefs globally (Williams *et al.*, 2019). By contrast, IPLC in the Global South contribute little to greenhouse gas (GHG) emissions but are some of the most susceptible to climate impacts (Wolff *et al.*, 2015). As a result, local conservation efforts aiming to empower IPLC usually focus on addressing local-scale stressors such as fishing or water quality, and sometimes on initiatives like coral rehabilitation and restoration. While coral reef scientists agree that addressing local scale threats is important, differences in scale between climate change and local stressors has caused disagreement among coral reef conservationists about which threats and solutions to prioritize; some suggest that focusing on local stressors to reefs is a waste of time and resources until we have addressed GHG emissions (Braverman, 2016) while others argue that both are important and necessary for the long-term survival of coral reefs (e.g. Abelson, 2020). The voices of IPLC are not often represented in these debates; despite the location of most reefs in the South, research on coral reefs is produced by people, non-governmental organizations (NGOs), and academic institutions based in the Global North (Ahmadia *et al.*, 2021).

The geographic inequalities in coral reef research are similar to those in other conservation fields and EEB more broadly (Pyšek *et al.*, 2008; Tydecks *et al.*, 2018; Hazlett *et al.*, 2020; Patel, 2022). While efforts to address the lingering racism in conservation that stem from its colonial roots also apply to coral reef conservation, it is unclear to what extent coral reef conservationists have engaged with these calls. Addressing discrimination and increasing diversity at research institutions are integral for coral reef science to become more equitable, which also makes conservation practice more effective (Chaudhury and Colla, 2021; Cronin *et al.*, 2021; Rudd *et al.*, 2021; Fidler *et al.*, 2022). Still, as calls to end ‘parachute science’ – in which scientists from the Global North conduct research in the South without engaging with local communities or ensuring that the work benefits them (de Vos, 2020; Stefanoudis *et al.*, 2021; de Vos and Schwartz, 2022; Genda *et al.*, 2022) – demonstrate, diversifying coral reef scientists in research institutions in the Global North will not necessarily change top-down approaches to research and conservation in the Global South. This is especially the case when the influence of scientific racism in conservation practice, conservation biology, and EEB more broadly go unchallenged in research norms and curriculum (Chaudhury and Colla, 2021; Kashwan *et al.*, 2021; Rudd *et al.*, 2021; Trisos, Auerbach and Katti, 2021).

Gaining an understanding of the narratives that coral reef conservationists use when discussing local reef degradation could reveal how coral reef conservationists have engaged with the longstanding critiques of conservation, and whether norms and practices have shifted in response to these critiques and calls for more justice and equitable approaches. Wilson’s Half Earth proposal, Hardin’s Tragedy of the Commons, and Ehrlich’s Population Bomb are examples of policy narratives, storylines that practitioners, bureaucrats, and policy makers use to guide

decision-making and convey simplified descriptions of complex situations (Roe, 1991; Campbell, 2002; Berdej, Andrachuk and Armitage, 2015). Policy narratives can intentionally or unintentionally privilege specific ways of thinking or marginalize others and may position different actors in pre-defined roles (Berdej, Andrachuk and Armitage, 2015); for example, as discussed above, fortress conservation narratives can cast IPLC as driving degradation, and conservationists as expert knowledge-holders. Different actors may also wield narratives to achieve specific outcomes, for example to claim rights to resources or to restrict the rights of others (Berdej, Andrachuk and Armitage, 2015). Policy narratives are overlapping and competing, and once established, can be extremely persistent, even when there is evidence contradicting them, as is the case with the Tragedy of the Commons (Roe, 1991). An understanding of various kinds of narratives in conservation and how they frame threats to biodiversity can help conservation biologists and practitioners by fostering critical reflection of goals, practices, and norms, which is critical because narratives can have material effects on design and implementation of conservation initiatives (Campbell, 2002; Berdej, Andrachuk and Armitage, 2015). Critically, investigating policy narratives can also reveal whether different ways of framing conservation problems inadvertently perpetuate systematic racism – in which the institutions and people driving conservation policy produce outcomes that deeply disadvantage or racialize communities by continuing to assign Indigenous or local groups a ‘bad actor’ status. Typically, this occurs without recognizing how conservation’s history has already dismantled highly adaptive and functional knowledge and governing systems, as is the case for fire-driven landscapes (Dickson-Hoyle *et al.*, 2022) as well as marine systems (Eckert *et al.*, 2018; Atlas *et al.*, 2021; Lepofsky *et al.*, 2021).

Conservation narratives are diverse and vary broadly, but can be grouped into two types that capture differences in how these narratives frame priorities, conceptualizations of human rights, and the beneficiaries of conservation action: crisis narratives and resilience narratives (Table 5.1) (Berdej, Andrachuk and Armitage, 2015). Initiatives such as the Half Earth proposal and overpopulation narratives are examples of crisis narratives, which stress the urgency of conservation interventions in response to an impending crisis. However, while crisis narratives are useful in that they can motivate fast actions to halt environmental degradation, they tend to overlook or minimize interactions between people and resources (Berdej, Andrachuk and Armitage, 2015), which can lead to neglecting ethical considerations and may drive human rights abuses; for example, conservationists have defended militarized conservation tactics as necessary for protecting against mass extinction (Duffy *et al.*, 2019). Crisis narratives privilege scientific knowledge and lean heavily on ideas of wilderness as an Edenic and human-evacuated landscape, leading to a reliance on ‘top down’ policy solutions that exclude people from nature or may portray IPLC who do not comply as poachers and criminals (Campbell, 2002).

Table 5.1. Features of crisis and resilience narratives.

	Crisis Narratives	Resilience Narratives
Pros	Can motivate action, generate support and funding	Ensures that IPLC are not overlooked or “written out”
Cons	Overlook people and their rights; urgency incentivizes extreme approach	May not communicate legitimate urgency
Conservation Motivations	Restoring ecosystems to a pre-human baseline	Facilitating adaptation and resilience
Epistemologies	Science is the only legitimate way to reveal truth	There are many ways of knowing and all are valid
Power Concentration	Centralized, top-down	Decentral, bottom-up
Relationships between people and nature	Human/nature dualism	Humans as a part of nature
Examples	Fortress conservation; 30 x 30; the Half Earth Initiative; militarized conservation	Community-based conservation; pro-poor conservation; rights-based conservation

By contrast, resilience narratives reflect ideas of adaptation and resilience and facilitate greater recognition of human relationships with the environment. Unlike crisis narratives, resilience narratives are local, decentralized, and often community driven (Campbell, 2002). Resilience policy narratives emerged alongside social-ecological systems theory, which aimed to understand how environmental systems can support healthy societies, and vice versa; resilience narratives arose to challenge dominant perspectives that assumed the existence of ecological equilibriums (Folke, 2006). Living up to the promise of resilience narratives requires that governments, NGOs, and scientists transfer decision-making power to IPLC; without this, resilience framings remain rhetorical, undermining trust and creating conflict (Campbell, 2002; Dressler *et al.*, 2010; Kamat, 2018; Büscher and Fletcher, 2019). Berdej *et al.* (2015) suggested that combining the beneficial aspects of crisis and resilience narratives could combat the weaknesses in each, leading to a more balanced, just, and effective policy narrative that also

recognizes the reality of the urgent need to combat degradation. Still, this will require finding a way to reconcile conflicts between the two narratives; for example, resilience narratives emphasize building trust between practitioners and IPLC, which takes time, while crisis narratives specifically emphasize expediency (Büscher and Fletcher, 2019; Jacobs *et al.*, 2022). These narrative types are a way to understand how people think and talk about conservation problems and can provide information about underlying assumptions held by different actors. Importantly, any conservation problem can be framed through resilience or crisis narratives; the difference between them is not an objective representation of the problem itself, but how a given person thinks about and conceptualizes that problem.

Here, I take advantage of a long-standing listserv for coral reef information and news, the Coral List, which is hosted by the United States National Ocean and Atmospheric Administration's (NOAA) Coral Health and Monitoring Program (CHAMP), to search for and identify trends in how coral reef conservationists have engaged with the longstanding critiques of conservation, and whether norms and practices have shifted in response to calls for more justice and equitable approaches. I use narrative analysis to conduct an interdisciplinary investigation exploring how participants on the Coral List discussed the local threats to coral reefs, the actors involved, the drivers of these threats, their perceived solutions, and how these discussions have changed over time, and searched for evidence of persistent use of crisis or resilience narratives among coral reef conservationists. The results illuminate trends in how Coral List participants communicate about the drivers of local threats to reefs and who they view as responsible for reef degradation.

5.2 Methods

The Coral List, a long-standing email listserv for coral reef information and news hosted by NOAA CHAMP, provides a unique opportunity to understand how coral reef conservationists and concerned citizens employ policy narratives when discussing threats to coral reefs, and how these narratives have shifted over time (NOAA CHAMP, 2019). According to NOAA CHAMP, the list is meant to “provide a forum for Internet discussions and announcements pertaining to coral reef ecosystem research, conservation, and education. The list is primarily for use by coral reef ecosystem researchers, scientists, and educators, but is of course open to everybody” (2019). The listserv started in May 1995, and since then the number of subscribers has ballooned to over 9,900 as of March 2022 (M. Jankulak, personal communication, 15 March 2022).

I used a mixed methods, qualitative and quantitative approach that combined narrative policy analysis (Roe, 1994), thematic coding (Saldana, 2009; Marshall and Rossman, 2016; Leavy, 2017), and the statistical methods described below to investigate how the coral reef conservation community discusses local threats to coral reefs, their distal drivers, the actors involved, and their solutions using the Coral List listserv archives, for two different time periods: May 1995 through December 2000, and January 2015 through December 2020. The Coral List archives are publicly available online for each month that the coral list has operated, starting in May 1995 (NOAA CHAMP, 2019). As such, the University of British Columbia Behavioral Research Ethics Board did not require us to apply for ethics approval for this project. However, I do not name individuals here and because the archives are publicly available online, I have paraphrased quotations where necessary to conceal participants’ identities and to maintain the focus on the

community more broadly, with the goal of identifying system-wide challenges and spaces for improvement.

I thematically coded conversational emails about local threats to coral reefs sent via the Coral List between 1995 - 2000 and 2015 – 2020 in NVivo for Windows release 1.0 (QSR International Pty Ltd., 2020). I identified emails that were informal and conversational (excluding all formal text, such as job postings, publication announcements, and press releases) and created a decision-making flow chart to guarantee uniformity (Appendix D.1). I excluded conversations that were solely about global threats to reefs (climate change and ocean acidification) but identified where people discussed interactions between global and local threats. I did not include emails that discussed symptoms of local drivers without specifically attributing them to a local threat. For example, I ignored emails discussing outbreaks of the predatory crown-of-thorns (CoT) starfish (*Acanthaster planci*), which have been linked to water quality and overfishing but can occur absent those stressors (Pratchett *et al.*, 2017), unless the emails attributed outbreaks to anthropogenic stressors. I did not code emails discussing coral diseases, phase shifts, macroalgal blooms, or other potential symptoms of local anthropogenic stressors unless the participants specifically mentioned those stressors themselves, because some of these symptoms may also occur after natural disasters such as storms (Fabricius *et al.*, 2008).

I tracked the participants in the list during the two time periods by creating an individual case for each person who sent an email meeting the criteria above, and used the participant's email signature (when included) to track their affiliation, geography (where they were based at the time of posting), and their role in coral reef conservation (e.g., scientist, dive professional, aquarium

hobbyist, environmental consultant, university student, etc.). In cases where people were not identifiable from their emails (e.g., they did not include a signature or I was unable to identify them from their email address), I used their email address to track their participation. I grouped the locations of Coral List participants into the global regions used by the World Bank, following Ahmadia *et al.* (2021). I also created an individual case to track each email meeting the above criteria using its message-ID, a unique value assigned to each email by the listserv software, and its date. I linked the emails to their senders to identify the most active participants on the list.

For each email, I identified the geography of the coral reefs that participants discussed (if provided), the threat itself, the actors, and proposed solutions (if provided). I coded threats iteratively, using the terminology employed by the participants, and grouped topic codes together as appropriate. I distinguished between proximate and distal drivers of reef degradation following the recommendations of Forster *et al.* (2017), who demonstrated that understanding the distal drivers of degradation is important for addressing the root causes of threats to reefs; local, proximate stressors are those that act directly upon the reef to produce negative impacts on reef health, for example fishing or water quality, while distal drivers of local threats are those that are physically removed from the reef, but underlie proximate impacts, such as population growth or economic pressures that could influence how IPLC and/or local stakeholders utilize resources (Forster *et al.*, 2017). Finally, I grouped sub-codes into top-level codes that captured the types of threats most commonly discussed by listserv participants, using a hierarchical coding structure (Appendix D.2).

Past work has found that the view of different threats facing coral reefs varied by gender, age, educational level, and career attributes (Kleypas and Eakin, 2007). While there is immense value in demographic information, particularly for evaluating the diversity of list participants and whether perceptions of threats vary by groups, I opted against attempting to identify the demographics of Coral List participants. Automated methods either misrepresent people who are transgender or non-binary or fail to represent them entirely (Mihaljević *et al.*, 2019), and collecting demographics responsibly necessitates either direct outreach to list participants, or further research into their identities (Ahmadia *et al.*, 2021), both of which were not feasible given the already broad scope of this project.

5.2.1 Statistical analysis

Statistical analyses and figures were done using R statistical software version 4.1.1 (R Core Team, 2021) and RStudio version 2021.09.0 Build 351 (RStudio Team, 2020). Figures were created with the R packages ggplot2 (Wickham, 2016), ggalluvial (Brunson, 2017), and iGraph (Csardi and Nepusz, 2006). I used Welch's two-sampled t-tests to check for statistically significant differences across groups and time periods. For statistical tests evaluating changes in the number of participants or number of emails, I used the number per month to calculate the annual average number (emails or participants) first, and then conducted t-tests across periods (annual mean $n \sim$ period). To account for potential interannual variation in participation (which could be caused by low participation during fieldwork seasons or academic teaching schedules), I normalized values within each year before testing for differences across periods to account for interannual variation in participation, as this could be influenced by field seasons or academic teaching schedules. For t-tests evaluating changes in the percent of emails mentioning a given

threat, actor, solution, or distal driver, I used the mean monthly percent of emails and assessed differences in means across the two periods (percent ~ period).

To identify similarities or differences in how List participants discussed actors, threats to reefs, or solutions, I calculated the Jaccard's similarity score of coding similarities in NVivo for all combinations of nodes within each of the four categories: actors, distal drivers of local threats, local threats, and solutions. To classify the nodes by their similarities to either crisis or resilience narratives, I also calculated the Jaccard similarity scores between nodes for actors, threats, distal drivers, or solutions, and the nodes for crisis and resilience narratives. Then, I calculated the difference between the Jaccard similarity scores for the two narrative types to classify each node into either crisis narratives, resilience narratives, or both. The nodes that I considered both were those that with a difference of less than 0.05 between the narrative types.

I used the R packages *readtext* (Benoit and Obeng, 2021), *qdapRegex* (Rinker, 2017), and *quanteda* (Benoit *et al.*, 2018) to count the total number of emails (including those not meeting our criteria), using the unique message identification values for the whole dataset. I also estimated the unique number of participants posting to the list using the number of unique email addresses, but this is only a rough estimate; in the first few years, the Coral List administrators often forwarded emails manually to the listserv, people on the list often forwarded information from other individuals who did not post on the list themselves, and I also did not account for individuals who used more than one email address.

The Coral List administrators do not have records of the number of subscriptions over time, although they have posted the total number of subscribers on the list informally on occasion (personal communication, M. Jankulak, 15 March 2022). I used these values to linearly interpolate an estimate for the number of subscribers and how this changed over time during each of the two periods I analyzed.

5.2.2 Terminology

The participants of the list sometimes referred to people or locations using out-of-date or problematic terminology. I did not use these terms to identify actors in the statistical analysis and avoid using them in the results and discussion, except where I use direct quotations from the participants themselves, because these terms may reveal the underlying assumptions inherent in crisis or resilience narratives that I aim to identify here. Any quotes I use below reflect the exact language used by the authors of the emails. For example, I use the terms Global North and Global South throughout this paper. People posting on the Coral List often used different terms, including developed versus developing, or poor versus wealthy, interchangeably with Global North and Global South. While I understand that these terms are not interchangeable and have distinct meanings, I grouped these terms together in our coding to reflect the ways that people on the list used them.

I recognize that Indigenous peoples hold inherent, internationally recognized rights to access and make decisions about the lands and waters they have stewarded for millennia, and that these rights supersede those of local people and stakeholders (Ornelas, 2015). However, I use Indigenous Peoples and Local Communities (IPLC) in lieu of the term Indigenous because of the

latter's complexity in many parts of the world. For example, in the Pacific Islands, people who live on their traditional and ancestral territories may not necessarily identify as Indigenous despite meeting some definitions of the term (Gagné and Salaün, 2012). Also, non-Indigenous local communities may also hold localized and traditional knowledge, have long-lasting relationships between lands and waters, and are marginalized in various parts of the world (Dowie, 2009). For these reasons, IPLC is a more inclusive way of capturing these complexities, although I understand that it might also obscure important differences between Indigenous peoples and local communities, in particular the unalienable rights that Indigenous peoples hold to access resources (Ornelas, 2015).

5.3 Results

Informal conversations about local threats to coral reefs and their solutions accounted for about 16% of all unique emails (1,811 of 11,474) sent to the Coral List during these two periods (12% of 4,103 in the first period and 19% of 7,371 in the second period). About 4,470 people posted to the coral list during both periods, but this is a rough approximation. Based on this estimate, the people who participated in the discussions analysed here represent about 11% of the total individuals who posted to the list during our study periods.

5.3.1 Coral List participants

The average number of people participating in discussions about local threats to reefs each month did not change significantly across the two periods (from a mean of 6 in the first period to 10 in the second period, respectively, Welch's two-sample t-test, $p = 0.12$), despite the increase in the number of subscribers to the list. The total number of emails more than doubled between periods, from 506 in the first period to 1,375 in the second period, but the average number of emails per month (10 in the first period and 19 in the second period) was only marginally significant ($p = 0.06$). Participation in the list was uneven, with about 58% of the participants (277) only sending one email, and thirty participants (6%) accounted for over half of the emails sent across both periods. The percent of subscribers (not participants) represented by the emails I analyzed did not exceed 2% over all ten years and remained below 0.1% in the second period. Participation was also uneven among the active posters on the list; the most active poster sent 120 emails, while the tenth most active poster sent twenty-three.

I was unable to identify the roles of more than half of the participants using their email signatures or how they described themselves in conversations. I identified roles for 219 participants (45%). About 53% were scientists/researchers (117), including academics/professors (58), government researchers (14), independent researchers and consultants (36), graduate students and postdoctoral researchers (23). Following scientists, the second most common role was NGO employees or representatives, but this accounted for only about 6% of the people participating (28). The remaining roles each represented less than 1% of the participants. While I am unable to say for certain how well this represents the people who sent the emails I analyze here, I was able to find the roles for 81% of the thirty most active participants, and the results were similar; half were scientists or researchers, while the other half were in roles with less than five individuals so I do not report them here.

Identification of the location of participants (possible in 75% of cases) revealed that participants in the United States and Canada, Australia, and Europe were most prevalent, and would discuss reefs located all over the world, while people in Latin America and Southeast Asia were more likely to participate in discussions that were specific to reefs within their regions (Figure 5.1). People in the United States and Canada accounted for 39% of posters (188), followed by people in western Europe (56, 12%), Latin America and the Caribbean (39, 8%), Australia (30, 6%), and East Asia and the Pacific (30, 6%). Fewer than ten participants were in each of three regions – the Middle East and North Africa, South Asia, and Sub-Saharan Africa – with each representing about 1% of the total participants.

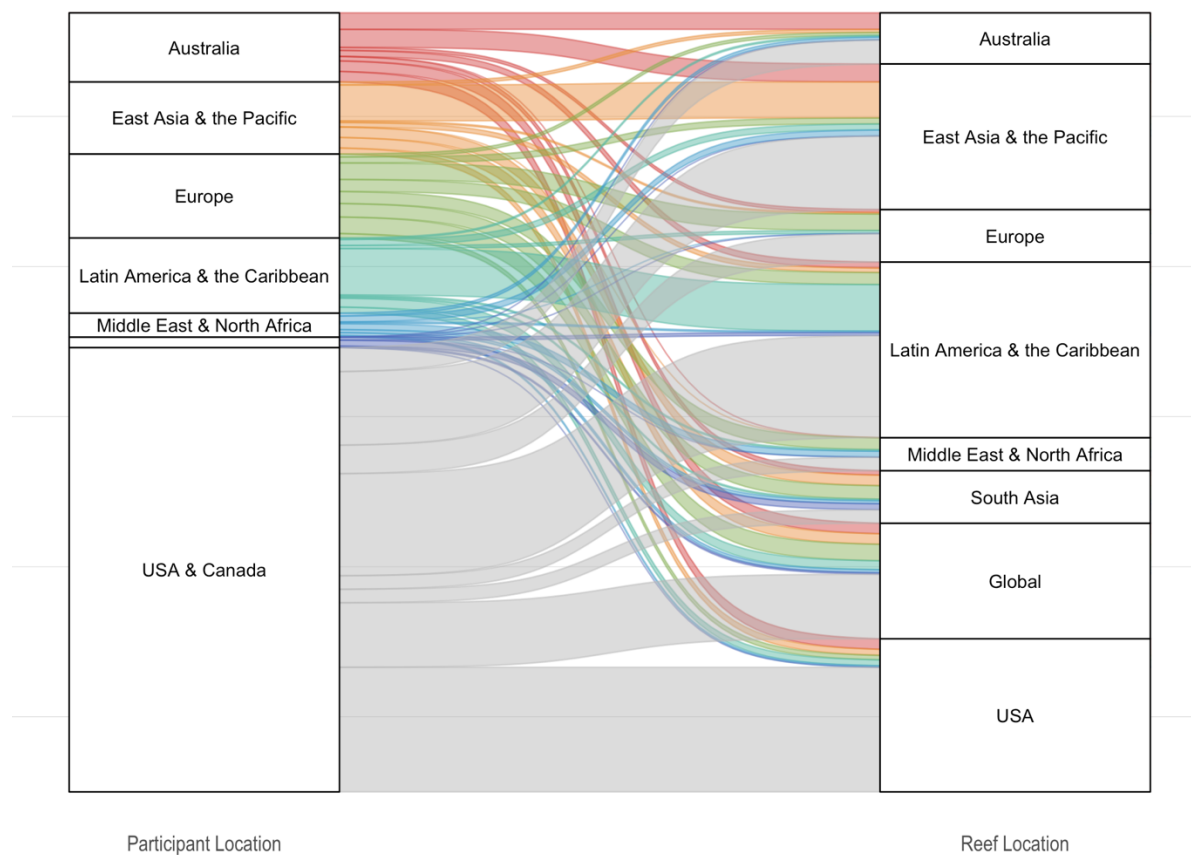


Figure 5.1. Participant location and the locations of reefs they discussed. I omitted participants from Sub-Saharan Africa here because there were fewer than five.

Here, I share relevant findings from the quantitative results representing how frequently participants discussed actors, threats, and solutions. The full quantitative results are described in detail in Appendices D.3 and D.4 (actors) and D.5 (threats and solutions). The results demonstrated that debates were common on the List and these discussions drove the number of emails about controversial topics; the threats that participants discussed most frequently were not necessarily the most pressing threats to coral reefs. For example, in the second period of the list, sunscreen pollution accounted for 27% (95) of emails discussing water quality and pollution (347); in the first period, sunscreen only accounted for 2% of emails (3) about water quality and

pollution ($p < 0.01$). As discussed further below, scientists do not consider sunscreen a major threat to reefs, especially when compared to global climate change or fishing and water pollution, but they disagree about whether it is a threat at all and if banning harmful ingredients in sunscreen is justified (Beisch, 2019). I found a similar effect for coral restoration and rehabilitation efforts in response to interactions between climate change and local threats. Despite almost a quarter of the emails discussing rehabilitation and restoration also referencing interactions between climate change and local threats, I found no evidence that anyone posting to the list considered rehabilitation and restoration a solution to climate-related stressors. Instead, some participants on the list argued that rehabilitation and restoration was a tool to help reefs recover, alongside other strategies, while others list argued that restoration was a waste of time until climate-driven stressors are addressed. The debates inflated the number of emails on the list about these topics.

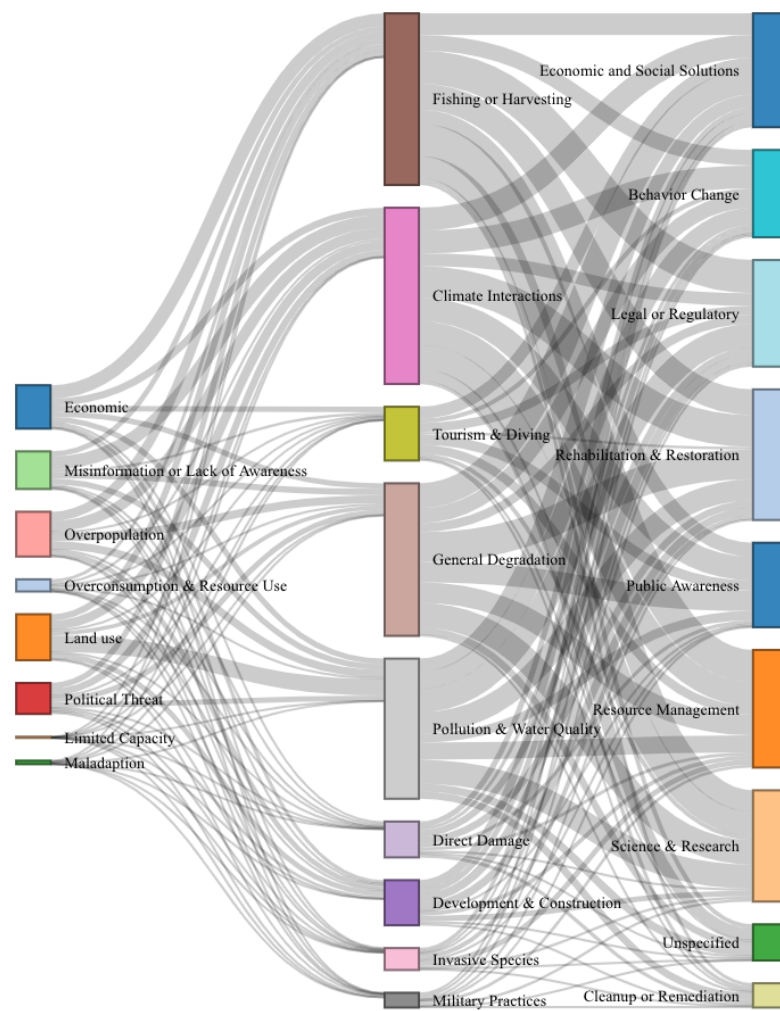


Figure 5.2. Distal drivers of threats to reefs (left), direct threats (center), and proposed solutions (right) for all time periods combined. An interactive version of this plot is available online at <https://rpubs.com/secannon/corallistdiscussions>.

5.3.2 Role of narratives

Coral List participants used features of both resilience framings and crisis framings in discussions about threats to coral reefs, often within the same email, sentence, or paragraph.

Features of crisis narratives were more common in the Coral List discussions than resilience narratives, and most of the individual nodes for actors, distal drivers, local threats, and solutions

were more similar to crisis narratives or both crisis and resilience narratives together than resilience narratives alone (Figure 5.4; all Jaccard similarity scores are available in Appendix D.3). In 1997, none of the comments I coded used resilience narratives, while in 2019, almost 40% of the posts on the list used resilience narratives, the highest of all years in our dataset. I manually reviewed the comments from 1997 and found that the dearth of resilience narratives coincided with the start of a mass bleaching event, and most emails during the latter half of the year were from individuals sharing bleaching observations, which were not the focus of this analysis. The ratio of narrative types remained steady on average across both periods and the means did not differ significantly for either narrative type (resilience narratives increased on average from 13% to 24%, $p = 0.13$, while crisis narratives increased from 50% to 58%, $p = 0.30$).

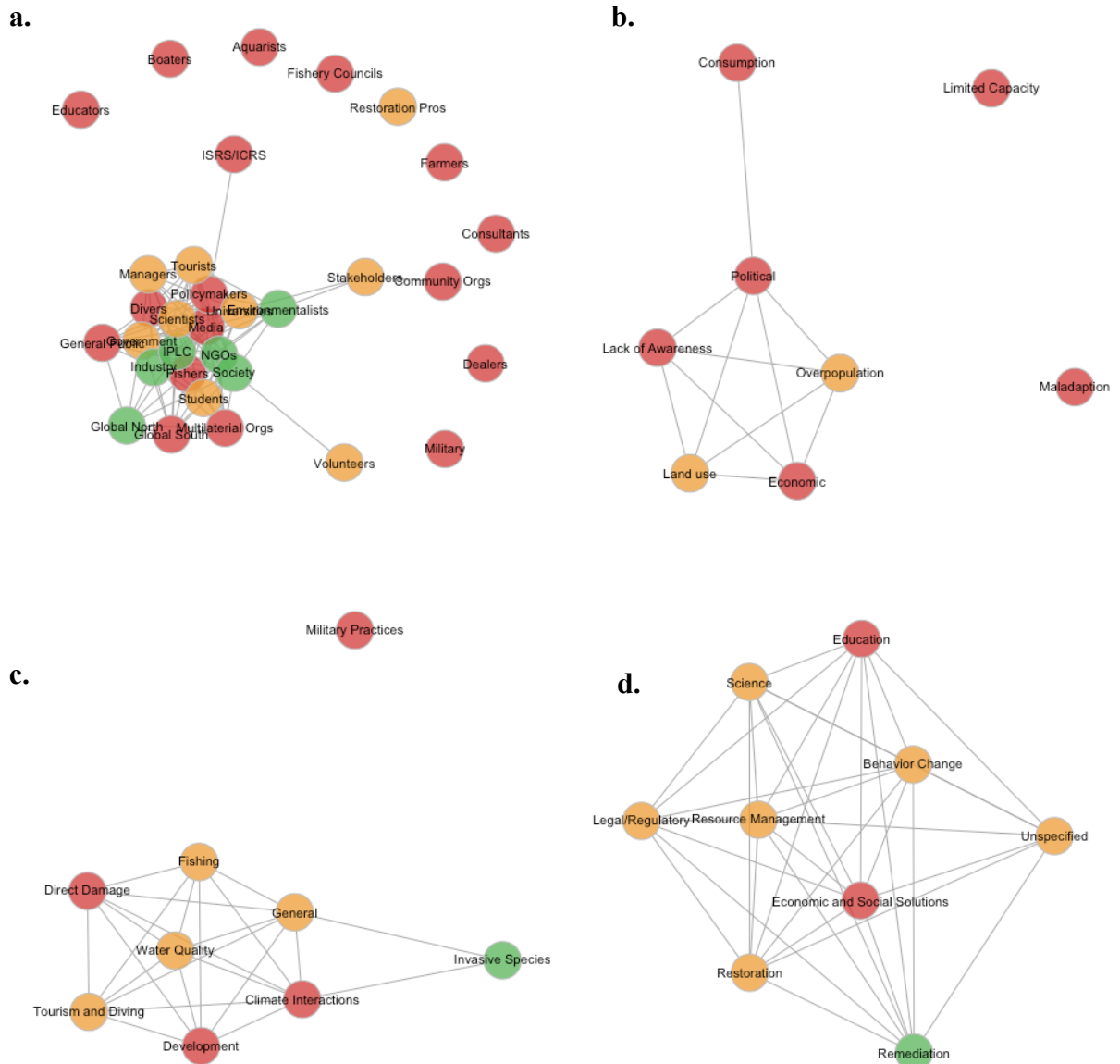


Figure 5.3. Clustering by Jaccard similarity scores based on coding similarities for a. actors, b. distal drivers of local threats, c. local threats, and d. solutions (bottom right). Green are nodes that had greater similarity to resilience narratives, orange indicates more similarity to crisis narratives, while red indicates nodes that were equally similar.

Some members of the Coral List community actively resisted features of resilience thinking. For example, here a participant responds to critiques of the pristine wilderness concept:

“[Redacted]brought to my attention the divide that exists between those who believe that the old tools and tactics of classic environmental conservation no longer apply in this century. They argue that our goals are misplaced and unrealistic. We need to change our views of the natural world and become more pragmatic. They say we need to stop advocating for pristine wilderness and instead find solace in ‘the swamp at the edge of town’. Nature, we are told is not so fragile and impoverished. I guess that suggests that many of us are old-school in that we don’t mind admitting that we place a higher value on the sense of wonder that can only be found in the relatively undisturbed, still-wild versions of nature.” [2015; q1]

The use of narratives also strongly aligned with the global versus local debate described above; people using resilience narratives discussed local solutions more than people using crisis narratives. For example:

The notion that there is nothing we can do locally is defeatist. Communities must have a way to respond; water quality and fishing management are two ways we maintain healthier reefs even in the face of events like this. [2015; q2]

Again, crisis narratives were more common than resilience narratives, and because participants often used aspects of both narratives in emails, it was rare for participants to post emails that employed only resilience narratives. One example of this blend of narratives was the way that many participants discussed or addressed uncertainty. Although embracing uncertainty is a feature of resilience narratives (Berdej, Andrachuk and Armitage, 2015), the Coral List

participants often incorporated uncertainty into crisis narratives, for example to urge conservation interventions in lieu of further research or to argue for embracing the precautionary principle and erring on the side of caution.

Participants often situated actors into distinct roles in Coral List discussions, for example as driving degradation or holding responsibility for enacting solutions, and these differed depending on the narrative types they employed. Those using crisis narratives were more likely to give agency over solutions to external or non-local actors, while resilience narratives situated IPLC as actors with agency (Table 5.2). For example, in one participant considered coastal dwellers (coded as IPLC) the actors driving degradation while conservation agencies, dive magazines, resorts, NGOs, marine scientists, and “all with an interest in coral reefs” were their defenders (q3 in Table 5.2); this framing placed IPLC at odds with those who have an interest in coral reefs, rather than including them within that group. By contrast, a self-described scientist positioned the scientific community and governments as failing to meet their responsibility to conserve coral reefs (Table 5.2, q5). Although the author mentioned direct threats to reefs, they did not directly attribute causation to actors; for example, they mention bringing an end to destructive boating and fishing practices but do not mention fishers or boaters. Finally, another example of a crisis narrative described IPLC as victims of circumstance who had no choice but to overfish (Table 5.2, q7). While the drivers of overfishing are complex and alternative livelihood programs may or may not benefit IPLC, that example is a crisis narrative because the impetus is on external actors to provide the alternatives; the fishers themselves have no agency.

By contrast, participants who used resilience narratives tended to consider IPLC a part of solutions. For example, one Coral List participant used a resilience narrative to discuss protected areas as a solution to overfishing on coral reefs (Table 5.2, q4). Like the examples of crisis narratives, the participant situated fishers as driving reef degradation. However, they also positioned fishers as central in ending overfishing, whereas the examples of crisis narratives instead positioned governments, NGOs, and scientists as responsible for implementing solutions. In the next example, a Coral List participant acknowledges that poor people contribute to reef degradation but points to economic development as a distal driver that results in overexploitation (Table 5.2, q6). By contrast, they situate people in the Global North as driving this degradation through colonialism and social injustice. In the last example of a typical way participant used resilience narratives, the participant centered managers as actors with the power to address local threats to reefs (Table 5.2, q8). They argue that while addressing local stressors will not necessarily make reefs more resistant to climate threats, doing so is still necessary and worthwhile.

Participants also framed the beneficiaries of conservation differently depending on the narrative type (Table 5.2). Crisis narratives tended to emphasize that conservation would benefit to large numbers of people at broad spatial scales. While they claim to benefit greater numbers of people, the material benefits from these narratives were sometimes vague. By contrast, resilience narratives, when they did occur, were more likely to emphasize IPLC and their ability to access resources and exercise their rights (Table 5.2).

Table 5.2. Excerpts illustrating differences in actors across narrative types from Coral List conversations about local threats to coral reefs.

Crisis	Resilience
<p>The coral reefs in the Asia Pacific islands are under siege by coastal dwellers using cyanide and dynamite to procure fish. This practice has been vehemently condemned by conservation agencies, scuba diving magazines, dive resorts, NGOs (non governmental organizations) and marine scientists as well as all that have their vested interest in the coral reef environment. If the practice continues, it is estimated by the year 2020, all coral reefs in the region will be destroyed. [1996; q3]</p>	<p>IF FISHERMEN FIND THEIR CATCHES INCREASING AFTER THE ESTABLISHMENT OF A MARINE RESERVE, THEY WILL BECOME ITS STRONGEST, indeed, it's [sic] only effective defenders. This is the key that makes preserves work- if the fishermen don't want it or don't care, the preserve will fail, if they do want it, it has a good chance, especially if they are supported. This makes community-based preserves an imperative. [1997; q4]</p>
<p>We scientists have documented the demise of reefs and are getting better at it every day. Each story is worse than the last. But research will not stop the carnage. Management has failed. Governments have failed. Conservation has failed..... [sic] Time to get people engaged rather than pontificate. Time to start doing rather than documenting. Keep it simple – stop over-fishing, stop destructive anchoring, bombing, clean up sewage, and make the diving industry responsible for their destructive practices as well. [2017; q5]</p>	<p>You point out the environmental damage poor people contribute to. It is extremely important that we 'first worlders' [sic] recognize that most of them do that for us. I don't know of any indigenous [sic] people today who overfish or over cut for their own subsistence using their own traditional systems. As soon as we get in there and 'help' them develop economically (Eg [sic] become more western), and 'help' them manage their resources using our approaches, then yes both culture and environment break down. Let's [sic] please not look at these as straight forward issues – they are immensely complex and social injustice and colonialism has driven a great deal of it. [2019; q6]</p>
<p>To simply shut down an industry that you do not agree with is reckless from the standpoint that you have not offered these people any alternatives for sustaining themselves. Perhaps you would rather see them support logging or gold mining operations and all the wonderful runoff issues associated with them?? [2000; q7]</p>	<p>I don't understand the logic in arguing managers should give up because climate change has had significant impacts on corals. I've said it a million times: local impacts need to be mitigated. We all agree on that. I think you're underestimating managers and local conservation capacity. (All the managers I know acknowledge climate change but aren't giving up). As the Ocean Optimism symposium highlighted over the weekend, local successes are realistic and very much meaningful and worthwhile. [2017; q8]</p>

These dynamics are visible in conversations debating a UK-driven protected area in the Chagos Archipelago, a group of islands and atolls in the Indian Ocean, where local people were forcibly evicted fifty years ago by the UK so that the United States could build a military base to one of the islands. The UK and Mauritius continue to fight for control of the Chagos via international courts (see Twyman-Ghoshal (2021) and Sheppard and Sheppard (2019) for opposing views of

this history). Because much of this controversy occurred during the study period, I was able to track how participants used crisis and resilience narratives to communicate their views about the protected area and the actors they judged would benefit versus who they saw as responsible for degradation (Table 5.3). The authors using crisis narratives described humanity and “the people of the Indian Ocean rim” as beneficiaries without any mention of the Chagossian people; by contrast, the resilience narratives considered the Chagossians both conservationists and beneficiaries of conservation. The participants using crisis narratives did not clarify how a protected area in the Chagos Archipelago benefits the peoples of the Indian Ocean rim when the islands remain off limits to everyone but scientists and military personnel (Sand, 2012). For example, a Coral List participant positioned Mauritius’ choice over whether to exercise their rights as detrimental to marine science and conservation (Table 5.3, q13).

Table 5.3: Crisis and Resilience Narratives when discussing the Chagos Archipelago, from 2015.

Crisis Narratives	Resilience Narratives
It is a tragedy that the UN court has judged the creation of the British Indian Ocean Territory Marine Protected Area to have been illegal. The tragedy is for all of us, who will lose the benefits of this rich and protected place and especially for the people of the Indian Ocean rim. [q9]	To suggest that Mauritius will now somehow degrade the Chagos reefs is neither supported by the facts, nor by their past conduct in Chagos. It also ignores the public commitment by Chagossians (many of whom are also Mauritians) to protect their homeland and its environment pending their forthcoming resettlement. [q10]
Anyone who might crow about this being a success story must be anti conservation [sic] and pro the pillage of some of the best reefs in the Indian Ocean. [q11]	This decision marks a landmark for the transition of the Chagos from a territory which has been governed by the UK in secrecy and with a colonial arrogance to one where the rules of law, international and national, must now be respected by all concerned. The Government of Mauritius is to be commended for achieving this in a struggle that has been likened to David and Goliath [q12].
On the one hand it [Mauritius] could say that having had these rights legally recognized it did not want to exercise them, but rather to have its scientists and conservationists join the international conservation efforts to maintain a world-class fully protected marine reserve for the huge benefit of millions of people in Indian Ocean States. That would indeed be a new beginning for Chagos conservation and one which we and others concerned with marine conservation would heartedly welcome. Or they [Mauritius] could seek to exercise those rights, which would be a setback to marine conservation and science, though how big a setback would of course depend on the scale, locale, and enforcement of the fishing [q13].	The situation with Mauritius is quite tense. The US should leave Diego Garcia now unless the Chagossians choose to keep them there. The UK should transport Chagossians back to their homeland and pay them significant compensation. The Chagossians should determine the conservation of their waters. The world should support them and the sustained conservation of the Chagos and surrounding waters on a legitimate footing [q14].

Coral List participants who advocated for more restrictive conservation interventions often referred to the necessity of urgent action to justify what they saw as required actions to save reefs, or even humanity (Table 5.4, q15). What posters considered ‘more aggressive’ approaches had different meanings for different people on the list, but they often pointed to science and rationality to support their views (discussed further below). On one end of the spectrum, many people pointed out that exclusionary approaches to conservation have not worked to conserve coral reefs, but argued that this was because of lack of enforcement, not the methods themselves,

These participants called for more aggressive approaches, like restrictive but better enforced protected areas (Table 5.4, q16 and q17), although often without describing who was responsible for the enforcement or its implementation (q17).

Some participants pointed to existential threats to reefs as motivation for more extreme interpretations of aggressive conservation interventions. I found several examples of anti-humanist viewpoints; for example, more than once, participants referred to humans as “a cancer on the earth”, reflecting neo-Malthusian talking points (Table 5.4, q18). For others, these anti-humanist viewpoints led to more aggressive approaches included authoritarianism and encroaching on human rights (e.g. ecofascism).

Participants discussed authoritarian solutions most frequently in response to overpopulation, a regular subject of debate on the List; 52 participants posted about overpopulation (11% of participants), many of whom are influential, highly cited researchers in coral reef science. As described above, participants connected overpopulation (a distal threat) to fishing and harvesting, water pollution, and interactions between local threats and climate impacts. In Table 5.4, q19 is an example of an ecofascist argument in response to overpopulation concerns, in which the author describes non-voluntary population reduction as the kindest, least traumatic, and most merciful means of saving humanity (and presumably, coral reefs along with them). Another example (Table 5.4, q20) demonstrates how overpopulation narratives redirect blame to the Global South, while the remaining examples (Table 5.4, q21 and q22) demonstrate ethically concerning and eco-fascist or neo-Malthusian examples of solutions, including withholding medical care (to “stop trying to prevent every death”) and an unspecified solution that the author

says is too difficult for “people in the west” to think about; this could be insinuating eugenics programs.

Table 5.4: Examples of crisis narratives and "aggressive" approaches to conservation.

I believe we should, in the face of what may be considered time constraints on the survival of this ecosystem, carefully scrutinize past conservation management failures and keep our minds open to innovative and more aggressive practices. [1999, q15]

To wit: most reefs except those impossibly remote ones are being exploited, and most are being over-exploited. So 1) seek to cut fishing pressure, 2) seek to eliminate fishing methods that destroy habitat and other species, 3) seek to ensure that existing fishing rules are obeyed, and protected actually protected. [2017, q16]

Many MPAs have been created at least on paper, and have been documented when they are well-enforced to increase fish stocks (but evidence they increase total fish catch is slim to non-existent). Most aren't well-enforced, resistance is very high, particularly among people in developed countries ... [2018, q17]

I agree with Hern⁴ that the human growth behavior has the characteristics of a cancer. As we outgrow our habitat, we move onto other lands looking for life support. That is why humans are not limited in distribution to just Africa. This has been going on for 100's of thousands of years with loss of major species everywhere we move to, as we ate them to extinction (Harari⁵ does a great job of summarizing this history). [2019, q18]

What we have learned here is very clear – that population reduction measures will unfortunately not be effective unless they are not voluntary, not left up to human decision processes once implemented and are applied using methods equally affecting the global population. Clearly, not easy or likely to be popular – but technically possible today, and we are coming close to those dread[sic] 'life boat' survival priorities⁶ – sooner than later ... I firmly believe based on the changes in global ecosystems that I have seen over the past 50 years, the research I've done on the subject – that it is the only way that we will avoid a catastrophic human population collapse. The longer we wait, the more extreme the efforts will have to be to survive ... I know non-voluntary reproduction limit impositions seem extreme, but given the economic/finite critical resource collapse that is otherwise inevitable in about 30 years ... A couple generations with minimal births is by far the least traumatic, kindest, merciful and most preferential means that is effective in not only reducing marine anthropogenic impacts – including reducing anthropogenic species extinctions, but likely necessary in saving our entire species. [2017, q19]

I am very familiar with the social justice take on overpopulation, and while yes, most of us 1st worlders[sic] consume more stuff per day than a very poor person in Bangladesh, the very poor people have high levels of pollution because of concentrated human density. So it is all of us, each in our own way contributing to the problem. And as global population increases, so does famine, armed conflict, rates of poverty and destruction of the environment. The immigration issues can be linked back to human populations being over the carrying capacity of the regions the people are fleeing ... The rate at which environmental degradation has accelerated follows the human population curve. Soon there will be nothing worthwhile left to save. [2017, q20]

There is a cure. It is currently far too difficult for most people in the west to even think about, much less their political representatives. Consequently, they don't realize the outcome of doing nothing is essentially the same as only addressing anthropogenic toxic symptoms - if the source of the problem isn't addressed. However, other less sensitive international leaderships are undoubtedly considering overpopulation solutions more drastic that will favor their existence even at the expense of other nations. [2015, q21]

Every new mouth on Earth demands more food production, and more land use for food production. So we need both to control birth rates, stop trying to prevent every death, and reduce our consumption of animal products as recommended by the IPCC 2019 April report. [2020, q22]

⁴ The participant is referencing the work of William M. Hern, who compared human population growth to a planetary disease and arguing that human population has the growth characteristics of a cancer on the earth (Hern, 1993).

⁵ This is referencing the book *Sapiens: A Brief History of Humankind* (Harari, 2014).

Even among those using crisis narratives to discuss overpopulation as a root cause of local threats to coral reefs, the solutions that some participants proposed were controversial (Table 5.5). Many argued for what they viewed as more just approaches to population control, for example, by arguing that empowering women around the globe (through access to education and health care) can address overpopulation without resorting to authoritarianism (Table 5.5, q23 through q26). Those who posted often about overpopulation, included some highly cited researchers in the field, commonly described themselves as censored or unable to openly share their views in other venues (Table 5.5.5, q27 and q28), insinuating that they received a more welcomed reception on the Coral List. The final example in Table 5.5 demonstrates how overpopulation narratives can easily veer into xenophobia (q29), discussed further below. Participants rarely employed resilience narratives to discuss overpopulation, which reflects the different scales associated with each of the narratives; crisis narratives framed problems as having broad-scale or global solutions, while resilience narratives framed problems as having local solutions.

⁶ The participant is referring to Hardin's lifeboat ethics, in which he equates helping the poor to bringing people onboard an already overloaded lifeboat; the lifeboat represents wealthy nations, while the swimmers are poor nations (Robertson, 2012).

Table 5.5: Aspects of overpopulation narratives per the Coral List.

I strongly support free voluntary family planning for everyone around the world who wants it but can't afford it. Reducing population growth now will indeed reduce future problems, larger populations multiply other problems caused by things like development and consumption. [2015, q23]
I don't think we can use population reduction to save reefs. Which doesn't mean that we shouldn't work to make voluntary family planning available to all who want it. That should help slow the rate of population growth and benefit the environment in the long run. [2015, q24]
Improving education, women's status, and income all help population efforts. [1997, q25]
Population growth rates usually come down with development as people get more education, equality, job opportunities, and ability to control their family size. [2015, q26]
The elephant in the room is really 7 billion people on the planet.....and no one wants to talk about it as though it would be upsetting some moral taboo. [2016, q27]
I have noticed something very interesting. Coral-List subscribers that agree that human overpopulation is the major issue write to me privately and not the whole list. Those of you who think over-consumption is the whole problem and have a knee-jerk social justice reaction to how do we reduce human population size? issue, write to the list. Wonder why that is? [2019, q28]
The developed world could stop having babies. Then we could just sit back and let the third world proliferate and overwhelm us. [2019, q29]

Participants employed crisis narratives to emphasize or defend using purely scientific methods and rationality for decision-making, which they viewed as being at odds with sentimentality and sometimes used to discount solutions proposed by those using resilience framings (Table 5.6). This is ironic given that people using crisis narratives were not immune to emotional arguments in defense of coral reefs (for example, see the arguments in favor of the Chagos Marine Protected Area in Table 5.3). Some participants also felt that decision-makers were actively undermining or attacking science, especially after voters in the United States elected Donald Trump as president in 2016 (for example, Table 5.6, q39). The reliance on rationality and science-based decision-making sometimes obscured ethical concerns in the approaches different participants recommended; for example, a participant portrays emotion as a weakness that has contributed to the refusal to reduce global populations (Table 5.6, q37).

Table 5.6: Narrative types and forms of knowledge.

Crisis Narratives	Resilience Narratives
<p>The point is that to have a working conservation program today we need to know how things were working yesterday. The stabilization of Central American politics is resulting in an increase exploitation of the coastal resources, at a rate that far exceeds development of scientific knowledge. [1995, q30]</p>	<p>The conservation logic is clear yet challenging to the scientific community as science to action in the field must upend some aspects of authority and change the process; best science must be carefully negotiated into the terms and practices of local custom and leadership. This can be achieved through a personal and intimate project of social inclusion and indigenous [sic] privilege that will test and modify controlled structure and methods. [2015, q31]</p>
<p>As usual the debate over coral harvesting seems to be based more on emotion and gut reactions than any sort of scientific basis rooted in facts. [1999, q32]</p>	<p>The more I reflect on all of this, the more I ascribe the reef problems right to this lack of modesty, sensitivity and will to give up comfort, emerging even [sic] from emails circulating on such [sic] selective and educated list. If this is the way we look at nature and our relationship to it, no wonder we are in this situation. [2015, q33]</p>
<p>Overpopulation survival priority is biologically the ultimate logic for any species. We should also consider that humans are one of the last evolving species, and the world was doing just fine, if not arguably better before we arrived. We should recognize our presence on the planet is and [sic] become demonstrably and undeniably biologically unnecessary to the planet's wellbeing. [2017, q34]</p>	<p>We also have to consider that if we as a community of researchers are going to support [redacted] we need a very good story concerning what happens to the other stakeholders worldwide who are in some way tied to coral reef communities. This includes many indigenous peoples who rely on coral reefs for subsistence fishing and gleaning. Even if you would argue that we have enough knowledge of coral reef community function to choose which are the 10% of reefs we will save, there are many other stakeholders that have a right to be a part of the discussion before that decision can be finalized. I think it's premature to write off the other 90% when so many people are dependent on these reefs. In fact, we are but one stakeholder on this issue and though we should take positions on policy issues like this one, we should not advocate decision processes that fail to give other stakeholders adequate time to respond. [2017, q36]</p>
<p>I suggest that we try to convince coral reef MPA managers worldwide that they need to carefully control recreational snorkeling and scuba diving both in terms of number of divers allowed and diver/snorkeler behavior. We should help provide them the tools to do that; specific recommendations, legal language, and science-based justification. [2015, q35]</p>	
<p>Population wise there also seems to be additional layers. Emotional/psychological components involved in resisting population reduction. Part of which is perhaps intellectual embarrassment and resulting denial and or an unwillingness to accept the blame for letting our population get so far beyond sustainable levels. [2017, q37]</p>	<p>While the "us against them" saga continues, our fellows from other branches of the conservation sciences are unveiling surprising things such as: the power of collaborative learning and management; the importance of conservation marketing; the value of local knowledge embedded into decision making and enforcement. And – hard to believe – some of them get results! [2015, q38]</p>
<p>In order for coral reefs to survive, we may be in need of more than an effective scientific message. We may in fact be in need of a full-blown campaign to restore the symbolic legitimacy of science. [2016, q39]</p>	<p>I agree with [redacted] below – this should not just be linked to the science, but also to traditional and local ecological knowledge ... ultimately, it should be about reef management, and for that we need a campaign that will bring people together. [2017, q40]</p>

5.3.3 Coral List Environment

As with most Listservs (Papadakis, 2003), examples of incivility and hostility were evident on the Coral List, which may have influenced who participated in the conversations documented here. In the earlier period of the list, administrators sometimes intervened to address antagonism on the list, and in a couple of cases, banned people from participating after they began name-calling and using profanity. Still, the Coral List administrators have had to remind participants to behave professionally at least once in each period. In this example from the second period of the list, an administrator reminds everyone that the list is public, with (at the time) almost 9,000 subscribers:

*“Come on, folks! Surely you are more articulate than to use profanity/slang to get your point(s) across! I still get messages in the queue with profanity. Just remember that this is a U.S. Government sponsored list, and even though some of the words you might want to toss into your message may seem to be commonly used, as though you were having a nice conversation with your friends at the bar, please try your best to be a little more circumspect. You may even be tempted to do what one other Coral-Lister did and throw in the typical cartoon representation of a swear word: *#^@&, but ask yourself if that’s how you want to be seen by almost 9,000 people who will read your post. Think of it this way: you wouldn’t write that way if you were writing for a peer-review journal or a magazine. We try to keep Coral-List a cut above mud-slinging and profanity, so please do your part. Please re-read what you intend to write before pushing the Send key.” [2015, q41]*

Despite these reminders, discussions on the list grew contentious often and sometimes constituted bullying. For example, I documented examples of established, mid-career researchers criticizing students and early-career researchers (ECRs) who posted questions to the list. The

tone of debates remained contentious throughout and sometimes turned personal in both list periods. I found additional examples of personal attacks in the later period and one participant described the coral reef conservation community as a whole as “toxic negative” after reading the Coral List (suggesting that some participants view the List as representing the community).

In addition to bullying, criticism, and contentious debates that turned personal, I also found specific examples of remarks which were racially insensitive at best. I documented remarks about people who are Indigenous, of Chinese descent, from South America, people in developing countries, and immigrants along the southern border of the United States and, in Europe, from the Middle East. In one case, a participant espoused replacement theory (Table 5.5, q29), the idea that white populations in the United States are declining out demographically because of immigration (Davey and Ebner, 2019; Turner and Bailey, 2022), although four people quickly and publicly condemned that viewpoint. In another example, a participant compared coral restoration to a triage situation in “poor villages in South America”, a position they had stated publicly in other contexts (Braverman, 2016, 2018); no one publicly objected to this language. Instead, multiple Coral List participants expressed solidarity and understanding.

“He said that in the emergency room they don’t have the resources to attend all the babies and little children at once. When in a triage situation, they only help the babies that are crying. Because if they are crying, it means they are strong enough, they still have some life left in them, and the medical treatment will be useful.

For the babies that don’t cry, there’s no help.

We are now in triage. We cannot save every coral reef through conservation: marine protected areas and other tools. We can only save the coral reefs that are still crying. Crying for help. Because they still hold enough life that the conservation effort will be useful.” [2017, q42]

5.4 Discussion

These findings illustrate that the Coral List is an active site of discussions and debate about local threats facing coral reefs, their drivers, the actors involved, and their solutions. These beliefs can influence research and proposed solutions, particularly when scientists fail to examine their values and biases (Chan, 2008). Unfortunately, I am unable to say to what extent the views I have described here are representative of coral reef conservation professionals; only a small number of active posters sent most of the emails, and the proportion of subscribers participating in list discussions declined over time. However, some of the most active posters on the list are also some of the most well-known scientists in coral reef conservation, suggesting that their views may have outsized influence on normative practices (Parker, Lortie and Allesina, 2010). Most people participating in discussions were scientists, and most scientists were also academics or professors. They also had a large audience, given that the list had almost 10,000 subscribers at the end of 2020. Some participants in the list implied that they felt the list was representative of the coral reef scientific community, as did the media when quoting participants using the list to debate sunscreens (discussed further below) (Beisch, 2019).

The locations of people on the list reflected the geographic bias in the published literature on coral reefs, with researchers based in the Global North overrepresented amongst participants.

Coral List participants who were based in the Global North discussed reefs located in multiple regions, while those in the Global South tended to post about the regions of their affiliations. This is similar to the findings of Ahmadi et al. (2021), who examined researcher's locations versus the location of coral reefs in publications from top-tier science journals and found that people in the Global North published about multiple locations while people in the South published more commonly about where they lived. Studies of geographic biases conservation biology and EEB research found the same overall pattern (White *et al.*, 2005; Pyšek *et al.*, 2008; Wilson *et al.*, 2016; Hazlett *et al.*, 2020).

5.4.1 Actors

In general, participants saw themselves as responsible for creating the science that would drive or inform conservation policy. Most participants using crisis narratives described conservation as benefiting society or the global population. When discussing fishing, they also saw IPLC as perpetrators of degradation but not a part of the solution. Instead, when the participants used crisis narratives, they usually assigned responsibility to experts, scientists, NGOs, or governments. Even when conservation actions were meant to benefit local peoples, participants using crisis narratives either excluded them by favoring top-down decision-making or did not mention them at all. Leaving specific actors out of the discussions meant it was not always clear who participants thought should implement solutions. In other cases, participants employed crisis narratives to place responsibility on the coral reef conservation community, either by name or by using in-group pronouns (e.g. "our" or "we") when discussing conservation strategies. By contrast, in emails using resilience narratives, participants talked about IPLC and fishers or

harvesters as part of the solution, although they disagreed on how much IPLC cause or contribute to degradation.

Coral List participants mentioned fishers and harvesters less frequently in the second period than in the first period, while references to industry and private sector increased from the first to second period. A hopeful interpretation of these changes would be that participants are shifting their views about the actors that drive coral reef degradation. However, I am unable to support this empirically without further research.

5.4.2 Threats to reefs

I found that the conversations on the Coral List tended to discuss more controversial topics and did not necessarily represent what participants considered the most important threats to coral reefs. For example, a survey of almost three-hundred coral reef conservation community members, identified through the Coral List and registrations for the 2004 International Coral Reef Symposium, ranked the most pressing threats as (in order of importance): overfishing, coastal development, water quality (sedimentation and nutrient enrichment), habitat-destructive fishing, and industrial and urban pollution (Kleypas and Eakin, 2007). By contrast, on the Coral List, water quality and pollution, and fishing and harvesting independently accounted for 21% of emails discussing local threats, and development only accounted for 7%.

Participants discussed water quality and pollution frequently, but this was due to several long-lasting email threads about sunscreen as a threat to reefs, which I coded as a child node nested within water quality and pollution (see codebook, Appendix D.2). Specifically, participants

debated whether there is scientific evidence supporting that toxic ingredients in sunscreen harm corals in situ, and proposed bans of sunscreen with toxic ingredients in tourist locations. Evidence that chemicals in sunscreen are toxic to corals is questionable (Moeller *et al.*, 2021). Still, proponents of sunscreen bans argued that they were justified in accordance with the precautionary principle. Some opponents thought the discussion about sunscreens was a distraction from climate change, which they viewed as the greatest threat facing reefs globally; they also worried that banning sunscreen with oxybenzone would make people feel that they were protecting coral reefs, without taking meaningful action in favor of conservation. These debates clearly had effects outside of the listserv; the Washington Post published an article describing the debate and quoting excerpts from the Coral List (Beisch, 2019). Participants were concerned that by making such disagreement public, the discussion on the list had undermined the general public's trust in scientists.

Despite the clear influence of controversial topics, I also found some results that might indicate shifts in perceptions of threats amongst the coral reef conservation community. For example, unsurprisingly, the conversations discussing interactions between local stressors and climate change increased across both periods; in the first period, coral reefs underwent the first global bleaching event, while the second period began amid another major global bleaching event (Hughes, Kerry, *et al.*, 2017). The literature on coral reefs and climate change grew exponentially after the end of the first period (Comte and Pendleton, 2018), which likely drove the greater awareness and increasing mentions in the later period of the list .

5.4.3 Solutions

Despite changes in the threats that participants discussed, I did not document statistically significant changes in the specific solutions proposed by the participants between the two periods, with one exception: participants were more likely to talk about the need for more science and research in the latter period than the first, and this was marginally significant ($p = 0.09$). Participants were more likely to discuss solutions in the later period of the list than in the first.

Like the threats to reefs, controversy also affected how frequently participants mentioned certain solutions. For example, some emails linked climate interactions to restoration practices as a solution, but this was not because participants believed restoration could solve climate impacts. Rehabilitation and restoration were controversial topics on the list because some people believe they are useful exercises while others have argued they're wasting time and resources that could go to efforts to halt climate change (Braverman, 2018). As a result, there were several long debates about the utility of restoration efforts.

5.4.4 Role of narratives

Many of the participants placed the responsibility for conservation action on Coral List participants, and discussions and debates usually revolved around about what the posters felt were the most pressing concerns facing coral reefs and potential solutions. The results support past research on narratives in conservation, showing that trends in different fields of conservation apply to the Coral List community. They also add further detail to studies from coral reef conservation specifically. For example, while embracing uncertainty was a defining feature of

resilience narratives in the Coral Triangle Initiative (Berdej, Andrachuk and Armitage, 2015), these findings showed that participants also appealed to uncertainty as a part of crisis narratives (Campbell, 2000), for example to advocate for action despite uncertainty or to appeal to erring on the side of caution as shown here:

“If we wait for perfect knowledge on complex ecosystems, we will never do anything, since we will never have that knowledge. Other people are not hesitating to do a lot, most of which is destructive. We need to use the best available scientific information, and we need to save reefs when we can.” [1995 – 2000, q43]

Crisis narratives play an integral role in conveying legitimate urgency of threats facing coral reefs and are also useful for garnering support and securing conservation funding (Berdej, Andrachuk and Armitage, 2015). I found that this urgency could backfire in that it sometimes produced existential anxiety that pushed people to recommend increasingly “aggressive” conservation approaches, which they viewed as justified because of the scale and severity of threats facing coral reefs. What Coral List participants considered aggressive varied; many people advocated for increased enforcement of protected areas, for example. Others, while more rare, suggested solutions with neo-Malthusian leanings; indeed, participants often referred to Malthusian concepts regarding overfishing (Pauly, 1990) and to Hardin’s Tragedy of the Commons, suggesting that these narratives remain normative despite efforts from researchers to change this (Steneck, 2009).

Participants who used crisis narratives to advocate for aggressive solutions employed a chain of logic reminiscent of those used by eugenicists: perceptions of existential crises combined with

scientific, non-emotional, ‘rational’ solutions led participants to support these aggressive approaches as straightforward and logical, leading, in some cases, to solutions with ecofascist and/or neo-Malthusian leanings. For example, a popular topic amongst a subset of participants on the list was overpopulation, with several vocal Coral List participants posting regularly to assert that overpopulation is the greatest distal threat driving coral reef degradation.

Overpopulation narratives claim that increasing global population puts pressure on local resources; however, because population growth rates have declined in the Global North, population control or population reduction initiatives usually target people in the Global South. These views on overpopulation are emblematic of neo-Malthusianism, the view that overpopulation is driving environmental degradation globally and that solving overpopulation will require global population control (Schultz, 2021). People on the Coral List were either unfamiliar with or dismissive of social science research about population narratives and the material effects such narratives have supported, which almost always impact the most vulnerable in society (Hartmann, 1994). Indeed, while directly addressing misconceptions and inaccuracies in posts on the Coral List, some of the assertions used by proponents of overpopulation narratives are easily disproven (for example, poverty and population densities do not correlate with elevated levels of pollution) (Boyce, 1994).

Some, not all, of the views on the list in reference to overpopulation and its perceived effects (e.g. fishing, pollution) also meet the definition of ecofascism. People concerned with environmental degradation tend to assume that ecofascism is rare or the consequence of rogue political factions, but this assumption is unfortunately not supported by evidence (Murdock, 2021) and could itself be harmful; by giving people using ecofascist arguments the benefit of the

doubt on the Coral List and elsewhere, the community is inadvertently signaling that there is space for such viewpoints within their ranks. In addition, people mentioned overpopulation more frequently in the second period of the list (albeit when accounting for the proportion of emails mentioning distal threats, the increase was only by 3%). Still, others have argued that overpopulation narratives, along with other extreme narratives that misplace blame for environmental degradation, will only become more common as climate change intensifies (Hassan, 2021; Thomas and Gosink, 2021), and our findings provide limited support to this effect.

There were responses opposing overpopulation narratives. For example, participants argued that such narratives ignore crucial differences between the Global North and South in terms of consumption, resource use, and industrialization. However, these responses were less common than the overpopulation emails themselves, except for one comment in which a participant espoused the white supremacist replacement theory in response to a discussion about population that four people responded to immediately (Table 5.5, q29). Although such blatant examples of racism were rare during the study periods, it is important to recognize how overpopulation narratives can and have led to anti-immigrant viewpoints (Turner and Bailey, 2022), and I found at least five additional emails using less obvious language that hinted at xenophobia.

While these numbers are low compared to the total number of emails, they occurred during email debates receiving high engagement from the list and received long chains of email responses that sometimes continued for weeks; there is no denying that people read them. Participants' engagement with ecofascist, racist, or discriminatory posts without actively confronting their

authors may have even inadvertently boosted these views and signaled acceptance. Indeed, that I found only one example of people directly condemning racism in the study periods shows that people on the Coral List are either unaware of the more subtle ways such views can seep into conservation practice and perpetuate systemic racism, did not find xenophobia problematic, or were avoiding confrontation. Also, the people who posted about overpopulation narratives were usually active participants on the Coral List, while those who responded highlighting the problems in these narratives participated less frequently. Those posting rebuttals often sent one or two emails and then did not engage further, possibly because in some cases, people using of overpopulation narratives were dismissive (for example, one participant referred to these rebuttals as ‘the knee-jerk, social justice take on overpopulation’, Table 5.5) and the conversations tended to last for a week or more. A lack of response does not mean that all, or even most, participants agree with these views. However, the lack of objection might signal that the coral reef conservation community accepts them and that the Coral List is a safe environment for expressing such views (Miriti, 2020; Watson, 2021).

Given that discussions about overpopulation occurred regularly on the Coral List, it was surprising to find that the people who posted most about overpopulation felt censored in other forums. This was especially interesting given that some of well-established, late career researchers who had broad influence while coral reef science was first becoming established have published neo-Malthusian viewpoints (e.g. Sale, 2011; Wilkinson and Salvat, 2012), in one case with multiple publication spanning decades (e.g. Sheppard, 2002, 2003, 2014, 2015). I did not find any evidence that the participants on the Coral List found these topics unacceptable for the List except where proponents of overpopulation narratives said so themselves (e.g. Table

5.5). To the contrary, list participants discussed overpopulation more than any other distal threat except economic drivers, and again, the proportion of emails discussing overpopulation narratives increased over time. Paul Ehrlich claimed to have written *The Population Bomb* for because population control was unacceptable to discuss prior to its publication in 1968, suggesting that proponents of the overpopulation narrative have always considered themselves underdogs (Mann, 2018). Notably, in the previously mentioned survey of the coral reef conservation community, survey respondents identified overpopulation as the greatest global threat facing coral reefs today, placing it even above climate change (although the survey occurred before two mass bleaching events that may have changed people's views on climate change in the rankings) (Kleypas and Eakin, 2007). Again, this suggests that the views I documented from conversations on the Coral List may be representative of the coral reef conservation community more broadly, although I cannot say so definitively without further research.

While I agree with Berdej et al. (2015) that combining crisis and resilience narratives would theoretically produce a more justice-centered narrative that can adequately convey the urgency of conservation problems facing coral reefs while also ensuring that projects do not neglect IPLC, our findings suggest that changing the narratives alone will not be enough to influence conservation practice and its material effects on people. While employing resilience narratives to frame conservation problems helps to address one of the key limitations of crisis narratives— their tendency to erase or “write out” IPLC, as shown here— the resilience framing can also undermine conservation when these changes remain rhetorical. For example, resilience narratives without corresponding changes in power structures may undermine trust between IPLC and

conservationists or portray IPLC as responsible for degradation without considering additional, non-local, or external sources of threats to ecosystems (Campbell, 2000; Baker-Médard and Sasser, 2020). In many cases, despite the local framings, local threats may be driven by industry under the banner of sustainable development, a symptom of the broader neo-liberalization of conservation (Kashwan *et al.*, 2021). For example, a “community-based” MPA in Kenya claimed to empower local communities and involve them in management decisions, but instead excluded local fishers from the park’s boundaries to protect what conservationists had portrayed as a fragile ecosystem in need of protection. This left fishers understandably confused and angered when the government improved the construction of a gas pipeline through the MPA, and the relationship between the conservationists managing the park and the local community is now strained (Kamat, 2018). While there are many benefits to resilience narratives, specifically that they recognize IPLC as autonomous peoples with agency, they have also proven difficult to enact in practice, particularly in cases where conservationists employ them in name only (Dressler *et al.*, 2010).

5.4.5 Creating an inclusive Coral List environment

Some of those who posted to the Coral List shared that they did not find it to be a supportive environment. Participants were especially hostile to ECRs in the first period. Some Coral List participants described the list, or the entire coral reef conservation community, as hostile or “toxic-negative”, and in their words, depicted coral reef scientists as territorial, exceedingly rude, nasty, and overly sensitive.

The Coral List has a code of conduct, which is posted on the NOAA website (NOAA CHAMP, 2019) and periodically sent out to subscribers along with reminders to behave professionally, as shown above. Administrators loosely monitor messages sent to the list, and they had to manually approve emails in the later period. Still, the pure volume of emails on the list makes reading each email in detail next to impossible; an administrator explained that they do their best but often skim the messages. I cannot say how many messages the administrators have declined to post.

I did not quantify or systematically track perceptions of the Coral List, as it was not the focus of this research. Instead, I provide examples of problematic and racially-insensitive emails to show that they are normalized and to highlight the need to collectively confront legacies of racism and colonialism among the coral reef conservation community. However, not everyone found the environment negative, or at least not entirely so; participants often thanked the list administrators for the tremendous amount of work they did to keep the list running, and several individuals mentioned that they found funding, jobs, academic programs, and other opportunities through the listserv. It clear that through disseminating these opportunities, the Coral List has provided an important service to the coral list conservation community, and it is a laudable that they have done so for almost 30 years. However, given the treatment of ECRs in the earliest period, and the evidence of insensitive posts from both periods, people's opinions of the Coral List and its environment will most likely be different based on their identities and whether they were members of the majority (specifically, academics from the Global North).

5.4.6 Moving Forward

Ongoing efforts to diversify conservation through increasing access to institutions in the Global North are important and valuable. However, if we continue to train conservationists to rely on purely scientific evidence and do not teach the history of these viewpoints or encourage critical reflection of their impacts, we are predisposing trainees, regardless of their backgrounds, to repeat problematic norms stemming from the colonial history of EEB (Trisos, Auerbach and Katti, 2021). Increasing the diversity among conservationists will not necessarily change conservation norms and practices. This is particularly the case when most conservation biologists and institutions conducting research on tropical ecosystems, including but not limited to coral reefs (Ahmadia *et al.*, 2021), are based in the Global North.

The issues I have highlighted here are relevant to coral reef conservation, but also exemplify patterns observed in both realms of conservation – science and practice – more broadly (Rudd *et al.*, 2021). At the very least, there is an urgent need for conservationists to engage with literature on the colonial history of conservation and how this history continues to affect conservation today (e.g. Cannon, 2019). This context must also become a central part of the curriculum used to train conservation scientists and practitioners (Trisos, Auerbach and Katti, 2021). Such engagement will be necessary to challenge and move away from the Malthusian norms that still permeate coral reef conservation and ignore the distal drivers of localized environmental degradation. We must confront the aspects of conservation narratives that perpetuate and excuse racism, but doing so will require sustained efforts to educate ourselves on what those narratives are; I hope that this work will be a first step in that direction. We also need to be aware (so that we can guard against them) that the negative aspects of crisis narratives may become more

common, especially as climate change intensifies and continues to degrade coral reefs. In addition, given that people on the far right are actively targeting scientists and academics (Ciccariello-Maher, 2017), it is essential that conservationists become familiar with ecofascist talking points and their roots in environmentalism and conservation, to enable us to take an active part in combatting ecofascism and continued human rights abuses occurring in the name of conservation.

Conservation scientists who are from the Global North must also learn about and work to center IPLC in the places where we conduct our research. This includes understanding our positionalities—the ways that our positions within social systems, including geographies, race, gender, and social class, might influence our research (Baker, Eichhorn and Griffiths, 2019; see Section 5.5). It also requires exploring how sharing and co-producing knowledge can enhance conservation efforts, and shifting our understandings of knowledge to not only respect place-based epistemologies, but to hold them on equal footing with Western science (Jacobs *et al.*, 2022). This shift will not be easy (‘Decolonizing ecology and evolution is a long road’, 2021). As the List has shown, some participants are resistant to challenging conventional conservation norms, and in some cases, we will have to make difficult choices. For example, addressing the harms caused by conservation and research may also require interrogating whether it is appropriate for researchers from the Global North to continue their research in the Global South, especially if such work does not engage with and support IPLC (Baker, Eichhorn and Griffiths, 2019). At the very least, a code of conduct in marine conservation could require researchers to consider how conservation affects people, and might catalyze shifting conservation norms towards more people-centered, just, and equitable approaches (Bennett *et al.*, 2017).

Following Chan (2008), conservation biology “must become an integrated interdisciplinary field that includes social sciences and humanities, in which all conservation biologists are conversant in the ethical underpinnings of their work.” When Soulé first introduced conservation biology as a field, he envisioned it as interdisciplinary (Soulé, 1985), but by characterizing conservation as a crisis discipline, he may have inadvertently precluded such overlap between fields (given that crisis narratives often discount qualitative research). Scholars have proposed several new, justice-centered, decolonial, and ethical conservation narratives that could potentially address the limitations of crisis narratives while preventing the difficulties in implementation that are common with resilience narratives, for example convivial conservation (Büscher and Fletcher, 2019), regenerative conservation (Kashwan *et al.*, 2021), or an Indigenized version of the North American model of conservation (Hessami *et al.*, 2021), and many others (e.g. Salomon *et al.*, 2018; Asase *et al.*, 2022; Jacobs *et al.*, 2022). Coral reef conservationists, and conservationists more broadly, must engage with this literature; otherwise, we risk remaining stuck within the limitations of crisis or resilience framings, which in addition to perpetuating harms can also undermine conservation outcomes. By documenting trends in conservation narratives among Coral List participants and highlighting how these trends can, advertently or inadvertently, perpetuate and entrench systemic racism and colonialism, I hope to trigger an important shift in awareness in coral reef conservation. Ultimately, confronting these oppressive systems and centering the people who are most affected by coral reef degradation will not only lead to more ethical conservation, but will lead to greater efficacy of conservation outcomes.

5.5 Positionality Statement

I am a Ph.D. candidate at the University of British Columbia, a university located in Vancouver, Canada on the traditional, ancestral, and unceded territory of the x^wməθk^wəyəm (Musqueam) people. I am a white, queer cisgender woman of European settler descent and am a citizen of the United States with permanent residency in Canada. I recognize that I benefit from the systems discussed here, and I see myself (and other non-Indigenous white conservationists who are from and/or trained in the Global North) as responsible for doing the labour required to change them. I am also a marine biologist with 10 years of experience working in the Micronesia region of the Pacific, specifically in Yap, Federated States of Micronesia, the Republic of Kiribati, and the Republic of the Marshall Islands. I have subscribed to the Coral List since approximately 2010 and am a part of the coral reef conservation community; this allows me to understand and interpret the discussions from the Coral List because I understand the terminology and much of the context.

Chapter 6: Conclusion

In this dissertation, I evaluate open questions in coral reef conservation science and practice in the context of climate change. Specifically, I investigated how local and global anthropogenic stressors interact to influence reef health and recovery after multiple stressors, methods used by coral reef scientists to assess reef degradation, and finally, the ways the coral reef conservation community talk about local threats affecting reef health and their drivers. Collectively, I find that while local people do influence benthic coral reef communities, the results are often unpredictable and counter what we would expect from long-standing paradigms in coral reef ecology. This suggests that moving forward, scientists and conservationists will have to challenge longstanding ecological paradigms as they may not reliably predict the future of coral reefs as climate change intensifies (Williams *et al.*, 2019). I have demonstrated this throughout each of the research chapters, as summarized below.

6.1 Local human disturbance and recovery after heat stress

My first chapter demonstrates that at sites in the Gilbert Islands of the Republic of Kiribati, contrary to expectations, fewer local human-driven stressors does not increase coral reef resilience to climate-driven heat stress. By comparing how benthic communities had changed between 2012 and 2018, I found that sites with a lower local anthropogenic footprint (those in Abaiang and N. Tarawa) were more affected by bleaching than those in S. Tarawa, where reefs were highly degraded because of fishing and pollution. This was because in S. Tarawa, an opportunistic coral species, *Porites rus*, dominated the benthic communities of most reefs. This species can outcompete other benthic taxa that are more sensitive to nutrients, sedimentation, and heat stress (Darling *et al.*, 2012; Lenz and Edmunds, 2017). As a result, reefs in Tarawa were

less affected by heat stress than those in Abaiang, where more sensitive coral taxa like branching coral genera *Acropora* and *Pocillopora* experienced widespread mortality. In Abaiang, a CoTs outbreak then decimated any corals that survived the heat stress events, most of which were large, long-lived, mounding taxa (e.g. massive *Porites*). Sites in Abaiang may be able to recover to more diverse coral assemblages over time and may therefore be more resilient to bleaching overall, but I found that changes in overall coral cover were minor during the study period such that recovery in Abaiang will depend on whether there are future stressor events and how they influence the current benthic communities. In Tarawa, the opposite is the case; reefs were not necessarily *resilient* because they shifted to dominance by *P. rus* and this may not be reversible without intervention, and it is unclear whether these reefs will continue to function similarly to reefs that host higher biodiversity with greater structural complexity. Reefs in Tarawa were, however, *resistant* to multiple stressors in that they were less affected in the first place (Côté and Darling, 2010).

This work has important implications for coral reef conservation. For example, no-take or limited-take marine protected areas (MPAs) are the most widespread approach to coral reef conservation (Strain *et al.*, 2019). Proponents suggest that MPAs can increase coral reef resilience to climate-driven heat stress by increasing the biomass and diversity of reef fish, especially herbivores (e.g. Mellin *et al.*, 2016; Shaver, Burkepile and Silliman, 2018). By feeding on turf and macroalgae, herbivores may create space and reduce competition for corals, creating a more hospitable environment that allows them to recolonize after bleaching. My dissertation suggest that this approach could backfire by facilitating the growth of sensitive taxa that are less resistant to heat stress, which are more likely to face widespread mortality during sustained

periods of high SSTs (Côté and Darling, 2010; Bates *et al.*, 2019). While I do not suggest that local degradation benefits reefs, or that coral reefs dominated by a single hard species of coral (such as those in Tarawa) are more desirable than those in Abaiang, these findings suggest that reducing local stressors may come with trade-offs, and these are not well understood.

Collectively, my results demonstrate that coral reef scientists cannot unquestionably rely on methods that worked for addressing local stressors to increase resilience to climate-driven stressors. Instead, more nuanced approaches to conservation are necessary, particularly as the climate continues to warm (Mumby, 2017; Darling *et al.*, 2019).

6.2 Interactions between local human disturbance and climate-driven heat stress on coral reefs

In my second chapter, I show that local benthic communities and the taxa that are present prior to bleaching events will influence how reefs respond to and recover from local and global anthropogenic stressors. The taxa that compose a given benthic community, and their responses to different stressors, dictated whether local and global stressors interacted synergistically or antagonistically. When comparing reefs in Kiribati to those in the RMI, I found that benthic communities at sites that were most affected by local human disturbance (Majuro in the RMI and S. Tarawa in Kiribati) were the most similar, despite sites in the Gilbert Islands experiencing more frequent heat stress due to the higher interannual variability in SSTs in this region. By contrast, the variation of past SST did influence benthic communities in the atolls with smaller populations and less local human-driven degradation. This is contrary to coarser resolution findings from Bruno and Valdivia (2016), who found that signatures of local human stressors

were undetectable because they were swamped by climate-driven stressors.

I found that the variability of past SST, a proxy for exposure to bleaching-level heat stress, and local human disturbance acted synergistically to increase the percent cover of hard corals in Tarawa, because of the high prevalence of the opportunistic coral species *P. rus*. However, when investigating interactions between the variability of SST and local human disturbance at the taxa level, half of the interactions were antagonistic. These findings challenge the idea that climate change and local threats to coral reefs will interact synergistically and negatively. In Tarawa, the interaction between stressors was correlated with an increase in coral cover because of *P. rus*. In addition, half of the taxa I tested exhibited antagonistic interactions. Instead of uniformly negative, synergistic interactions, these results suggest that the context in which these threats occur is important for predicting ecosystem responses. The taxa that are present at a given reef will dictate the interactions present between stressors, and while local human stressors may benefit some taxa through preconditioning (e.g. *P. rus*), this will likely come at the expense of other, more sensitive taxa (e.g. *Acropora* spp.).

6.3 Macroalgae as a proxy for reef health and the effects of human disturbance

Next, I investigated the utility of a common proxy used by scientists to indicate reef health or degradation, total macroalgae cover. This, along with the theory that the percent cover of macroalgae on coral reefs is driven by herbivory and nutrients, has led to the common assumption that reefs disturbed by local anthropogenic stressors are likely to have high cover of macroalgae (Bruno and Valdivia, 2016; Smith *et al.*, 2016). However, even reefs that are far from people may have naturally high cover of macroalgae (Vroom and Braun, 2010; Vroom,

2011; Bruno *et al.*, 2014). My master's research focused in the Marshall Islands found that some genera of macroalgae were negatively correlated with local human disturbance while others were more positively correlated, suggesting that total percent of macroalgae cover could actually obscure signatures of degradation on reefs (Cannon *et al.*, 2019). Building upon that work, in a meta-analysis of data collected 46 scientists across 1,205 sites from the Indian and Pacific Oceans, I tested the assumption that total macroalgae cover is correlated with local human degradation and examined whether local human footprints are more detectable when identifying macroalgae taxa to the genera level. I found that total macroalgae cover is not correlated with human disturbance, and that distinct genera have diverse and often opposing responses to various sources of human disturbance (for example, nutrients from agriculture, fishing pressure, or development).

Again, my findings challenge widely held perceptions about coral reef health and signatures of local human disturbance on coral reefs (Bruno and Valdivia, 2016; Smith *et al.*, 2016; Ceccarelli *et al.*, 2018). The idea that macroalgae creates an inhospitable environment for corals and that coral-dominated reefs are more desirable than macroalgae-dominated ones (Littler and Littler, 2007) has led to a body of literature that focuses on negative interactions between corals and macroalgae (see, for example, Mumby, Foster and Fahy, 2005; Littler, Littler and Brooks, 2006; Littler and Littler, 2007; Birrell *et al.*, 2008; Del Monaco *et al.*, 2017; Ceccarelli *et al.*, 2018), and a shortage of studies that investigate how individual macroalgae taxa respond to local human-driven disturbance (but see McClanahan *et al.*, 2004; Brown *et al.*, 2017). This overlooks the services provided by macroalgae, some of which can benefit corals and many of which support ecosystem functioning (Fulton *et al.*, 2019; Duarte *et al.*, 2022; Wilson *et al.*, 2022). This

chapter demonstrates how blind spots held by scientists can undermine our ability to respond to the multiple stressors facing coral reefs and raises important questions for estimating reef health. I hope it will also catalyze much-needed discussion and research into the services and functions supported by less studied taxa on reefs.

6.4 Legacies of racism and colonialism in coral reef conservation

In my final research chapter, I analyzed two periods of emails spanning a total of ten years (1995 – 2000 and 2015 – 2020) on a popular, long running listserv for coral reef conservationists to investigate how participants discussed local threats to reefs, the actors involved, and potential solutions. I used a multidisciplinary approach that combined discourse analysis with quantitative methods to demonstrate how the racist and colonialist history of Western science still influences coral reef conservation. For example, the concept of carrying capacity remains influential in ecology today, and this way of thinking can shape how ecologists view threats to ecosystems.

Coral reef conservationists mostly used crisis narratives to discuss threats facing coral reefs, with some features of resilience narratives. Both narrative types have benefits and weaknesses; while resilience narratives can undermine the legitimate urgency of threats facing coral reefs, they also are more people-oriented and avoid the more problematic implications of crisis narratives, which convey a sense of urgency that is important for catalyzing fast responses but can privilege Western scientific approaches and rationality often at the expense of IPLC. My analysis found that the features of crisis narratives were associated with participants who suggested extreme, neo-Malthusian and in some cases, ecofascist solutions to the local threats facing coral reefs. While the number of people participating in these discussions were low overall, I found that such

viewpoints were normalized and rarely confronted, and that this did not change over the study period. Although I am unable to say whether the email list represents the coral reef conservation community more broadly, many of the regular participants on the list are well known in coral reef conservation and have considerable influence over the field; as prominent academics, these individuals have considerable power over the success of students and early career researchers, as well as to set or influence research norms and practices (Lane *et al.*, 2019; Hernandez *et al.*, 2020). The prominence of these participants in coral reef conservation may also affect the willingness of others to participate in list discussions, especially white women and Black, Indigenous, and people of color (BIPOC) who are already underrepresented in the natural sciences (Fry, Kennedy and Funk, 2021). I show through the words of some Coral List participants themselves, most of whom were academic scientists based in the Global North, that there is an urgent need to confront racism and white supremacy in coral reef conservation, as in conservation more broadly. Without naming and calling out racism when it occurs, coral reef scientists risk continuing to unknowingly perpetuate assumptions that cause further harm to already marginalized communities.

6.5 Future research

This work raises several important questions that will only become more critical in the future as threats to coral reefs continue to intensify. Given that most reefs are in the Global South, and that climate change is driven by people in the Global North and is broadly accepted by as the greatest threat facing reefs today (Hughes, Barnes, *et al.*, 2017), coral reef conservation is not just a matter of conserving a diverse ecosystem; it is also a matter of justice. Millions of people

globally depend on coral reefs, and those who would be the most harmed by their loss are also least likely to contribute to their demise (Wolff *et al.*, 2015).

6.5.1 Coral reef functioning

Coral reef scientists still do not agree about what constitutes a healthy reef. However, the focus in the literature on coral reef conservation has begun to shift towards focusing on quantifying coral reef functioning instead of health (Brandl *et al.*, 2019). This shift reflects the growing acknowledgment that benthic coral reef communities are changing and due to climate change, will continue to change despite conservation efforts; it may not be possible for conservation to return reefs to a pre-human or ‘pristine’ state (Darling *et al.*, 2019). Indeed, the focus on defining a healthy reef as ‘pristine’ reflects the limited nature of the wilderness concept defined in Chapter 5, in that it assumes the existence of a pre-human baseline (e.g. Sandin *et al.*, 2008; Smith *et al.*, 2016).

By shifting the focus in coral reef conservation from restoring reef health to maintaining reef functioning – the processes of energy flow and information exchange performed by living systems that also supports their ability to provide services (Bellwood *et al.*, 2019; O’Connor *et al.*, 2021) – conservation efforts can focus on ensuring that reefs continue to benefit people who depend upon them, for example by supporting reef fish populations, maintaining structural complexity that protects shorelines from erosion, or producing sediments that contribute to island growth. While much research has been dedicated to preserving the ability of reefs to provide these services, such work has tended to assume that less-degraded reefs provide greater services to people because they host higher biodiversity (Bellwood and Hughes, 2001; Plaisance *et al.*,

2011; Brandl *et al.*, 2019). By providing a mechanistic link between biodiversity and the services reefs provide to people, research on ecosystem functioning brings together two key conservation priorities.

The focus on reef functioning is relatively recent, and little is known about how reef degradation influences ecosystem functioning, particularly when degradation is driven by both local and global anthropogenic impacts (Bellwood *et al.*, 2019; Brandl *et al.*, 2019). In a recent review of the existing literature, Brandl *et al.* (2019) described eight core ecological processes that contribute to coral reef functioning: calcium carbonate production, bioerosion, primary production, herbivory, secondary production, predation, nutrient uptake, and nutrient release. Most literature to date has aimed to quantify a single function, for example calcium carbonate production, (e.g. Courtney *et al.*, 2020), or relationships between a few of these functions, such as calcium carbonate production and bioerosion (e.g. Perry and Alvarez-Filip, 2018), or primary production and herbivory (e.g. Poore *et al.*, 2012). By contrast, research that investigates how these processes interact to contribute to overall reef functioning has largely focused on quantifying the functioning of reefs that host high biodiversity (Brandl *et al.*, 2019; Topor *et al.*, 2019), but as my first chapter demonstrates, greater biodiversity of coral taxa does not necessarily confer resilience to heat stress. This may be the result of feedbacks between biodiversity, ecosystem functioning, and human wellbeing (BEHs) relationships, which are currently not well understood (O'Connor *et al.*, 2021).

Because Tarawa and Abaiang in the Gilbert Islands, Kiribati may foreshadow how reefs in other parts of the world respond to the projected increasing frequency of heat stress-driven bleaching

events in the future (Donner, Heron and Skirving, 2009), they provide an opportunity for investigating how heat stress interacts with local stressors to influence reef functioning, and for identifying potential feedbacks in BEH relationships. The unique benthic communities at these atolls would allow an examination of how coral communities dominated by a single coral species, such as the *P. rus* dominated reefs in Tarawa described in Chapters 2 and 3, are functioning today, and this could foreshadow how reefs in other places will function in the future. This understanding would fill an important gap in the literature, while providing useful information for people in the Pacific Islands that would potentially help urban populations near coral reefs prepare for the ways reefs will change in the future. For example, scientists currently do not know whether reefs dominated by *P. rus* can provide the same services as more diverse reefs, even though they are more resistant to heat stress. However, Tarawa's reefs are more rugose than reefs in Abaiang and thus provided more protection to shorelines from wave energy, even though Abaiang's reefs are less degraded by local human stressors (Summers and Donner, 2022). In addition, comparing reef functions in Tarawa and Abaiang to those in Majuro and Arno would also allow isolating the effects of local versus global stressors and how they interact to influence reef functioning (Table 1.1).

Future work in Kiribati and the RMI could be modelled to investigate how the processes described by Brandl et al. (2019) interact to influence overall reef functioning. This might start by repeating the benthic surveys conducted in Chapter 1 and Chapter 2 to investigate whether the patterns observed here have remained consistent since 2018 and to estimate primary productivity. Fish surveys would be useful to investigate herbivory, predation, and secondary productivity, as it is unclear whether *P. rus*-dominated reefs can still support local subsistence

fisheries and how those fisheries influence fish populations. In S. Tarawa, an outstanding question is whether local reef fish diversity is linked to the biodiversity and complexity of the benthic communities at these locations, as has been found elsewhere (Strain *et al.*, 2019). Additionally, settlement plates could provide information about coral recruitment and whether and how recruitment varies. This would indicate whether the benthic compositions at given sites and atolls are driven by limitations in recruitment (Cruz and Harrison, 2017), or other drivers that prevent recruits from establishing and growing, such as water quality, and would potentially allow predictions of calcium carbonate production and bioerosion over long time scales. Estimating calcification rates at each site using the percent cover from benthic surveys (Husband, Perry and Lange, 2022) would allow a greater understanding of how local and global impacts influence coral reefs ability to continue growing fast enough to keep up with rising sea levels, across gradients of local and global impacts. Finally, collecting water samples to evaluate nutrients across a gradient of human impacts would provide insight into how different benthic communities process and release nutrients across sites in S. Tarawa and parts of Majuro, as these sites experience relatively high nutrient inputs from land, versus those in parts of Abaiang and Arno, while also considering the potential influence of climate-driven heat stress. While all these suggestions are specific to Kiribati and the RMI, similarly to the work in Chapters 2 and 3, they have broad implications for reefs globally, particularly as the climate continues to warm.

In addition, Chapter 4 demonstrated that coral reef scientists know little about the drivers of macroalgae cover on coral reefs, and we know even less about individual macroalgae taxa or the services that tropical macroalgal communities provide to people. However, like corals, some macroalgae are threatened by climate-driven heat stress, including the canopy-forming genus

Sargassum (Fulton *et al.*, 2019), and similarly to coral reefs (Alvarez-Filip *et al.*, 2009), heat stress is driving *Sargassum* and other canopy-forming taxa to lose complexity and ‘flatten’ over time as the climate warms (Fulton *et al.*, 2019). These taxa provide important habitat for reef fish, supporting small-scale fisheries and may also help to facilitate reef recovery after bleaching and other disturbance events (Sievers *et al.*, 2020; Wilson *et al.*, 2022). However, I showed in Chapter 4 that distinct macroalgae genera respond differently to diverse sources of human disturbance, and there are few studies investigating these dynamics at the genus level, except for common taxa like *Sargassum*. A greater awareness of the services provided by macroalgal-dominated reefs, how they differ depending on the taxa that are present, and the functions these taxa perform that support those services, will be required for understanding reef functioning overall. In addition, understanding how local and global stressors affect specific macroalgae taxa will help to make predictions about coral reefs and tropical macroalgal communities going forward. Again, Kiribati and the RMI provide a unique opportunity for investigating these dynamics as they allow for comparisons of fish and benthic community surveys across both gradients of human influence and past temperature stress.

6.5.2 Distal drivers of threats facing coral reefs

Another important aspect of applying the lessons from the Coral List in practice will be for conservationists to pay closer attention to the distal drivers of threats to coral reefs, as argued by Forster *et al.* (2017). I showed in Chapter 5 that even during informal conversations, participants often overlooked the distal drivers of local threats facing reefs, although this improved over time. However, both social and environmental vulnerability to coral bleaching might be more related to socio-economic components than ecological ones, according to work from the Caribbean

(Siegel *et al.*, 2019). This work also found that sovereign nations were less vulnerable to coral bleaching than overseas territories. To my knowledge, there has been no similar work in the Pacific Islands, although there are several overseas territories in the Pacific. However, I and others have argued that legacies of colonialism have made people in the Pacific Islands more vulnerable to the impacts of climate change (Bordner, Ferguson and Ortolano, 2020; Cannon, 2020), which could support the hypothesis that sovereign nations are less vulnerable to coral bleaching in the Pacific. Expanding the work of Siegel *et al* (2019) from the Caribbean to the Pacific and beyond could provide insights that would support conservation efforts undertaken by sovereign nations in the Pacific and/or provide evidence in favor of decolonization and the rights of IPLC.

6.5.3 The coral reef conservation community

The analysis of the Coral List showed that racism and colonialism influence the ways coral reef scientists talk about the local threats facing reefs today, with implications for conservation practice. This analysis raised several questions that were beyond the scope of the original investigation but that offer opportunities for future research. For example, I did not consider emails that discussed only global stressors facing coral reefs in Chapter 5. An analysis of these emails using methods like the analyses in Chapter 5 might provide valuable insight into how coral conservationists talk about climate change, who they view as responsible, and what they consider solutions.

Also, expanding the analysis to incorporate gender and race would provide insight into whether participation and the views held by participants differed across identities. A survey of the coral

reef conservation community found that conservationists ranked the threats facing coral reefs and their solutions differently depending on their gender (Kleypas and Eaken, 2007), while another study found that women were more likely to use hopeful narratives when discussing threats to reefs (Braverman, 2016). I decided against attempting to identify the gender of participants in Chapter 5 because automated methods for estimating gender representation can harm people who are non-binary and transgender by excluding, misgendering, and otherwise “othering” them (Mihaljević *et al.*, 2019), and collecting information about the gender and race of participants ethically requires researching the public personas of list participants (e.g. Ahmadia *et al.*, 2021), which was beyond the scope of Chapter 5. However, gathering this information and incorporating it into an analysis of the list and the narratives that participants used, along with additional demographic information that is usually publicly available (for example, career stage), would allow an understanding of how participation or engagement differed by identity.

While the Coral List has almost 10,000 subscribers, few of them participated in the exchanges I analyzed in Chapter 5, and as a result, the list archives only provided a limited snapshot of the coral conservation community. In addition, people likely have different perceptions of the Coral List depending on their identities and whether they are academic scientists from the Global North (as were the majority of participants). A formal survey or interviews of Coral List subscribers would allow me to test this hypothesis. A study that uses surveys or interviews to investigate the list environment would give subscribers an opportunity to describe their experiences themselves. Interviews could help explain what drives participation on the list, what participants and subscribers see as benefits or drawbacks to participation, and whether these are equally distributed among the participants. Conducting an anonymous survey would allow the collection

of potentially sensitive demographics information to facilitate a more intersectional approach to answering these questions. Finally, opening the survey to coral reef conservationists beyond the Coral List, alongside special efforts to ensure participation from conservationists in the Global South who were underrepresented among the Coral List participants, could reveal whether the List represents the community globally.

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Appendices

Appendix A Appendix to Chapter 2

A.1 Environmental variables, coordinates, and years we collected data for 19 study sites visited between 2012 and 2018.

Atoll	Site	Years Visited (20)				Lat	Long	Exposure Metric ¹	Mean NDV ²	Population Metric ³	CV _{SSR} ⁴	Mean Chl-a (mg m ⁻³)	# of CoTs scars (2014)
		12	14	16	18								
Abaiang	ABG001					1.8577	172.8796	0.48	0.33	4.07	3.24	0.57	18
	ABG002					1.8820	172.8180	0.60	0.41	5.95	3.23	0.19	0
	ABG003					1.7143	172.9865	0.46	0.38	5.29	3.20	0.57	85
	ABG004					1.8626	172.8802	0.17	0.35	4.09	3.33	0.19	81
	ABG005					1.9209	172.8039	0.23	0.38	4.89	3.16	0.17	--
	ABG006					1.8972	172.7772	0.15	0.35	4.98	3.20	0.17	--
	ABG010					1.8784	172.8463	0.50	0.45	4.74	3.17	1.03	8
	ABG011					1.8033	172.9088	0.26	0.36	3.37	3.24	0.29	1
	TRW005					1.6325	172.9673	0.74	0.21	5.55	3.31	0.17	29
	TRW007					1.6178	172.9336	0.63	0.27	5.67	3.18	0.15	0
Tarawa	TRW002					1.3332	173.0217	0.13	0.30	7.42	3.27	0.17	0
	TRW008					1.3581	173.1446	0.59	0.26	7.60	3.28	0.27	--
	TRW010					1.3302	172.9634	0.48	0.11	7.56	3.30	0.17	6
	TRW011					1.3570	173.0790	0.70	0.26	8.73	3.31	0.18	--
	TRW012					1.3246	172.9951	0.66	0.19	7.42	3.29	0.17	--
	TRW013					1.3463	172.9241	0.64	0.26	9.47	3.31	0.23	0
	TRW014					1.4209	172.9146	0.26	0.45	7.81	3.23	0.39	0
	TRW015					1.3506	173.0466	0.73	0.26	8.56	3.34	0.18	--
	TRW016					1.3911	173.1507	0.54	0.31	7.40	3.32	0.16	--

¹Metric calculated using the prevailing wind direction and a compass heading perpendicular to the reef crest (see Wind and Wave Exposure). Lower values are more sheltered, while higher values are more exposed.

²A human disturbance metric using the National Difference Vegetation Index (see Human disturbance). These values range from -1.0 to 1.0, with higher values equal to lower human disturbance.

³A human disturbance metric using the distance of each site to the nearest village divided by the population of that village (see Human disturbance). Higher values equal greater human disturbance.

⁴Coefficient of variation for daily Sea Surface Temperature (from 1985 – 2018; see Oceanographic Data).

A.2 Coral order, family, and species observed in Tarawa and Abaiang Atolls (as reported by Lovell et al, 2000).

Class & Order	Family	Species
Class ANTHOZOA, subclass ZOOANTHERIA, order SCLERACTINIA		
	THAMNASTERIIDAE	
		<i>Psammocora (P.) haimeana</i> (Edwards and Haime, 1851)
		<i>Psammocora profundacella</i> (Gardiner, 1898)
	POCILLOPORIDAE	
		<i>Pocillopora damicornis</i> (Linnaeus, 1758)
		<i>Pocillopora eydouxi</i> (Edwards & Haime, 1860)
		<i>Seriatopora hystrix</i> (Dana, 1846)
		<i>Stylophora pistallata</i> (Esper, 1797)
	ACROPORIDAE	
		<i>Acropora (A.) abrotanoides</i> (Lamark, 1816)
		<i>Acropora (A.) anthrocercis</i> (Brook, 1891)
		<i>Acropora (A.) cerealis</i> (Dana, 1846)
		<i>Acropora (A.) digitifera</i> (Dana, 1846)
		<i>Acropora (A.) divaricate</i> (Dana, 1846)
		<i>Acropora (A.) echinate</i> (Dana, 1846)
		<i>Acropora (A.) gemmifera</i> (Brook, 1892)
		<i>Acropora (A.) grandis</i> (Brook, 1892)
		<i>Acropora (A.) humilis</i> (Dana, 1846)
		<i>Acropora (A.) hyacinthus</i> (Dana, 1846)
		<i>Acropora (A.) intermedia</i> (Dana, 1846)
		<i>Acropora (A.) latistella</i> (Brook, 1892)
		<i>Acropora (A.) lovelli</i> (Veron and Wallace, 1984)
		<i>Acropora (A.) microphthalma</i> (Verrill, 1869)
		<i>Acropora (A.) muricata</i> (Dana, 1846)
		<i>Acropora (A.) nana</i> (Studer, 1878)
		<i>Acropora (A.) nasuta</i> (Dana, 1846)
		<i>Acropora (A.) paniculata</i> (Verrill, 1902)
		<i>Acropora (A.) robusta</i> (Dana, 1846)
		<i>Acropora (A.) secale</i> (Studer, 1878)
		<i>Acropora (A.) selago</i> (Studer, 1878)
		<i>Acropora (A.) spicifera</i> (Dana, 1846)

		<i>Acropora (A.) tenuis</i> (Dana, 1846)
		<i>Acropora (A.) tortuosa</i> (Dana, 1846)
		<i>Acropora (A.) valida</i> (Dana, 1846)
		<i>Acropora (A.) verweyi</i> (Veron and Wallace, 1984)
		<i>Acropora (A.) sp.</i>
		<i>Astreopora listeri</i> (Bernard, 1896)
		<i>Astreopora myriophthalma</i> (Lamarck 1816)
		<i>Montipora efflorescens</i> (Bernard, 1897)
		<i>Montipora foveolate</i> (Dana, 1846)
		<i>Montipora grisea</i> (Bernard, 1897)
		<i>Montipora hispida</i> (Dana, 1846)6)
		<i>Montipora hoffmeisteri</i> (Wells, 1954)
		<i>Montipora informis</i> (Bernard, 1897)
		<i>Montipora peltiformis</i> (Bernard, 1897)
		<i>Montipora terbuculosa</i> (Lamarck, 1816)
		<i>Montipora venosa</i> (Ehrenberg, 1834)
		<i>Montipora verrucose</i> (Lamarck, 1816)
	AGARICIIDAE	
		<i>Gardineroseris planulata</i> (Dana, 1846)
		<i>Leptoseris mycetoseroides</i> (Wells, 1954)
		<i>Pachyseris speciosa</i> (Dana, 1846)
		<i>Pavona cactus</i> (Forskal, 1775)
		<i>Pavona clavus</i> (Dana, 1846)
		<i>Pavona explanulata</i> (Lamarck, 1816)
		<i>Pavona maldivensis</i> (Gardiner, 1905)
		<i>Pavona minuta</i> (Wells, 1954)
		<i>Pavona varians</i> (Verrill, 1864)
	SIDERASTREIDAE	
		<i>Coscinaraea column</i> (Dana, 1846)
	FUNGIIDAE	
		<i>Cycloseris costulata</i>
		<i>Fungia (D.) horrida</i> (Dana, 1846)
		<i>Fungia (D.) valida</i> (Verrill, 1864)
		<i>Fungia (F.) fungites</i> (Linnaeus, 1758)
		<i>Fungia (P.) scutaria</i> (Lamarck, 1801)
		<i>Fungia (V.) concinna</i> (Verrill, 1864)
		<i>Fungia (V.) granulosa</i> (Klunzinger, 1879)
		<i>Fungia (V.) repanda</i> (Dana, 1846)
		<i>Halomitra pileus</i> (Linnaeus, 1758)
		<i>Herpolitha limax</i> (Houttuyn, 1772)
		<i>Podobacia crustacea</i> (Edwards and Haime, 1849)
		<i>Sandalolitha robusta</i> (Quelch, 1886)

	PORITIDAE	
		<i>Goniopora stutchburyi</i> (Wells, 1955)
		<i>Gonipora</i> sp.
		<i>Porites</i> (P.) <i>cylindrica</i> (Dana, 1846)
		<i>Porites</i> (P.) <i>lichen</i> (Dana, 1846)
		<i>Porites</i> (P.) <i>lobata</i> (Dana, 1846)
		<i>Porites</i> (P.) <i>lutea</i> (Edward & Haime, 1860)
		<i>Porites</i> <i>rus</i> (Forskal, 1775)
		<i>Porites</i> (S.) <i>rus</i> (Forskal, 1775)
		<i>Porites</i> sp.
	FAVIIDAE	
		<i>Cyphastrea microphthalma</i> (Lamarck, 1816)
		<i>Cyphastrea serailia</i> (Forskal, 1775)
		<i>Echinopora horrida</i> (Dana, 1846)
		<i>Echinopora lamellosa</i> (Esper, 1795)
		<i>Favia favius</i> (Forskal, 1775)
		<i>Favia matthaii</i> (Vaughan, 1918)
		<i>Favia pallida</i> (Dana, 1846)
		<i>Favia rotumana</i> (Gardiner, 1899)
		<i>Favia stelligera</i> (Dana, 1846)
		<i>Favites chinensis</i> (Verrill, 1866)
		<i>Favites flexuosa</i> (Dana, 1846)
		<i>Favites pentagona</i> (Esper, 1794)
		<i>Favites russelli</i> (Wells, 1954)
		<i>Goniastrea aspera</i>
		<i>Goniastrea edwardsi</i> (Chevalier, 1971)
		<i>Goniastrea favulus</i> (Dana, 1846)
		<i>Goniastrea pectinate</i> (Ehrenberg, 1834)
		<i>Leptastrea bewickensis</i> (Veron, Pinchon, and Wijsman-best, 1977)
		<i>Leptastrea pruinosa</i> (Crossland, 1952)
		<i>Leptastrea purpurea</i> (Dana, 1846)
		<i>Leptastrea</i> sp.
		<i>Leptoria phrygia</i> (Ellis & Solander, 1786)
		<i>Montastrea curta</i> (Dana, 1846)
		<i>Montastrea magnistellata</i> (Chevalier, 1971)
		<i>Oulophyllia crispa</i> (Lamarck, 1816)
		<i>Platygyra daedalea</i> (Ellis & Solander, 1786)
		<i>Platygyra sinensis</i> (Edward & Haime, 1849)
	MERULINIDAE	
		<i>Hydnophora exesa</i> (Pallas, 1766)
		<i>Hydnophora microconos</i> (Lamarck, 1816)
		<i>Hydnophora rigida</i> (Dana, 1846)
		<i>Merulina ampliata</i> (Ellis & Solander, 1786)

	MUSSIDAE	
		<i>Acanthastrea echinate</i> (Dana, 1846)
		<i>Lobophyllia corymbose</i> (Forskal, 1775)
		<i>Lobophyllia hemprichii</i> (Ehrenberg, 1834)
		<i>Symphyllia radians</i> (Edwards & Haime, 1849)
	PECTINIIDAE	
		<i>Echinophyllia echinata</i> (Saville-Kent, 1871)
		<i>Echinophyllia</i> sp.
		<i>Mycedium elephantotos</i> (Pallas, 1766)
		<i>Oxypora lacera</i> (Verrill, 1864)
	CARYPHYLLIDAE	
		<i>Plerogyra simplex</i> (Rehberg, 1892)
	DENDROPHYLLIIDAE	
		<i>Tubastrea micrantha</i> (Ehrenberg, 1834)
		<i>Turbinaria frondens</i> (Dana, 1846)
		<i>Turbinaria mesenterina</i>
		<i>Turbinaria reinformis</i> (Bernard, 1896)
		<i>Turbinaria</i> sp.
Class HYDROZOA, order COENOTHECALIA		
	HELIOPORIDAE	
		<i>Heliopora coerulea</i> (Pallas, 1766)
Order MILLEPORINA		
	MILLEPORIDAE	
		<i>Millepora platyphylla</i> (Hemprich & Ehrenberg, 1834)
		<i>Millepora</i> sp.
	STYLASTERIDAE	
		<i>Distochopora violacea</i> (Pallas, 1776)

A.3 Results of linear mixed effects models for each key benthic category, including additional LMM for subsets of the data.

	<i>All Sites</i>				<i>Sites affected by CoTs</i>				<i>Sites Visited Every Year</i>			
Categories	χ^2	p	Marg R ²	Cond R ²	χ^2	p	Marg R ²	Cond R ²	χ^2	p	Marg R ²	Cond R ²
<i>Hard Coral Taxa</i>												
All Live Coral	8.36	0.04	0.03	0.89	3.29	0.35	0.04	0.77	6.76	0.08	0.08	0.82
<i>Acropora</i>	<u>7.74</u>	<u>0.05</u>	<u>0.18</u>	<u>0.19</u>	4.04	0.26	0.19	0.19	6.94	0.07	0.26	0.26
Favids	15.00	<0.01	0.32	0.49	5.74	0.12	0.07	0.07	10.44	0.02	0.37	0.53
<i>Heliopora</i>	8.59	0.04	0.05	0.79	8.01	0.05	0.11	0.83	11.07	0.01	0.13	0.82
<i>Montipora</i>	16.41	<0.01	0.35	0.45	11.61	0.01	0.44	0.56	6.73	0.08	0.25	0.29
<i>Pocillopora</i>	14.77	<0.01	0.14	0.68	<u>6.16</u>	<u>0.10</u>	<u>0.22</u>	<u>0.50</u>	<u>6.88</u>	<u>0.08</u>	<u>0.19</u>	<u>0.48</u>
<i>Porites</i> (Massive)	9.62	0.02	0.07	0.79	<u>6.53</u>	<u>0.09</u>	<u>0.07</u>	<u>0.85</u>	<u>7.31</u>	<u>0.06</u>	<u>0.05</u>	<u>0.86</u>
<i>P. rus</i>	<u>6.75</u>	<u>0.08</u>	<u>0.02</u>	<u>0.91</u>	3.15	0.37	0.05	0.73	3.21	0.36	0.03	0.81
<i>Macroalgae Taxa</i>												
All Macroalgae	19.68	<0.01	0.29	0.53	9.73	0.02	0.44	0.55	13.00	<0.01	0.40	0.63
<i>Halimeda</i>	14.27	<0.01	0.26	0.55	10.02	0.02	0.36	0.52	12.77	0.01	0.32	0.62
<i>Lobophora</i>	5.15	0.16	0.09	0.33	5.28	0.15	0.19	0.47	1.98	0.58	0.07	0.24
<i>Other Benthic Categories</i>												
CCA*	7.95	0.05	0.14	0.38	5.69	0.13	0.12	0.68	4.35	0.23	0.16	0.26
Corallimorphs	4.06	0.26	0.12	0.51	3.86	0.28	0.17	0.52	5.52	0.14	0.15	0.50
Cyanobacteria	5.21	0.16	0.08	0.41	4.35	0.23	0.20	0.23	2.41	0.49	0.10	0.26
Rubble	9.81	0.02	0.14	0.53	5.87	0.12	0.26	0.26	<u>6.21</u>	<u>0.10</u>	<u>0.20</u>	<u>0.50</u>
Sand	<u>6.33</u>	<u>0.10</u>	<u>0.06</u>	<u>0.71</u>	2.74	0.43	0.08	0.57	2.20	0.53	0.05	0.59
Soft Coral	1.48	0.69	0.04	0.40	5.16	0.16	0.17	0.57	1.40	0.70	0.04	0.63
Sponges	14.09	<0.01	0.16	0.64	18.22	<0.01	0.63	0.63	11.51	0.01	0.34	0.63
Turf algae	14.34	<0.01	0.17	0.66	14.92	<0.01	0.28	0.82	11.64	0.01	0.28	0.70

A.4 Turkey results for Linear Mixed Effects Models (Percent ~ Year + (1|Site).

All p-values have been adjusted for multiple comparisons. Results significant at sigma = 0.05 are in bold; those significant at sigma = 0.10 are underlined.

Model results for dataset including all sites.

Hard coral taxa

All hard coral

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-7.589	2.768	-2.741	0.031
<u>2012 – 2016</u>	<u>-6.497</u>	<u>2.644</u>	<u>-2.446</u>	<u>0.068</u>
2012 – 2018	-5.382	2.535	-2.123	0.144
2014 – 2016	1.111	2.385	0.466	0.966
2014 – 2018	2.196	2.341	0.938	0.783
2016 – 2018	1.085	2.178	0.498	0.959

Acropora

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	0.464	0.268	1.731	0.307
2012 – 2016	-0.221	0.277	-0.798	0.855
2012 – 2018	-0.119	0.245	-0.485	0.962
<u>2014 – 2016</u>	<u>-0.685</u>	<u>0.277</u>	<u>-2.470</u>	<u>0.065</u>
<u>2014 – 2018</u>	<u>-0.583</u>	<u>0.244</u>	<u>-2.382</u>	<u>0.080</u>
<u>2016 – 2018</u>	<u>0.103</u>	<u>0.255</u>	<u>0.402</u>	<u>0.978</u>

Favids

Years	Estimate	St. Error	z-value	p-value
<u>2012 – 2014</u>	<u>-1.125</u>	<u>0.479</u>	<u>-2.349</u>	<u>0.086</u>
<u>2012 – 2016</u>	<u>-1.132</u>	<u>0.478</u>	<u>-2.366</u>	<u>0.083</u>
2012 – 2018	0.270	0.442	0.611	0.928
2014 – 2016	-0.007	0.457	-0.014	1.000
2014 – 2018	1.395	0.420	-3.322	0.005
2016 – 2018	1.402	0.415	3.375	0.004

Heliopora

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-0.089	0.969	-0.092	1.000
2012 – 2016	-1.893	0.924	-2.050	0.169

2012 – 2018	-1.895	0.912	-2.077	0.160
2014 – 2016	-1.804	0.833	-2.165	0.132
2014 – 2018	-1.806	0.819	-2.204	0.121
2016 – 2018	-0.002	0.780	-0.002	1.000

Montipora

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-0.089	0.126	-0.711	0.892
2012 – 2016	-0.205	0.116	-1.764	0.289
2012 – 2018	0.212	0.113	1.885	0.233
2014 – 2016	-0.116	0.116	-0.996	0.750
2014 – 2018	0.301	0.112	2.704	0.035
2016 – 2018	0.417	0.100	4.182	<0.001

Pocillopora

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-0.219	0.391	-0.560	0.943
2012 – 2016	-0.213	0.376	-0.565	0.942
2012 – 2018	0.840	0.356	2.344	0.087
2014 – 2016	0.007	0.338	0.020	1.000
2014 – 2018	1.059	0.236	3.249	0.006
2016 – 2018	1.053	0.307	3.429	0.003

Porites (Massive)

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-0.893	0.650	-1.373	0.515
2012 – 2016	-1.920	0.640	-3.000	0.014
<u>2012 – 2018</u>	<u>-1.424</u>	<u>0.611</u>	<u>-2.330</u>	<u>0.091</u>
2014 – 2016	-1.027	0.573	-1.794	0.275
2014 – 2018	-0.532	0.563	-0.945	0.780
2016 – 2018	0.496	0.547	0.906	0.801

Porites rus

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-5.582	2.835	-1.969	0.199
2012 – 2016	0.111	2.681	0.041	1.000
2012 – 2018	-0.047	2.569	-0.018	1.000
2014 – 2016	5.693	2.530	2.250	0.110
2014 – 2018	5.536	2.492	2.221	0.117
2016 – 2018	-0.158	2.287	-0.069	1.000

Macroalgae taxa*All macroalgae genera*

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-14.735	3.528	-4.177	<0.001
2012 – 2016	-15.528	3.436	-4.519	<0.001
2012 – 2018	-11.729	3.334	-3.518	0.002
2014 – 2016	-0.793	3.018	-0.263	0.994
2014 – 2018	3.006	2.888	1.041	0.724
2016 – 2018	3.799	2.771	1.371	0.515

Halimeda

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-13.990	4.470	-3.130	0.009
2012 – 2016	-19.125	4.611	-4.147	<0.001
2012 – 2018	-12.950	4.435	-2.920	0.018
2014 – 2016	-5.134	4.024	-1.276	0.577
2014 – 2018	1.040	3.805	0.273	0.993
2016 – 2018	6.175	4.053	1.523	0.422

Lobophora

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-3.506	1.995	-1.757	0.292
2012 – 2016	-0.132	1.884	-0.070	1.000
2012 – 2018	-0.319	1.837	-0.168	0.998
2014 – 2016	3.374	1.749	1.929	0.214
2014 – 2018	3.197	1.710	1.869	0.240
2016 – 2018	-0.177	1.547	-0.114	0.999

Other benthic taxa*Crustose-coralline algae*

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	3.678	1.698	2.166	0.131
2012 – 2016	4.529	1.651	2.743	0.031
2012 – 2018	3.270	1.558	2.099	0.152
2014 – 2016	0.850	1.482	0.573	0.940
2014 – 2018	-0.409	1.393	-0.293	0.991
2016 – 2018	-1.259	1.335	-0.943	0.780

Cyanobacteria

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	0.186	1.778	0.104	1.000
2012 – 2016	-0.346	1.724	-0.200	0.997
2012 – 2018	-2.584	1.630	-1.585	0.385
2014 – 2016	-0.531	1.547	-0.343	0.986
2014 – 2018	-2.770	1.463	-1.893	0.229
2016 – 2018	-2.239	1.396	-1.604	0.374

Rubble

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	3.919	1.406	2.787	0.027
2012 – 2016	2.249	1.360	1.654	0.346
2012 – 2018	0.899	1.289	0.698	0.897
2014 – 2016	-1.167	1.220	-1.369	0.517
2014 – 2018	-1.302	1.161	-2.600	0.045
2016 – 2018	-1.350	1.103	-1.224	0.610

Sand

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	4.490	2.919	1.538	0.411
2012 – 2016	-0.949	2.904	-0.327	0.988
2012 – 2018	-0.004	2.854	-0.001	1.000
<u>2014 – 2016</u>	<u>-5.439</u>	<u>2.368</u>	<u>-2.297</u>	<u>0.097</u>
2014 – 2018	-4.494	2.292	-1.961	0.200
2016 – 2018	0.945	2.231	0.424	0.974

Soft Coral

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	0.097	0.101	0.956	0.774
2012 – 2016	0.101	0.101	0.998	0.750
2012 – 2018	0.062	0.094	0.658	0.912
2014 – 2016	0.004	0.101	0.042	1.000
2014 – 2018	-0.035	0.094	-0.373	0.982
2016 – 2018	-0.039	0.904	-0.419	0.975

Sponges

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-2.409	0.708	-3.404	0.004
2012 – 2016	-0.453	0.682	-0.664	0.910
2012 – 2018	-0.710	0.648	-1.096	0.690
2014 – 2016	1.956	0.612	3.193	0.007
2014 – 2018	1.698	0.588	2.891	0.020
2016 – 2018	-0.257	0.555	-0.464	0.967

Turf algae

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	16.882	5.035	3.353	0.004
2012 – 2016	18.669	4.850	3.849	<0.001
2012 – 2018	13.382	4.613	2.901	0.019
2014 – 2016	1.787	4.356	0.410	0.976
2014 – 2018	-3.500	4.184	-0.836	0.836
2016 – 2018	-5.290	3.950	-1.339	0.536

Model results for dataset containing only the sites that were affected by COTs (ABG001, ABG003, ABG004, ABG010, ABG011, TRW005, TRW010).

Hard coral taxa

All live hard coral

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-5.371	2.751	-1.953	0.206
2012 – 2016	<u>-6.719</u>	<u>2.847</u>	<u>-2.360</u>	<u>0.085</u>
2012 – 2018	-3.127	2.751	-1.137	0.666
2014 – 2016	-1.348	2.751	-0.490	0.961
2014 – 2018	2.244	2.503	0.896	0.806
2016 – 2018	3.593	2.751	1.306	0.558

Acropora

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	0.551	0.417	1.321	0.549
2012 – 2016	-0.111	0.457	-0.242	0.995
2012 – 2018	0.028	0.417	0.067	1.000
2014 – 2016	-0.662	0.417	-1.586	0.385
2014 – 2018	-0.523	0.373	-1.402	0.497
2016 – 2018	0.139	0.417	0.332	0.987

Favids

Years	Estimate	St. Error	z-value	p-value
<u>2012 – 2014</u>	-1.701	0.595	-2.859	0.022
2012 – 2016	<u>-1.579</u>	<u>0.620</u>	<u>-2.546</u>	<u>0.053</u>
2012 – 2018	0.080	0.579	0.138	0.999
2014 – 2016	0.122	0.595	0.205	0.997
2014 – 2018	1.781	0.537	3.315	0.005
2016 – 2018	1.658	0.579	2.866	0.022

Heliopora

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	1.348	1.178	1.144	0.662
2012 – 2016	-2.312	1.218	-1.898	0.228
2012 – 2018	-1.396	1.178	-1.185	0.636
2014 – 2016	-3.660	1.178	-3.106	0.010
2014 – 2018	<u>-2.744</u>	<u>1.074</u>	<u>-2.556</u>	<u>0.052</u>
2016 – 2018	0.916	1.178	0.777	0.865

Montipora

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-0.162	0.115	-1.409	0.493
2012 – 2016	-0.245	0.120	-2.046	0.171
2012 – 2018	0.176	0.111	1.578	0.391
2014 – 2016	-0.084	0.115	-0.728	0.886
2014 – 2018	0.338	0.104	3.258	0.006
2016 – 2018	0.421	0.111	3.778	<0.001

Pocillopora

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-0.137	0.494	-0.277	0.993
2012 – 2016	-0.493	0.525	-0.940	0.783
2012 – 2018	1.082	0.494	2.190	0.126
2014 – 2016	-0.357	0.494	-0.722	0.888
2014 – 2018	1.219	0.443	2.753	0.030
2016 – 2018	1.575	0.494	3.189	0.008

Porites (massive)

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-1.095	0.959	-1.142	0.663
2012 – 2016	-2.556	0.987	-2.591	0.050
2012 – 2018	-2.148	0.952	-2.255	0.108
2014 – 2016	-1.462	0.959	-1.525	0.422
2014 – 2018	-1.054	0.875	-1.204	0.624
2016 – 2018	0.408	0.952	0.428	0.974

Porites rus

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-3.980	4.015	-0.991	0.754
2012 – 2016	1.444	4.174	0.343	0.986
2012 – 2018	1.362	4.015	0.339	0.987
2014 – 2016	5.414	4.015	1.348	0.531
2014 – 2018	5.343	3.641	1.467	0.457
2016 – 2018	-0.071	4.015	-0.018	1.000

Macroalgae Taxa*All Macroalgae*

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-18.866	5.683	-3.320	0.005
2012 – 2016	-22.636	6.053	-3.739	0.001
2012 – 2018	-18.044	5.683	-3.175	0.008
2014 – 2016	-3.770	5.683	-0.663	0.911
2014 – 2018	0.822	5.089	0.162	0.998
2016 – 2018	0.459	5.683	0.808	0.850

Halimeda

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-18.465	5.820	3.172	0.008
2012 – 2016	-26.728	6.204	-4.308	<0.001
2012 – 2018	-18.595	5.820	-3.195	0.008
2014 – 2016	-8.264	5.820	-1.420	0.486
2014 – 2018	-0.130	5.211	-0.025	0.999
2016 – 2018	0.814	5.820	1.397	0.500

Lobophora

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-0.438	1.836	-0.238	0.995
2012 – 2016	3.996	1.935	2.065	0.164
2012 – 2018	0.391	1.767	0.221	0.996
<u>2014 – 2016</u>	<u>4.433</u>	<u>1.856</u>	<u>2.415</u>	<u>0.074</u>
2014 – 2018	0.826	1.657	0.500	0.959
2016 – 2018	-3.605	1.767	-2.041	0.173

Other Benthic Taxa

CCA

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	2.879	2.057	1.399	0.499
<u>2012 – 2016</u>	<u>5.522</u>	<u>2.161</u>	<u>2.556</u>	<u>0.052</u>
2012 – 2018	2.689	2.057	1.307	0.558
2014 – 2016	2.643	2.057	1.285	0.572
2014 – 2018	-0.190	1.853	-0.103	0.999
2016 – 2018	-2.833	2.057	-1.377	0.513

Cyanobacteria

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-1.065	1.574	-0.677	0.906
2012 – 2016	0.423	1.724	0.245	0.995
2012 – 2018	0.982	1.574	0.624	0.924
2014 – 2016	1.488	1.574	0.946	0.779
2014 – 2018	2.047	1.407	1.455	0.464
2016 – 2018	0.560	1.563	-0.956	0.773

Rubble

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	4.049	1.821	2.223	0.117
2012 – 2016	5.361	1.929	2.779	0.028
2012 – 2018	1.521	1.821	0.835	0.837
2014 – 2016	1.312	1.821	0.721	0.889
2014 – 2018	-2.528	1.634	-1.547	0.408
2016 – 2018	-3.841	1.821	-2.109	0.150

Sand

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	3.469	4.029	0.861	0.825
2012 – 2016	0.295	4.248	0.069	1.000
2012 – 2018	-0.369	4.029	-0.092	1.000
2014 – 2016	-3.174	4.029	-0.788	0.860
2014 – 2018	-3.837	3.622	-1.059	0.714
2016 – 2018	-0.664	4.029	-0.165	0.998

Soft Coral

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	0.186	0.110	1.697	0.325
2012 – 2016	0.191	0.110	1.745	0.300
2012 – 2018	0.077	0.107	0.721	0.889
2014 – 2016	0.005	0.110	0.048	1.000
2014 – 2018	-0.109	0.107	-1.018	0.739
2016 – 2018	-0.114	0.107	-1.067	0.709

Sponges

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-0.864	0.498	-1.737	0.303
<u>2012 – 2016</u>	<u>1.345</u>	<u>0.545</u>	<u>2.468</u>	<u>0.065</u>
2012 – 2018	0.840	0.498	1.688	0.329
2014 – 2016	2.209	0.480	4.440	<0.001
2014 – 2018	1.704	0.445	3.829	<0.001
2016 – 2018	-0.505	0.498	-1.015	0.740

Turf Algae

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	20.539	4.232	4.853	<0.001
2012 – 2016	20.476	4.392	4.662	<0.001
2012 – 2018	19.157	4.232	4.527	<0.001
2014 – 2016	-0.063	4.232	-0.015	1.000
2014 – 2018	-1.382	3.843	-0.360	0.984
2016 – 2018	-1.319	4.232	-0.312	0.989

Model results for dataset containing only the sites that were visited each year (ABG001, ABG002, ABG003, TRW002, and TRW010).

Hard coral taxa

All Live Coral

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-4.812	2.989	-1.500	0.438
<u>2012 – 2016</u>	<u>-7.642</u>	<u>2.989</u>	<u>-2.557</u>	<u>0.052</u>
2012 – 2018	-5.220	2.989	-1.747	0.300
2014 – 2016	-3.160	2.989	-1.057	0.716
2014 – 2018	-0.739	2.989	-0.247	0.995
2016 – 2018	2.422	2.989	0.810	0.850

Acropora

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	1.145	1.679	0.682	0.904
2012 – 2016	-0.131	1.860	-0.071	1.000
2012 – 2018	1.164	1.754	0.663	0.911
2014 – 2016	-1.277	1.790	-0.713	0.892
2014 – 2018	0.018	1.679	0.011	1.000
2016 – 2018	1.295	1.860	0.696	0.898

Favids

Years	Estimate	St. Error	z-value	p-value
<u>2012 – 2014</u>	<u>-1.322</u>	<u>0.526</u>	<u>-2.514</u>	<u>0.058</u>
2012 – 2016	-1.485	0.526	-2.824	0.024
2012 – 2018	-0.260	0.526	-0.494	0.960
2014 – 2016	-0.163	0.526	-0.310	0.990
2014 – 2018	1.062	0.526	2.020	0.181
<u>2016 – 2018</u>	<u>1.225</u>	<u>0.526</u>	<u>2.330</u>	<u>0.091</u>

Heliopora

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-8.171	10.197	-0.801	0.853
2012 – 2016	-3.580	9.038	-0.396	0.979
2012 – 2018	1.067	10.197	0.105	1.000
2014 – 2016	4.591	9.038	0.508	0.957
2014 – 2018	9.238	10.197	0.906	0.801
2016 – 2018	4.647	9.038	0.514	0.955

Montipora

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-2.064	7.489	-0.276	0.993
2012 – 2016	-2.779	8.204	-0.339	0.987
2012 – 2018	13.862	7.783	1.781	0.282
2014 – 2016	-0.714	7.489	-0.095	1.000
2014 – 2018	15.926	7.025	2.267	0.105
2016 – 2018	16.640	7.783	2.138	0.141

Pocillopora

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-3.610	7.103	-0.508	0.957
2012 – 2016	2.057	5.800	0.353	0.985
2012 – 2018	-4.340	6.484	-0.669	0.908
2014 – 2016	5.657	7.103	0.796	0.855
2014 – 2018	-0.730	7.672	-0.095	1.000
2016 – 2018	-6.387	6.484	-0.985	0.756

Porites (massive)

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	11.827	8.634	1.370	0.518
<u>2012 – 2016</u>	<u>11.654</u>	<u>8.634</u>	<u>1.350</u>	<u>0.531</u>
2012 – 2018	12.356	8.634	1.431	0.479
2014 – 2016	-0.173	8.027	-0.022	1.000
2014 – 2018	0.529	8.027	0.066	1.000
2016 – 2018	0.701	8.037	0.087	1.000

Porites rus

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-22.332	6.299	-3.545	0.002
2012 – 2016	-27.203	5.539	-4.911	<0.001
2012 – 2018	-21.945	6.299	-3.484	0.819
2014 – 2016	-4.872	5.595	-0.871	0.819
2014 – 2018	0.387	6.293	0.061	1.000
2016 – 2018	5.259	5.595	0.940	0.782

Macroalgae taxa**All macroalgae**

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	16.797	4.976	3.375	0.004
2012 – 2016	21.383	4.976	4.297	<0.001
2012 – 2018	14.629	4.976	2.940	0.018
2014 – 2016	4.586	4.976	0.922	0.793
2014 – 2018	-2.168	4.976	-0.436	0.972
2016 – 2018	-6.753	4.976	-1.357	0.526

Halimeda

Years	Estimate	St. Error	z-value	p-value
<u>2012 – 2014</u>	<u>14.788</u>	<u>5.82</u>	<u>2.541</u>	<u>0.053</u>
2012 – 2016	22.536	5.82	3.872	<0.001
2012 – 2018	16.217	5.82	2.786	0.028
2014 – 2016	7.748	5.82	1.331	0.543
2014 – 2018	1.429	5.82	0.245	0.995
2016 – 2018	-6.319	5.82	1.086	0.698

Lobophora

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	1.963	2.938	0.668	0.909
2012 – 2016	-1.102	2.938	-0.375	0.982
2012 – 2018	-1.533	2.938	-0.522	0.954
2014 – 2016	-3.065	2.938	-1.043	0.724
2014 – 2018	-3.495	2.938	-1.190	0.633
2016 – 2018	-0.431	2.938	-0.147	0.999

Other benthic taxa**CCA**

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	2.220	2.336	0.951	0.777
2012 – 2016	4.272	2.336	1.829	0.260
2012 – 2018	3.755	2.336	1.608	0.374
2014 – 2016	2.051	2.336	0.878	0.816
2014 – 2018	1.534	2.336	0.657	0.913
2016 – 2018	-0.517	2.336	-0.221	0.996

Cyanobacteria

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	1.491	2.592	0.575	0.940
2012 – 2016	0.122	2.592	0.047	1.000
2012 – 2018	3.286	2.592	1.268	0.584
2014 – 2016	-1.369	2.592	-0.528	0.952
2014 – 2018	1.795	2.592	0.692	0.900
2016 – 2018	3.164	2.592	1.221	0.614

Rubble

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	3.139	1.807	1.737	0.304
2012 – 2016	3.945	1.807	2.183	0.128
2012 – 2018	1.009	1.807	0.558	0.944
2014 – 2016	0.805	1.807	0.446	0.971
2014 – 2018	-2.130	1.807	-1.179	0.640
2016 – 2018	-2.954	1.807	-1.624	0.365

Sand

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	3.659	3.552	1.030	0.732
2012 – 2016	0.233	3.552	0.065	1.000
2012 – 2018	-0.881	3.552	-0.248	0.995
2014 – 2016	-3.436	3.552	-0.965	0.770
2014 – 2018	-4.540	3.552	-1.278	0.577
2016 – 2018	-1.114	3.552	-0.314	0.989

Soft coral

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	-0.097	0.096	-1.005	0.746
2012 – 2016	-0.101	0.096	-1.049	0.720
2012 – 2018	-0.046	0.096	-0.480	0.964
2014 – 2016	-0.004	0.096	-0.044	1.000
2014 – 2018	0.050	0.096	0.525	0.953
2016 – 2018	0.055	0.096	0.569	0.941

Sponges

Years	Estimate	St. Error	z-value	p-value
2012 – 2014	0.097	0.107	0.899	0.805
2012 – 2016	0.101	0.107	0.939	0.784
2012 – 2018	0.046	0.107	0.429	0.973
2014 – 2016	0.004	0.107	0.040	1.000

2014 – 2018	-0.050	0.107	-0.470	0.966
2016 – 2018	-0.054	0.107	-0.509	0.957

Turf algae

Years	Estimate	St. Error	z-value	p-value
<u>2012 – 2014</u>	<u>15.844</u>	<u>6.298</u>	<u>2.516</u>	<u>0.057</u>
2012 – 2016	23.062	6.298	3.662	0.001
2012 – 2018	14.061	6.298	2.232	0.114
2014 – 2016	7.218	6.298	1.146	0.661
2014 – 2018	-1.784	6.298	-0.283	0.992
2016 – 2018	-9.002	6.298	-1.429	0.481

A.5 Results of Size Frequency statistical analyses.

Results including all years

Welch's ANOVA of size-frequency statistics between years, with significant results bolded.

Taxa	Mean ¹			Coefficient of Variation			Kurtosis			Skewness		
	F	p	df ²	F	p	df ²	F	p	df ²	F	p	df ²
<i>Acropora</i>	1.35	0.47	1.69	0.58	0.68	1.99	--	--	--	--	--	--
Favids	2.06	0.36	1.81	1.57	0.41	2.05	0.24	0.86	1.85	0.17	0.91	1.71
<i>Heliopora</i>	1.89	0.39	1.71	1.07	0.51	2.09	7.90	0.13	1.83	<u>9.36</u>	<u>0.10</u>	<u>2.03</u>
<i>Montipora</i>	4.37	0.21	1.86	37.23	0.04	1.67	--	--	--	0.74	0.63	1.77
<i>Pocillopora</i>	1.77	0.41	1.70	6.97	0.12	2.12	40.20	0.04	1.68	5.36	0.15	2.08
Massive <i>Porites</i>	7.63	0.13	1.82	139.35	0.01	2.02	0.55	0.70	1.77	0.95	0.57	1.70

¹ Mean size in cm

² df is the denominator degrees of freedom. Numerator degrees of freedom equals 1 for all tests.

Kolmogorov-Smirnov (KS) test results comparing size distributions across years within each atoll, with Bonferroni correction. Results that are significant are in bold.

Taxa	All years						2012 & 2018					
	Abaiang			Tarawa			Abaiang			Tarawa		
	D	p	p-adj	D	p	p-adj	D	p	p-adj	D	p	p-adj
<i>Acropora</i>	0.45	0.61	1.00	0.22	0.66	1.00	0.45	0.07	0.44	0.32	0.43	1.00
Favids	0.82	<0.01	<0.01	0.14	0.82	1.00	0.69	<0.01	<0.01	0.15	0.70	1.00
<i>Heliopora</i>	0.51	<0.01	<0.01	0.25	0.03	0.25	0.74	<0.01	<0.01	0.51	<0.01	<0.01
<i>Montipora</i>	0.58	0.39	1.00	0.33	0.89	1.00	0.36	0.83	1.00	0.53	0.17	0.87
<i>Pocillopora</i>	0.23	0.43	1.00	0.19	0.40	1.00	0.70	<0.01	<0.01	0.39	<0.01	<0.01
Massive <i>Porites</i>	0.53	<0.01	<0.01	0.61	0.14	1.00	0.76	<0.01	<0.01	0.49	0.18	0.87

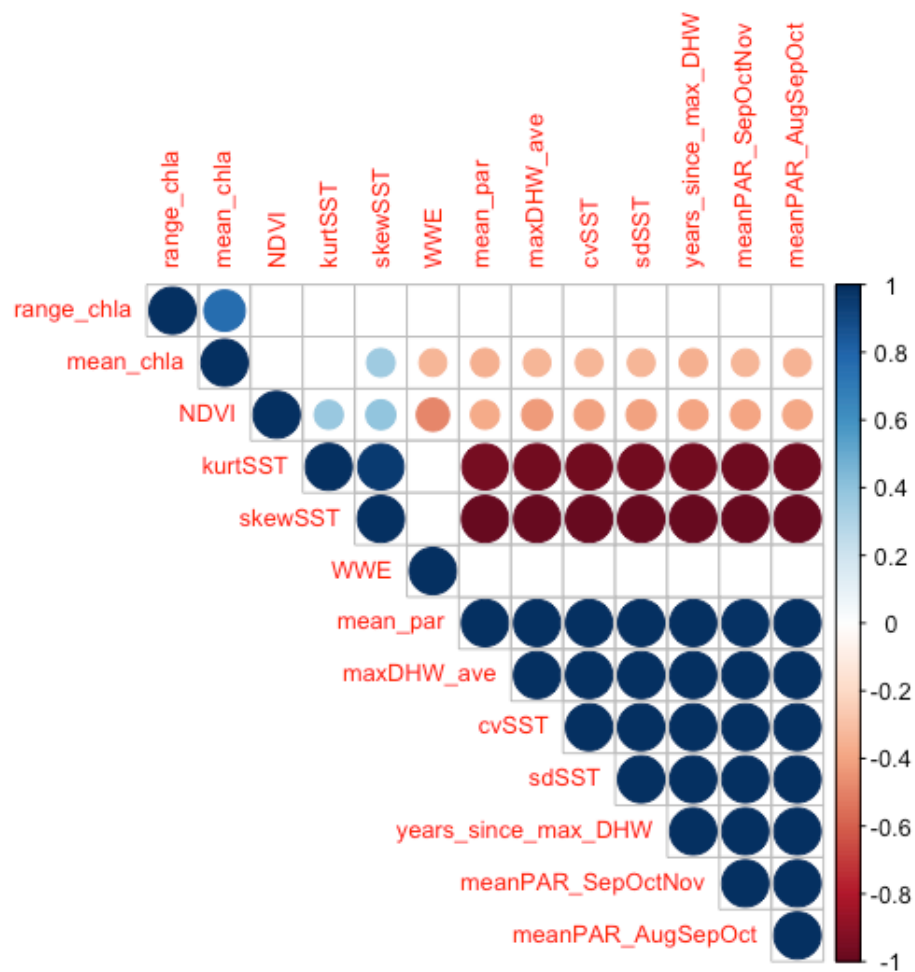
Appendix B Appendix to Chapter 3

B.1 List of sites and variables.

Site	Atoll	Country	Lat	Long	SD SST	CV SST	SST KURT	SST SKEW	DHW MAX	Yrs DHW MAX	Annual μ DHW MAX	WWE	PAR _{μ}	PAR _{μ} Sep- Nov	PAR _{μ} Aug- Oct	chl- a _R	chl- a _{μ}	NDVI scaled	Inverse NDVI
ARN001	Arno	RMI	7.0631	171.5452	0.68	2.38	-	0.01	3.66	2	0.59	0.04	42.80	41.80	44.07	3.17	0.57	1.00	0.00
ARN002	Arno	RMI	7.0411	171.5694	0.68	2.38	-	0.03	3.50	2	0.53	0.03	42.80	41.80	44.07	0.27	0.19	0.65	0.35
ARN003	Arno	RMI	6.9928	171.6089	0.68	2.36	-	0.04	3.73	2	0.51	0.14	42.00	42.40	44.18	3.17	0.57	0.69	0.31
ARN004	Arno	RMI	6.9959	171.6421	0.68	2.36	-	0.04	3.73	2	0.51	0.07	42.00	42.40	44.18	0.27	0.19	0.40	0.60
ARN005	Arno	RMI	7.0040	171.5896	0.68	2.38	-	0.03	3.50	2	0.53	0.01	42.80	41.80	44.07	0.85	0.17	0.75	0.25
ARN006	Arno	RMI	6.9553	171.7485	0.67	2.36	-	0.03	3.29	2	0.47	0.02	42.00	42.40	44.18	0.27	0.17	0.83	0.17
ARN007	Arno	RMI	6.9623	171.7259	0.67	2.36	-	0.03	3.29	2	0.47	0.04	42.00	42.40	44.18	3.17	0.57	0.74	0.26
ARN008	Arno	RMI	6.9813	171.6959	0.68	2.36	-	0.03	3.44	2	0.49	0.01	42.00	42.40	44.18	3.17	0.57	0.79	0.21
ARN009	Arno	RMI	7.1179	171.5646	0.68	2.39	-	0.00	3.68	2	0.55	0.07	42.80	41.80	44.07	2.23	0.29	0.93	0.07
ARN010	Arno	RMI	7.0843	171.5529	0.68	2.38	-	0.02	3.67	2	0.55	0.03	42.80	41.80	44.07	1.82	1.03	0.79	0.21
ARN011	Arno	RMI	7.1508	171.5873	0.69	2.39	-	0.01	3.80	2	0.53	0.02	42.80	41.80	44.07	2.23	0.29	0.98	0.02
ARN012	Arno	RMI	7.1881	171.6088	0.69	2.39	-	0.01	3.52	2	0.51	0.01	42.80	41.80	44.07	3.62	0.75	0.89	0.11
ARN013	Arno	RMI	7.2430	171.6326	0.69	2.40	-	0.02	3.79	2	0.51	0.02	42.80	41.80	44.07	3.17	0.57	0.81	0.19
MAJ001	Majuro	RMI	7.0747	171.1667	0.68	2.38	-	0.01	3.21	2	0.55	0.17	42.80	41.80	44.07	2.25	0.67	0.73	0.27
MAJ002	Majuro	RMI	7.0665	171.2955	0.68	2.38	-	0.01	2.49	2	0.50	1.78	42.80	41.80	44.07	0.51	0.11	0.39	0.61
MAJ003	Majuro	RMI	7.0794	171.3435	0.68	2.38	-	0.00	2.57	4	0.51	1.85	42.80	41.80	44.07	0.38	0.09	0.55	0.45
MAJ004	Majuro	RMI	7.2211	171.0562	0.68	2.39	-	0.01	3.11	2	0.56	0.00	42.80	41.80	44.07	0.14	0.07	0.92	0.08

MAJ005	Majuro	RMI	7.1974	171.0971	0.68	2.38	0.00	-	0.02	2.95	2	0.51	2.98	42.80	41.80	44.07	0.16	0.07	0.66	0.34	
MAJ006	Majuro	RMI	7.1571	171.2031	0.69	2.39	0.01	-	0.03	3.05	2	0.50	0.21	42.80	41.80	44.07	0.32	0.14	0.87	0.13	
MAJ007	Majuro	RMI	7.1433	171.0271	0.68	2.37	0.00	-	0.01	3.44	2	0.59	0.02	42.80	41.80	44.07	0.15	0.07	0.94	0.06	
MAJ008	Majuro	RMI	7.1040	171.0810	0.68	2.38	0.00	-	0.01	3.23	2	0.53	0.18	42.80	41.80	44.07	0.14	0.07	0.72	0.28	
MAJ009	Majuro	RMI	7.1036	171.3823	0.68	2.38	0.01	-	0.03	3.40	2	0.54	2.25	42.80	41.80	44.07	0.39	0.07	0.08	0.92	
MAJ010	Majuro	RMI	7.1302	171.3161	0.68	2.38	0.00	-	0.03	3.68	2	0.57	2.36	42.80	41.80	44.07	0.37	0.11	0.76	0.24	
MAJ012	Majuro	RMI	7.0762	171.3769	0.68	2.38	0.00	-	0.03	3.13	2	0.55	2.22	42.80	41.80	44.07	0.77	0.15	0.22	0.78	
ABG001	Abaiang	KBT	1.8577	172.8796	0.92	3.20	-	-	0.14	0.49	13.35	14	3.87	0.06	47.73	50.11	50.54	0.61	0.12	0.60	0.40
ABG002	Abaiang	KBT	1.8820	172.8180	0.93	3.21	-	-	0.15	0.49	13.31	14	3.95	0.32	47.73	50.11	50.54	1.76	0.32	0.82	0.18
ABG003	Abaiang	KBT	1.7143	172.9865	0.92	3.20	-	-	0.14	0.49	13.35	14	3.87	0.01	47.73	50.11	50.54	0.21	0.09	0.74	0.26
ABG005	Abaiang	KBT	1.9209	172.8040	0.93	3.21	-	-	0.14	0.50	13.56	14	3.77	0.03	47.73	50.11	50.54	0.14	0.07	0.74	0.26
ABG006	Abaiang	KBT	1.8972	172.7772	0.93	3.23	-	-	0.17	0.49	13.11	14	3.95	0.01	47.73	50.11	50.54	0.95	0.09	0.66	0.34
ABG011	Abaiang	KBT	1.8033	172.9088	0.92	3.19	-	-	0.13	0.50	13.53	14	3.77	0.00	47.73	50.11	50.54	0.15	0.07	0.77	0.23
TRW005	Abaiang	KBT	1.6325	172.9673	0.93	3.23	-	-	0.15	0.50	13.59	14	4.26	2.16	47.73	50.11	50.54	0.37	0.17	0.27	0.73
TRW007	Abaiang	KBT	1.6178	172.9336	0.94	3.25	-	-	0.17	0.49	13.81	14	3.99	0.01	47.73	50.11	50.54	0.08	0.15	0.93	0.07
TRW002	Tarawa	KBT	1.3332	173.0217	0.95	3.28	-	-	0.13	0.51	14.66	14	4.05	2.12	47.52	50.54	50.54	0.27	0.17	0.52	0.48
TRW008	Tarawa	KBT	1.3581	173.1446	0.94	3.27	-	-	0.12	0.52	13.53	14	3.87	0.07	47.52	50.54	50.54	0.27	0.16	0.41	0.59
TRW010	Tarawa	KBT	1.3302	172.9634	0.95	3.29	-	-	0.14	0.50	15.19	14	4.43	0.03	47.73	50.11	50.54	0.41	0.17	0.00	1.00
TRW011	Tarawa	KBT	1.3570	173.0790	0.94	3.27	-	-	0.12	0.51	14.16	14	4.02	2.14	47.52	50.54	50.54	2.19	0.18	0.41	0.59
TRW012	Tarawa	KBT	1.3246	172.9951	0.95	3.29	-	-	0.14	0.50	15.19	14	4.43	2.11	47.73	50.11	50.54	0.41	0.17	0.22	0.78
TRW013	Tarawa	KBT	1.3463	172.9241	0.95	3.30	-	-	0.16	0.50	15.05	14	4.45	0.52	47.73	50.11	50.54	3.02	0.23	0.41	0.59
TRW015	Tarawa	KBT	1.3506	173.0466	0.94	3.27	-	-	0.13	0.51	14.80	14	4.19	2.13	47.52	50.54	50.54	2.19	0.18	0.41	0.59
TRW016	Tarawa	KBT	1.3911	173.1507	0.95	3.28	-	-	0.11	0.52	13.04	14	3.87	2.16	47.52	50.54	50.54	0.32	0.16	0.55	0.45

B.2 Correlation analysis of variables used in statistics.



B.3 Results of full multiple linear regression equations for all taxa using the equation:

$$\text{Percent} \sim \text{NDVI} + \text{CV}_{\text{SST}} + \text{NDVI} * \text{CV}_{\text{SST}}.$$

Category	Residual Standard Error	Multiple R ²	Adjusted R ²	F _{3,36}	p-value
Hard coral taxa					
All live coral	11.73	0.31	0.25	5.32	<0.01
<i>Acropora</i>	<i>0.04</i>	<i>0.16</i>	<i>.09</i>	<i>2.22</i>	<i>0.10</i>
Favids	<0.01	0.28	0.22	4.74	<0.01
<i>Heliopora</i>	<i>2.63</i>	0.32	0.27	5.72	<0.01
<i>Isopora</i>	<i>1.94</i>	0.78	0.21	4.39	0.01
<i>Pocillopora</i>	0.95	0.51	0.47	12.65	<0.01
Massive	7.54	0.21	0.15	3.26	0.03
<i>Porites</i>					
<i>Porites rus</i>	9.382	0.57	0.53	15.60	<0.01
Macroalgae taxa					
<i>All macroalgae</i>	<i>17.58</i>	<i>0.19</i>	<i>0.13</i>	<i>2.87</i>	<i>0.05</i>
Halimeda	14.00	0.23	0.16	3.49	0.03
Hypnea	3.79	0.21	0.15	3.27	0.03
<i>Lobophora</i>	<i>5.06</i>	<i>0.10</i>	<i>0.03</i>	<i>1.36</i>	<i>0.27</i>
<i>Microdictyon</i>	<i>5.63</i>	<i>0.19</i>	<i>0.12</i>	<i>2.77</i>	<i>0.06</i>
Other categories					
CCA	3.92	0.16	0.09	2.29	0.10
Corallimorphs	1.89	0.40	0.35	7.85	<0.01
Cyanobacteria	4.37	0.45	0.40	9.79	<0.01
Sponges	0.01	0.37	0.32	7.06	<0.01
<i>Turf algae</i>	<i>12.52</i>	<i>0.16</i>	<i>0.09</i>	<i>2.32</i>	<i>0.09</i>

Results that are significant at $\alpha = 0.05$ are in bold, while those that are significant at $\alpha = 0.10$ are in italics. Note that for taxa that were not present at all sites, these results may differ from the tobit regression results presented in the manuscript (tobit regressions are more accurate).

Appendix C Appendix to Chapter 4

C.1 Description of variables thought to influence total macroalgae percent cover on coral reefs.

	Name	Resolution and/or Units	Description and Reasoning	Source
Connectivity	<i>Connections between coral reefs can influence local ecological communities through larval dispersal with impacts for resilience and management (Magris et al., 2016). Some macroalgae may travel long distances during various parts of their lifecycles. Additionally, the ability of hard coral taxa to compete with macroalgae after disturbances may be influenced by coral larval supply (Beyer et al., 2018).</i>			
1	Connectivity Score	5 km resolution, no units	A metric estimating the level of connectivity of sites to other reefs, including outgoing larval settlement (including self-recruitment) and larval export estimated via a larval connectivity model (Beyer et al., 2018).	Andrello et al., 2021
2	Reef Area (15 km)	Number of reefs cells falling within a 15-km buffer multiplied by the area of a cell (0.25 km ²).	15-km is the upper range of larval dispersion distances for most reef fishes, which can influence macroalgae percent cover through herbivory (Green et al., 2015).	Yeager et al., 2017

	Name	Resolution and/or Units	Description and Reasoning	Source
3	Reef Area (200 km)	Number of reefs cells falling within a 200-km buffer multiplied by the area of a cell (0.25 km ²).	200-km is the upper range of larval dispersal distances for large-bodied fish species (Green <i>et al.</i> , 2015). Some macroalgae can also disperse across large distances.	Yeager <i>et al.</i> , 2017
Geography <i>Geography influences the oceanography and climate of a given reef. These variables will also account for geographical bias in the dataset and spatial autocorrelation across sites.</i>				
4	Latitude	Decimal degrees	We used the latitude and longitude to account for spatial autocorrelation in the dataset.	Data contributors
5	Longitude	Decimal degrees	We used the latitude and longitude to account for spatial autocorrelation in the dataset.	Data contributors
6	Region	Decimal degrees	We used the regions defined here to assess and account for regional differences in tropical macroalgal communities across sites.	Kleypas, Danabasoglu and Lough, 2008
Heat Stress <i>Heat stress can kill corals and may exacerbate local human impacts, depending on the coral taxa present (Darling <i>et al.</i>, 2012). Macroalgae cover may increase as a result of declining coral cover,, but some macroalgae may also be vulnerable to heat stress (Fulton <i>et al.</i>, 2019).</i>				
7	SST _{CV}	5 km resolution, no units	The coefficient of variation for sea surface temperature represents the range of temperature values at a given site.	CRW Version 3.1 Daily Global Satellite Products (1995 – 2020) from NOAA Coral Reef Watch (2020)
8	Number of DHW > 4	5 km resolution, no units	Degree heating weeks greater than 4 represent a bleaching warning as defined by Coral Reef Watch, indicating that coral bleaching is possible.	CRW Version 3.1 Daily Global Satellite Products (1995 – 2020) from NOAA Coral Reef Watch (2020)

	Name	Resolution and/or Units	Description and Reasoning	Source
9	Number of DHW > 8	5 km resolution, no units	When degree heating weeks exceed 8, Coral Reef Watch issues a bleaching warning, indicating that coral bleaching is likely.	CRW Version 3.1 Daily Global Satellite Products (1995 – 2020) from NOAA Coral Reef Watch (2020)
10	SST _{kurt}	5 km resolution, no units	The kurtosis of SST is the distribution by frequency, with positive values indicating a steeper distribution than normal, and negative values indicating a broader distribution than normal.	CRW Version 3.1 Daily Global Satellite Products (1995 – 2020) from NOAA Coral Reef Watch (2020)
11	MaxDHW (all)	5 km resolution, no units	The maximum Degree Heating Weeks, a metric for cumulative heat stress, in the entire time period (between 1995 and 2020).	CRW Version 3.1 Daily Global Satellite Products (1995 – 2020) from NOAA Coral Reef Watch (2020)
12	Mean of annual maxDHW	5 km resolution, no units	The mean of the highest DHW from each year between 1995 and 2020.	CRW Version 3.1 Daily Global Satellite Products (1995 – 2020) from NOAA Coral Reef Watch (2020)
13	MMM	5 km resolution, expressed in °C	The Maximum Monthly Mean is the highest value among the 12 monthly mean SST climatologies at a given site. Prolonged SSTs that are 1°C greater than the MMM may induce coral bleaching (Liu et al., 2018).	CRW Version 3.1 Daily Global Satellite Products (1995 – 2020) from NOAA Coral Reef Watch (2020)
14	Overall Climate Score	5 km resolution, No units	A metric for the heat stress experienced at each site, incorporating historic, recent, and estimated future heat stress and trends (Beyer et al., 2018)	Andrello <i>et al.</i> , 2021
15	Historic Climate Stress Score	5 km resolution, No units	A metric for the historic heat stress experienced at each site, from 1985 - 2017 (Beyer et al., 2018)	Andrello <i>et al.</i> , 2021

	Name	Resolution and/or Units	Description and Reasoning	Source
16	Recent Thermal Stress Score	5 km resolution, No units	A metric representing the more recent thermal heat stress experienced at each site from the two previous warm seasons, specifically 1 Jan 2015 – 31 Dec 2016 in the northern hemisphere and 24 April 2015 – 24 April 2017 in the southern hemisphere (Beyer <i>et al.</i> , 2018).	Andrello <i>et al.</i> , 2021
17	SST _{sd}	5 km resolution, expressed in °C	The standard deviation of SST represents the amount that sea surface temperatures.	CRW Version 3.1 Daily Global Satellite Products (1995 – 2020) from NOAA Coral Reef Watch (2020)
18	SST _{skew}	5 km resolution, expressed in °C	The skewness of SST indicates whether the frequency of daily temperatures are normally distributed or skewed towards lower or higher temperature values.	CRW Version 3.1 Daily Global Satellite Products (1995 – 2020) from NOAA Coral Reef Watch (2020)
Human Disturbance	<i>Scientists use macroalgae as a metric for estimating reef health and may assume that coral reefs with high macroalgae percent cover are degraded (Littler and Littler, 2007). We collected a wide range of variables representing several aspects of human disturbance on coral reefs to test this assumption and whether macroalgae percent cover is useful as an indication of coral reef ecosystem health.</i>			
19	Cumulative Human Impact Score	5 km resolution, No units	An estimate of cumulative human impacts on coral reefs, including small scale fishing pressure, coastal population, industrial development, tourism, and two types of water pollution (sedimentation and nitrogen from agriculture).	Andrello <i>et al.</i> , 2021

	Name	Resolution and/or Units	Description and Reasoning	Source
20	Distance to Market	N/A; expressed in km	The distance between each site and the nearest population center, where smaller distances represent low human disturbance and vice versa. This metric captures disturbances associated with nearby populations (such as fishing and eutrophication) but does not account for population size or density.	Yeager et al., 2017
21	Market Gravity	10 km grid cells; expressed as the number of people / (travel time to nearest market in hours) ²	The population of a major market divided by the squared travel time between a reef site and market, representing fishing pressure (Cinner et al., 2018). Fishing pressure can increase herbivory on coral reefs, which may increase macroalgae percent cover.	Andrello et al., 2021
22	HII-100	1 km ² cells aggregated from 1995 – 2004	The aggregated global Human Influence Index within a 100-km radius around each site. HII incorporates population density, land use and infrastructure, and human aspects (including coastlines, roads, railroads, and rivers), which are known to predict local human impacts on coral reefs (Baumann et al., 2022).	Global Human Influence Index v2 (1995-2004) from the NASA Socioeconomic Data and Applications Center, downloaded from Baumann et al. (2022)
23	HII-10	1 km ² cells aggregated from 1995 – 2004	The aggregated global Human Influence Index within a 10-km radius around each site.	Global Human Influence Index v2 (1995-2004) from the NASA Socioeconomic Data and Applications Center, downloaded from Baumann et al. (2022)

	Name	Resolution and/or Units	Description and Reasoning	Source
24	HII-25	1 km ² cells aggregated from 1995 – 2004	The aggregated global Human Influence Index within a 25-km radius around each site.	Global Human Influence Index v2 (1995-2004) from the NASA Socioeconomic Data and Applications Center, downloaded from Baumann et al. (2022)
25	HII-50	1 km ² cells aggregated from 1995 – 2004	The aggregated global Human Influence Index within a 50-km radius around each site.	Global Human Influence Index v2 (1995-2004) from the NASA Socioeconomic Data and Applications Center, downloaded from Baumann et al. (2022)
26	HII-70	1 km ² cells aggregated from 1995 – 2004	The aggregated global Human Influence Index within a 70-km radius around each site.	Global Human Influence Index v2 (1995-2004) from the NASA Socioeconomic Data and Applications Center, downloaded from Baumann et al. (2022)
27	Population density	0.25 km ² grid cell resolution, Number of people within a 20-km radius of each site per 1,256 km ²	As human population densities increase, associated threats, including coastal development, nutrient pollution, and fishing pressure, may also increase. A 20-km radius represents the distance travelled by most subsistence fishers (Clark et al., 2002, Chuenpagdee et al., 2006) and the scale at which land-use change has the largest impact on nutrient loading (Yeager et al., 2017).	Yeager <i>et al.</i> , 2017

	Name	Resolution and/or Units	Description and Reasoning	Source
28	Population density	0.25 km ² grid cell resolution, Number of people within a 50-km radius of each site per 7,850 km ²	A 50-km radius represents the upper limit of small-scale or semi-commercial coastal fisheries (Chuenpagdee et al., 2006), and watershed-scale impacts of nutrient loading and sedimentation (Delvin and Brodie, 2005).	Yeager <i>et al.</i> , 2017
29	Land area-15	0.25 km ² grid cell resolution, 15km radius, expressed in km ²	Land area within a 15-km radius of each site. Nutrient inputs from land-derived sources are commonly detectable within primary producers up to 15 km from shore (Lapointe and Clark 1992).	Yeager <i>et al.</i> , 2017
30	Land area-50	0.25 km ² grid cell resolution, 50 km radius, expressed in km ²	Land area within a 50 km radius of each site. Rivers can transport nutrients from land-use activities 50 km or more from the coast	Yeager <i>et al.</i> , 2017
31	Scaled mean NDVI	1 km radius (3.14 km ² area) resolution, no units	The mean Normalized Difference Vegetation Index of land within a 1-km radius circle around each site, and an indication of nearby development. We calculated the NDVI values using LandSat8 data from the United States Geological Survey. We scaled mean NDVI values for each site to between 0 and 1 within each of the contributed datasets to account for climate-driven variation in vegetation across sites and regions. Coastal development can influence water quality by increasing the amount of sediment and nutrients from land.	Please see Cannon et. al. (2019, 2021) for detailed methods

	Name	Resolution and/or Units	Description and Reasoning	Source
32	Number of Ports	5 km resolution, no units	A proxy for pressures from industrial development, including dredging. Includes all ports within 5km ² as this is the maximum likely distance of dredging impacts (Wenger <i>et al.</i> , 2020).	Andrelo et al., 2021
33	Nutrients from agriculture	5 km resolution, no units	An estimate of nitrogen pollution produced via a settlement plume model. This metric will underestimate nitrogen pollution because it does not include eutrophication caused by wastewater discharge (Andrelo et al., 2021).	Nitrogen delivery to coral reefs from agriculture, from Andrelo et al (2021)
34	Population (coastal)	5 km resolution, no units	An estimate of the number of people living within a 5 km buffer of each coral reef cell using a global data layer of 2020 human populations.	Andrelo et al., 2021
35	Tourism	5 km resolution, no units	The estimated number of tourist trip equivalents for global coral reefs using tourism activity from 2005 – 2012. Intensive tourist use can cause physical injury to corals, sediment-associated tissue necrosis, and disease (Lamb <i>et al.</i> , 2014), all of which may increase macroalgae percent cover.	Andrelo et al., 2021
36	Sedimentation	5 km resolution, expressed as tons of sediment per km ²	Estimated sediment exposure as predicted by a sediment plume model described in Andrelo et al. (2021).	Andrelo et al., 2021
Methodology & Site Characteristics	<i>We included methodology and site characteristics here because they may account for any sampling noise associated with the data, for example from methodological differences or geographic bias. Site features such as the type of habitat and depth may also influence the benthic communities present at each site (Magris et al., 2016).</i>			

	Name	Resolution and/or Units	Description and Reasoning	Source
37	Contributor	Categorical	The person(s) contributing a dataset to the analysis. We included this to account for any methodological differences driving sampling noise associated with the data.	Contributors
38	Depth	Meters	Depth of the ecological survey in meters. Depth influences the amount of light available for photosynthesis, local temperature, and exposure to wind and waves.	Contributors
39	Habitat	Categorical	Whether the survey site was located on a backreef, reef crest, reef flat, reef slope, or another habitat (such as terrace reefs and those in a channel). Each habitat type has different physical features that influence exposure to drivers of benthic community compositions. For example, sites on a reef crest experience higher wind and wave exposure than those on a backreef.	Contributors
40	Management	Categorical	Whether sites were open to fishing with no restrictions (open access), fishing was allowed but with restrictions (restricted access) or fishing was banned (no access) (Darling <i>et al.</i> , 2019). Fishing pressure can decrease herbivory on coral reefs and might trigger increases in some taxa of macroalgae.	Contributors
41	Methods	Categorical	Whether the survey used a point intercept transect, line intercept transect, or photo quadrat method. Methodological differences may account for potential noise in the dataset (Darling <i>et al.</i> , 2019).	Contributors

	Name	Resolution and/or Units	Description and Reasoning	Source
Net Primary Productivity	<i>Net primary productivity (NPP) on coral reefs is determined by light, water temperature, and nutrient availability (Yeager et al., 2017). Many taxa of macroalgae may be nutrient-limited (Littler and Littler, 2007) and increasing nutrient availability (represented by NPP or chl_a) may drive increasing percent cover of macroalgae.</i>			
42	Chl _a CV	4 km ² monthly resolution, no units	Chlorophyll-a concentration (chl _a) is widely used to indicate net primary productivity (Siegel et al., 2005). The coefficient of variation (CV) represents the variation in NPP.	MODIS-Ocean Color Data from NASA (2014)
43	Kurtosis of chl _a	4 km ² monthly resolution, no units	The distribution of chl _a concentration by frequency at each site, with positive values indicating a steeper distribution than normal, and negative values indicating a broader distribution than normal.	MODIS-Ocean Color Data from NASA (2014)
44	Mean chl _a	4 km ² monthly resolution, Mg m ⁻³	The average monthly chl _a value at each site.	MODIS-Ocean Color Data from NASA (2014)
45	Chl _a SD	4 km ² monthly resolution, no units	The standard deviation of chl _a representing the amount of variation in chl _a concentration experienced at each site.	MODIS-Ocean Color Data from NASA (2014)
46	Skewness of Chl _a	4 km ² monthly resolution, no units	The skewness of chl _a indicates whether the frequency of daily temperatures are normally distributed or skewed towards lower or higher temperature values.	MODIS-Ocean Color Data from NASA (2014)
47	Mean Chl _a for the year of survey	4 km ² monthly resolution, Mg m ⁻³	The average chl _a for the year of the survey.	MODIS-Ocean Color Data from NASA (2014)
48	NPP _{max}	mg C m ⁻² day ⁻¹	Mean annual maximum net primary productivity of carbon	Yeager et al., 2017
49	NPP _{mean}	mg C m ⁻² day ⁻¹	Overall mean net primary productivity of carbon	Yeager et al., 2017

	Name	Resolution and/or Units	Description and Reasoning	Source
50	NPP _{min}	mg C m ⁻² day ⁻¹	Mean annual minimum net primary productivity of carbon	Yeager <i>et al.</i> , 2017
51	NPP _{SD}	mg C m ⁻² day ⁻¹	Intra-annual standard deviation of the net primary productivity of carbon	Yeager <i>et al.</i> , 2017
Seasonality	<i>Several studies have found that macroalgae communities can be seasonal in nature, with blooms occurring at regular annual intervals, and that light and/or ocean temperatures may drive seasonal growth cycles (Fulton et al., 2014; Brown et al., 2020).</i>			
52	Mean SST of survey month	5 km	The average sea surface temperature of the month when the surveys were conducted.	CRW Version 3.1 Daily Global Satellite Products (1995 – 2020) from NOAA Coral Reef Watch (2018)
53	Mean PAR of survey month	4 km	Average photosynthetically available radiation of the survey month.	MODIS-Ocean Color Data from NASA (2014)
54	Rank of survey month by SST	Month	The month of the survey corrected by the months ranked from hottest to coldest.	CRW Version 3.1 Daily Global Satellite Products (1995 – 2020) from NOAA Coral Reef Watch (2018)
Storms and Cyclones	<i>Tropical storms and cyclones drive strong wind and waves that have the potential to break corals. They may also cause high storm surges that wash debris from land onto reefs, causing further damage. In some cases, macroalgae cover on coral reefs has increased immediately following storms that caused severe damage to corals.</i>			

	Name	Resolution and/or Units	Description and Reasoning	Source
55	Average number of storms	Annual	The average number of total storms per year passing within 100 km of each site. 100 km is the estimated maximum distance at which storms can cause damage to coral reefs (Fabricius <i>et al.</i> , 2008).	Storm tracks for all storms after 1989 from NOAA National Centers for Environmental Information (NCEI) International Best Track Archive for Climate Stewardship (IBTrACS) (Knapp <i>et al.</i> , 2018) and extracted in ArcMap.
56	Number of storms (class tropical storms or stronger)	Total number of tropical storms or stronger passing within 100 km of each site in 10 years	The total number of tropical storms or greater passing within 100 km of each site as defined by Saffir-Simpson Hurricane Scale, in the 10 years preceding each survey.	Storm tracks were downloaded from NOAA NCEI IBTrACS (Knapp <i>et al.</i> , 2018) and extracted in ArcMap.
57	Number of storms of type 3 or stronger	Total number of Type 3 storms or stronger passing within 100 km of each site in 10 years	The total number of storms of Type 3 or greater passing within 100 km of each site as defined by the Saffir Simpson Hurricane Scale, in the 10 years preceding each survey.	Storm tracks were downloaded from NOAA NCEI IBTrACS (Knapp <i>et al.</i> , 2018) and extracted in ArcMap.
58	Number of tropical storms or stronger	Total number of tropical storms or stronger passing within 100 km of each site in 5 years	The total number of tropical storms or greater passing within 100 km of each site as defined by Saffir-Simpson Hurricane Scale, in the 5 years preceding each survey.	Storm tracks were downloaded from NOAA NCEI IBTrACS (Knapp <i>et al.</i> , 2018) and extracted in ArcMap.

	Name	Resolution and/or Units	Description and Reasoning	Source
59	Number of storms of type 3 or stronger	Total number of Type 3 storms or stronger passing within 100 km of each site in 10 years	The total number of storms of Type 3 or greater passing within 100 km of each site as defined by the Saffir Simpson Hurricane Scale, in the 5 years preceding each survey.	Storm tracks were downloaded from NOAA NCEI IBTrACS (Knapp et al., 2018) and extracted in ArcMap.
60	Cyclone Score	5 km resolution, No units	A metric for cyclone activity from 1985 – 2014 incorporating three damaging aspects of cyclones for coral reefs: average annual days of exposure, the maximum annual number of days of exposure to cyclones (winds of gale force or higher), and the inverse of the return time interval of at least one day of exposure per year (Beyer et al., 2018).	Andrello <i>et al.</i> , 2021
Wind and wave exposure		<i>Wind and wave exposure can drive benthic community compositions by selecting for taxa that can withstand the local environment (Page-Albins et al., 2012).</i>		
61	Aspect	Decimal degrees	The direction from each site to the greatest depth in the surrounding area. Because there were too many sites to measure the direction each site faced manually, we assumed that greater depths indicated the open ocean and used the direction between the site and the greatest depth in the bathymetry layer in ArcGIS. We randomly spot-checked the sites manually to ensure accuracy.	Calculated in ArcGIS.

	Name	Resolution and/or Units	Description and Reasoning	Source
62	Mean wave energy	3-hour temporal resolution for a span of 31 years (1979-2009). Expressed in kW m^{-1}	Wave energy flux (the power transmitted per unit of wavefront width), overall mean.	Yeager <i>et al.</i> , 2017
63	Mean annual wind direction	Decimal degrees	The prevailing wind direction at each site.	Prevailing wind direction was calculated with data from NCDC Blended Sea Winds (Zhang, Reynolds and Bates, 2006) using the methods described in Cannon et al. (2021)
64	Wind and Wave Exposure	Decimal degrees	The angle of each site (using the Aspect) to the prevailing wind.	Calculated with data from NCDC Blended Sea Winds (Zhang, Reynolds and Bates, 2006) using the methods described in Cannon et al. (2021)

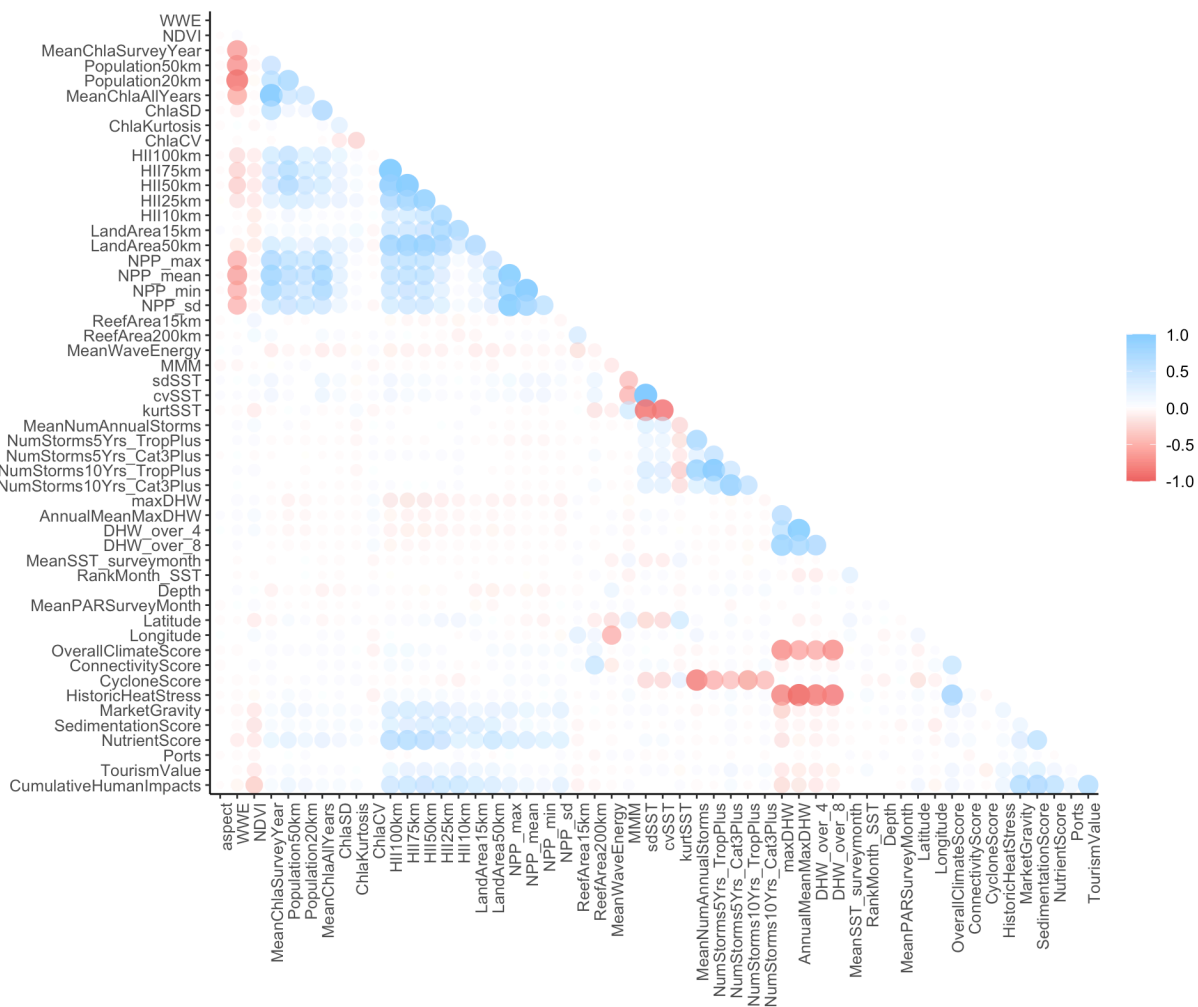
C.2 Algae genera identified in surveys across the Indian and Pacific Oceans.

	Code	Genus	Divisions
1	ACI	<i>Actinotrichia</i>	Red
2	ACN	<i>Acanthopora</i>	Red
3	AMA	<i>Amansia</i>	Red
4	AMP	<i>Amphiroa</i>	Red
5	ASP	<i>Asparagopsis</i>	Red
6	AVR	<i>Avrainvillea</i>	Green
7	BMA	Brown macroalgae (Other)	Brown
8	BOE	<i>Boergesenia</i>	Green
9	BOO	<i>Boodlea</i>	Green
10	BRY	<i>Bryopsis</i>	Green
11	CAL	<i>Callophyllis</i>	Red
12	CAN	<i>Canistrocarpus</i>	Brown
13	CER	<i>Ceratodictyon</i>	Red
14	CHE	<i>Cheilosporum</i>	Red
15	CHL	<i>Chlorodesmis</i>	Green
16	CHN	<i>Chondrus</i>	Red
17	CPY	<i>Chondrophycus</i>	Red
18	CHP	<i>Champia</i>	Red
19	CLA	<i>Claudea</i>	Red
20	CLD	<i>Cladophora</i>	Green
21	CLP	<i>Caulerpa</i>	Green
22	CLS	<i>Cladophoropsis</i>	Green
23	COD	<i>Codium</i>	Green
24	COL	<i>Colpomenia</i>	Brown
25	COR	<i>Corallina</i>	Red
26	CRP	<i>Carpopeltis</i>	Red
27	CYS	<i>Cystoseiria</i>	Brown
28	DCH	<i>Dichotomaria</i>	Red
29	DCT	<i>Dictosphaeria</i>	Green
30	DEL	<i>Delisea</i>	Red
31	DER	<i>Derbesia</i>	Green
32	DIC	<i>Dictyota</i>	Brown
33	DIG	<i>Digenea</i>	Red
34	DIH	<i>Dichotomaria</i>	Red
35	DIT	<i>Distromium</i>	Brown
36	DPT	<i>Dictyopteris</i>	Brown
37	DUD	<i>Dudresnaya</i>	Red
38	ECK	<i>Ecklonia</i>	Brown
39	ECP	<i>Eckloniopsis</i>	Brown
40	END	<i>Endosiphonia</i>	Red
41	EUC	<i>Eucheuma</i>	Red

42	GEL	<i>Gelidium</i>	Red
43	GIB	<i>Gibsmithia</i>	Red
44	GIG	<i>Gigartina</i>	Red
45	GLA	<i>Galaxaura</i>	Red
46	GMA	Green macroalgae (other)	Green
47	GRA	<i>Gracilaria</i>	Red
48	GRT	<i>Grateloupia</i>	Red
49	HA	<i>Halimeda</i>	Green
50	HEM	<i>Helminthocladia</i>	Red
51	HET	<i>Heterosiphonia</i>	Red
52	HLA	<i>Halymenia</i>	Red
53	HRM	<i>Hormophysa</i>	Brown
54	HYP	<i>Hypnea</i>	Red
55	JAN	<i>Jania</i>	Red
56	KAL	<i>Kallymenia</i>	Red
57	LAU	<i>Laurencia</i>	Red
58	LIA	<i>Liagora</i>	Red
59	LIP	<i>Lithophyllum</i>	Red
60	LPA	<i>Lobophora</i>	Brown
61	MA	Macroalgae (fleshy) - other	
62	MAR	<i>Martensia</i>	Red
63	MEI	<i>Meristotheca</i>	Red
64	MIC	<i>Microdictyon</i>	Green
65	NEO	<i>Neomeris</i>	Green
66	NRM	<i>Neurymenia</i>	Red
67	PAD	<i>Padina</i>	Brown
68	PAL	<i>Palisada</i>	Red
69	PEN	<i>Penicillus</i>	Green
70	PLO	<i>Plocamium</i>	Red
71	POL	<i>Polysiphonia</i>	Red
72	POR	<i>Portieria</i>	Red
73	PRE	<i>Predaea</i>	Red
74	PRI	<i>Prionitis</i>	Red
75	PRT	<i>Portieria</i>	Red
76	PTE	<i>Pterocladia</i>	Red
77	PTI	<i>Ptilophora</i>	Red
78	PYS	<i>Peyssonellia</i>	Red
79	RHI	<i>Rhipidosiphon</i>	Green
80	RHO	<i>Rhodopeltis</i>	Red
81	RHY	<i>Rhodymenia</i>	Red
82	RMA	Red macroalgae (Other)	Red
83	SPT	<i>Spatoglossum</i>	Brown
84	SPY	<i>Spyridia</i>	Red

85	SAR	<i>Sargassopsis</i>	Brown
86	SRG	<i>Sargassum</i>	Brown
87	SPO	<i>Sporochnus</i>	Brown
88	STP	<i>Styopodium</i>	Brown
89	TIT	<i>Titanophora</i>	Red
90	TOL	<i>Tolypiocladia</i>	Red
91	TRB	<i>Turbinaria (algae)</i>	Brown
92	TRI	<i>Tricleocarpa</i>	Red
93	TYD	<i>Tydemanina</i>	Green
94	UDO	<i>Udotea</i>	Green
95	ULV	<i>Ulva</i>	Green
96	UMB	<i>Umbraulva</i>	Green
97	VAN	<i>Vanvoorstia</i>	Red
98	VEN	<i>Ventricaria</i>	Green
99	ZEL	<i>Zellera</i>	Red
100	ZON	<i>Zonaria</i>	Brown

C.3 Results from correlation analysis of variables.



C.4 Variable Inflation Factors (VIF) used to exclude variables before running

PERMANOVAs.

All Sites	
Variable	VIF
Contributor	305.18
Latitude	22.64
Month (ranked by SST)	4.98
Storms within 5 years (Type 3 Plus)	3.95
maxDHW	8.44
Cumulative human impact	8.71
Habitat	4.15
Nutrients (agriculture)	5.00
Mean wave energy	4.31
Longitude	10.93
Cyclone score	11.51
NPP _{SD}	7.16
Climate score	16.54
SST _{SD}	7.16
Market gravity	13.34
MMM	2.15
Depth	2.65
Reef area (200 km)	3.29
SST (kurtosis)	67.29
Connectivity score	11.86
Management	6.77
NDVI	1.96
Mean PAR (survey month)	5.00
WWE	457.30
Aspect	3.12
Chl _a (kurtosis)	1.87

Realm 9. Mid-tropical North Pacific	
Variable	VIF
Month (ranked by SST)	39.86
sdSST	1399.22
Mean PAR (survey month)	17.98
Cyclone score	27.09
Mean wave energy	53.88
MMM	87.97
Connectivity score	12.84
Contributor	2243.78
Latitude	12401.24
SST (kurtosis)	948.99
Storms within 5 years (type 3 plus)	2.97
Nutrients (agriculture)	7.98

Realm 13. Indo-Pacific seas & Indian Ocean	
Variable	VIF
Contributor	323.15
SST _{SD}	57.29
Month (ranked by SST)	13.86
Longitude	414.91
Cumulative human impacts	12.36
Chl _a (kurtosis)	2.12
Latitude	89.97
Reef area (200 km)	7.31
Depth	1.98
Market gravity	20.75
Management	10.20
NPP _{SD}	14.22
NDVI	1.49
Mean SST (month of survey)	2.09
Reef area (15km)	3.61
Nutrients (agriculture)	11.63
SST (kurtosis)	44.96
Mean wave energy	3.31
Climate score (overall)	41.52
Connectivity score	15.41

Realm 16. Coral Sea	
Variable	VIF
Contributor (max)	19113.93
Human population (20 km)	1535.29
MaxDHW	11.29
Nutrients (agriculture)	4.79
NDVI	4.42
Connectivity score	38.02
Climate score (overall)	35.05
Latitude	50.24
Chl _a (kurtosis)	5.67
Mean wave energy	4.42
Storms within 5 years (Type 3 plus)	1.49
Mean PAR (survey month)	15.71
Month (ranked by SST)	553.32
Mean SST (survey month)	104.94
Reef area (200 km)	13.76
Management	10.09
Cyclone score	16.87
NPP _{SD}	1.99

Realm 17. Mid South Tropical Pacific	
Variable	VIF
Contributor (max)	19113.93
Cyclone score	109.21
Management	3.79
Aspect	1.26
Depth	1.40
Market Gravity	14.57
NDVI	1.65
Mean PAR (survey month)	3.83
Latitude	1356.94
MaxDHW	99.48

Realm 20. Offshore West Pacific	
Variable	VIF
Contributor	662.17
Month (ranked by SST)	6177.86
Longitude	513.55
MaxDHW	86.85
Mean SST (survey month)	3401.77
Reef area (200 km)	901.62
Connectivity score	163.17
NDVI	5.86
WWE	5.34
Aspect	5.39
Market gravity	357.29
Mean wave energy	3.62
Storms within 5 years (Type 3 Plus)	161.77
SST _{SD}	1443.77
MMM	116.86
Latitude	8939.16
SST (kurtosis)	5442.84
Cumulative human impacts	46.51
Habitat	11.85
Human population (20 km)	22.96
Mean PAR (survey month)	39.86
Cyclone score	1808.99
Climate score (overall)	1476.10

Realm 29. NW Pacific	
Variable	VIF
Contributor	60.62
Depth	10.38
Chl_a (kurtosis)	4.38
Connectivity score	11.38
Nutrients (agriculture)	3.27
Management	8.51
WWE	1.91
Reef area (15 km)	17.82

C.5 SIMPER results

Realm 16 vs Realm 13

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.431	0.313	1.377	8.928	7.231	0.542	0.001	***
MIC	0.068	0.190	0.356	0.131	3.148	0.627	0.782	
SRG	0.060	0.169	0.355	2.139	1.054	0.702	0.001	***
LPA	0.055	0.139	0.393	0.751	0.639	0.771	1.000	
CLP	0.035	0.105	0.332	0.953	0.181	0.815	0.542	
PAD	0.035	0.108	0.321	0.261	0.457	0.858	0.991	
TRB	0.021	0.080	0.260	0.026	0.556	0.884	1.000	
CHL	0.017	0.078	0.218	0.191	0.029	0.905	0.149	
DIC	0.013	0.050	0.267	0.146	0.222	0.922	1.000	
DCT	0.012	0.049	0.248	0.062	0.243	0.937	0.792	
GLA	0.010	0.075	0.128	0.213	0.044	0.949	0.780	
ASP	0.009	0.058	0.146	0.018	0.134	0.960	0.975	
HYP	0.008	0.049	0.154	0.053	0.177	0.969	0.177	
LAU	0.007	0.031	0.221	0.287	0.006	0.978	0.005	**
UDO	0.005	0.035	0.132	0.162	0.000	0.984	0.001	***
DPT	0.003	0.018	0.152	0.155	0.000	0.987	0.999	
HLA	0.003	0.020	0.135	0.011	0.048	0.991	0.709	
CLS	0.002	0.017	0.125	0.000	0.073	0.993	0.532	
CER	0.002	0.014	0.150	0.000	0.063	0.996	0.999	
VAL	0.001	0.020	0.071	0.000	0.010	0.998	0.842	
NEO	0.001	0.015	0.070	0.000	0.010	0.999	0.994	
BRY	0.001	0.008	0.108	0.000	0.027	1.000	0.843	

Realm 16 vs Realm 19

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.301	0.315	0.958	8.928	1.000	0.328	0.925	
LPA	0.276	0.363	0.761	0.751	19.333	0.629	0.001	***
CLP	0.161	0.285	0.565	0.953	6.296	0.804	0.002	**
DIC	0.093	0.226	0.409	0.146	0.889	0.905	0.024	*
SRG	0.034	0.127	0.271	2.139	0.000	0.942	0.381	
PAD	0.013	0.067	0.188	0.261	0.000	0.956	0.997	
CHL	0.011	0.055	0.205	0.191	0.000	0.968	0.472	
LAU	0.006	0.029	0.208	0.287	0.000	0.975	0.152	
MIC	0.006	0.055	0.102	0.131	0.000	0.981	1.000	
GLA	0.005	0.059	0.083	0.213	0.000	0.986	0.737	
UDO	0.004	0.029	0.135	0.162	0.000	0.990	0.086	.
TRB	0.003	0.023	0.126	0.026	0.000	0.993	1.000	
DPT	0.002	0.017	0.147	0.155	0.000	0.996	0.718	
DCT	0.001	0.018	0.076	0.062	0.000	0.998	1.000	
HYP	0.001	0.007	0.152	0.053	0.000	0.999	0.951	
HLA	0.001	0.010	0.067	0.011	0.000	1.000	0.930	
ASP	0.000	0.004	0.091	0.018	0.000	1.000	0.998	

Contrast: 16_9

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p
HA	0.454	0.310	1.464	8.928	3.736	0.564	0.001 ***
PAD	0.078	0.204	0.384	0.261	0.833	0.661	0.002 **
LPA	0.074	0.157	0.474	0.751	0.600	0.753	0.774
SRG	0.043	0.148	0.288	2.139	0.000	0.806	0.451
MIC	0.036	0.128	0.281	0.131	0.612	0.851	0.994
CLP	0.033	0.109	0.302	0.953	0.027	0.891	0.567
DIC	0.026	0.097	0.264	0.146	0.258	0.923	0.754
CHL	0.017	0.073	0.229	0.191	0.000	0.944	0.328
TRB	0.008	0.042	0.196	0.026	0.071	0.954	1.000
LAU	0.008	0.034	0.223	0.287	0.000	0.963	0.106
GLA	0.006	0.070	0.090	0.213	0.000	0.971	0.843
NEO	0.006	0.036	0.154	0.000	0.095	0.978	0.113
ASP	0.005	0.031	0.171	0.018	0.095	0.984	0.940
UDO	0.005	0.037	0.142	0.162	0.000	0.991	0.090 .
DPT	0.003	0.020	0.155	0.155	0.000	0.995	0.875
DCT	0.002	0.022	0.083	0.062	0.000	0.997	1.000
HYP	0.002	0.009	0.163	0.053	0.000	0.999	0.986
HLA	0.001	0.014	0.071	0.011	0.000	1.000	0.949

Contrast: 16_17

Column1	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.403	0.312	1.290	8.928	3.721	0.477	0.005	**
LPA	0.107	0.187	0.570	0.751	2.115	0.604	0.005	**
TRB	0.056	0.136	0.407	0.026	1.202	0.669	0.001	***
DIC	0.054	0.141	0.386	0.146	1.080	0.734	0.001	***
SRG	0.045	0.144	0.316	2.139	0.153	0.787	0.346	
MIC	0.041	0.157	0.257	0.131	0.607	0.835	0.999	
CLP	0.039	0.119	0.329	0.953	0.129	0.882	0.257	
CHL	0.023	0.097	0.242	0.191	0.122	0.909	0.003	**
PAD	0.023	0.093	0.242	0.261	0.158	0.936	1.000	
ASP	0.019	0.094	0.198	0.018	0.229	0.958	0.053	.
GLA	0.015	0.082	0.187	0.213	0.243	0.976	0.135	
LAU	0.007	0.032	0.219	0.287	0.000	0.985	0.059	.
UDO	0.005	0.037	0.132	0.162	0.000	0.991	0.038	*
DPT	0.003	0.019	0.153	0.155	0.000	0.994	0.967	
DCT	0.003	0.024	0.108	0.062	0.021	0.997	1.000	
HYP	0.001	0.008	0.160	0.053	0.000	0.999	0.999	
HLA	0.001	0.017	0.060	0.011	0.000	1.000	0.993	

Contrast: 16_20

Column1	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.372	0.330	1.127	8.928	1.528	0.415	0.448	
LPA	0.073	0.180	0.406	0.751	0.679	0.496	0.855	
CLP	0.070	0.145	0.481	0.953	1.437	0.574	0.001	***
PAD	0.066	0.150	0.440	0.261	1.780	0.647	0.006	**
SRG	0.056	0.166	0.338	2.139	0.344	0.710	0.065	.
MIC	0.047	0.159	0.298	0.131	1.548	0.762	0.973	
CHL	0.032	0.096	0.332	0.191	0.583	0.798	0.001	***
CER	0.028	0.116	0.243	0.000	0.996	0.829	0.001	***
TRB	0.027	0.082	0.325	0.026	0.301	0.859	0.898	
DPT	0.026	0.088	0.292	0.155	1.232	0.888	0.001	***
DCT	0.023	0.061	0.374	0.062	0.989	0.913	0.008	**
AMA	0.015	0.070	0.210	0.000	0.876	0.929	0.001	***
DIC	0.013	0.064	0.208	0.146	0.213	0.944	1.000	
GLA	0.009	0.079	0.118	0.213	0.019	0.955	0.647	
LAU	0.008	0.035	0.225	0.287	0.004	0.963	0.031	*
HLA	0.006	0.030	0.215	0.011	0.098	0.971	0.007	**
NEO	0.006	0.033	0.196	0.000	0.370	0.978	0.016	*
UDO	0.005	0.040	0.126	0.162	0.000	0.983	0.088	.
VAL	0.004	0.025	0.166	0.000	0.333	0.988	0.036	*
VEN	0.003	0.023	0.123	0.000	0.212	0.991	0.009	**
BRY	0.002	0.019	0.130	0.000	0.130	0.994	0.040	*
CLS	0.002	0.016	0.134	0.000	0.159	0.996	0.449	
HYP	0.002	0.011	0.166	0.053	0.001	0.998	0.984	
ASP	0.002	0.009	0.183	0.018	0.029	1.000	0.999	

Contrast 16
vs 19

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.413	0.376	1.100	8.928	0.633	0.439	0.035	*
LPA	0.160	0.233	0.686	0.751	2.017	0.609	0.001	***
NRM	0.055	0.135	0.410	0.000	0.933	0.668	0.001	***
CLP	0.046	0.148	0.308	0.953	0.129	0.716	0.151	
SRG	0.046	0.155	0.294	2.139	0.005	0.764	0.378	
PAD	0.043	0.158	0.270	0.261	0.408	0.809	0.499	
GLA	0.032	0.100	0.319	0.213	0.179	0.843	0.010	**
SPT	0.029	0.098	0.293	0.000	0.582	0.874	0.001	***
CHL	0.025	0.116	0.220	0.191	0.002	0.901	0.066	.
LAU	0.021	0.060	0.349	0.287	0.141	0.923	0.001	***
AMA	0.019	0.075	0.248	0.000	0.401	0.943	0.008	**
TRB	0.011	0.075	0.143	0.026	0.001	0.954	1.000	
DPT	0.009	0.056	0.167	0.155	0.045	0.964	0.199	
MIC	0.009	0.079	0.112	0.131	0.000	0.973	1.000	
DIC	0.007	0.032	0.223	0.146	0.038	0.981	1.000	
HYP	0.007	0.033	0.211	0.053	0.057	0.989	0.294	
UDO	0.006	0.047	0.129	0.162	0.003	0.995	0.072	.
DCT	0.002	0.023	0.085	0.062	0.000	0.997	1.000	
HLA	0.002	0.024	0.062	0.011	0.000	0.999	0.786	
VAL	0.001	0.005	0.116	0.000	0.004	0.999	0.831	
ASP	0.001	0.006	0.095	0.018	0.000	1.000	1.000	
NEO	0.000	0.001	0.220	0.000	0.003	1.000	0.989	

Contrast: 13_19

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p
LPA	0.271	0.359	0.754	0.639	19.333	0.302	0.001 ***
HA	0.256	0.262	0.978	7.231	1.000	0.587	0.991
CLP	0.148	0.278	0.533	0.181	6.296	0.752	0.003 **
DIC	0.086	0.198	0.434	0.222	0.889	0.848	0.035 *
MIC	0.054	0.168	0.325	3.148	0.000	0.909	0.474
SRG	0.020	0.100	0.203	1.054	0.000	0.931	0.806
PAD	0.016	0.065	0.251	0.457	0.000	0.949	0.976
TRB	0.014	0.060	0.227	0.556	0.000	0.965	0.968
DCT	0.009	0.037	0.232	0.243	0.000	0.974	0.583
ASP	0.006	0.045	0.141	0.134	0.000	0.981	0.671
HYP	0.005	0.041	0.123	0.177	0.000	0.987	0.261
GLA	0.003	0.030	0.098	0.044	0.000	0.990	0.962
CLS	0.002	0.015	0.120	0.073	0.000	0.992	0.146
CER	0.002	0.012	0.146	0.063	0.000	0.994	0.930
CHL	0.002	0.013	0.124	0.029	0.000	0.996	1.000
HLA	0.002	0.011	0.141	0.048	0.000	0.997	0.602
VAL	0.001	0.009	0.090	0.010	0.000	0.998	0.663
BRY	0.001	0.007	0.104	0.027	0.000	0.999	0.326
NEO	0.001	0.010	0.071	0.010	0.000	1.000	0.884
LAU	0.000	0.003	0.052	0.006	0.000	1.000	1.000

Contrast: 13_9

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p
HA	0.368	0.272	1.353	7.231	3.736	0.492	0.582
MIC	0.093	0.212	0.439	3.148	0.612	0.617	0.091 .
PAD	0.077	0.186	0.415	0.457	0.833	0.720	0.004 **
LPA	0.068	0.148	0.457	0.639	0.600	0.810	0.919
DIC	0.031	0.093	0.329	0.222	0.258	0.851	0.504
SRG	0.026	0.118	0.220	1.054	0.000	0.886	0.948
TRB	0.021	0.075	0.280	0.556	0.071	0.914	0.988
ASP	0.013	0.063	0.213	0.134	0.095	0.932	0.400
DCT	0.012	0.045	0.257	0.243	0.000	0.947	0.650
CLP	0.011	0.036	0.295	0.181	0.027	0.962	1.000
HYP	0.007	0.050	0.136	0.177	0.000	0.971	0.287
NEO	0.006	0.036	0.176	0.010	0.095	0.979	0.060 .
GLA	0.004	0.038	0.112	0.044	0.000	0.985	0.982
CHL	0.002	0.019	0.125	0.029	0.000	0.988	1.000
CLS	0.002	0.018	0.130	0.073	0.000	0.991	0.384
CER	0.002	0.014	0.159	0.063	0.000	0.994	0.968
HLA	0.002	0.013	0.153	0.048	0.000	0.997	0.761
VAL	0.001	0.014	0.092	0.010	0.000	0.998	0.655
BRY	0.001	0.009	0.113	0.027	0.000	1.000	0.487
LAU	0.000	0.004	0.057	0.006	0.000	1.000	1.000

Contrast: 13_17

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.340	0.279	1.222	7.231	3.721	0.427	1.000	
LPA	0.097	0.174	0.556	0.639	2.115	0.548	0.060	.
MIC	0.094	0.221	0.425	3.148	0.607	0.666	0.007	**
TRB	0.063	0.136	0.461	0.556	1.202	0.745	0.001	***
DIC	0.058	0.135	0.430	0.222	1.080	0.817	0.001	***
SRG	0.029	0.115	0.252	1.054	0.153	0.854	0.979	
PAD	0.025	0.081	0.309	0.457	0.158	0.885	1.000	
ASP	0.025	0.100	0.245	0.134	0.229	0.916	0.001	***
CLP	0.017	0.065	0.258	0.181	0.129	0.937	1.000	
GLA	0.013	0.061	0.219	0.044	0.243	0.953	0.255	
DCT	0.012	0.046	0.256	0.243	0.021	0.968	0.762	
CHL	0.009	0.055	0.164	0.029	0.122	0.979	0.990	
HYP	0.007	0.049	0.134	0.177	0.000	0.988	0.335	
CLS	0.002	0.017	0.128	0.073	0.000	0.990	0.424	
CER	0.002	0.014	0.155	0.063	0.000	0.993	0.990	
HLA	0.002	0.013	0.144	0.048	0.000	0.996	0.907	
VAL	0.001	0.019	0.074	0.010	0.001	0.997	0.750	
NEO	0.001	0.014	0.074	0.010	0.000	0.999	0.964	
BRY	0.001	0.008	0.111	0.027	0.000	1.000	0.684	
LAU	0.000	0.004	0.056	0.006	0.000	1.000	1.000	

Contrast: 13_20

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.326	0.292	1.116	7.231	1.528	0.376	1.000	
MIC	0.099	0.223	0.447	3.148	1.548	0.490	0.014	*
PAD	0.065	0.135	0.483	0.457	1.780	0.566	0.002	**
LPA	0.062	0.162	0.383	0.639	0.679	0.637	0.997	
CLP	0.050	0.108	0.466	0.181	1.437	0.695	0.015	*
SRG	0.039	0.140	0.280	1.054	0.344	0.740	0.620	
TRB	0.034	0.089	0.387	0.556	0.301	0.780	0.480	
DCT	0.030	0.069	0.435	0.243	0.989	0.815	0.001	***
CER	0.030	0.112	0.264	0.063	0.996	0.849	0.001	***
DPT	0.023	0.086	0.269	0.000	1.232	0.876	0.001	***
DIC	0.021	0.077	0.271	0.222	0.213	0.900	0.978	
CHL	0.017	0.048	0.359	0.029	0.583	0.920	0.220	
AMA	0.015	0.069	0.212	0.000	0.876	0.936	0.002	**
ASP	0.010	0.061	0.161	0.134	0.029	0.948	0.762	
NEO	0.007	0.036	0.207	0.010	0.370	0.956	0.002	**
GLA	0.007	0.054	0.132	0.044	0.019	0.965	0.878	
HLA	0.007	0.025	0.273	0.048	0.098	0.973	0.003	**
HYP	0.007	0.050	0.137	0.177	0.001	0.981	0.278	
VAL	0.006	0.033	0.174	0.010	0.333	0.987	0.002	**
CLS	0.004	0.023	0.184	0.073	0.159	0.992	0.035	*
BRY	0.003	0.019	0.168	0.027	0.130	0.996	0.007	**
VEN	0.003	0.023	0.123	0.000	0.212	0.999	0.013	*
LAU	0.001	0.012	0.083	0.006	0.004	1.000	1.000	

Contrast: 13_29

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.405	0.328	1.236	7.231	0.633	0.430	0.042	*
LPA	0.140	0.211	0.667	0.639	2.017	0.579	0.004	**
MIC	0.072	0.204	0.353	3.148	0.000	0.655	0.487	
NRM	0.052	0.127	0.413	0.000	0.933	0.711	0.001	***
PAD	0.042	0.137	0.302	0.457	0.408	0.755	0.570	
SRG	0.028	0.124	0.224	1.054	0.005	0.784	0.852	
SPT	0.027	0.094	0.289	0.000	0.582	0.813	0.001	***
GLA	0.026	0.074	0.349	0.044	0.179	0.841	0.038	*
CLP	0.022	0.093	0.235	0.181	0.129	0.864	0.944	
TRB	0.020	0.083	0.246	0.556	0.001	0.886	0.948	
AMA	0.018	0.072	0.249	0.000	0.401	0.905	0.014	*
DIC	0.018	0.065	0.272	0.222	0.038	0.923	0.968	
DCT	0.014	0.055	0.249	0.243	0.000	0.938	0.421	
HYP	0.013	0.064	0.203	0.177	0.057	0.952	0.053	.
LAU	0.012	0.044	0.272	0.006	0.141	0.965	0.023	*
ASP	0.011	0.072	0.151	0.134	0.000	0.976	0.498	
DPT	0.006	0.045	0.122	0.000	0.045	0.982	0.496	
CHL	0.004	0.039	0.105	0.029	0.002	0.986	0.999	
VAL	0.003	0.029	0.094	0.010	0.004	0.989	0.175	
CER	0.003	0.016	0.157	0.063	0.000	0.992	0.937	
CLS	0.003	0.019	0.129	0.073	0.000	0.995	0.325	
HLA	0.002	0.016	0.143	0.048	0.000	0.997	0.557	
NEO	0.002	0.019	0.088	0.010	0.003	0.999	0.654	
BRY	0.001	0.009	0.112	0.027	0.000	1.000	0.361	
UDO	0.000	0.001	0.179	0.000	0.003	1.000	0.994	

Contrast: 19_9

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p
LPA	0.302	0.371	0.815	19.333	0.600	0.347	0.001 ***
HA	0.216	0.232	0.932	1.000	3.736	0.596	0.997
CLP	0.163	0.306	0.531	6.296	0.027	0.783	0.001 ***
DIC	0.103	0.203	0.508	0.889	0.258	0.902	0.015 *
PAD	0.050	0.155	0.320	0.000	0.833	0.959	0.328
MIC	0.024	0.099	0.247	0.000	0.612	0.987	0.902
NEO	0.005	0.030	0.150	0.000	0.095	0.992	0.133
ASP	0.004	0.026	0.153	0.000	0.095	0.997	0.719
TRB	0.003	0.021	0.141	0.000	0.071	1.000	0.993

Contrast: 19_17

Column1	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p
LPA	0.311	0.361	0.862	19.333	2.115	0.353	0.001 ***
HA	0.190	0.234	0.816	1.000	3.721	0.569	1.000
CLP	0.157	0.292	0.536	6.296	0.129	0.746	0.001 ***
DIC	0.117	0.223	0.524	0.889	1.080	0.879	0.005 **
TRB	0.042	0.113	0.375	0.000	1.202	0.927	0.247
MIC	0.028	0.123	0.226	0.000	0.607	0.958	0.936
ASP	0.014	0.073	0.193	0.000	0.229	0.974	0.232
GLA	0.008	0.044	0.187	0.000	0.243	0.983	0.409
CHL	0.006	0.044	0.128	0.000	0.122	0.990	0.834
SRG	0.004	0.026	0.173	0.000	0.153	0.995	0.998
PAD	0.004	0.023	0.165	0.000	0.158	0.999	1.000
DCT	0.001	0.011	0.073	0.000	0.021	1.000	1.000
VAL	0.000	0.000	0.075	0.000	0.001	1.000	0.984

Contrast: 19_20

Column1	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
LPA	0.288	0.373	0.774	19.333	0.679	0.311	0.001	***
CLP	0.176	0.287	0.615	6.296	1.437	0.501	0.001	***
HA	0.142	0.228	0.622	1.000	1.528	0.654	1.000	
DIC	0.103	0.236	0.436	0.889	0.213	0.765	0.005	**
PAD	0.041	0.106	0.389	0.000	1.780	0.809	0.418	
MIC	0.035	0.132	0.264	0.000	1.548	0.847	0.818	
CER	0.024	0.101	0.238	0.000	0.996	0.873	0.069	.
DPT	0.021	0.080	0.259	0.000	1.232	0.895	0.077	.
DCT	0.018	0.051	0.355	0.000	0.989	0.914	0.231	
TRB	0.016	0.049	0.331	0.000	0.301	0.932	0.820	
SRG	0.014	0.079	0.171	0.000	0.344	0.946	0.894	
AMA	0.013	0.064	0.205	0.000	0.876	0.960	0.075	.
CHL	0.013	0.036	0.357	0.000	0.583	0.974	0.393	
NEO	0.006	0.030	0.186	0.000	0.370	0.980	0.105	
HLA	0.004	0.020	0.225	0.000	0.098	0.985	0.167	
VAL	0.004	0.024	0.159	0.000	0.333	0.989	0.089	.
VEN	0.003	0.022	0.120	0.000	0.212	0.992	0.030	*
GLA	0.002	0.025	0.085	0.000	0.019	0.994	0.854	
CLS	0.002	0.015	0.131	0.000	0.159	0.996	0.261	
BRY	0.002	0.013	0.142	0.000	0.130	0.998	0.132	
ASP	0.001	0.007	0.152	0.000	0.029	0.999	0.950	
LAU	0.001	0.007	0.076	0.000	0.004	1.000	0.935	
HYP	0.000	0.001	0.105	0.000	0.001	1.000	0.979	

Contrast: 19_29

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
LPA	0.358	0.374	0.957	19.333	2.017	0.380	0.002	**
CLP	0.175	0.324	0.541	6.296	0.129	0.565	0.002	**
HA	0.151	0.285	0.531	1.000	0.633	0.726	1.000	
DIC	0.129	0.280	0.461	0.889	0.038	0.862	0.005	**
NRM	0.044	0.113	0.389	0.000	0.933	0.909	0.016	*
SPT	0.023	0.085	0.268	0.000	0.582	0.933	0.014	*
AMA	0.015	0.065	0.235	0.000	0.401	0.950	0.086	.
GLA	0.015	0.038	0.398	0.000	0.179	0.966	0.265	
PAD	0.014	0.097	0.143	0.000	0.408	0.980	0.912	
LAU	0.009	0.036	0.253	0.000	0.141	0.990	0.155	
DPT	0.004	0.034	0.125	0.000	0.045	0.994	0.426	
HYP	0.004	0.023	0.171	0.000	0.057	0.999	0.397	
SRG	0.001	0.004	0.123	0.000	0.005	0.999	0.977	
VAL	0.000	0.003	0.123	0.000	0.004	1.000	0.547	
CHL	0.000	0.002	0.123	0.000	0.002	1.000	0.964	
NEO	0.000	0.001	0.221	0.000	0.003	1.000	0.641	
UDO	0.000	0.001	0.171	0.000	0.003	1.000	0.538	
TRB	0.000	0.001	0.129	0.000	0.001	1.000	1.000	

Contrast: 9_17

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.316	0.264	1.195	3.736	3.721	0.406	0.999	
LPA	0.124	0.193	0.644	0.600	2.115	0.565	0.008	**
DIC	0.076	0.159	0.480	0.258	1.080	0.663	0.001	***
PAD	0.069	0.192	0.363	0.833	0.158	0.752	0.009	**
MIC	0.066	0.181	0.367	0.612	0.607	0.838	0.636	
TRB	0.060	0.136	0.440	0.071	1.202	0.914	0.003	**
ASP	0.025	0.095	0.258	0.095	0.229	0.946	0.035	*
GLA	0.011	0.053	0.206	0.000	0.243	0.960	0.462	
CLP	0.011	0.055	0.192	0.027	0.129	0.974	1.000	
CHL	0.008	0.055	0.144	0.000	0.122	0.984	0.925	
SRG	0.006	0.031	0.189	0.000	0.153	0.991	1.000	
NEO	0.006	0.036	0.161	0.095	0.000	0.999	0.086	.
DCT	0.001	0.013	0.080	0.000	0.021	1.000	1.000	

Contrast: 9_20

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.289	0.279	1.035	3.736	1.528	0.340	1.000	
PAD	0.113	0.221	0.513	0.833	1.780	0.474	0.001	***
LPA	0.087	0.184	0.472	0.600	0.679	0.576	0.424	
MIC	0.073	0.186	0.394	0.612	1.548	0.662	0.488	
CLP	0.051	0.110	0.466	0.027	1.437	0.723	0.068	.
DIC	0.035	0.118	0.298	0.258	0.213	0.764	0.309	
CER	0.032	0.122	0.259	0.000	0.996	0.801	0.001	***
DPT	0.026	0.095	0.274	0.000	1.232	0.832	0.001	***
TRB	0.026	0.065	0.399	0.071	0.301	0.862	0.814	
DCT	0.023	0.060	0.389	0.000	0.989	0.890	0.026	*
SRG	0.019	0.097	0.192	0.000	0.344	0.912	0.967	
CHL	0.017	0.043	0.390	0.000	0.583	0.932	0.340	
AMA	0.016	0.075	0.216	0.000	0.876	0.951	0.005	**
NEO	0.013	0.050	0.252	0.095	0.370	0.966	0.003	**
ASP	0.006	0.032	0.197	0.095	0.029	0.973	0.825	
HLA	0.006	0.024	0.252	0.000	0.098	0.980	0.051	.
VAL	0.005	0.027	0.172	0.000	0.333	0.986	0.084	.
GLA	0.003	0.035	0.096	0.000	0.019	0.990	0.918	
VEN	0.003	0.025	0.124	0.000	0.212	0.993	0.074	.
CLS	0.002	0.017	0.135	0.000	0.159	0.996	0.429	
BRY	0.002	0.016	0.144	0.000	0.130	0.999	0.127	
LAU	0.001	0.010	0.083	0.000	0.004	1.000	0.979	
HYP	0.000	0.003	0.077	0.000	0.001	1.000	1.000	

Contrast: 9_29

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.378	0.333	1.136	3.736	0.633	0.410	0.426	
LPA	0.172	0.224	0.767	0.600	2.017	0.596	0.001	***
PAD	0.103	0.258	0.398	0.833	0.408	0.707	0.003	**
NRM	0.062	0.138	0.449	0.000	0.933	0.774	0.001	***
MIC	0.037	0.132	0.276	0.612	0.000	0.814	0.939	
DIC	0.036	0.125	0.288	0.258	0.038	0.853	0.324	
SPT	0.032	0.103	0.305	0.000	0.582	0.887	0.001	***
GLA	0.024	0.054	0.442	0.000	0.179	0.912	0.096	.
AMA	0.021	0.079	0.265	0.000	0.401	0.935	0.013	*
CLP	0.015	0.085	0.175	0.027	0.129	0.951	0.974	
LAU	0.013	0.046	0.291	0.000	0.141	0.966	0.022	*
NEO	0.007	0.043	0.169	0.095	0.003	0.974	0.064	.
DPT	0.006	0.046	0.141	0.000	0.045	0.981	0.421	
ASP	0.006	0.036	0.167	0.095	0.000	0.987	0.775	
HYP	0.006	0.030	0.194	0.000	0.057	0.993	0.420	
TRB	0.004	0.028	0.158	0.071	0.001	0.998	1.000	
SRG	0.001	0.005	0.138	0.000	0.005	0.999	0.999	
VAL	0.001	0.004	0.138	0.000	0.004	1.000	0.702	
CHL	0.000	0.002	0.138	0.000	0.002	1.000	1.000	
UDO	0.000	0.001	0.191	0.000	0.003	1.000	0.797	

Contrast: 17_20

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.244	0.255	0.957	3.721	1.528	0.278	1.000	
LPA	0.115	0.205	0.560	2.115	0.679	0.409	0.006	**
MIC	0.076	0.204	0.373	0.607	1.548	0.496	0.375	
TRB	0.069	0.140	0.497	1.202	0.301	0.575	0.001	***
DIC	0.064	0.155	0.413	1.080	0.213	0.648	0.001	***
CLP	0.056	0.122	0.463	0.129	1.437	0.712	0.006	**
PAD	0.055	0.127	0.433	0.158	1.780	0.775	0.092	.
CER	0.029	0.117	0.251	0.000	0.996	0.809	0.001	***
DPT	0.024	0.090	0.272	0.000	1.232	0.837	0.001	***
DCT	0.023	0.060	0.384	0.021	0.989	0.863	0.008	**
SRG	0.023	0.098	0.231	0.153	0.344	0.889	0.969	
CHL	0.022	0.066	0.340	0.122	0.583	0.914	0.048	*
ASP	0.021	0.098	0.210	0.229	0.029	0.938	0.076	.
AMA	0.015	0.072	0.214	0.000	0.876	0.955	0.001	***
GLA	0.013	0.065	0.206	0.243	0.019	0.971	0.281	
NEO	0.007	0.034	0.198	0.000	0.370	0.978	0.020	*
HLA	0.006	0.023	0.240	0.000	0.098	0.985	0.035	*
VAL	0.004	0.026	0.169	0.001	0.333	0.990	0.040	*
VEN	0.003	0.024	0.124	0.000	0.212	0.993	0.002	**
BRY	0.003	0.022	0.118	0.000	0.130	0.996	0.050	*
CLS	0.002	0.017	0.135	0.000	0.159	0.999	0.435	
LAU	0.001	0.013	0.069	0.000	0.004	1.000	0.994	

Contrast: 17_29

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.289	0.290	0.997	3.721	0.633	0.310	1.000	
LPA	0.203	0.239	0.849	2.115	2.017	0.528	0.001	***
DIC	0.070	0.170	0.414	1.080	0.038	0.604	0.002	**
TRB	0.063	0.153	0.414	1.202	0.001	0.672	0.008	**
NRM	0.057	0.134	0.427	0.000	0.933	0.733	0.001	***
MIC	0.044	0.175	0.250	0.607	0.000	0.780	0.909	
GLA	0.036	0.086	0.417	0.243	0.179	0.819	0.003	**
SPT	0.030	0.101	0.299	0.000	0.582	0.851	0.001	***
CLP	0.028	0.116	0.244	0.129	0.129	0.882	0.722	
ASP	0.025	0.116	0.212	0.229	0.000	0.908	0.063	.
PAD	0.022	0.113	0.196	0.158	0.408	0.932	0.977	
AMA	0.019	0.076	0.256	0.000	0.401	0.953	0.007	**
LAU	0.014	0.052	0.267	0.000	0.141	0.968	0.009	**
CHL	0.009	0.062	0.147	0.122	0.002	0.978	0.823	
SRG	0.007	0.034	0.203	0.153	0.005	0.985	0.999	
DPT	0.006	0.050	0.125	0.000	0.045	0.992	0.466	
HYP	0.006	0.031	0.182	0.000	0.057	0.998	0.449	
DCT	0.001	0.014	0.079	0.021	0.000	0.999	1.000	
VAL	0.001	0.005	0.125	0.001	0.004	1.000	0.790	
NEO	0.000	0.001	0.232	0.000	0.003	1.000	0.929	
UDO	0.000	0.001	0.183	0.000	0.003	1.000	0.899	

Contrast: 20_29

Genus	Average	SD	Ratio	Average (Group A)	Average (Group B)	Cumulative Sum	p	
HA	0.184	0.251	0.733	1.528	0.633	0.195	1.000	
LPA	0.177	0.252	0.701	0.679	2.017	0.382	0.001	***
PAD	0.077	0.180	0.426	1.780	0.408	0.463	0.009	**
CLP	0.068	0.156	0.433	1.437	0.129	0.534	0.007	**
NRM	0.059	0.140	0.419	0.000	0.933	0.596	0.001	***
MIC	0.048	0.167	0.291	1.548	0.000	0.647	0.868	
AMA	0.036	0.107	0.333	0.876	0.401	0.685	0.001	***
CER	0.034	0.135	0.253	0.996	0.000	0.721	0.002	**
DPT	0.033	0.112	0.300	1.232	0.045	0.757	0.001	***
GLA	0.032	0.090	0.354	0.019	0.179	0.790	0.021	*
SPT	0.031	0.102	0.298	0.000	0.582	0.823	0.001	***
TRB	0.029	0.084	0.343	0.301	0.001	0.853	0.681	
DCT	0.026	0.066	0.388	0.989	0.000	0.880	0.023	*
SRG	0.023	0.115	0.203	0.344	0.005	0.905	0.891	
CHL	0.018	0.048	0.385	0.583	0.002	0.924	0.249	
DIC	0.018	0.081	0.227	0.213	0.038	0.944	0.890	
LAU	0.016	0.055	0.286	0.004	0.141	0.960	0.003	**
NEO	0.008	0.036	0.210	0.370	0.003	0.968	0.072	.
HLA	0.007	0.028	0.245	0.098	0.000	0.976	0.040	*
HYP	0.007	0.035	0.192	0.001	0.057	0.983	0.318	
VAL	0.005	0.028	0.196	0.333	0.004	0.989	0.066	.
BRY	0.004	0.032	0.114	0.130	0.000	0.992	0.035	*

VEN	0.003	0.026	0.124	0.212	0.000	0.996	0.057
CLS	0.002	0.017	0.135	0.159	0.000	0.998	0.370
ASP	0.001	0.009	0.167	0.029	0.000	1.000	0.976
UDO	0.000	0.001	0.177	0.000	0.003	1.000	0.851

C.6 Regional descriptions of macroalgal communities by biogeographic realm

All Sites (1205 Total)				
Genus	Division	Mean	Maximum	Median
All Macroalgae	--	12.80	88.20	6.79
<i>Sargassum</i>	Brown	13.00	62.00	6.25
<i>Microdictyon</i>	Green	12.00	69.70	5.00
<i>Halimeda</i>	Green	8.02	77.30	4.44
<i>Amansia</i>	Red	6.34	13.50	4.96
<i>Cladophoropsis</i>	Green	4.76	9.30	4.51
<i>Dictyopteris</i>	Brown	4.60	14.60	4.00
<i>Ceratodictyon</i>	Red	4.44	20.00	1.23
<i>Lobophora</i>	Brown	3.89	82.70	1.31
<i>Padina</i>	Brown	3.21	24.40	2.08
<i>Spatoglossum</i>	Brown	3.17	12.20	0.53

9. Mid-tropical North Pacific (101)				
Genus	Division	Mean	Maximum	Median
All Macroalgae	--	6.83	24.40	5.13
<i>Padina</i>	Brown	5.41	11.60	4.82
<i>Halimeda</i>	Green	5.16	21.60	4.39
<i>Microdictyon</i>	Green	3.98	12.60	2.43
<i>Asparagopsis</i>	Red	3.09	3.33	3.09
<i>Neomeris</i>	Green	3.08	3.35	3.08
<i>Lobophora</i>	Brown	2.24	9.30	1.99
<i>Liagora</i>	Red	1.68	1.68	1.68
<i>Turbinaria</i>	Brown	1.53	3.33	0.93
<i>Dictyota</i>	Brown	1.27	5.83	0.31
<i>Caulerpa</i>	Green	0.22	0.51	0.17

13. Indo-Pacific seas & Indian Ocean				
Genus	Division	Mean	Maximum	Median
All Macroalgae	--	18.40	88.20	14.80
<i>Microdictyon</i>	Green	12.80	69.70	3.66
<i>Sargassum</i>	Brown	10.10	62.00	4.92
<i>Halimeda</i>	Green	8.16	77.30	4.94
<i>Cystoseiria</i>	Brown	7.12	26.40	3.53
<i>Cladophoropsis</i>	Green	4.12	6.23	4.10
<i>Jania</i>	Red	3.56	6.54	3.66
<i>Turbinaria</i>	Brown	3.00	29.50	1.07
<i>Padina</i>	Brown	2.91	12.40	1.64
<i>Lobophora</i>	Brown	2.77	27.60	0.60
<i>Spyridia</i>	Red	2.46	2.46	2.46

16. Coral Sea [324]				
Genus	Division	Mean	Maximum	Median
All Macroalgae	--	15.60	78.50	9.74
<i>Galaxaura</i>	Red	26.10	35.20	26.10
<i>Sargassum</i>	Brown	22.40	59.10	19.70
<i>Halimeda</i>	Green	14.10	44.60	11.20
<i>Sargassopsis</i>	Brown	8.20	37.20	4.25
<i>Hydroclathrus</i>	Brown	5.59	13.60	5.75
<i>Dictosphaeria</i>	Green	5.04	14.10	0.76
<i>Dictyopteris</i>	Brown	4.75	10.20	4.25
<i>Caulerpa</i>	Green	4.50	30.00	1.43
<i>Lobophora</i>	Brown	3.07	23.60	0.69
<i>Laurencia</i>	Brown	3.05	13.70	1.67

17. Mid South Tropical Pacific [166]				
Genus	Division	Mean	Maximum	Median
All Macroalgae	--	11.40	37.90	9.07
<i>Microdictyon</i>	Green	9.11	12.30	9.31
<i>Lobophora</i>	Brown	6.33	28.50	4.52
<i>Turbinaria</i>	Brown	5.67	26.10	4.50
<i>Padina</i>	Brown	4.73	6.00	5.00
<i>Chlorodesmis</i>	Green	4.58	8.33	4.17
<i>Halimeda</i>	Green	4.26	22.80	2.38
<i>Sargassum</i>	Brown	3.83	6.00	4.00
<i>Asparagopsis</i>	Red	3.81	8.00	3.33
<i>Galaxaura</i>	Red	3.58	7.48	4.45
<i>Dictyota</i>	Brown	3.31	15.30	1.71

19. Offshore Indian Ocean [12]				
Genus	Division	Mean	Maximum	Median
All Macroalgae	--	34.20	82.70	21.30
<i>Lobophora</i>	Brown	43.50	82.70	43.70
<i>Caulerpa</i>	Green	28.30	35.30	28.30
<i>Halimeda</i>	Green	4.50	5.00	4.50

20. Offshore West Pacific [114]				
Genus	Division	Mean	Maximum	Median
All Macroalgae	--	12.70	85.40	4.70
<i>Eckloniopsis</i>	Brown	31.50	40.80	31.50
<i>Ptilophora</i>	Red	25.00	37.90	25.00
<i>Microdictyon</i>	Green	16.10	43.90	15.40
<i>Ventricaria</i>	Green	15.70	15.70	15.70
<i>Vanvoorstia</i>	Red	12.80	12.80	12.80
<i>Corallina</i>	Red	11.80	20.50	11.80
<i>Ceratodictyon</i>	Red	11.50	20.00	10.50
<i>Prionitis</i>	Red	11.40	11.40	11.40
<i>Cladophoropsis</i>	Green	9.30	9.30	9.30
<i>Amansia</i>	Red	9.06	13.50	9.12

29. NW Pacific [57]				
Genus	Division	Mean	Maximum	Median
All Macroalgae	--	5.70	22.10	2.66
<i>Padina</i>	Brown	8.54	17.00	8.54
<i>Caulerpa</i>	Green	5.40	5.40	5.40
<i>Amansia</i>	Red	3.63	11.60	1.45
<i>Spatoglossum</i>	Brown	3.17	12.20	0.53
<i>Neomeris</i>	Green	2.93	11.50	1.45
<i>Gracilaria</i>	Red	2.41	2.41	2.41
<i>Lobophora</i>	Brown	1.97	8.53	0.99
<i>Actinotrichia</i>	Red	1.68	1.68	1.68
<i>Halimeda</i>	Green	1.43	11.00	0.27
<i>Dudresnaya</i>	Red	1.20	1.20	1.20

C.7 Full results for linear mixed effects models.

Genus / Category	R ²		Cumulative Human Impacts		Log (Population 20km)		Market Distance		Market Gravity		NDVI		Nutrients	
	Marg	Cond	Est	p	Est	p	Est	p	Est	p	Est	p	Est	p
All Macroalgae	0.00	0.01	-0.02	0.03	0.03	< 0.01	-0.02	< 0.01	-0.02	< 0.01	-0.01	0.30	0.02	< 0.01
All Brown Macroalgae	0.06	0.91	0.09	0.21	0.06	0.17	-0.01	0.73	0.07	0.19	0.12	< 0.01	0.01	0.82
<i>Dictyota</i>	0.11	0.75	0.28	< 0.01	-0.26	< 0.01	-0.05	0.17	0.04	0.45	0.07	0.10	0.11	0.02
<i>Dictyopteris</i>	0.03	1.00	0.04	0.61	0.05	0.24	0.00	0.92	-0.08	0.16	0.04	0.32	0.14	< 0.01
<i>Lobophora</i>	0.01	0.85	-0.07	0.31	0.05	0.04	0.02	0.61	0.09	0.10	-0.00	0.94	-0.04	0.37
<i>Padina</i>	0.07	0.66	0.03	0.61	0.16	< 0.01	0.10	< 0.01	-0.01	0.79	0.04	0.29	<i>0.07</i>	<i>0.09</i>
<i>Spatoglossum</i>	0.02	0.17	-0.03	0.62	0.02	0.54	0.06	0.10	0.13	< 0.01	0.05	0.22	-0.10	0.02
<i>Sargassum</i>	0.03	0.94	0.09	0.23	0.03	0.43	<i>0.07</i>	<i>0.07</i>	0.02	0.67	0.13	< 0.01	-0.04	0.37
<i>Turbinaria</i>	0.05	0.78	0.08	0.25	-0.02	0.55	0.04	0.24	0.17	< 0.01	0.00	0.97	-0.01	0.78
All Green Macroalgae	0.11	0.77	-0.38	< 0.01	0.14	< 0.01	-0.10	< 0.01	-0.05	0.27	-0.08	0.04	0.17	< 0.01
<i>Bryopsis</i>	0.05	1.00	-0.19	< 0.01	0.13	< 0.01	0.06	0.11	0.12	0.02	0.04	0.39	0.18	< 0.01
<i>Chlorodesmis</i>	0.03	0.90	-0.11	0.12	-0.03	0.52	0.05	0.24	0.07	0.21	-0.04	0.35	0.19	< 0.01
<i>Caulerpa</i>	0.02	0.72	-0.14	0.04	0.04	0.32	0.08	0.03	0.01	0.83	-0.03	0.41	0.15	< 0.01
<i>Cladophoropsis</i>	0.05	1.00	0.00	0.99	-0.00	0.94	-0.06	0.10	0.06	0.23	0.01	0.78	0.15	0.16
<i>Dictosphaeria</i>	0.03	0.99	-0.09	0.23	0.16	< 0.01	0.04	0.28	-0.02	0.66	0.01	0.84	0.13	< 0.01
<i>Halimeda</i>	0.11	0.40	-0.28	< 0.01	0.04	0.31	-0.12	< 0.01	0.03	0.59	-0.15	< 0.01	<i>0.09</i>	<i>0.05</i>
<i>Microdictyon</i>	0.06	0.98	-0.24	< 0.01	0.14	< 0.01	<i>-0.08</i>	<i>0.05</i>	-0.13	< 0.02	0.05	0.22	<i>0.08</i>	<i>0.09</i>
<i>Neomeris</i>	0.01	0.99	0.02	0.81	0.05	0.25	0.03	0.49	-0.01	0.88	-0.01	0.85	0.08	0.11
<i>Udotea</i>	0.01	0.08	-0.03	0.62	-0.08	0.04	0.00	0.97	0.05	0.35	<i>-0.07</i>	<i>0.06</i>	0.01	0.81
All Red Macroalgae	0.13	0.34	0.03	0.62	0.11	< 0.01	0.01	0.71	0.06	0.18	-0.01	0.71	0.25	< 0.01
<i>Amansia</i>	0.03	0.83	-0.06	0.39	<i>0.08</i>	<i>0.07</i>	0.04	0.32	0.02	0.73	0.01	0.87	0.16	< 0.01
<i>Asparagopsis</i>	0.02	0.96	0.10	0.17	-0.09	0.13	-0.02	0.62	<i>0.11</i>	<i>0.05</i>	0.05	0.26	-0.06	0.17
<i>Ceratodictyon</i>	0.06	1.00	0.00	0.78	<i>-0.11</i>	<i>0.09</i>	0.08	0.03	<i>0.09</i>	<i>0.08</i>	0.05	0.25	0.22	< 0.01
<i>Galaxaura</i>	0.01	0.99	-0.11	0.12	-0.01	0.81	0.02	0.61	0.05	0.35	-0.05	0.24	0.14	< 0.01
<i>Halymenia</i>	0.10	0.55	-0.07	0.29	0.15	< 0.01	0.04	0.27	0.02	0.73	-0.01	0.76	0.28	< 0.01
<i>Hypnea</i>	0.04	0.99	0.06	0.15	0.06	0.43	-0.08	0.05	0.08	0.12	0.04	0.34	0.02	0.66
<i>Laurencia</i>	0.01	0.65	0.02	0.78	-0.05	0.22	-0.04	0.27	-0.06	0.25	0.10	0.02	0.04	0.39
<i>Neurymenia</i>	0.02	0.27	-0.02	0.77	0.03	0.40	0.02	0.65	0.07	0.13	0.00	0.98	<i>0.07</i>	<i>0.09</i>
<i>Peyssonellia</i>	0.02	0.14	0.03	0.64	0.16	< 0.01	0.10	0.90	-0.01	0.33	0.04	0.10	0.07	0.04

C.8 Full PERMANOVA results for each biogeographic realm.

a. All sites.				
<i>Formula = percent ~ Month of survey (ranked by SST) + storms within 5 years (Type 3+) + maxDHW + cumulative human impacts + habitat + nutrients (agriculture) + mean wave energy + NPPSD + SSTSD + MMM + Depth + reef area (200 km) + management + NDVI + mean PAR (survey month) + aspect + Chl_a (kurtosis)</i>				
	Sum of Squares	R ²	Pseudo-F	p-value
Model	29.08	0.10	2.62	< 0.01
Residual	266.23	0.90		
Total	295.30	1.00		
Variables				
Month (ranked by SST)	9.26	0.03	2.16	< 0.01
Storms within 5 years (Type 3+)	0.79	0.00	2.21	0.02
MaxDHW	0.99	0.00	2.79	< 0.01
Cumulative human impacts	1.72	0.01	4.81	< 0.01
Habitat	5.52	0.02	5.14	< 0.01
Nutrients (agriculture)	0.37	0.00	1.02	0.42
Mean wave energy	0.72	0.00	1.99	0.03
NPP _{SD}	0.43	0.00	1.19	0.28
Reef area (200km)	1.46	0.00	4.06	< 0.01
Management	3.27	0.01	4.56	< 0.01
NDVI	0.90	0.00	2.51	< 0.01
Mean PAR (survey month)	0.79	0.00	2.22	0.02
Aspect	0.23	0.00	0.65	0.81
<i>Chl_a (kurtosis)</i>	<i>0.67</i>	<i>0.00</i>	<i>1.87</i>	<i>0.05</i>
Residual	424.38	0.96		
Total	443.18	1.00		

b. Realm 9. Mid-tropical North Pacific				
<i>Formula = percent ~ Storms within 5 years (Type 3+) + nutrients (agriculture)</i>				
	Sum of Squares	R ²	Pseudo-F	p-value
<i>Model</i>	9.97	0.05	1.63	0.08
Residual	19.30	0.94		
Total	19.27	1.00		
Variables				
Population (20 km)	0.38	0.02	3.94	< 0.01
Depth	0.59	0.01	2.21	0.03
Residual	18.30	0.94		
Total	19.27	1.00		

c. Realm 13. Indo-Pacific seas & Indian Ocean				
<i>Formula = percent ~ Chl_a (kurt) + reef area (200 km) + depth + NDVI + mean SST (survey month) + reef area (15 km) + mean wave energy</i>				
	Sum of Squares	R ²	Pseudo-F	p-value
Model	15.27	0.12	7.50	< 0.01
Residual	111.74	0.88		
Total	127.01	1.00		
Variables				
Chl _a (kurtosis)	1.11	0.01	3.81	< 0.01
Reef area (200 km)	1.83	0.01	6.27	< 0.01
Depth	2.56	0.02	8.79	< 0.01
NDVI	2.26	0.02	7.76	< 0.01
Mean SST (survey month)	0.91	0.01	3.11	< 0.01
Reef area (15 km)	6.01	0.05	20.68	< 0.01
Mean wave energy	0.60	0.01	2.06	0.04
Residual	111.74	0.88		
Total	126.01	1.00		

d. Realm 16. Coral Sea.				
<i>Formula = percent ~ nutrients (agriculture) + NDVI + chl_a (kurtosis) + mean wave energy + storms within 5 years (type 3+) + NPP_{SD}</i>				
	Sum of Squares	R ²	Pseudo-F	p-value
Model	16.28	0.21	9.88	< 0.01
Residual	60.13	0.79		
Total	76.41	1.00		
Variables				
Nutrients (agriculture)	4.58	0.06	16.66	< 0.01
NDVI	3.05	0.04	11.12	< 0.01
Chl _a (kurtosis)	1.26	0.02	4.59	< 0.01
Mean wave energy	2.97	0.04	10.81	< 0.01
Storms within 5 years (Type 3+)	0.92	0.01	3.36	< 0.01
NPP _{SD}	3.50	0.05	12.76	< 0.01
Residual	60.13	0.79		
Total	76.41	1.00		

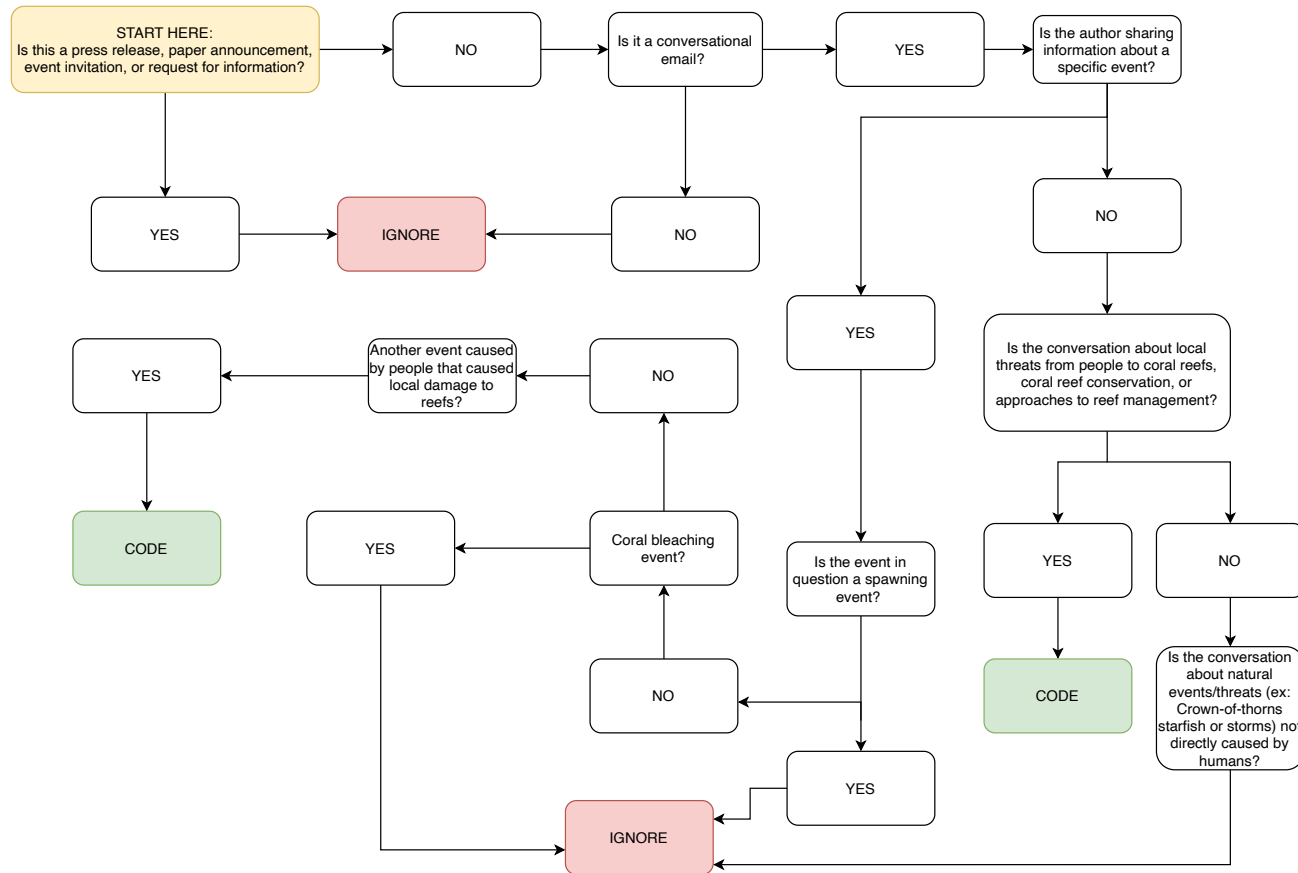
e. Realm 17. Mid South Tropical Pacific				
<i>Formula = percent ~ management + aspect + depth + NDVI + mean PAR (survey month)</i>				
	Sum of Squares	R ²	Pseudo-F	p-value
Model	10.76	0.18	5.80	< 0.01
Residual	48.26	0.82		
Total	59.02	1.00		
Variables				
Management	5.00	0.08	8.08	< 0.01
Aspect	0.17	0.02	0.54	0.83
Depth	2.57	0.04	8.29	< 0.01
NDVI	0.89	0.02	2.87	< 0.01
Mean PAR (survey month)	2.14	0.04	6.91	< 0.01
Residual	48.26	0.82		
Total	59.02	1.00		

f. Realm 20. Offshore West Pacific				
<i>Formula = percent ~ NDVI + WWE + aspect + mean wave energy</i>				
	Sum of Squares	R ²	Pseudo-F	p-value
Model	3.28	0.07	1.99	< 0.01
Residual	46.62	0.93		
Total	49.90	1.00		
Variables				
NDVI	1.31	0.03	3.16	< 0.01
WWE	0.49	0.01	1.19	0.26
Aspect	0.42	0.01	1.01	0.42
Mean wave energy	1.06	0.02	2.58	< 0.01
Residual	46.62	0.93		
Total	49.90	1.00		

g. Realm 29. NW Pacific				
<i>Formula = percent ~ chl_a (kurtosis) + nutrients + management + WWE</i>				
	Sum of Squares	R ²	Pseudo-F	p-value
Model	0.54	0.02	1.36	< 0.01
Residual	19.74	0.84		
Total	23.57	1.00		
Variables				
Chl _a (kurtosis)	0.54	0.02	1.36	0.12
Nutrients (agriculture)	0.85	0.04	2.16	< 0.01
Management	2.09	0.09	2.65	< 0.01
WWE	0.35	0.01	0.88	0.62
Residual	19.74	0.86		
Total	23.57	1.00		

Appendix D Appendix to Chapter 5

D.1 Coding decision-making flow chart



D.2 Codebook

- Actors
 - Activists or Environmentalists
 - Aquarists
 - Boaters
 - Community organizations
 - Consultants
 - Dealers
 - Educators
 - Farmers
 - Fishers or harvesters
 - General public or laypeople
 - Global North
 - Global South
 - Government agencies
 - Industry or private sector
 - Scuba industry
 - ISRS or ICRS
 - Locals and local communities
 - Managers
 - Media
 - Military
 - Multilateral organizations
 - Nonprofits or NGOs
 - Policymakers/politicians
 - Recreational divers
 - Restoration practitioners
 - Scientists & researchers or the scientific community
 - Stakeholders
 - Students
 - Tourists
 - Universities/research institutions
 - Volunteers
- Distal drivers
 - Economic
 - General consumption or resource use
 - Land use
 - Limited capacity
 - Maladaptation
 - Misinformation or lack of awareness
 - Political
 - Population density or growth
- Local threats to reefs
 - Development and construction

- Development for tourism and diving
 - Dredging/quarrying
 - Drilling/mineral extraction
 - Island building/land reclamation
 - Direct damage
 - Boat groundings
 - Research-related
 - Trash or debris
 - Fishing or harvesting
 - Coral harvesting
 - Destructive fishing practices
 - Live fish market
 - Poaching
 - Shark finning
 - Technological advancements
 - General or unspecified degradation
 - Interactions with climate change
 - Invasive species
 - Military practices
 - Pollution and water quality
 - Eutrophication
 - Oil spills
 - Sedimentation
 - Sunscreen
 - Tourism and diving
- Narratives
 - Crisis
 - Resilience
- Solutions
 - Public awareness, education, or training
 - Rehabilitation and restoration
 - Resource management
 - Individual actions (e.g. behavioral change)
 - Legal or regulatory (includes policy)
 - Science (improvements in knowledge or understanding)
 - Unspecified intervention or strategy
 - Cleanup or remediation
 - Economic or social solutions
 - Access fee or tax
 - Alternative incomes
 - Conservation or research funding
 - Economic valuations
 - Fines, penalties, compensation
 - Insurance
 - International aid

- Market-driven
- Population control
- Social capital
- Sustainable development
- Traditional approaches

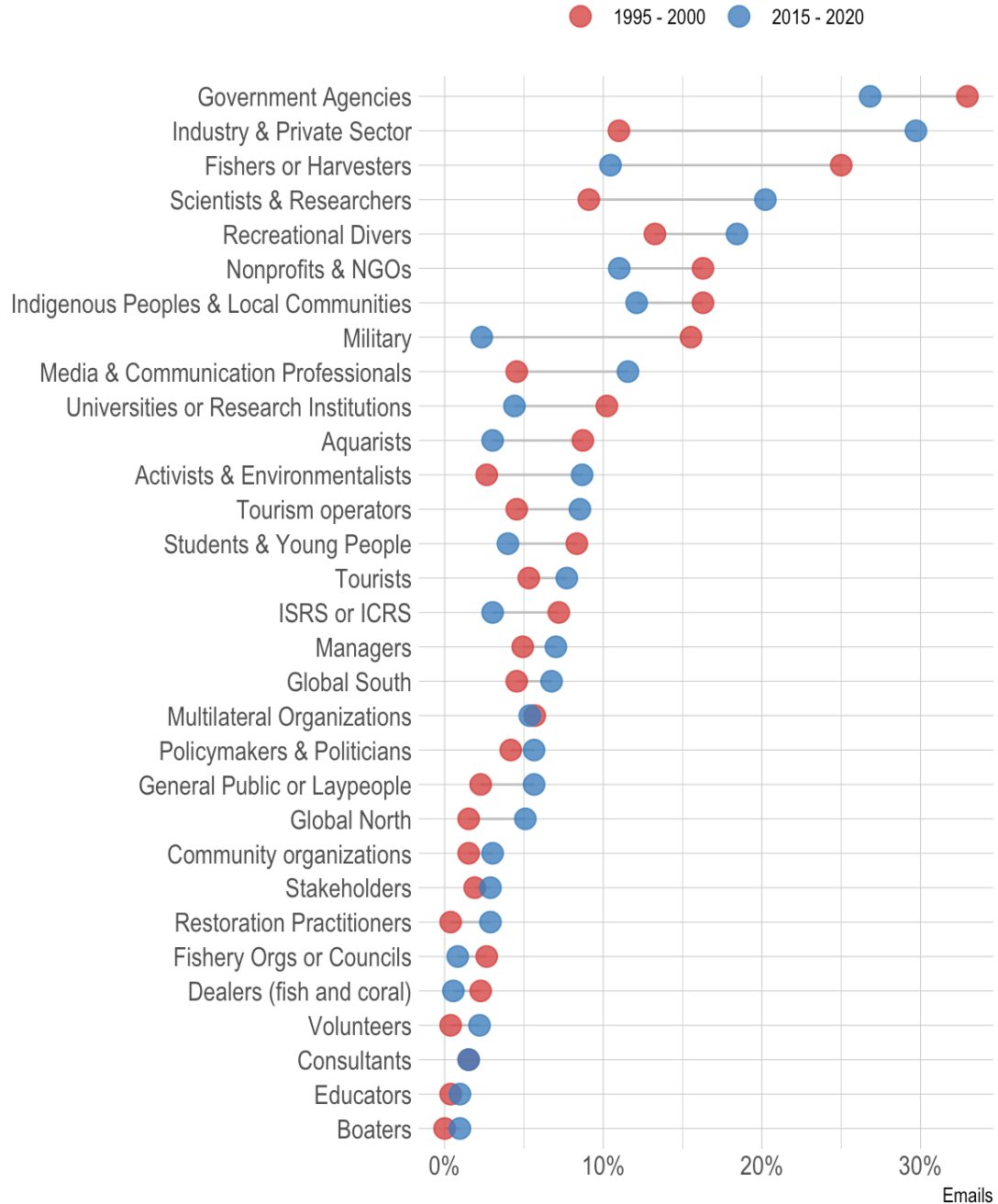
D.3 Actors in discussions of local threats

When discussing local threats to coral reefs, participants in Coral List discussions referenced specific actors 53% of the time (991 emails). Participants mentioned fishers and harvesters in 14% of all emails that mentioned actors (142), and they mentioned IPLC in 13% (131). Actors were included more frequently in discussions on average in the second period (mean 53% of monthly emails) compared to the first (41%), and means were significantly different across periods (Welch's two-sample t-test, $p = 0.01$).

The specific actors mentioned during list discussions also changed over time (Figure 5.2). The largest changes were for industry and private sector, which Coral List participants mentioned in an average 12% of monthly emails during the first period and increased to 28% in the second period ($p = 0.01$). Fishers and harvesters also changed by 15% across periods, declining from 26% of monthly emails during the first period to 11% in the second period, but the means were only marginally significantly different across periods ($p = 0.06$). Participants also mentioned scientists and researchers or the scientific community in a higher proportion of emails in the second period (mean 22% of monthly emails) than the first (9%, $p = 0.02$). The proportion of emails referencing the remaining actors did not change significantly. Mentions of military actors decreased by 13% across the two periods – from 16% (41) to 2% (17) – but the differences in the mean percent of monthly emails mentioning actors was not significant (8% in the first period to 2% in the second period, $p = 0.31$). This discrepancy between the percent of total emails mentioning military actors and the mean percent of monthly emails mentioning the military in the first period was caused by a specific debate about the effects of military activities on coral

reefs in 1999. Participants sent 35 emails mentioning military actors in 1999 alone, but only seven additional emails total that mentioned military actors in the remaining four years.

D.4 Actors in Coral List discussions, by percent of emails mentioning actors.



D.5 Threats to reefs and their solutions

Participants mentioned distal drivers of local threats to reefs in 24% of all emails (443). They discussed distal drivers (those that do not directly act to influence coral reefs but may underly direct, or proximate, stressors) more frequently in the second period (27% of monthly emails on average) than the first (mean 10% of monthly emails), and the means were significantly different across periods (Welch's two-sample t-test, $p < 0.01$). The participants most frequently discussed economic distal drivers, including poverty, inequality, and food insecurity (128, 29% of emails discussing distal threats) and population growth or density (123, 28%), followed by lack of awareness or misinformation (97, 22%), political drivers (such as disagreements between national governments over control over or access to resources, 90, 20%), and land use (activities on land that can influence coral reefs such as farming or deforestation, 80, 18%).

The distal drivers that participants discussed changed over time. Economic drivers accounted for a greater total proportion of emails in the earlier period (33, 44%) than in the latter period (95, 26%), but the monthly mean percent of emails was not significantly different across periods (32% versus 25%, $p = 0.52$). Political drivers accounted for 7% of monthly emails on average mentioning distal drivers in the earlier period but increased to 24% of emails in the latter period ($p < 0.01$). The proportion of emails discussing land use as a distal driver of local threats to reefs declined, from a mean of 32% of emails mentioning distal drivers to 17% ($p = 0.14$). The total proportion of emails discussing population density or growth increased marginally from a mean of 19% of monthly emails of emails discussing distal drivers to 29%, but the means did not differ significantly across periods ($p = 0.11$).

When looking at both study periods combined, participants often linked the economic distal drivers to fishing and harvesting (46, or 31% of emails about economic drivers) or interactions with climate change (25, 17%), while they usually discussed population density or growth in emails discussing interactions between local threats and climate change (37, 24% of emails discussing population density or growth), fishing or harvesting (32, 21%), general or unspecified degradation (28, 18%), and pollution and water quality (27, 17%) (Figure 5.3). Misinformation or lack of awareness was most frequently linked with interactions with climate change (45, 35% of emails mentioning misinformation or lack of awareness), general degradation (17%, 22), or pollution and water quality (20, 15%), and participants discussed political threats alongside interactions with climate change (24, 22%) and fishing or harvesting (20, 19%).

The most discussed proximate threat to coral reefs was pollution or water quality (478 emails, 21% of emails discussing proximate threats), followed by fishing and harvesting (478, 21%), interactions with climate change (425, 19%), and general or unspecified degradation (383, 17%). The number of emails discussing proximate threats interacting with climate change increased from an average of 3% of monthly emails in the first period to 48% in the latter period ($p < 0.01$), while discussions about fishing or harvesting declined from a mean of 50% of emails in the first period to 31% in the second period ($p < 0.01$). Discussions about live coral harvesting for the aquarium trade accounted for over half (100, 53%) of all emails discussing fishing and harvesting between 1995 and 2000 (I coded these conversations in a node nested within fishing and harvesting), while in the second period, emails about the aquarium trade only accounted for 10% of those discussing fishing and harvesting, which aligns with evidence that this threat has

become less important over time as coral gardening projects and mariculture facilities have replaced much of the supply that used to be harvested (Pomeroy, Parks and Balboa, 2006). The other proximate threats changed by less than five percentage points between the two periods.

The Coral List participants discussed five categories of solutions at almost equal frequencies: economic and social solutions (329, 15% of emails discussing solutions), science and research (325, 15%), legal and regulatory solutions (321, 15%), rehabilitation and restoration (301, 14%), and resource management (297, 14%). The proportions of emails mentioning the solutions increased from 44% on average in the first period to 60% on average in the second period ($p < 0.01$). The specific solutions changed by less than 5% across periods and the means were not significantly different across periods, with one exception: scientific solutions increased from a mean of 22% of emails mentioning solutions to 34%, and the difference between means was marginally significant ($p = 0.09$).

The participants mentioned specific solutions in the context of different threats to reefs (Figure 5.3); for example, when considering both periods together, they discussed economic and social solutions more frequently in the context of general or unspecified degradation (86, 22% of emails discussing economic and social solutions), interactions with climate change (79, 20%), or fishing or harvesting (75, 19%). People posting to the list discussed legal or regulatory solutions most frequently in the context of fishing and harvesting (115, 31% of emails mentioning legal or regulatory solutions) than any other threat, and individual actions such as behavioral changes were most frequently mentioned in the context of interactions between local threats and climate change (79, 26% of emails about individual actions), and pollution or water quality (59, 20%).

Emails most frequently linked rehabilitation and restoration solutions with interactions between climate change and local threats to reefs (110, 24% of emails discussing rehabilitation and restoration), followed by general or unspecified degradation (103, 23%), fishing and harvesting (89, 20%), and pollution and water quality (73, 16%).

D.6 Jaccard similarity coefficients

<i>Actors</i>		
Code A	Code B	Jaccard's coefficient
Resilience Narratives	Locals and Local Communities	0.65
Locals and Local Communities	Industry & Private Sector	0.64
Government Agencies	Crisis Narratives	0.63
Industry & Private Sector	Government Agencies	0.60
Locals and Local Communities	Fishers or Harvesters	0.60
Resilience Narratives	Industry & Private Sector	0.60
Nonprofits & NGOs	Government Agencies	0.58
Recreational Divers	Industry & Private Sector	0.56
Locals and Local Communities	Government Agencies	0.56
Scientists & Researchers or Scientific Community	Government Agencies	0.56
Fishers or Harvesters	Crisis Narratives	0.56
Resilience Narratives	Nonprofits & NGOs	0.56
Nonprofits & NGOs	Fishers or Harvesters	0.55
Resilience Narratives	Crisis Narratives	0.55
Resilience Narratives	Fishers or Harvesters	0.55
Scientists & Researchers or Scientific Community	Crisis Narratives	0.54
Industry & Private Sector	Crisis Narratives	0.54
Government Agencies	Fishers or Harvesters	0.54
Fishers or Harvesters	Actors	0.54
Resilience Narratives	Government Agencies	0.53
Scientists & Researchers or Scientific Community	Industry & Private Sector	0.52
Recreational Divers	Crisis Narratives	0.52
Resilience Narratives	Recreational Divers	0.52
Resilience Narratives	Actors	0.52
Recreational Divers	Government Agencies	0.51
Locals and Local Communities	Crisis Narratives	0.51
Nonprofits & NGOs	Locals and Local Communities	0.51
Scientists & Researchers or Scientific Community	Nonprofits & NGOs	0.51
Nonprofits & NGOs	Industry & Private Sector	0.51
Scientists & Researchers or Scientific Community	Locals and Local Communities	0.51

Industry & Private Sector	Fishers or Harvesters	0.51
Recreational Divers	Actors	0.50
Developing Countries	Developed Countries	0.50
Scientists & Researchers or Scientific Community	Media	0.50
Scientists & Researchers or Scientific Community	Resilience Narratives	0.49
Scientists & Researchers or Scientific Community	Recreational Divers	0.49
Locals and Local Communities	Actors	0.49
Scientists & Researchers or Scientific Community	Actors	0.49
Universities or Research Institutions	Nonprofits & NGOs	0.49
Nonprofits & NGOs	Actors	0.48
Recreational Divers	Locals and Local Communities	0.48
Scientists & Researchers or Scientific Community	Fishers or Harvesters	0.47
Resilience Narratives	Media	0.47
Nonprofits & NGOs	Crisis Narratives	0.46
Universities or Research Institutions	Fishers or Harvesters	0.46
Students & Young People	Media	0.46
Media	Government Agencies	0.46
Media	Crisis Narratives	0.45
Nonprofits & NGOs	Media	0.45
Recreational Divers	Nonprofits & NGOs	0.45
Recreational Divers	Fishers or Harvesters	0.44
Universities or Research Institutions	Government Agencies	0.44
Recreational Divers	Media	0.43
Media	Industry & Private Sector	0.43
Universities or Research Institutions	Locals and Local Communities	0.42
Scientists & Researchers or Scientific Community	Policymakers & Politicians	0.42
Nonprofits & NGOs	International Governance	0.42
Students & Young People	Nonprofits & NGOs	0.41
Tourists	Industry & Private Sector	0.41
Humanity or Society	Future Generations	0.41
Media	Locals and Local Communities	0.41
General Public or Laypeople	Developed Countries	0.40
Managers	Fishers or Harvesters	0.40

Universities or Research Institutions	Scientists & Researchers or Scientific Community	0.40
Media	Actors	0.40
Students & Young People	Resilience Narratives	0.40
Scientists & Researchers or Scientific Community	Managers	0.40
International Governance	Developing Countries	0.40
Universities or Research Institutions	Resilience Narratives	0.40
Tourists	Recreational Divers	0.39
Scientists & Researchers or Scientific Community	General Public or Laypeople	0.39
Locals and Local Communities	Developing Countries	0.39
Locals and Local Communities	Developed Countries	0.39
Students & Young People	Locals and Local Communities	0.39
Students & Young People	Scientists & Researchers or Scientific Community	0.39
Tourists	Media	0.39
Fishers or Harvesters	Activists & Environmentalists	0.38
Universities or Research Institutions	Crisis Narratives	0.38
Managers	Locals and Local Communities	0.38
Universities or Research Institutions	Industry & Private Sector	0.38
Universities or Research Institutions	Actors	0.38
Managers	Industry & Private Sector	0.37
Policymakers & Politicians	Nonprofits & NGOs	0.37
Tourists	Scientists & Researchers or Scientific Community	0.37
Universities or Research Institutions	Students & Young People	0.37
Managers	Government Agencies	0.36
Industry & Private Sector	Developing Countries	0.36
Scientists & Researchers or Scientific Community	Humanity or Society	0.36
Managers	Crisis Narratives	0.36
Students & Young People	Industry & Private Sector	0.36
Media	Humanity or Society	0.36
Policymakers & Politicians	Locals and Local Communities	0.36
Media	Fishers or Harvesters	0.36
Fishers or Harvesters	Developing Countries	0.36
Students & Young People	Recreational Divers	0.36
Nonprofits & NGOs	Activists & Environmentalists	0.36

Universities or Research Institutions	Recreational Divers	0.36
Resilience Narratives	Humanity or Society	0.36
Students & Young People	Crisis Narratives	0.36
International Governance	Humanity or Society	0.36
Tourists	Humanity or Society	0.35
Universities or Research Institutions	Managers	0.35
Policymakers & Politicians	International Governance	0.35
Policymakers & Politicians	Government Agencies	0.35
Policymakers & Politicians	Fishers or Harvesters	0.35
Policymakers & Politicians	Crisis Narratives	0.35
Locals and Local Communities	International Governance	0.35
Resilience Narratives	Developing Countries	0.35
ISRS or ICRS	Bad Actors' (for example climate deniers)	0.35
Managers	Humanity or Society	0.35
Government Agencies	Developing Countries	0.34
Resilience Narratives	Developed Countries	0.34
Industry & Private Sector	Developed Countries	0.34
Tourists	Resilience Narratives	0.34
Students & Young People	Fishers or Harvesters	0.34
Tourists	Activists & Environmentalists	0.34
Tourists	Government Agencies	0.34
Students & Young People	International Governance	0.34
Media	Managers	0.34
Nonprofits & NGOs	Developing Countries	0.34
Industry & Private Sector	Humanity or Society	0.34
Policymakers & Politicians	Industry & Private Sector	0.34
Humanity or Society	Developing Countries	0.33
Humanity or Society	General Public or Laypeople	0.33
International Governance	Developed Countries	0.33
Locals and Local Communities	Activists & Environmentalists	0.33
Policymakers & Politicians	Activists & Environmentalists	0.33
Policymakers & Politicians	General Public or Laypeople	0.33
Recreational Divers	Humanity or Society	0.33
Recreational Divers	Policymakers & Politicians	0.33
Scientists & Researchers or Scientific Community	Developing Countries	0.33
Stakeholders	Community organizations	0.33

Students & Young People	Government Agencies	0.33
Industry & Private Sector	General Public or Laypeople	0.33
Tourists	Locals and Local Communities	0.33
Resilience Narratives	Activists & Environmentalists	0.33
Nonprofits & NGOs	Humanity or Society	0.33
Managers	Actors	0.33
Media	General Public or Laypeople	0.33
Media	Activists & Environmentalists	0.33
Tourists	Managers	0.33
Tourists	Crisis Narratives	0.33
Humanity or Society	Developed Countries	0.33
International Governance	Industry & Private Sector	0.32
Resilience Narratives	International Governance	0.32
Recreational Divers	General Public or Laypeople	0.32
Locals and Local Communities	Humanity or Society	0.32
Media	International Governance	0.32
Students & Young People	Developing Countries	0.32
Resilience Narratives	Policymakers & Politicians	0.32
International Governance	Fishers or Harvesters	0.32
Policymakers & Politicians	Humanity or Society	0.32
Fishers or Harvesters	Developed Countries	0.32
Policymakers & Politicians	Media	0.32
Future Generations	Developing Countries	0.32
Recreational Divers	Managers	0.32
Tourists	Nonprofits & NGOs	0.32
Locals and Local Communities	General Public or Laypeople	0.31
Universities or Research Institutions	Stakeholders	0.31
Scientists & Researchers or Scientific Community	Activists & Environmentalists	0.31
Universities or Research Institutions	Policymakers & Politicians	0.31
Students & Young People	Actors	0.31
Government Agencies	Developed Countries	0.31
Resilience Narratives	General Public or Laypeople	0.31
Universities or Research Institutions	Media	0.31
Students & Young People	Policymakers & Politicians	0.31
Policymakers & Politicians	ISRS or ICRS	0.31
Stakeholders	Activists & Environmentalists	0.31
Resilience Narratives	Managers	0.30

Developing Countries	Crisis Narratives	0.30
Tourists	Policymakers & Politicians	0.30
General Public or Laypeople	Crisis Narratives	0.30
Volunteers	Humanity or Society	0.30
Humanity or Society	Activists & Environmentalists	0.30
Government Agencies	General Public or Laypeople	0.30
International Governance	Government Agencies	0.30
Managers	Community organizations	0.30
Humanity or Society	Fishers or Harvesters	0.30
Media	Community organizations	0.30
Policymakers & Politicians	Actors	0.30
Humanity or Society	Crisis Narratives	0.30
Universities or Research Institutions	International Governance	0.30
Nonprofits & NGOs	Managers	0.29
Students & Young People	Activists & Environmentalists	0.29
Humanity or Society	Government Agencies	0.29
Industry & Private Sector	Activists & Environmentalists	0.29
Scientists & Researchers or Scientific Community	International Governance	0.29
Scientists & Researchers or Scientific Community	Developed Countries	0.29
Recreational Divers	Developing Countries	0.29
Tourists	Actors	0.29
Tourists	Fishers or Harvesters	0.29
Developed Countries	Bad Actors' (for example climate deniers)	0.29
ISRS or ICRS	Activists & Environmentalists	0.29
Locals and Local Communities	Community organizations	0.29
Recreational Divers	Activists & Environmentalists	0.29
Stakeholders	Locals and Local Communities	0.29
Students & Young People	Aquarists	0.29
Recreational Divers	International Governance	0.28
Managers	Activists & Environmentalists	0.28
Universities or Research Institutions	Developing Countries	0.28
Managers	International Governance	0.28
Developing Countries	Actors	0.28
Future Generations	Activists & Environmentalists	0.28
ISRS or ICRS	Future Generations	0.28
Nonprofits & NGOs	Developed Countries	0.28

International Governance	Crisis Narratives	0.27
Policymakers & Politicians	Developed Countries	0.27
Students & Young People	General Public or Laypeople	0.27
Tourists	Community organizations	0.27
Stakeholders	Managers	0.27
ISRS or ICRS	Humanity or Society	0.27
General Public or Laypeople	Developing Countries	0.27
Industry & Private Sector	Community organizations	0.27
Stakeholders	Industry & Private Sector	0.27
Stakeholders	Resilience Narratives	0.26
Students & Young People	Developed Countries	0.26
Universities or Research Institutions	Military	0.26
Fishers or Harvesters	Aquarists	0.26
Boaters	Bad Actors' (for example climate deniers)	0.26
General Public or Laypeople	Bad Actors' (for example climate deniers)	0.26
Policymakers & Politicians	Developing Countries	0.26
Crisis Narratives	Activists & Environmentalists	0.26
Developed Countries	Crisis Narratives	0.26
International Governance	General Public or Laypeople	0.26
Students & Young People	Humanity or Society	0.26
Government Agencies	Activists & Environmentalists	0.26
Policymakers & Politicians	Managers	0.26
Scientists & Researchers or Scientific Community	Bad Actors' (for example climate deniers)	0.26
Universities or Research Institutions	Tourists	0.26
Humanity or Society	Community organizations	0.26
International Governance	Actors	0.26
Tourists	Developed Countries	0.25
Media	Aquarists	0.25
Universities or Research Institutions	Activists & Environmentalists	0.25
Nonprofits & NGOs	Future Generations	0.25
Scientists & Researchers or Scientific Community	ISRS or ICRS	0.25
Consultant	Bad Actors' (for example climate deniers)	0.25
Media	Developing Countries	0.25
Military	Community organizations	0.25

Restoration Practitioners	Bad Actors' (for example climate deniers)	0.25
Stakeholders	Media	0.25
Stakeholders	Military	0.25
Stakeholders	Nonprofits & NGOs	0.25
Students & Young People	Managers	0.25
Universities or Research Institutions	Developed Countries	0.25
General Public or Laypeople	Actors	0.25
Nonprofits & NGOs	General Public or Laypeople	0.25
Recreational Divers	Developed Countries	0.25
Resilience Narratives	Community organizations	0.25
Military	Locals and Local Communities	0.25
Scientists & Researchers or Scientific Community	Community organizations	0.25
Managers	Developing Countries	0.25
Tourists	Developing Countries	0.25
Tourists	Stakeholders	0.24
Aquarists	Activists & Environmentalists	0.24
International Governance	Future Generations	0.24
Volunteers	Activists & Environmentalists	0.24
Media	Bad Actors' (for example climate deniers)	0.24
Universities or Research Institutions	Community organizations	0.24
General Public or Laypeople	Fishers or Harvesters	0.24
Developing Countries	Activists & Environmentalists	0.24
Recreational Divers	Community organizations	0.24
Military	International Governance	0.24
Nonprofits & NGOs	ISRS or ICRS	0.24
Stakeholders	International Governance	0.24
Community organizations	Activists & Environmentalists	0.24
Future Generations	Developed Countries	0.24
Media	ISRS or ICRS	0.24
Tourists	International Governance	0.24
Industry & Private Sector	Future Generations	0.24
Humanity or Society	Consultant	0.24
Volunteers	Educators	0.24
Resilience Narratives	Aquarists	0.23
Humanity or Society	Actors	0.23
Resilience Narratives	Future Generations	0.23

Nonprofits & NGOs	Community organizations	0.23
Volunteers	ISRS or ICRS	0.23
Tourists	Students & Young People	0.23
International Governance	Activists & Environmentalists	0.23
Managers	ISRS or ICRS	0.23
Students & Young People	Stakeholders	0.23
Educators	Community organizations	0.23
Policymakers & Politicians	Bad Actors' (for example climate deniers)	0.23
Fishers or Harvesters	Community organizations	0.23
Industry & Private Sector	Bad Actors' (for example climate deniers)	0.23
Stakeholders	Fishers or Harvesters	0.23
ISRS or ICRS	General Public or Laypeople	0.23
Volunteers	Developing Countries	0.23
Developed Countries	Actors	0.22
Consultant	Community organizations	0.22
Government Agencies	Community organizations	0.22
Nonprofits & NGOs	Bad Actors' (for example climate deniers)	0.22
Stakeholders	Consultant	0.22
Volunteers	Future Generations	0.22
Recreational Divers	Military	0.22
Resilience Narratives	Bad Actors' (for example climate deniers)	0.22
Managers	General Public or Laypeople	0.22
Policymakers & Politicians	Aquarists	0.22
General Public or Laypeople	Future Generations	0.22
ISRS or ICRS	International Governance	0.22
Volunteers	Tourists	0.22
Media	Developed Countries	0.22
Nonprofits & NGOs	Aquarists	0.22
Policymakers & Politicians	Future Generations	0.22
Students & Young People	Bad Actors' (for example climate deniers)	0.22
Military	Industry & Private Sector	0.22
Volunteers	General Public or Laypeople	0.22
Actors	Activists & Environmentalists	0.22
Locals and Local Communities	Aquarists	0.21

Scientists & Researchers or Scientific Community	Aquarists	0.21
Volunteers	Community organizations	0.21
Volunteers	Policymakers & Politicians	0.21
Locals and Local Communities	Consultant	0.21
Government Agencies	Aquarists	0.21
Locals and Local Communities	Future Generations	0.21
Nonprofits & NGOs	Military	0.21
Recreational Divers	Bad Actors' (for example climate deniers)	0.21
Scientists & Researchers or Scientific Community	Future Generations	0.21
Volunteers	Resilience Narratives	0.21
Government Agencies	Future Generations	0.21
Managers	Developed Countries	0.21
Volunteers	International Governance	0.21
Volunteers	Scientists & Researchers or Scientific Community	0.21
Developing Countries	Bad Actors' (for example climate deniers)	0.21
International Governance	Community organizations	0.21
Stakeholders	Scientists & Researchers or Scientific Community	0.21
Military	Fishers or Harvesters	0.21
Volunteers	Media	0.21
Universities or Research Institutions	Humanity or Society	0.21
Developed Countries	Consultant	0.21
ISRS or ICRS	Industry & Private Sector	0.21
Industry & Private Sector	Aquarists	0.21
Crisis Narratives	Community organizations	0.20
Stakeholders	Crisis Narratives	0.20
Students & Young People	Community organizations	0.20
Volunteers	Recreational Divers	0.20
Stakeholders	Recreational Divers	0.20
Developed Countries	Community organizations	0.20
Future Generations	Bad Actors' (for example climate deniers)	0.20
Humanity or Society	Boaters	0.20
Locals and Local Communities	Bad Actors' (for example climate deniers)	0.20

Managers	Future Generations	0.20
Stakeholders	Developed Countries	0.20
Tourists	ISRS or ICRS	0.20
Locals and Local Communities	ISRS or ICRS	0.20
Tourists	General Public or Laypeople	0.20
Military	Managers	0.20
Developed Countries	Activists & Environmentalists	0.20
Stakeholders	Government Agencies	0.20
Tourists	Future Generations	0.20
Stakeholders	Humanity or Society	0.20
Future Generations	Fishers or Harvesters	0.19
Resilience Narratives	Military	0.19
Future Generations	Crisis Narratives	0.19
Scientists & Researchers or Scientific Community	Consultant	0.19
Volunteers	Nonprofits & NGOs	0.19
ISRS or ICRS	Consultant	0.19
Volunteers	Bad Actors' (for example climate deniers)	0.19
Aquarists	Actors	0.19
Community organizations	Aquarists	0.19
Stakeholders	Aquarists	0.19
Government Agencies	Bad Actors' (for example climate deniers)	0.19
Recreational Divers	Future Generations	0.19
Policymakers & Politicians	Community organizations	0.19
Stakeholders	Policymakers & Politicians	0.19
Military	Media	0.19
Industry & Private Sector	Consultant	0.19
Future Generations	Consultant	0.19
Crisis Narratives	Aquarists	0.18
General Public or Laypeople	Activists & Environmentalists	0.18
ISRS or ICRS	Crisis Narratives	0.18
Managers	Bad Actors' (for example climate deniers)	0.18
Students & Young People	Future Generations	0.18
Fishers or Harvesters	Bad Actors' (for example climate deniers)	0.18
Resilience Narratives	ISRS or ICRS	0.18

Volunteers	Industry & Private Sector	0.18
Military	Government Agencies	0.18
Future Generations	Community organizations	0.18
International Governance	Educators	0.18
Stakeholders	Future Generations	0.18
Universities or Research Institutions	General Public or Laypeople	0.18
Universities or Research Institutions	ISRS or ICRS	0.18
Students & Young People	Military	0.18
Military	Consultant	0.18
Universities or Research Institutions	Future Generations	0.18
Humanity or Society	Aquarists	0.18
ISRS or ICRS	Developing Countries	0.18
Tourists	Bad Actors' (for example climate deniers)	0.18
Nonprofits & NGOs	Consultant	0.18
Universities or Research Institutions	Consultant	0.18
Students & Young People	Restoration Practitioners	0.18
ISRS or ICRS	Government Agencies	0.17
Recreational Divers	ISRS or ICRS	0.17
Volunteers	Fishers or Harvesters	0.17
Crisis Narratives	Bad Actors' (for example climate deniers)	0.17
Military	Developed Countries	0.17
Stakeholders	Developing Countries	0.17
Volunteers	Managers	0.17
Media	Future Generations	0.17
Military	Crisis Narratives	0.17
Educators	Boaters	0.17
Educators	Developing Countries	0.17
International Governance	Aquarists	0.17
International Governance	Bad Actors' (for example climate deniers)	0.17
Nonprofits & NGOs	Fishery Orgs or Councils	0.17
Restoration Practitioners	Farmers	0.17
Volunteers	Boaters	0.17
Volunteers	Developed Countries	0.17
ISRS or ICRS	Fishers or Harvesters	0.16
Universities or Research Institutions	Aquarists	0.16

Universities or Research Institutions	Bad Actors' (for example climate deniers)	0.16
Policymakers & Politicians	Military	0.16
Resilience Narratives	Consultant	0.16
Community organizations	Actors	0.16
Military	Actors	0.16
Recreational Divers	Aquarists	0.16
Stakeholders	Actors	0.16
Fishers or Harvesters	Consultant	0.16
General Public or Laypeople	Community organizations	0.16
Bad Actors' (for example climate deniers)	Activists & Environmentalists	0.16
Policymakers & Politicians	Educators	0.16
Scientists & Researchers or Scientific Community	Military	0.16
Community organizations	Bad Actors' (for example climate deniers)	0.16
Restoration Practitioners	Humanity or Society	0.16
Stakeholders	Bad Actors' (for example climate deniers)	0.16
Fishery Orgs or Councils	Community organizations	0.15
International Governance	Consultant	0.15
Military	Fishery Orgs or Councils	0.15
Restoration Practitioners	Boaters	0.15
Stakeholders	Fishery Orgs or Councils	0.15
Tourists	Aquarists	0.15
Volunteers	Locals and Local Communities	0.15
Future Generations	Actors	0.15
ISRS or ICRS	Community organizations	0.15
Stakeholders	ISRS or ICRS	0.15
Volunteers	Universities or Research Institutions	0.15
Fishery Orgs or Councils	Fishers or Harvesters	0.15
Managers	Consultant	0.15
Dealers	Aquarists	0.15
Developing Countries	Community organizations	0.15
General Public or Laypeople	Aquarists	0.15
Universities or Research Institutions	Restoration Practitioners	0.15
Media	Consultant	0.15
Government Agencies	Consultant	0.14

ISRS or ICRS	Actors	0.14
Consultant	Activists & Environmentalists	0.14
Developing Countries	Consultant	0.14
Tourists	Military	0.14
Volunteers	Crisis Narratives	0.14
Volunteers	Fishery Orgs or Councils	0.14
Volunteers	Government Agencies	0.14
Recreational Divers	Fishery Orgs or Councils	0.14
Managers	Aquarists	0.14
Students & Young People	ISRS or ICRS	0.14
Military	Humanity or Society	0.14
ISRS or ICRS	Boaters	0.14
ISRS or ICRS	Educators	0.14
Bad Actors' (for example climate deniers)	Actors	0.14
Developing Countries	Boaters	0.14
Recreational Divers	Consultant	0.13
Resilience Narratives	Fishery Orgs or Councils	0.13
Boaters	Activists & Environmentalists	0.13
Dealers	Activists & Environmentalists	0.13
Educators	Activists & Environmentalists	0.13
Military	General Public or Laypeople	0.13
Restoration Practitioners	Nonprofits & NGOs	0.13
Tourists	Boaters	0.13
Scientists & Researchers or Scientific Community	Restoration Practitioners	0.13
Restoration Practitioners	ISRS or ICRS	0.13
Students & Young People	Consultant	0.13
Developed Countries	Boaters	0.13
General Public or Laypeople	Consultant	0.13
Volunteers	Students & Young People	0.13
Industry & Private Sector	Fishery Orgs or Councils	0.13
Dealers	Community organizations	0.13
Humanity or Society	Educators	0.13
Restoration Practitioners	Policymakers & Politicians	0.13
Stakeholders	Boaters	0.13
Stakeholders	Educators	0.13
Military	Developing Countries	0.12

ISRS or ICRS	Developed Countries	0.12
Students & Young People	Boaters	0.12
Students & Young People	Educators	0.12
Tourists	Fishery Orgs or Councils	0.12
Consultant	Aquarists	0.12
Crisis Narratives	Consultant	0.12
Restoration Practitioners	Community organizations	0.12
Military	Activists & Environmentalists	0.12
Policymakers & Politicians	Fishery Orgs or Councils	0.12
Fishery Orgs or Councils	Developed Countries	0.12
General Public or Laypeople	Boaters	0.12
Media	Boaters	0.12
Universities or Research Institutions	Fishery Orgs or Councils	0.12
Nonprofits & NGOs	Boaters	0.12
Nonprofits & NGOs	Dealers	0.12
Managers	Educators	0.12
Future Generations	Fishery Orgs or Councils	0.12
Restoration Practitioners	Media	0.12
Locals and Local Communities	Educators	0.11
Scientists & Researchers or Scientific Community	Boaters	0.11
Scientists & Researchers or Scientific Community	Educators	0.11
Humanity or Society	Fishery Orgs or Councils	0.11
International Governance	Dealers	0.11
Restoration Practitioners	General Public or Laypeople	0.11
Students & Young People	Fishery Orgs or Councils	0.11
Developing Countries	Aquarists	0.11
Volunteers	Actors	0.11
Consultant	Boaters	0.11
Dealers	Consultant	0.11
Government Agencies	Fishery Orgs or Councils	0.11
Policymakers & Politicians	Consultant	0.11
Restoration Practitioners	Recreational Divers	0.11
Scientists & Researchers or Scientific Community	Fishery Orgs or Councils	0.11
General Public or Laypeople	Fishery Orgs or Councils	0.11
Boaters	Aquarists	0.11
Educators	Aquarists	0.11

Developed Countries	Aquarists	0.11
Resilience Narratives	Boaters	0.11
International Governance	Fishery Orgs or Councils	0.11
Restoration Practitioners	Consultant	0.11
Fishers or Harvesters	Educators	0.10
Restoration Practitioners	Resilience Narratives	0.10
Consultant	Actors	0.10
Policymakers & Politicians	Farmers	0.10
Farmers	Activists & Environmentalists	0.10
Industry & Private Sector	Boaters	0.10
Industry & Private Sector	Educators	0.10
Policymakers & Politicians	Boaters	0.10
Volunteers	Restoration Practitioners	0.10
Nonprofits & NGOs	Educators	0.10
Scientists & Researchers or Scientific Community	Farmers	0.10
Media	Farmers	0.10
Fishery Orgs or Councils	Developing Countries	0.10
Students & Young People	Farmers	0.10
Fishery Orgs or Councils	Aquarists	0.10
Locals and Local Communities	Boaters	0.10
Locals and Local Communities	Dealers	0.10
Volunteers	Stakeholders	0.10
Fishery Orgs or Councils	Consultant	0.10
Restoration Practitioners	Locals and Local Communities	0.10
Students & Young People	Dealers	0.10
Developed Countries	Dealers	0.09
Educators	Developed Countries	0.09
Recreational Divers	Educators	0.09
Locals and Local Communities	Fishery Orgs or Councils	0.09
Educators	Bad Actors' (for example climate deniers)	0.09
Fishery Orgs or Councils	Crisis Narratives	0.09
Managers	Boaters	0.09
Resilience Narratives	Dealers	0.09
Restoration Practitioners	Government Agencies	0.09
Restoration Practitioners	Managers	0.09
Fishers or Harvesters	Boaters	0.09

Fishers or Harvesters	Dealers	0.09
Fishery Orgs or Councils	Activists & Environmentalists	0.09
Military	Bad Actors' (for example climate deniers)	0.09
General Public or Laypeople	Educators	0.09
Managers	Fishery Orgs or Councils	0.09
Stakeholders	General Public or Laypeople	0.09
Farmers	Community organizations	0.08
Future Generations	Boaters	0.08
Future Generations	Educators	0.08
International Governance	Boaters	0.08
Military	Future Generations	0.08
Stakeholders	Farmers	0.08
Restoration Practitioners	Crisis Narratives	0.08
Restoration Practitioners	International Governance	0.08
Locals and Local Communities	Farmers	0.08
Community organizations	Boaters	0.08
Fishery Orgs or Councils	Actors	0.08
Fishery Orgs or Councils	Bad Actors' (for example climate deniers)	0.08
Military	Dealers	0.08
Military	Educators	0.08
Restoration Practitioners	Future Generations	0.08
Stakeholders	Dealers	0.08
Universities or Research Institutions	Boaters	0.08
Universities or Research Institutions	Educators	0.08
Volunteers	Consultant	0.08
Bad Actors' (for example climate deniers)	Aquarists	0.08
Government Agencies	Boaters	0.08
Government Agencies	Educators	0.08
Dealers	Boaters	0.08
Developing Countries	Dealers	0.08
Educators	Dealers	0.08
ISRS or ICRS	Aquarists	0.08
Recreational Divers	Boaters	0.08
Stakeholders	Restoration Practitioners	0.08
Tourists	Farmers	0.08
Media	Dealers	0.08

Media	Educators	0.08
Tourists	Dealers	0.08
Tourists	Educators	0.08
Resilience Narratives	Educators	0.07
Military	Aquarists	0.07
Tourists	Restoration Practitioners	0.07
Crisis Narratives	Boaters	0.07
Dealers	Crisis Narratives	0.07
Educators	Crisis Narratives	0.07
Farmers	Aquarists	0.07
Media	Fishery Orgs or Councils	0.07
Restoration Practitioners	Educators	0.07
Industry & Private Sector	Dealers	0.07
Restoration Practitioners	Industry & Private Sector	0.07
Managers	Farmers	0.07
Managers	Dealers	0.07
Government Agencies	Dealers	0.07
Tourists	Consultant	0.07
Restoration Practitioners	Actors	0.06
Farmers	Developed Countries	0.06
Fishery Orgs or Councils	Dealers	0.06
Fishery Orgs or Councils	Educators	0.06
Humanity or Society	Farmers	0.06
Recreational Divers	Dealers	0.06
Universities or Research Institutions	Farmers	0.06
Humanity or Society	Dealers	0.06
Resilience Narratives	Farmers	0.06
Restoration Practitioners	Developed Countries	0.06
Restoration Practitioners	Fishery Orgs or Councils	0.06
Universities or Research Institutions	Dealers	0.06
Fishers or Harvesters	Farmers	0.06
Restoration Practitioners	Fishers or Harvesters	0.06
Boaters	Actors	0.06
Dealers	Actors	0.06
Educators	Actors	0.06
Farmers	Consultant	0.06
Industry & Private Sector	Farmers	0.06
Military	ISRS or ICRS	0.06

Volunteers	Aquarists	0.06
Government Agencies	Farmers	0.05
Educators	Consultant	0.05
Volunteers	Farmers	0.05
Farmers	Developing Countries	0.05
Volunteers	Dealers	0.05
Future Generations	Aquarists	0.05
Restoration Practitioners	Developing Countries	0.05
Farmers	Actors	0.05
Nonprofits & NGOs	Farmers	0.05
Policymakers & Politicians	Dealers	0.05
Scientists & Researchers or Scientific Community	Dealers	0.05
Farmers	Bad Actors' (for example climate deniers)	0.05
ISRS or ICRS	Farmers	0.04
Future Generations	Farmers	0.04
Farmers	Crisis Narratives	0.04
Future Generations	Dealers	0.04
Military	Boaters	0.04
ISRS or ICRS	Fishery Orgs or Councils	0.04
Restoration Practitioners	Military	0.04
Restoration Practitioners	Aquarists	0.03
Volunteers	Military	0.03
Recreational Divers	Farmers	0.03
Restoration Practitioners	Activists & Environmentalists	0.03
General Public or Laypeople	Farmers	0.03
General Public or Laypeople	Dealers	0.03
International Governance	Farmers	0.03
Dealers	Bad Actors' (for example climate deniers)	0.00
Farmers	Boaters	0.00
Farmers	Dealers	0.00
Farmers	Educators	0.00
Fishery Orgs or Councils	Boaters	0.00
Fishery Orgs or Councils	Farmers	0.00
ISRS or ICRS	Dealers	0.00
Military	Farmers	0.00
Restoration Practitioners	Dealers	0.00

Distal drivers of local threats		
Code A	Code B	Jaccard's coefficient
Resilience Narratives	Economic	0.55
Resilience Narratives	Crisis Narratives	0.55
Economic	Crisis Narratives	0.51
Resilience Narratives	Population Density or Growth (Human)	0.50
Population Density or Growth (Human)	Economic	0.49
Political Threat	Economic	0.49
Resilience Narratives	Political Threat	0.46
Political Threat	Misinformation or Lack of Awareness, Misunderstanding	0.44
Resilience Narratives	Land use	0.44
Political Threat	Crisis Narratives	0.44
Population Density or Growth (Human)	Crisis Narratives	0.43
Population Density or Growth (Human)	Political Threat	0.43
Resilience Narratives	Misinformation or Lack of Awareness, Misunderstanding	0.40
Land use	Economic	0.39
Misinformation or Lack of Awareness, Misunderstanding	Crisis Narratives	0.39
Misinformation or Lack of Awareness, Misunderstanding	Economic	0.39
Political Threat	Land use	0.38
Population Density or Growth (Human)	Land use	0.37
Land use	Crisis Narratives	0.36
Misinformation or Lack of Awareness, Misunderstanding	Land use	0.36
Population Density or Growth (Human)	Misinformation or Lack of Awareness, Misunderstanding	0.34
Political Threat	General Consumption or Resource Use	0.31

Population Density or Growth (Human)	General Consumption or Resource Use	0.29
Misinformation or Lack of Awareness, Misunderstanding	General Consumption or Resource Use	0.28
Land use	General Consumption or Resource Use	0.24
Resilience Narratives	General Consumption or Resource Use	0.22
General Consumption or Resource Use	Economic	0.22
General Consumption or Resource Use	Crisis Narratives	0.17
Maladaptation	Limited Capacity	0.13
Limited Capacity	Economic	0.09
Limited Capacity	Land use	0.09
Resilience Narratives	Limited Capacity	0.07
Misinformation or Lack of Awareness, Misunderstanding	Limited Capacity	0.07
Population Density or Growth (Human)	Limited Capacity	0.06
Limited Capacity	Crisis Narratives	0.05
Misinformation or Lack of Awareness, Misunderstanding	Maladaptation	0.05
Resilience Narratives	Maladaptation	0.05
Maladaptation	Land use	0.04
Political Threat	Maladaptation	0.04
Political Threat	Limited Capacity	0.04
Maladaptation	Economic	0.04
Maladaptation	Crisis Narratives	0.03
Limited Capacity	General Consumption or Resource Use	0.00
Maladaptation	General Consumption or Resource Use	0.00
Population Density or Growth (Human)	Maladaptation	0.00

Local threats		
Code A	Code B	Jaccard's coefficient
Pollution & Water Quality	Fishing or harvesting	0.75
Pollution & Water Quality	Crisis Narratives	0.72
Fishing or harvesting	Crisis Narratives	0.72
General or Unspecified Degradation	Crisis Narratives	0.70
General or Unspecified Degradation	Fishing or harvesting	0.64
Pollution & Water Quality	General or Unspecified Degradation	0.63
Interactions with Climate Change	General or Unspecified Degradation	0.61
Development and construction	Crisis Narratives	0.58
Resilience Narratives	Fishing or harvesting	0.57
Pollution & Water Quality	Development and construction	0.57
Fishing or harvesting	Development and construction	0.56
General or Unspecified Degradation	Development and construction	0.55
Interactions with Climate Change	Crisis Narratives	0.55
Resilience Narratives	Crisis Narratives	0.55
Interactions with Climate Change	Fishing or harvesting	0.54
Resilience Narratives	Development and construction	0.54
Resilience Narratives	Interactions with Climate Change	0.53
Resilience Narratives	Pollution & Water Quality	0.53
Resilience Narratives	General or Unspecified Degradation	0.51
Pollution & Water Quality	Interactions with Climate Change	0.51
Interactions with Climate Change	Development and construction	0.51
Resilience Narratives	Direct Damage	0.48
Tourism and Diving	Crisis Narratives	0.48
Pollution & Water Quality	Direct Damage	0.47
Tourism and Diving	Resilience Narratives	0.46
Direct Damage	Crisis Narratives	0.45
Fishing or harvesting	Direct Damage	0.45
Tourism and Diving	Interactions with Climate Change	0.44
General or Unspecified Degradation	Direct Damage	0.43
Direct Damage	Development and construction	0.42
Tourism and Diving	Fishing or harvesting	0.42
Tourism and Diving	General or Unspecified Degradation	0.41
Tourism and Diving	Pollution & Water Quality	0.40
Interactions with Climate Change	Direct Damage	0.40
Invasive Species	Interactions with Climate Change	0.39

Tourism and Diving	Development and construction	0.37
Tourism and Diving	Direct Damage	0.37
Resilience Narratives	Invasive Species	0.35
Invasive Species	General or Unspecified Degradation	0.33
Invasive Species	Development and construction	0.29
Invasive Species	Direct Damage	0.28
Invasive Species	Crisis Narratives	0.26
Invasive Species	Fishing or harvesting	0.26
Pollution & Water Quality	Invasive Species	0.25
Tourism and Diving	Invasive Species	0.24
Military Practices	Direct Damage	0.20
Resilience Narratives	Military Practices	0.17
Military Practices	Development and construction	0.16
Military Practices	Fishing or harvesting	0.13
Military Practices	Crisis Narratives	0.13
Military Practices	Interactions with Climate Change	0.12
Pollution & Water Quality	Military Practices	0.12
Military Practices	Invasive Species	0.12
Tourism and Diving	Military Practices	0.12
Military Practices	General or Unspecified Degradation	0.11

<i>Solutions</i>		
Code A	Code B	Jaccard's coefficient
Science (Improvements in knowledge and understanding)	Economic and Social Solutions	0.70
Rehabilitation & Restoration	Economic and Social Solutions	0.67
Science (Improvements in knowledge and understanding)	Crisis Narratives	0.67
Resource Management	Economic and Social Solutions	0.67
Resource Management	Individual Actions (e.g. Behavior Change)	0.66
Resource Management	Crisis Narratives	0.66
Science (Improvements in knowledge and understanding)	Rehabilitation & Restoration	0.66
Science (Improvements in knowledge and understanding)	Resource Management	0.65
Legal or Regulatory (includes Policy)	Crisis Narratives	0.65
Resource Management	Rehabilitation & Restoration	0.64
Science (Improvements in knowledge and understanding)	Legal or Regulatory (includes Policy)	0.64
Science (Improvements in knowledge and understanding)	Public awareness, education, or training	0.63
Resource Management	Legal or Regulatory (includes Policy)	0.63
Economic and Social Solutions	Crisis Narratives	0.63
Legal or Regulatory (includes Policy)	Economic and Social Solutions	0.61
Public awareness, education, or training	Crisis Narratives	0.61
Science (Improvements in knowledge and understanding)	Resilience Narratives	0.60
Rehabilitation & Restoration	Crisis Narratives	0.59
Individual Actions (e.g. Behavior Change)	Crisis Narratives	0.59
Legal or Regulatory (includes Policy)	Individual Actions (e.g. Behavior Change)	0.59
Public awareness, education, or training	Economic and Social Solutions	0.58
Resilience Narratives	Economic and Social Solutions	0.58
Individual Actions (e.g. Behavior Change)	Economic and Social Solutions	0.58
Resilience Narratives	Public awareness, education, or training	0.57
Rehabilitation & Restoration	Legal or Regulatory (includes Policy)	0.57

Rehabilitation & Restoration	Individual Actions (e.g. Behavior Change)	0.55
Resource Management	Resilience Narratives	0.55
Resilience Narratives	Crisis Narratives	0.55
Science (Improvements in knowledge and understanding)	Individual Actions (e.g. Behavior Change)	0.54
Rehabilitation & Restoration	Public awareness, education, or training	0.54
Public awareness, education, or training	Individual Actions (e.g. Behavior Change)	0.54
Public awareness, education, or training	Legal or Regulatory (includes Policy)	0.53
Resilience Narratives	Legal or Regulatory (includes Policy)	0.53
Resource Management	Public awareness, education, or training	0.51
Resilience Narratives	Rehabilitation & Restoration	0.51
Resilience Narratives	Individual Actions (e.g. Behavior Change)	0.50
Resilience Narratives	Cleanup or Remediation	0.38
Unspecified Intervention or Strategy	Resilience Narratives	0.37
Unspecified Intervention or Strategy	Rehabilitation & Restoration	0.35
Unspecified Intervention or Strategy	Cleanup or Remediation	0.34
Unspecified Intervention or Strategy	Individual Actions (e.g. Behavior Change)	0.34
Unspecified Intervention or Strategy	Science (Improvements in knowledge and understanding)	0.34
Science (Improvements in knowledge and understanding)	Cleanup or Remediation	0.33
Economic and Social Solutions	Cleanup or Remediation	0.33
Unspecified Intervention or Strategy	Public awareness, education, or training	0.32
Unspecified Intervention or Strategy	Economic and Social Solutions	0.32
Individual Actions (e.g. Behavior Change)	Cleanup or Remediation	0.32
Unspecified Intervention or Strategy	Crisis Narratives	0.32
Legal or Regulatory (includes Policy)	Cleanup or Remediation	0.32
Crisis Narratives	Cleanup or Remediation	0.31
Resource Management	Cleanup or Remediation	0.31
Public awareness, education, or training	Cleanup or Remediation	0.30
Rehabilitation & Restoration	Cleanup or Remediation	0.30
Unspecified Intervention or Strategy	Resource Management	0.30

Unspecified Intervention or Strategy	Legal or Regulatory (includes Policy)	0.28
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