Insight into coral reef ecosystems: Investigations into the application of acoustics to monitor coral reefs and how corallivorous fish respond to mass coral mortality.

by

Sean Dimoff

BSc, University of Hawai‘i, 2016

A Thesis Submitted in Partial Fulfillment

of the Requirements for the Degree of

MASTER OF SCIENCE

in the Department of Biology

University of Victoria

Supervisory Committee

Insight into coral reef ecosystems: Investigations into the application of acoustics to monitor coral reefs and how corallivorous fish respond to mass coral mortality.

by

Sean Dimoff

BSc, University of Hawaiʻi, 2016

Supervisory Committee

Dr. Julia K. Baum, Supervisor
Department of Biology

Dr. Francis Juanes, Departmental Member
Department of Biology

Dr. William H. Halliday, Outside Member
School of Earth and Ocean Sciences

Abstract

Coral reefs around the world are threatened by a variety of sources, from localized impacts, including overfishing and coastal development, to global temperature increases and ocean acidification. Conserving these marine biodiversity havens requires both global and local action informed by scientific research. In this thesis, I use data collected from the coral reefs around Kiritimati atoll (Republic of Kiribati) in the central equatorial Pacific, first to assess the applicability of two common metrics used in passive underwater acoustic research, and second to examine the effects of a marine heatwave and local human disturbance on an assemblage of corallivorous fish. Using acoustic data recorded in 2017 and 2018 on reefs around Kiritimati, I assess how sound pressure level (SPL) and the acoustic complexity index (ACI) respond to changes in fish sounds in a low frequency band (160 Hz – 1 kHz) and snapping shrimp snaps in a high frequency band (1 kHz – 22 kHz). I found that while SPL was positively correlated with increases in fish sounds and snap density, changes in ACI were dependent upon the settings chosen for its calculation, with the density of snaps negatively correlated with ACI across all settings. These findings provide evidence that despite its quick and prolific adoption, acoustic metrics like ACI should be thoroughly field-tested and standardized before they are applied to new ecosystems like coral reefs. Next, using underwater visual censuses (UVCs) of reef fish assemblages, I quantified how two functional groups of corallivores, obligate and facultative, responded to a mass coral mortality event created by the 2015-2016 El Niño. Declines in abundance of both groups were largely driven by the response of coral-associated damselfishes, *Plectroglyphidodon johnstonianus* in the obligate group and *Plectroglyphidodon dickii* in the facultative group, to heat stress and subsequent coral mortality. I also observed a significant decline in the species richness of obligate corallivores, and a continued decline in the abundance of obligate corallivores three years after the mass coral mortality event. Additionally, facultative corallivore abundance increased with disturbance, although the effect was modulated by year, likely due to their more adaptable diets. Corallivore assemblage structure was also influenced by the heat stress event, recovery, and local human disturbance. These results detail how an entire corallivorous assemblage is impacted by a coral mortality event and incidentally provide a timeline for corallivore decline. Together, these results provide information about new ways of monitoring coral reefs, and the ways in which two components of the reef fish community, obligate and facultative corallivores, respond to a mass coral mortality event.

Table of Contents

List of Tables

List of Figures

Acknowledgements

This thesis would not have been possible without the efforts of my mentors, collaborators, teachers, and friends. First, I would like to thank Dr. Julia Baum for her guidance throughout the last two years and for always pushing me to achieve my best. You have supported me through some supremely difficult times and pushed me forward when it was needed. Your passion and dedication to exceptional science are inspiring. I would also like to thank my committee members – Dr. William Halliday and Dr. Francis Juanes – your assistance, compassion, and advice helped guide me through this thesis. Thank you to Bill for guiding me through the field of underwater acoustics and consistently handling my many questions with grace and patience, and to Francis for providing me with thought provoking questions to make me think more deeply about how I approach the questions that intrigue me.

This thesis relies on data that was collected by an incredible group of people that I would like to take the opportunity to acknowledge here. Thank you to Scott Clark, for taking me under your wing on my first trip to Kiritimati. Your leadership and good humor made that expedition one that I will never forget. To Matt Pine, for sharing your passion of acoustics with me and showing me the adventurous life that it can lead to. To Tyler Phelps, thank you for being one of the best friends and dive buddies I could ever ask for, for making me laugh through the stress, and for always pushing me to be the best that I can be. I am forever grateful for your friendship. To Kevin Bruce, thank you for putting up with all that I could throw at you, for listening to me and for taking care of me when it was needed. And to Kristina Tietjen, thank you for your support and your help through my studies, you helped me when I was down and supported me through some of my roughest patches. I would also like to extend my thanks to Jenn Magel, Jenny Smith, Sarah Franklin, Blake Hamilton, Niallan O’Brien, Kieran Cox, Hannah Epstein, and Danielle Claar for their assistance, guidance, leadership, and companionship during my several expeditions to Kiritimati.

This research would also not have been possible without an incredible community of people on Kiritimati. Ikari House and its staff have always provided a safe, clean, and enjoyable base of operations for the team to work. Thank you to Jacob, Lavinia and Dwayne Teem for all their help over the years, from shipping supplies to ensuring our stay was comfortable and our research was progressing. I would also like to thank Alfred, his family, and his team for their incredible work filling all our tanks each day and ensuring that we were always breathing safe air. Your kindness, patience, and hard work made the late nights and early mornings so much more enjoyable. Without the approval, supervision, and assistance of the Government of Kiribati our research could never have happened. Thank you Taratau and Tataua from the Ministries of Fisheries on Kiritimati for their help and continual support for our research program.

I was also fortunate to share lab space with many smart, talented, and compassionate people during my time at the University of Victoria. Both past and present members of both the Baum and Juanes labs have provided support, laughs, and incredible memories during my time in Victoria. From Christmas parties to road trip duets and lunchtime conversations about nothing, thank you for making my graduate school experience one that I might reflect on positively.

Aside from work, I would not be where I am today without the love and support of my family. Roy and Carrie, your unwavering support throughout this entire process has lightened my load, pushed me through the hard times, and provided me with a deep friendship that I am so fortunate for. Marjie and Keith, you have always reminded me of my worth and encouraged me to chase my dreams, thank you for always supporting me. To my closest friends - Marcus, Harrison, Alex, Chris, Dylan, and Weston - thank you all for the deep conversations and the light

ones, for pushing me, and for making me laugh. Finally, I would like to thank my wonderful girlfriend, Samara, for her support and encouragement throughout this arduous final year.

Finally, I would like to acknowledge the sources of funding that have made this research possible. My project would not have been possible without the MITACS Accelerate fellowship and the World Wildlife Fund for Nature (WWF). Fieldwork on Kiritimati was additionally supported by the National Science Foundation, the Rufford Maurice Laing Foundation, the Canadian Foundation for Innovation, the British Columbia Knowledge Development Fund, the Packard Foundation, the Pew Charitable Trusts, the University of Victoria Center for Asia-Pacific Initiatives, and the Government of Kiribati.

Dedication

To my father, Roy.

For your guidance and inspiration,

for teaching me to appreciate the natural world,

but most of all for your friendship.

Chapter 1 - Introduction

Coral reefs are among the most diverse ecosystems on the planet, providing important ecosystem services to human populations worldwide (Woodhead et al., 2019). Despite covering less than 1% of the ocean floor, coral reefs are home to over 4,000 species of fish and 800 types of coral (Burke et al., 2011a). Reef building scleractinian corals engineer their environment, providing the foundation for tropical coral reef ecosystems (Gillis et al., 2014) in addition to providing refuge for their highly diverse inhabitants (Graham et al., 2008). These structures play an important role in protecting coastal communities by reducing wave energy by up to 95%, benefitting an estimated 100 million people around the world (Ferrario et al., 2014), and reducing annual expected damages by storms by more than $4 billion USD annually (Beck et al., 2018). Tropical island nations worldwide depend on fishing coral reef ecosystems for a majority of their dietary protein (Bell et al., 2009; Maryann S. Watson et al., 2016). Additionally, tourism on coral reefs generates revenues in over 100 countries and territories worldwide and is valued at $35.8 billion USD annually (Spalding et al., 2017). However, despite the global ecological and economic role that they play, these essential ecosystems are under increasing threat (Hughes et al., 2018).

At both global and local scales, coral reef ecosystems are being threatened by human activity. Globally, anthropogenic carbon emissions are causing the world’s oceans to both warm and become more acidic (Hoegh-Guldberg et al., 2017), increasing stress on temperature and pH sensitive scleractinian corals and promoting coral bleaching events that can result in coral mortality (Hoegh-Guldberg, 2011). As global temperatures continue to rise, it is predicted that marine heatwaves, including El Niño events, could double in frequency and continue to increase in intensity (Cai et al., 2014). El Niño events are large-scale, natural climatic events that typically occur every 3-6 years, creating temporary changes in atmospheric circulation and oceanic conditions which lead to increased sea-surface temperatures (SSTs) in the central and eastern Pacific, with potentially catastrophic consequences for local fauna (Barber and Chavez, 1983; Reyes-Bonilla et al., 2002). In addition to increasing temperatures, anthropogenic carbon emissions are absorbed by the world's oceans, reducing pH and decreasing the calcium carbonate ($CaCO_3$) saturation state, commonly referred to as 'ocean acidification' (Doney et al., 2009). These changes to seawater chemistry result in reduced calcification rates and growth for a variety of invertebrates, including reef-building corals (Hoegh-Guldberg et al., 2017). Locally, coastal development can increase sedimentation in the water and combine with nutrient pollution to smother corals and increase macroalgal growth (Dubinsky and Stambler, 1996; Munday, 2004). When combined with overfishing of the herbivorous fishes that regulate algal biomass and increased temperatures, these local stressors can increase coral mortality eightfold, decimating coral ecosystems (Zaneveld et al., 2016). This destruction does not end with corals themselves, changes in coral cover and structure have lasting effects on inhabitants of coral reefs.

Reef fish communities are diverse and important components of coral reef ecosystems that are altered by coral reef destruction and overexploitation. These communities depend on scleractinian corals for both food (Rotjan and Lewis, 2008) and shelter (Darling et al., 2017; Hixon and Beets, 1993). Coral mortality events, caused by either coral bleaching or outbreaks of destructive corallivores like *Acanthaster planci* (Kayal et al., 2012) can result in restructuring of fish communities (Garpe et al., 2006; Viviani et al., 2019). Subsequent structural loss can then deplete both reef fish and invertebrate abundance (Nelson et al., 2016; Wilson et al., 2006). When coral mortality is combined with the depletion of local herbivores the dominance of live coral can be succeeded by macroalgae, resulting in a benthic phase-shift (McManus and

Polsenberg, 2004). These phase shifts can then lead to drastic reductions in fish abundance and significantly altered fish communities (Chong-Seng et al., 2012). Additionally, the depletion of targeted fishes through overfishing can reduce their ecosystem function, resulting in trophic restructuring (DeMartini et al., 2008). Overexploitation by collectors for the aquarium trade might also contribute to these reduced ecosystem functions by removing high value species from coral reefs (Tissot and Hallacher, 2003). Reef fish serve as an integral piece of the coral reef ecosystem, however, the destruction of their environment combined with overexploitation through fishing and aquarium collecting is resulting in major changes to their assemblage structure and functional role on reefs.

Monitoring coral reef fish communities and their functions is required to determine worthwhile management actions for their conservation. Historically, visual monitoring, typically referred to as underwater visual censuses (UVC), has provided most of the information used in quantifying coral reef fish assemblages (Bohnsack and Bannerot, 1986; Hill and Wilkinson, 2004). Visual monitoring provides the distinct advantage of providing first-hand observations of the ecosystem and has been used to aid in the creation and monitoring of marine protected areas (MPAs) on coral reefs around the world (Russ and Alcala, 1996; Williams et al., 2015). Unfortunately, this monitoring is often expensive and time consuming, limiting its utility on a large scale. Recent growth in the study of underwater acoustics has created new passive tools for the study and monitoring of coral reefs (Staaterman et al., 2017). New indices introduced by passive acoustic monitoring (PAM) studies are also being explored to determine their utility in describing the abundance and diversity of fish in the marine environment (Lindseth and Lobel, 2018). However, acoustic studies, particularly on coral reefs, are rarely connected with direct observations of the sound-making species, limiting the effectiveness of their application (Tricas and Boyle, 2014). Despite their limitations, each of these monitoring systems can provide worthwhile information to inform policy decisions (Daw et al., 2011; Rountree et al., 2006). Therefore, by establishing a foundation of knowledge concerning multiple monitoring systems, we can make informed decisions about which systems best suit a variety of conservation objectives.

1.1 Applying Acoustics to Coral Reefs

New applications in passive acoustics are expanding its usefulness as a tool for ecosystem monitoring. Since its inception over 80 years ago as a tool for marine fisheries, over 800 species of soniferous fishes have been identified around the world (Rountree et al., 2006). At the same time, studies have revealed that sound production plays a communicative role in fish behavior (Lobel, 2013; Lobel et al., 2010). Recently, the scope of underwater acoustics has broadened to investigate soundscapes produced by entire ecosystems (Lindseth and Lobel, 2018). This shift has allowed for spatial and temporal comparisons between ecosystems (Archer et al., 2018; Desjonquères et al., 2015; Wall et al., 2013) and has revealed links between ecosystem inhabitants and their associated soundscapes (Lillis et al., 2017; Nedelec et al., 2015). In one of the first soundscape studies conducted on coral reefs, Staaterman et al. (2013) compared reef soundscapes in Panama and the Caribbean and found that they were distinctly different, in part due to the presence/ absence and abundance of fish calls. Piercy et al. (2014) investigated differences in the soundscapes produced by protected and unprotected reefs in the central Philippines and found that higher coral cover and fish abundance was associated with louder sounds. A subsequent study by Kaplan et al. (2015), which explored spatial and temporal variations in sound production on reefs found that the strength of diurnal trends in their low frequency band (100 – 1000 Hz) was correlated with coral cover and fish density. Building from these initial studies, which connected the sounds of reef inhabitants with their overall biophony, new sound metrics are now being tested on coral reefs with the intention of capturing more specific components of reef health.

Two of the most commonly adopted sound metrics used in contemporary PAM studies are sound pressure level (SPL) and the acoustic complexity index (ACI) (Lindseth and Lobel, 2018). SPL, which presents the overall energy output of a soundscape in decibels (dB), is typically used to compare ecosystems and detect temporal patterns in the biophony (Buscaino et al., 2016; Staaterman et al., 2014). On coral reefs, ACI is the most widely adopted new acoustic index designed to measure the diversity of sounds on an acoustic recording and use them as a proxy for biodiversity (Lindseth and Lobel, 2018). To do this ACI calculates the differences in sound intensity between subsequent time steps, and then calculates the sum of those differences (Pieretti et al., 2011). Despite its prolific adoption, only two studies have attempted to ground truth the applicability of ACI to describe the diversity of fish sounds in high energy underwater environments (Bohnenstiehl et al., 2018; Bolgan et al., 2018).

1.2 Corallivore Communities

Most research concerning changing coral reef fish communities has been conducted using UVCs to assess and track changes in these ecosystems. As coral reefs continue to change in response to the combination of both local and global stressors, manual surveys can provide baselines for comparison over time (Wagner et al., 2015) or across a range of human disturbance (Sandin et al., 2008). One of the considerable focuses of this research has been to assess how coral reef fish are shifting in both biomass and community composition in response to global and local stressors (e.g. Bargahi et al., 2020; Bellwood et al., 2006; Brandl et al., 2016; Wilson et al., 2006). In tropical Pacific nations, subsistence fishing provides a majority of protein to most households (Bell et al., 2009; Watson et al., 2016), indicating the need to understand how coral reef stressors are affecting their associated fish assemblages. Previous research focuses on how reef fish communities are altered following coral mortality events, particularly in response to coral mortality caused by El Niño events (Spalding and Jarvis, 2002; Stuart-Smith et al., 2018), Crown-of-Thorns (*Acanthaster planci*) outbreaks (Sano, 2004) or by the direct effects of increased ocean temperatures (Magel et al., 2020). One consistent result is that corallivores, fish that eat live corals, decline in response to coral mortality (Cole et al., 2008). This result, however, only describes changes to the corallivorous functional group at the broadest of scales.

Understanding changes in corallivore populations requires an understanding of the varied ecological roles that they play on coral reefs. In addition to relying on corals for food, corallivores also play a regulatory role in coral growth, limiting the abundance and distribution of preferred species of corals (Cole et al., 2008). As a functional group, corallivores are responsible for up to 4% of the fish diversity in the Eastern Pacific (Kulbicki et al., 2005) and there are 128 species of corallivorous fishes from 11 families around the world (Cole et al., 2008). Corallivores are typically split into two further functional groups to better describe their reliance on corals for food and/or shelter (Rotjan and Lewis, 2008). Obligate species, fish that rely on corals as food to survive, make up roughly 1/3 of all corallivore species and are directly affected by changes in live coral cover (Graham et al., 2009) while facultative species, which include corals as only one part of their diverse diets (Nagelkerken et al., 2009), have been linked to changes in coral structure rather than live coral cover (Garpe et al., 2006; Graham et al., 2009). Roughly half of all corallivore species belong to butterflyfish (Chaetodontidae) (Rotjan and Lewis, 2008) and studies into corallivore behavior and ecology often reflect this, selecting only Chaetodontid species for study (Berumen and Pratchett, 2008; Crosby and Reese, 2005; Emslie et al., 2011; Graham et al., 2009; Pratchett et al., 2014).

Investigating how an entire corallivore assemblage is altered by an intense coral mortality event can reveal novel consequences for corallivore species composition and diversity. Previous work by Emslie et al. (2011) revealed that on the Great Barrier Reef, specialization in butterflyfishes plays a key role in determining their resilience to both physical and biological disturbances, as specialized species exhibited larger and more consistent declines when compared to facultative and generalist feeders. Pratchett et al. (2006) found that three species of obligate corallivores (*Chaetodon trifascialis, C. plebeius, and C. rainfordi*) disappeared entirely following a major coral mortality event. The loss of these specialized feeders can decrease biodiversity on coral reefs, particularly if coral mortality events precede algal phase shifts (Chong-Seng et al., 2012). Corallivore communities are the first to respond to coral mortality and the most impacted by changes in live coral cover, demonstrating that they will be the first major functional group severely altered by increased coral mortality. With El Niño events expected to increase in both frequency and intensity in the near future (Cai et al., 2014), understanding how an entire corallivore assemblage responds to coral mortality will be increasingly important to their conservation in the worlds oceans.

1.3 Thesis research

This thesis attempts to enhance our understanding of how two key monitoring systems used on tropical coral reef ecosystem can improve our understanding of coral reef ecology at different scales and using distinctly different information. Specifically, my collaborators and I examine the ability of 1) common metrics used in PAM to respond to changes in biogenic sound production on a coral reef, and 2) in-person surveys to describe changing corallivore communities on a coral reef in response to the interacting effects of a severe marine heatwave and local human disturbance. We use data collected from reefs around Kiritimati (Republic of Kiribati), a coral atoll in the central equatorial Pacific Ocean. During both 2015 and 2016, Kiritimati was at the center of an intense El Niño, resulting in a mass coral bleaching event on the surrounding reefs (Claar et al., 2020; Magel et al., 2020), with direct and lagged effects to the associated fish assemblages (Magel et al., 2020). Given the highly energetic soundscapes presented by coral reefs, I predicted that ACI would not reflect changes in the coral reef soundscape while SPL would correlate with changes in biogenic sounds. Concerning corallivores, I predicted that obligate communities would be more negatively affected by coral mortality than facultative species around Kiritimati but the effect on the entire corallivore assemblage would be influenced by the intensity of local human disturbance.

In Chapter 2, I investigated the potential for two commonly used acoustic metrics, ACI and SPL, to accurately respond to biological sounds on coral reefs. Using acoustic recordings from the coral reefs surrounding Kiritimati, I examined how responsive ACI and SPL were to changes in the number fish sounds in a low frequency band (160 Hz – 1 kHz) and the number of snapping shrimp snaps in a high frequency band (1 kHz – 22 kHz). This study provides evidence that ACI has limited applicability on highly energetic environments like coral reef ecosystems. I show that nearby fish sounds were partially responsible for changes in low frequency SPL in the morning, during crepuscular chorusing activity, but not at other times of day. Snapping shrimp snaps, however, were responsible for large changes in high frequency SPL. ACI results were dependent upon the frequency band chosen for their calculation, and the 31.2 Hz frequency resolution models were chosen as the best models in both frequency bands. These results contribute to a growing body of evidence against the use of ACI in its current form on highly energetic underwater ecosystems like coral reefs and highlight the importance of extensive field testing and standardization of new acoustic metrics prior to their adoption and proliferation.

In Chapter 3, I examine variability in the communities of obligate and facultative corallivorous reef fishes over the course of a decade on the world's largest atoll to determine the lasting and lagged effects of a coral mortality event. Using underwater reef fish surveys conducted between 2011 and 2019, I assess how the corallivore assemblage has changed in response to the 2015-2016 El Niño across the atoll's gradient of local human disturbance. I show that trends in both obligate and facultative corallivore abundance in response to the heat stress and coral morality are influenced by changes in the abundance of dominant coral-associated damselfishes within each functional group. I also show that obligate corallivore abundance and species richness are severely impacted by a coral mortality event, although the effects are lagged and can take years to manifest. In contrast, facultative corallivore abundance was largely unaffected by the coral mortality and was positively associated with local human disturbance. These results highlight the impact of coral mortality on coral-associated species and detail how these effects impact and alter an entire corallivore assemblage across a gradient of human disturbance.

In sum, the results of this thesis enhance our understanding of the applicability of ACI on coral reefs and investigate the effect of a major coral mortality event on an entire corallivore assemblage. As global climate change, increased coastal development, and overexploitation continue to threaten coral reefs around the world, the application of low-cost monitoring solutions like PAM will become increasingly necessary for world-wide conservation. However, when specific answers are needed, like which factors are driving the changes to reef fish communities, UVCs provide quantitative information at the species level. Our findings here provide an important warning about the adoption of new metrics without proper field-testing and add to the limited body of coral reef literature about how corallivore communities are altered by coral mortality and human disturbances.

Chapter 2 – The utility of different acoustic indicators to describe biological sounds of a coral reef soundscape

Sean Dimoff[1], William D. Halliday[1,2], Matthew K. Pine[1], Kristina L. Tietjen[1], Francis Juanes[1], Julia K. Baum[1,3]

[1]Department of Biology, University of Victoria, PO Box 1700 Station CSC, Victoria, British Columbia, V8W 2Y2, Canada

[2]Wildlife Conservation Society Canada, 169 Titanium Way, Whitehorse, Yukon, Y1A 0E9, Canada

[3]Hawai‘i Institute of Marine Biology, University of Hawai‘i, 46-007 Lilipuna Road, Kāne‘ohe, Hawai‘i, 96744, USA

Adapted from: Dimoff, S., Halliday, W.D., Pine M.K., Tietjen K.L., Juanes F., Baum J.K. 2021. In press. The utility of different acoustic indicators to describe biological sounds of a coral reef soundscape. Ecological Indicators.

2.1 Abstract

Monitoring coral reefs is vital to the conservation of these at-risk ecosystems. While most current monitoring methods are costly and time-intensive, passive acoustic monitoring (PAM) could provide a cost-effective, large scale reef monitoring tool. However, for PAM to be reliable, the results must be field tested to ensure that the acoustic methods used accurately represent the certain ecological components of the reef being studied. For example, recent acoustic studies have attempted to describe the diversity of coral reef fish using the Acoustic Complexity Index (ACI) but despite inconsistent results on coral reefs, ACI is still being applied to these ecosystems. Here, we investigated the potential for ACI and sound pressure level (SPL – another common metric used), to accurately respond to biological sounds on coral reefs when calculated using three different frequency resolutions (31.2 Hz, 15.6 Hz, and 4 Hz). Acoustic recordings were made over two to three-week periods in 2017 and 2018 at sites around Kiritimati (Christmas Island), in the central equatorial Pacific. We hypothesized that SPL would be positively correlated with the number of nearby fish sounds in the low frequency band and with snapping shrimp snaps in the high frequency band, but that ACI would rely on its settings, specifically its frequency resolution, to describe sounds in both frequency bands. We found that nearby fish sounds were partially responsible for changes in low frequency SPL in the morning, during crepuscular chorusing activity, but not at other times of day. Snapping shrimp snaps, however, were responsible for large changes in high frequency SPL. ACI results were reliant on the frequency band chosen, with the 31.2 Hz frequency resolution models being chosen as the best models. In the low frequency band, the effect of fish knocks was positive and significant only in the 31.2 Hz and 15.6 Hz models while in the high frequency band snapping shrimp snaps were negatively associated with ACI in all frequency resolutions. These results contribute to a

growing body of evidence against the continued use of ACI without standardization on highly energetic underwater ecosystems like coral reefs and highlight the importance of extensive field testing of new acoustic metrics prior to their adoption and proliferation.

2.2 Introduction

Coral reefs are among the most diverse ecosystems on the planet, providing important ecosystem services to human populations worldwide (Bell et al., 2009; Moberg and Folke, 1999). However, these essential ecosystems are threatened (Hughes et al., 2018) and of increasing conservation concern globally (Bellwood et al., 2019). At the global scale, anthropogenic carbon emissions are causing the world's oceans to warm and become more acidic, negatively impacting coral growth and survival (Hughes et al., 2017; Prada et al., 2017). Locally, stressors including pollution, coastal development, sedimentation and noise pollution exacerbate the stress on these systems (Cox et al., 2018; Magel et al., 2019; Slabbekoorn et al., 2010). Monitoring these ecosystems and their functions is vital to determine the management techniques that will be advantageous to their conservation. Historically, visual monitoring of coral reefs has provided most of the information used in determining coral reef health (Hill and Wilkinson, 2004), however, this monitoring is often expensive and time consuming, limiting its utility on a large scale. However, recent growth in the study of underwater acoustics has created new passive tools for the study and monitoring of these ecosystems (Staaterman et al., 2017).

For more than 80 years passive acoustics have been used both to describe fish vocal behaviour and as a tool in marine fisheries (Rountree et al., 2006). In one of the initial reviews of fish acoustics, Fish et al. (1952) detailed 26 species of North Atlantic sound-producing fish. Since then, over 800 species of soniferous (sound producing) fishes have been identified worldwide and behavioural studies have revealed the communicative role of sound production in fishes (Lobel, 2013; Rountree et al., 2006; Tricas and Boyle, 2014). Recently, the underwater acoustics field has shifted toward the study of spatial and temporal differences in sound production at the ecosystem level (Farina and James, 2016; Piercy et al., 2014; Wall et al., 2013), enabling comparisons between ecosystems and correlations linking ecosystem health to sound production.

On coral reefs, this shift to the ecosystem level has revealed links between coral reef acoustic communities and their associated soundscapes. In one of the first ecosystem-wide acoustic studies of coral reefs, Piercy et al. (2014) found that reefs with high coral cover and fish abundance produced louder sounds when compared with unprotected and overfished sites. Nedelec et al. (2015) found diel patterns in sound production and positive correlations between adult fish density, live coral cover, coral type and the acoustic output of the reef, suggesting that the acoustic output was determined by a variety of organisms on the reef. Along with these studies connecting reef inhabitants to the reef biophony (biological contributors to underwater soundscapes), new sound metrics suggest that acoustic approaches could be used to quantify specific components of reef health, rather than simply describing the overall sound output of an ecosystem (the soundscape).

Two of the most commonly applied sound metrics in contemporary fish acoustic studies are sound pressure level (SPL) and the acoustic complexity index (ACI) (Elise et al., 2019; Lindseth and Lobel, 2018). SPL is quantified by calculating the root mean square of the pressure level recorded (Lindseth and Lobel, 2018; Slabbekoorn et al., 2010) and represents the overall volume of a soundscape in decibels (dB). This makes it useful in comparing differences within and across ecosystems, and in identifying temporal patterns in the biophony (Archer et al., 2018;

McWilliam and Hawkins, 2013; Staaterman et al., 2014). Recently, several other acoustic metrics have been applied to coral reefs, with the intention of describing the diversity of sounds on a reef and using them as a proxy for biological diversity (McPherson et al., 2016; Sueur et al., 2014). The most popular of these is ACI, which describes acoustic complexity by comparing sound intensity at subsequent time steps by calculating and summing their differences. ACI was originally developed to study terrestrial avian communities (Pieretti et al., 2011) before being applied to underwater systems and proliferating in marine soundscape studies (e.g. Bertucci et al., 2016; Elise et al., 2019; Gordon et al., 2019; Kaplan et al., 2015; McWilliam and Hawkins, 2013; Staaterman et al., 2017, 2014).

Despite its frequent use in ecosystem experiments on coral reefs, only two studies have attempted to validate the ability of ACI to describe fish sounds. Bolgan et al. (2018) found that ACI was not able to distinguish between changes in sound abundance and call diversity and that ACI was dependent upon the settings used for its calculation, including temporal and frequency resolution. Bohnenstiehl et al. (2018) found that the diversity of fish calls in the marine environment was not necessarily responsible for assumed corresponding changes in ACI. Prior to these two validation studies, the use of ACI produced inconsistent results. Kaplan et al. (2015), found that ACI did not correlate with fish species composition at any of their sites on coral reefs, while Bertucci et al. (2016) found that low frequency ACI values were strongly correlated with fish diversity. Recent studies such as Lyon et al. (2019), however, found no correlation between ACI and fish diversity, evenness, or density. Discrepancies in results among these studies might be due to different frequency resolutions used, as there are no standards for ACI calculation (Bohnenstiehl et al., 2018). Despite these inconsistent results and repeated evidence highlighting ACI’s inability to describe highly energetic soundscapes (Bertucci et al., 2016; Bohnenstiehl et al., 2018; Bolgan et al., 2018; Kaplan et al., 2015), new studies continue to use it (e.g. Elise et al., 2019; Lyon et al., 2019).

We had three objectives in this study. First, we tested if SPL and ACI reliably respond to changes in the number of biological sounds on coral reefs. To do this, we counted fish vocalizations and snapping shrimp snaps in acoustic recordings made at five sites over two years on the world's largest coral atoll (Kiritimati (Christmas Island); central equatorial Pacific Ocean) and examined their relationship with SPL and ACI in low (160 Hz – 1 kHz) and high frequency bands (1 kHz – 22 kHz). We hypothesized that the number of fish calls would correlate with low frequency SPL and the number of snaps would correlate with high frequency SPL, because of the ability of reef inhabitants to influence SPL combined with SPL's capacity to encompass all sounds produced. In contrast, we hypothesized that neither fish calls nor snaps would be related to ACI because the high energy environment of a coral reef would overwhelm the ability of ACI to detect differences between sound production events. Second, we examined if the frequency resolution used to calculate ACI influenced its relationship to coral reef sounds in our study system and determined the best frequency resolution. Finally, we described the temporal patterns of the snapping shrimp and fish communities around Kiritimati over our entire deployments.

2.3 Methods

2.3.1 Study Site and Design

We deployed individual SoundTrap acoustic recorders (model: ST300 STD; Ocean Instruments, Auckland, New Zealand) at five sites on the forereef (10-12 m depth) of Kiritimati (Republic of Kiribati) in July 2017 and June 2018 (Figure 1). Acoustic recorders were secured roughly 1 meter above the reef by fastening them to stainless steel stakes that had been installed previously to denote site locations for our long-term monitoring program on this coral atoll. Underwater visual censuses (UVCs) of reef fishes conducted at our deployment sites reveal a highly diverse fish community (Magel et al., 2020) that contains several of the sound producing species identified by Tricas & Boyle (2014), including the acoustically active damselfish identified by Lobel et al. (2010). Acoustic recorders were set at a 96 kHz sample rate with the 'high gain' setting selected, and 5-minute duty cycles were recorded every 10 minutes in 2017 and every 15 minutes in 2018. The difference in duty cycle between years was not related to the goals of this study. Access to each site resulted in different deployment and recovery schedules, but we analyzed only the overlapping days within each year when all recorders were active at the same time (July 11-25, 2017; June 18-27, 2018) to maximize comparability between sites.

Located in the central equatorial Pacific Ocean (01°52'N 157°24'W), Kiritimati is the world's largest atoll by land mass. The atoll supports a population of approximately 6500 people (Beretitenti, 2012), the vast majority of which are highly dependent on reef resources for subsistence and income (Burke et al., 2011; Watson et al., 2016). Kiritimati's reefs experienced prolonged heat stress during the 2015-2016 El Niño event, resulting in the loss of approximately 90% of the atoll's live coral cover (J.K. Baum, unpublished data). Although at the time of this study, sites had less than 5% coral cover (J.K. Baum, unpublished data), reef fish abundances were similar to what they had been prior to the event (Magel et al., 2020). Using fishing pressure data from Watson et al. (2016) we replicated the methods described in Magel et al. (2020) combining the intensity of fishing pressure with the number of people living within a 2 km radius at each of our sites to serve as quantitative measure of local disturbance for our five sites.

2.3.2 Sound Analyses

Acoustic recordings were processed in MATLAB (version 2017a, Mathworks, Natick, Massachusetts, USA) to calculate root mean squared SPL. Both SPL and ACI were calculated in two frequency bands to determine the effects of distinct sound producers: 1) the high frequency band incorporated frequencies between 1 kHz and 22 kHz to separate the band with snapping shrimp snaps (Lillis et al., 2017); 2) the low frequency band included frequencies between 160 Hz and 1 kHz to represent the bandwidth of fish sounds. Most of the energy in herbivorous sounds, marked by a unique crunching sound in our samples, was below of the 1 kHz cut-off, however, some herbivorous sounds can extend beyond 1 kHz although they typically overlap the same range as fish sounds (Tricas and Boyle, 2014). The maximum frequency of 22 kHz was chosen to encompass the broad frequency range of snapping shrimp snaps and to resemble frequency ranges chosen by similar studies (Lillis et al., 2017), while the minimum frequency of 160 Hz was chosen to match the bandwidths used in Slabbekoorn et al. (2018) for sounds made by fish. Within each frequency band, SPL and ACI were calculated for each five-minute file, resulting in a single value for each file, and providing a time-series for the entire deployment from each year of data.

2.3.3 ACI Calculations

Each individual recording (across all sites and seasons) was processed in MATLAB using specifically written code for this study, whereby the variation in acoustic energy within each recording was calculated. We first produced spectrograms for the selected bandwidths (generated using Hanning windows of various sizes equating to 4 Hz (FFT = 24,000, $\Delta t = 0.25$ s), 15.6 Hz (FFT = 6,156, $\Delta t = 0.06$ s), and 31.2 Hz (FFT = 3,078, $\Delta t = 0.03$ s), with no overlap and no time averaging) before applying the *ACI* algorithm from Pieretti et al. (2011) with a 0.5 s temporal step. We then follow the steps outlined by Pieretti et al. (2011), the first of which calculates the absolute differences (d_k) between two adjacent sound pressures (intensities) in a single frequency bin within a matrix of intensities created from the *PSD* spectrogram:

$$d_k = \left| I_k - I_{(k+1)} \right|$$

where I_k and $I_{(k+1)}$ are the two adjacent intensities. The algorithm then sums all the d_k values within that particular temporal step of the recording (*j*, and defined by the temporal resolution of the *PSD* spectrogram):

$$D = \sum_{k=1}^{n} d_k$$

where *D* is the sum of all d_k contained in *j*. The result is then divided by the total sum of the intensity values contained in *j*:

$$ACI = \frac{D}{\sum_{k=1}^{n} I_k}$$

where ACI is for a single temporal step (*j*) and frequency bin (Δf_l). ACI was calculated for every temporal step within a single recording and for every individual frequency bin. The total ACI for each single frequency bin ($ACI_{(\Delta f_l)}$) was then calculated by

$$ACI_{(\Delta f_l)} = ACI_{(\Delta f_l)} = \sum_{j=1}^{m} ACI$$

where m = the number of temporal steps (j) in the entire recording. Finally, the broadband ACI (across all frequencies up to 24 kHz) was calculated by

$$ACI_{tot} = \sum_{l=1}^{q} ACI_{(\Delta f_l)}$$

where ACI_{tot} is the ACI value for the entire recording (Pieretti et al., 2011). Finally, the ACI_{tot} for each bandwidth (high frequency (1 – 22 kHz) and low frequency (160 Hz – 1 kHz)) was calculated.

2.3.4 Fish Sound Analysis

To test the relationships between each of our acoustic indicators (SPL and ACI) and fish sounds, we quantified three distinct types of fish sounds on a subset of our overall dataset. The amount of effort required for this manual bioacoustics analysis was quite large, therefore we subsampled the data. We subset each deployment to include five days from each of the five sites in both 2017 and 2018, with the proviso that days could only be included if no divers were in the water at any of the recording sites. This was to eliminate sounds made by divers and any influence that they caused on the reef fish community. We then subset each of the days (10 days x 5 sites) into four quarters (03:00, 09:00, 15:00, 21:00) and visually analyzed the first 5-minute file in each quarter. These times were chosen based on our initial exploratory analysis of daily patterns in SPL, which showed a peak at 09:00 at all sites and variations in sound levels at the other 3 sampled times.

Each of the 200 files included in this analysis were visually inspected by a single analyst using Raven Pro software (Version 1.5, Cornell Lab of Ornithology, Ithaca, New York, USA), with the window size set to 7000 samples, the frequency range set to 0 – 3000 Hz, and the time range of the view window set at 10 seconds. To ensure that only fish calls or herbivory sounds were counted, and all sounds were quantified consistently, each file was listened to by only one analyst and, in any cases of uncertainty, a second underwater acoustic expert was consulted. Within each visually inspected file, we recorded and summed the number of fish knocks (Figure 2C), fish long calls (Figure 2A), and herbivorous feeding sounds (Figure 2B). Fish knocks were determined to be of a short duration (<200 ms) and within the 160 – 1200 Hz frequency range (Figure 2C). Long calls, which were within the same frequency range as fish knocks, were identified by a longer duration (>200 ms; Figure 2C) and encompassed a variety of different call types including 'grunts', 'buzzes', 'chirps', 'purrs', and 'trumpeting' (Lobel et al., 2010). Herbivorous feeding sounds were identified through a combination of listening and visually inspecting each file to ensure that consistent sounds were counted. The energy in herbivorous sounds was typically between a 160 - 1000 Hz frequency range, although exceptions stretched beyond 1 kHz, and these long duration sounds (~250 ms) made a distinctive crunching sound (Figure 2B). If boat noise was observed in a file, then we removed the file from the overall sample, leading to the removal of 9 files (n = 191). Each file was also analyzed to ensure that weather, waves, and wind were not interfering with sound identification, however none of our samples revealed any obvious interference from these factors.

To investigate if there were changes in the sound intensity of individual sounds between our 4 sampled times, we also examined the characteristics of individual fish knocks from a small subset of files. Knocks were selected as they were a consistent call type present in all files. 20 acoustic files were selected, split between 2017 and 2018 and across all four of our sampling times (03:00, 09:00, 15:00, 21:00). Within each file we selected the first 10 individual knocks with a good signal-to-noise ratio using Raven Pro. We used the selection table tool in Raven Pro to collect different metrics on the individual knocks that were selected, including minimum and maximum frequency and time, peak frequency, and in-band power. We used in-band power as a metric of the uncalibrated received level of each call and converted these values to a calibrated received level by correcting for the end-to-end sensitivity of the individual recorder.

2.3.5 Snapping Shrimp Snap Analysis

Next, to test the relationships between each of our acoustic metrics and snapping shrimp sounds, we estimated the number of snaps in each 5-minute file from our overall dataset using a band limited energy detector on spectrograms in Raven Pro (version 1.5) with window size set to 7000 samples. The settings for the band limited energy detector were set to minimum frequency = 1.5 kHz, maximum frequency = 4.5 kHz, minimum duration = 0.036 s, maximum duration = 0.109 s, minimum separation = 0.036 s, minimum occupancy = 70%, signal-to-noise ratio threshold = 2 dB, block size = 10 s, and hop size = 5 s. We visually inspected a small subset of the detector results and determined that the detector was actually detecting snapping shrimp snaps rather than other extraneous sounds. We used our entire dataset for this analysis, resulting in a large sample size (n = 15,987).

2.3.6 Statistical Analysis

All statistical analyses were conducted using R version 3.6.1 (R Core Team 2019). Data and the code for figures and data analyses are available through GitHub at [repository to be made public upon manuscript acceptance].

To validate the responsiveness of SPL and ACI to the number of biogenic sounds recorded we fit linear mixed models (R package: *lme4*) for each of these two response variables, in both the low and high frequency bands. Our ‘low frequency band’ models included numbers of knocks, long calls, and herbivorous sounds as fixed effects (with each standardized to a mean of zero), and with lunar phase (continuous), fishing pressure (continuous), time of day (03:00, 09:00, 15:00, 21:00) and year (categorical) as fixed effects to assess changes in sound production responsible for the diurnal patterns observed in SPL (Figure 2C) and between our two sampling years. Due to boat noise, nine observations were removed from the low frequency dataset (n = 191). Our 'high frequency band' models included number of snapping shrimp snaps (continuous), day/night (categorical), year (categorical), lunar phase (continuous), and fishing pressure (continuous) as fixed effects, as well as the interaction between the snaps and day/night, to allow for the relationship between snaps and SPL to vary between night and day. Day/night was based on approximate times of sunrise and sunset near the equator (6:00 – 18:00). Due to irregular snap counts (< 200), three observations were removed from the high frequency dataset (n = 15,987). Prior to our analyses, all continuous parameters were standardized to a mean of zero and a standard deviation of 0.5 using the rescale function in the *arm* package (Gelman et al., 2020). For SPL models,, we ran models with all combinations of covariates described above and compared using small-sample corrected Akaike Information Criterion (AICc) to select the final model. To determine the best-fit models for ACI we first created models with all combinations of covariates described above for three different frequency resolutions. For ACI models, we first selected for the best model within each frequency resolution using AIC_c. We then compared the best ACI models from each frequency resolution using AIC_c to determine which frequency resolution best described variations in fish calls or snapping shrimp snaps.

Finally, we examined variation in the received levels of individual knocks through time based on the subset of knocks where we measured received levels (dB). We used a linear model in R (package: *Stats*; function: lm) with received level (dB) as the dependent variable and hour as a categorical independent variable. We tested all assumptions of this model (normality, homoscedasticity of variance), and it met all assumptions.

2.4 Results

2.4.1 Sound Pressure Level

Low frequency SPL was significantly influenced by knocks (Figure 2C), herbivory, time of day, year, and the interaction between knocks and time of day. The effect of knocks differed between the four hours sampled (Figure 3). Knocks had a significantly positive effect on low frequency at 09:00 (parameter estimate = 7.3, S.E. = 1.231, $t_{197} = 5.93$, $p < 0.0001$), but the interaction was not significant at the other sampled periods (03:00, 15:00, 21:00; Table 1). Herbivory also had a significant positive effect on low frequency SPL (parameter estimate = 1.28, S.E. = 0.395, $t_{197} = 3.23$, $p = 0.002$). Year was the only other significant factor and 2018 had significantly higher SPL than 2017 (parameter estimate = 3.53, S.E. = 0.348, $t_{197} = 10.15$, $p < 0.0001$). Lunar phase and fishing pressure were also included in the model although neither was significant (Table 1). This model explained 53.38% of variation in low frequency SPL. The only other model that fell within $\Delta AIC < 2$ was identical to the selected model except that it also included long calls, although they were non-significant (Table 1). Comparisons between knocks at each of the four sampling periods revealed that individual knocks had significantly higher received levels at 09:00 compared to knocks during the other three times examined (Supp. Figure 1; difference between 09:00 and 03:00 = 7.7 dB, S.E. = 0.9, $t_{197} = 8.1$, $p < 0.0001$; no significant difference between 03:00 and both 15:00 and 21:00, $p > 0.40$; model $R^2 = 0.33$; Supp. Table 7).

High frequency SPL was significantly influenced by snaps (Figure 2D), day/night, and their interaction, as well as lunar phase, year, and fishing pressure (Supp. Table 1). Snaps had a small but positive effect during the day (parameter estimate = 0.872, S.E. = 0.034, t_{15980} = 14.696, $p < 0.001$), and roughly twice the effect size at night compared to during the day (parameter estimate = 0.974, S.E. = 0.092, t_{15980} = 10.65, $p < 0.001$). Each of our abiotic parameters were also significant. Lunar phase had a positive effect (parameter estimate = 0.212, S.E. = 0.045, t_{15980} = 4.767, $p < 0.001$), 2018 had significantly higher SPL than 2017 (parameter estimate = 3.396, S.E. = 0.045, t_{15980}= 74.472, $p < 0.001$), and fishing pressure had a significant positive effect on high frequency SPL (parameter estimate = 1.004, S.E. = 0.0450, t_{15890} = 22.314, $p < 0.001$). Overall, this model explained 37.14 % of variation in high frequency SPL (Supp. Table 1).

2.4.2 Acoustic Complexity Index

For low frequency ACI, the best model according to AIC_c had a frequency resolution of 31.2 Hz and suggested that ACI was influenced by knocks, hour, herbivory, fishing pressure, and an interaction between knocks and hour. The effect of knocks was, however, different between the four times of day sampled (Table 2). The interaction was significant and positive at 09:00 (parameter estimate = 1.196, S.E. = 0.354, t_{179}= 2.347, $p = 0.020$) and 21:00 (parameter estimate = 1.331, S.E. = 0.358, t_{179}= 2.701, $p = 0.008$) but there was no significant difference between 03:00 and 15:00 (Table 2). Additionally, both herbivorous sounds (parameter estimate = 0.330, S.E. = 0.114, t_{179} = 2.905, $p = 0.004$) and fishing pressure (parameter estimate = 0.593, S.E. = 0.112, t_{179} = 5.280, $p < 0.001$) had a positive effect on low frequency ACI. This model explained 50.7% of the variation in low frequency ACI.

Both the 15.6 Hz and the 4 Hz frequency resolution models contained the same covariates as the selected 31.2 Hz model (Table 2) but had a diminished effect size of the interaction between knocks and time of day, and the main effect for knocks was no longer significant in either model. The 15.6 Hz model explained 41.8% of the variation in low frequency ACI. Within this model, the interaction between knocks and hour was significant at 09:00 (parameter estimate = 1.493, S.E. = 0.581, t_{179} = 2.570, p = 0.011), while herbivorous sounds and fishing pressure were both still significant (Supp. Table 2). The 4 Hz model explained only 40.6% in low frequency ACI and the interaction between knocks and hour was no longer significant at any time of day (Supp. Table 3).

In the high frequency band, the best model selected by AIC_c also had a frequency resolution of 31.2 Hz and was significantly influenced by snaps, day/night, and their interaction, as well as year and fishing pressure. Snaps had a statistically significant negative effect on ACI during the day (parameter estimate = -6.829, S.E. = 0.243, t_{15584}= -28.187, p < 0.001) and a smaller but still negative effect on ACI at night (parameter estimate = -5.904, S.E. = 0.374, t_{15584}= 2.47, p = 0.132). Year had a positive effect on ACI (parameter estimate = 12.78, S.E. = 0.187, t_{15584}= 68.495, p < 0.001), while fishing pressure had a negative effect (parameter estimate = -8.70, S.E. = 0.185, t_{15584} = -47.073, p < 0.001). Lunar phase was near-significant and had a small positive effect on ACI as well (Supp. Table 4). The selected model explained 37.03% of the variation in high frequency ACI. Of the high frequency ACI models, the selected models in all three frequency resolutions contained the same covariates (Supp. Table 4). The 15.6 Hz model explained 33.49% and the 4 Hz model explained 28.46%. While the effect sizes changed within each model, there were no differences in the significance or positivity/negativity of the covariates (Supp. Table 5, 6).

2.4.3 Diel Patterns

Diel patterns were present in both the low and high frequency SPL bands (Figure 4A, C). Low frequency SPL exhibited clear peaks in sound production at 09:00 and 22:00, and slightly higher levels of SPL produced at night compared to the day (Figure 4C). High frequency SPL maintained a higher SPL at night compared to the day (Figure 4A. The peaks in low frequency SPL also occurred around the times that high frequency SPL either increased (22:00) or decreased (09:00) (Figure 4A, C). Diel patterns in ACI, however, were only observed in the high frequency band (Figure 4B), where it appeared that ACI values were higher from 09:00 to 22:00, and slightly higher during the day compared to at night.

2.5 Discussion

Passive acoustic monitoring is potentially a useful tool for monitoring the health of coral reef ecosystems, however, its application must be based on field-tested evidence. The application and proliferation of new acoustic metrics to a variety of new ecosystems is common (Lindseth and Lobel, 2018), however, unless these new metrics are tested under a variety of conditions and in a variety of ecosystems, their results may reflect localized patterns rather than broadly applicable trends (Bolgan et al., 2018). Here, we tested two popular sound metrics to assess their applicability to coral reefs. Our SPL analyses partially supported our hypotheses that this metric would be representative of biogenic sounds on the coral reef: low frequency SPL responded to fish sounds, albeit only at certain times of day, and high frequency SPL was clearly driven by snapping shrimp snaps. As expected, ACI proved to be a less reliable metric. In the low frequency, the ability of each model to describe ACI was dependent upon the frequency resolution chosen for ACI calculation, while in the high frequency band it was negatively associated with the number of snaps. We speculate that the discrepancies between our SPL hypotheses and findings might be explained by the complex acoustic communities of coral reefs, whereas the differences between our ACI hypotheses and findings may be due to the reliance of

ACI on its calculation settings and its inability to separate independent calling events on high-energy systems like coral reefs.

2.5.2 Sound Pressure Level

In the low frequencies (160 – 1000 Hz), fish knocks were partially responsible for the peak in SPL at 09:00 (Figure 2C), with a positive relationship between the number of knocks and SPL at this time, but not at other times of day (Table 1). This peak in SPL appears to be evidence of chorusing behaviour of fishes (i.e. aggregations of fish vocalizing together) in Kiritimati. Although the number of knocks that we were able to count did not differ greatly between 09:00 and other times, the knocks that were recorded at 09:00 had a higher received level than knocks at other times (Supp. Figure 1), suggesting that fish were closer to the acoustic recorder when knocking, or that fish increased the source level of their knocks at 09:00. If more fish were making this knocking vocalization at 09:00, overlap and amplitude loss due to distance from the hydrophone might mask distant knocks so that they are lost in elevated background noise, compared to other times of day, when we were able to count more distant knocks with lower received levels because there were fewer knocks (i.e. less overlapping signals) and less background noise in the same frequency band (Figure 3). The phenomenon of fish increasing their sound intensity has been noted in both freshwater and marine species and can be a masking release strategy to overcome higher levels of background noise (Holt and Johnston, 2014; Luczkovich et al., 2016).

Fish choruses can be associated with reproduction and spawning events, and their timing and frequency range might be associated with avoiding overlap in the biophony (Lobel, 2013; McCauley and Cato, 2000). On coral reefs, several experiments have identified chorusing behaviour as a primary driver of low frequency SPL (Radford et al., 2014; Steinberg et al., 1965). McCauley and Cato (2000) on the Great Barrier Reef found that fish choruses raised ambient sound levels by 35 dB, representative of the impressive sound output fish can make together. The consistent increase in average SPL from 08:30 to 10:00 and 21:30 to 22:30 also suggest that chorusing activity is powerful enough to drive changes in SPL while non-chorusing behaviour is not. Here we define "non-chorusing behaviour" as periods when fish calls were present, but not in high enough intensity or quantity to create changes in SPL, which we observed at three of our four sampled times of day (03:00, 15:00, 21:00). However, to truly assess the influence of knocks and other fish calls on SPL at different times of day would require a more detailed analysis of received levels for each individual call, an extremely labour-intensive task considering the manual methodology we used, therefore we recommend an automated process for examining this relationship in the future.

In addition to knocks, herbivorous sounds also significantly affected low frequency SPL (Table 1). Although herbivorous sounds were infrequent in our dataset, they did contribute substantial acoustic energy to the soundscape when present (Figure 2B). Tricas and Boyle (2014) found that parrotfish feeding sounds in Hawaiʻi overlap with social fish vocalizations but occupy a much larger frequency range, which varies by species. In temperate reefs, the sounds of feeding sea urchins fill a similar frequency band and can contribute to choruses at dawn and dusk (C. Radford et al., 2008). Herbivorous sounds in our recordings typically fit within our low frequency band (160 Hz – 1000 Hz). Long calls, which consisted of grunts, buzzes, chirps, purrs, and trumpet calls were not significant in any of our top models (Table 1). It is interesting that long calls were not a significant component of low frequency SPL as they have been previously associated with chorusing activity on coral reefs (McCauley and Cato, 2000). However, their minimal input might be due to a low number of nearby long calls or high levels of different nearby sounds masking them.

Year was the only significant abiotic factor that we included in our low frequency model. SPL was roughly 3.5 dB higher in 2018 than 2017. Since weather conditions were similar between the two sampling years, this difference might be due to recordings taking place at different times of year; while both recordings were conducted in the summer, we sampled in June of 2017 and in July of 2018. These different months might be associated with differences in sound production related to reproductive events in fishes (Lobel et al., 2010). We also included lunar phase and fishing pressure, neither of which were significant, however these results might be due to our low sample size (n = 197). Conflicting results from Staaterman et al. (2014) found that lunar phase was significantly associated with changes in low frequency sound production at reefs in both Florida and Hawaiʻi, although using a sample size of over a year. Additionally, Piercy et al. (2014) found that reefs with higher coral cover and fish abundance were significantly louder than degraded reefs. Our use of fishing pressure does not provide a direct comparison of the biological health of a reef and is a proxy determined by distance from population centers and population density around Kiritimati (Magel et al., 2020). Therefore, fishing pressure might not adequately describe the contrast in the biological health of different reefs across the small scale used in this study.

In the high frequency band (1 – 22 kHz), snapping shrimp snaps generated large changes in SPL (Supp. Table 1). Their snaps are created for a variety of intra- and inter-specific behaviours (Herberholz and Schmitz, 1998; Lillis et al., 2017; Versluis, 2000) and the number of snaps created within a habitat is considered representative of the density and abundance of local snapping shrimp (Butler et al., 2017). On coral reefs, due to their three-dimensional structure, snapping shrimp populations can thrive, creating sounds that dominate the high frequencies (Enochs et al., 2011). Therefore, these results contribute to the growing body of evidence across a range of habitats that snapping shrimp snaps are responsible for changes in high frequency SPL (Bohnenstiehl et al., 2016; Johnson et al., 1947; Lillis et al., 2014; Lillis and Mooney, 2018; McWilliam and Hawkins, 2013; Nedelec et al., 2015; Radford et al., 2010). High frequency SPL was also significantly explained by year, lunar phase, and fishing pressure. The pattern in year matched the pattern seen in the low frequency SPL: SPL in the high frequency band was also roughly 3.4 dB higher in 2018 than 2017. This discrepancy between years might be explained by community structure changes or population growth by species associated with sound production. Lunar phases have been associated with changes in snapping shrimp snap production on both temperate reefs and tropical Caribbean coral reefs (Radford et al., 2008; Lillis and Mooney, 2018). Degradation of three-dimensional structure, often seen on degraded reefs, has also been associated with lower snapping shrimp populations (Butler et al., 2016), but this did not match the pattern that we saw in fishing pressure. However, this again might be because our calculated index of fishing pressure was not a direct a direct measure of the biological health of our different reefs.

2.5.3 Acoustic Complexity Index

As we hypothesized, the ability of ACI to reflect changes in biogenic sounds was determined, in part, by the frequency resolution used. In both low and high frequency bands, the 31.2 Hz frequency resolution was selected as the best model, followed by the 15.6 Hz resolution model and then the 4 Hz resolution model (Table 2, Supp. Table 4). These results contrast with the results of Bolgan et al. (2018), who found that the 15.6 Hz model with a temporal resolution of 0.5 s provided the best representation of sound abundance and diversity in both controlled and field experiments. This discrepancy might be due to differences in the habitats that were analyzed, as Bolgan et al. (2018) conducted their field experiments on a sandy bottom habitat in Calvi, France and experienced minimal sound input from only five different fish calls and boats. Our recordings include a large variety of sounds created by a diverse group of soniferous fish and invertebrate species, as recordings were conducted on high energy coral reef systems.

The best low frequency ACI model explained 50.7 % of the variation in ACI (Table 2), and included both knocks and herbivorous sounds as biogenic parameters, with the effect size of knocks changing between our four sampled time periods. These results resemble those found for low frequency SPL (Table 1), although the interaction between knocks and hour is significant at both 09:00 and 21:00 in the ACI model while it is only significant at 09:00 in the SPL model. This difference indicates that ACI might be more sensitive to subtle changes in knock volume or the number of knocks at 21:00 that were not discernable with SPL. Herbivorous sounds were loud and clear, obvious to identify in spectrograms (Figure 2), and had a positive effect on ACI. Interestingly, none of the selected models at any frequency resolution included long calls (Table 2, Supp. Table 2, 3), an important contributor to the biogenic soundscape in several environments (Bohnenstiehl et al., 2018; Bolgan et al., 2018; Locascio and Mann, 2008). This lack of significance in this experiment might be due to the low abundance of these calls and/or a lack of proximity to the hydrophones by the fish that made them. In a highly energetic environment like a coral reef, unless long calls are nearby and loud, they are difficult to identify and assess independently of constant background noise.

Year and fishing pressure were both significant abiotic factors that contributed to changes in ACI. The difference in ACI between 2017 and 2018 might, again, be due to differences in when the recordings took place in the year. As recordings were conducted in June 2017 and July

2018, fish reproductive events, which might be associated with different months could have created differences in the acoustic soundscape (Lobel et al., 2010). Fishing pressure had a significant positive effect on low frequency ACI, despite having no effect on low frequency SPL. Even though there was no significant change in SPL due to fishing pressure, degraded environments have less consistent and abundant biogenic sounds (Piercy et al., 2014), reducing the potential for "masking" changes in acoustic complexity (Bolgan et al., 2018; Staaterman et al., 2017). While it was included, we found no significant effect of lunar phase on low frequency ACI, unlike Staaterman et al. (2014), who observed lunar patterns in ACI on coral reefs in both Hawaii and Florida. This trend might have been obscured in this experiment by limited deployment durations and sampling due to the manual methods required for biogenic sounds in the low frequency band.

The 15.6 Hz and 4 Hz low frequency ACI models explained 41.84% and 40.57% of the variation, respectively. In the 15.6 Hz model, the interaction between knocks and hour was only significant at 09:00 while in the 4 Hz model, knocks no longer had a significant effect at any hour (Supp. Table 2, 3). These results resemble those reported by Bolgan et al. (2018), who found that ACI was significantly different when calculated using different frequency resolutions. Importantly, here we present evidence that changing the frequency resolution also affects the ability of ACI to respond to and reflect changes in the abundance of different biogenic sounds. In the 4Hz model, the only biogenic sound that had a significant effect on ACI was herbivorous sounds, which is likely due to their relatively high intensity in comparison to the other biogenic sounds recorded (Fig. 2B). The variable response by ACI to key biogenic sounds like knocks shows how important it is to test a variety of frequency resolutions on an ecosystem to determine a "best" resolution setting.

In the high frequency band, the selected model explained 37.03% of the variation in high frequency ACI. Despite this, increased snapping shrimp snaps resulted in a negative effect on high frequency ACI, indicating a potential drawback to its use in snap-dominated ecosystems (Supp. Table 4). Bohnenstiehl et al. (2018) similarly found that ACI reached a saturation threshold on a coral reef in the Bahamas while studies by Butler et al. (2016) in nearshore habitats in Florida and Staaterman et al. (2014) in reefs in both Florida and Hawai'i found that ACI followed diel patterns of snap frequency. These discrepancies in results might be due to differences in the number of snaps across different ecosystems and again raise questions about how comparable different ecosystems might be, even when using the same metric of complexity. The interaction between day/night and snapping shrimp snaps revealed that at night snaps had a significantly smaller negative effect on ACI, which could be associated with decreased snapping activity at night, reducing the "masking" effect that overwhelming and consistent sounds can have on ACI (Bolgan et al., 2018; Pieretti et al., 2011). Similar diurnal patterns in both low and high frequency ACI were observed by Staaterman et al. (2014) at reefs in Hawaii and Florida. Fishing pressure had a negative effect on ACI, similar to the results of a study by Bertucci et al. (2016), who found that MPA sites had significantly different ACIs compared to their adjacent non-MPA sites. 2018 had a significantly higher ACI than 2017 in the high frequency band as well, potentially due to differences in when the recordings took place in each year. Lunar phase was nearly significant in the high frequency band, similar to patterns observed in Staaterman et al. (2014) over a year-long study. Therefore, deployment limitations might have played a role in limiting its significance in our models.

In the high frequency models, changes in the frequency resolution did not create any differences in the significance or positive/negative slope of the covariates. Importantly, there was no change in the significant negative effect of snapping shrimp snaps among the three different frequency resolutions (Supp. Table 4, 5, 6). This is likely because regardless of frequency resolution, snapping shrimp snaps occurred in such high abundance that ACI was unable to detect changes in sound intensity between independent events. Pieretti et al. (2011) found similar results in terrestrial environments when assessing ACI's ability to encompass consistent sounds like insect buzzing or airplanes. With significant changes to temporal frequency prior to calculation, ACI might be able to detect changes in intensity between individual snaps, but it is more likely that such a consistent sound will be attributed a near constant intensity which produces low levels of ACI.

When calculating ACI, changing key settings like frequency resolution can create significant changes to results and limits comparisons between studies. In our experiment, adjusting the frequency resolution resulted in models with the same covariates explaining different amounts of variation in both low and high frequency bands (Table 2, Supp. Table 4). Across the literature, there doesn't appear to be any standardization in ACI settings prior to calculation. Bohnenstiehl et al. (2018) summarizes several key studies that use ACI and found that there was no consistent resolution used, even when studying the same ecosystem. Our results reveal that this discrepancy in frequency resolution could have a significant impact on the findings of each of these studies. A conclusion which is shared by Bolgan et al. (2018), who found that ACI was influenced by all settings, including temporal and frequency resolution, as well as the use of an amplitude filter. Our result might also be due to the inverse relationship between frequency and temporal resolution, in which our largest frequency resolution, 31.2 Hz, had the smallest temporal resolution and thus might have been better suited to detect short signals like fish knocks. Therefore, we recommend that more work is needed to standardize ACI calculations in the marine environment to provide a reliable and comparable metric of sound complexity.

2.5.4 Diel Patterns

Chorusing patterns are typically associated with changes in light, with dawn and dusk choruses being most prevalent (Butler et al., 2016; Radford et al., 2014; Staaterman et al., 2014). However, our results found a shifted chorusing pattern with peaks in sound production at roughly 09:00 and 22:00 (Figure 2.; Figure 3A, 3C). Sunrise and sunset in Kiritimati are typically near 06:30 and 18:30 in the summer months, roughly three hours from when our changes in sound production occurred. Not all choruses are associated with dawn and dusk, however, as nightly choruses have been recorded between dusk and midnight on the Great Barrier Reef (McCauley and Cato, 2000), and temperate fish such as the plainfin midshipman (*Porichthys notatus*) chorus in the middle of the night during the mating season (Halliday et al., 2018). While both fish and snapping shrimp chorusing activities have been linked to dawn/dusk choruses (Radford et al., 2008; Lillis and Mooney, 2018; Locascio and Mann, 2008), it is interesting that both snapping shrimp and fishes in this study showed changes in sound production around the same times despite not being associated with dawn or dusk.

Patterns in high frequency ACI were the inverse of patterns in high frequency SPL. These trends were also the opposite of those found by Staaterman et al. (2014), who found that acoustic complexity increased at night at both high and low frequencies. The opposing trends observed in high frequency SPL and ACI are likely due to the “masking effect”, in which a biogenic sound is produced frequently enough that it reduces ACI (Bohnenstiehl et al., 2018; Bolgan et al., 2018; Staaterman et al., 2017). The presence of this “masking effect” is exacerbated in underwater environments, like coral reefs, by the high sound propagation present in water, which allows for sounds to travel much further without losing intensity (Radford et al., 2011). Therefore, as SPL decreases during the day because of decreased snapping shrimp snap input, ACI is be better able to detect changes in complexity. In the low frequency band, no clear diurnal trends were present, unlike patterns seen in Hawaii and Florida (Staaterman et al., 2014). This could either indicate that there were no clear diurnal trends in sound diversity, or that ACI could not discern any trends with the settings used for its calculation (Bolgan et al., 2018).

2.5.5 Conclusions

Our results, which are in accordance with previous studies from across a range of ecosystems, indicate that ACI is not adequately developed to handle high energy systems like coral reefs (Bohnenstiehl et al., 2018; Kaplan et al., 2015; Staaterman et al., 2017). Despite its continued use in coral reef studies, ACI continues to produce inconsistent and non-significant results (Bertucci et al., 2016; Kaplan et al., 2015; Lyon et al., 2019). These inconsistencies might be a result of the lack of standardization in ACI settings and might require customizing ACI’s calculation at the ecosystem level (Bolgan et al., 2018). Meta-analyses investigating how distinct soundscapes create differing levels of complexity, and how to compare different ecosystems, might provide answers pertaining to the continued use of ACI and its potential to develop into a more useful acoustic metric.

Contemporary acoustic metrics are constantly evolving, and new technologies associated with event detection through machine learning techniques make passive acoustics more useful than ever before. While acoustic metrics can identify peaks in acoustic activity, they are not currently reliable enough to replace species-specific bioacoustic analyses. Current validation methodologies, such as the one used here, are labour-intensive and time-consuming and should eventually be replaced by automated detectors. Advances in machine learning is facilitating automation of passive acoustic monitoring with new studies investigating supervised and unsupervised methods of automatic biogenic sound detection (Lin et al., 2018, 2017), and these could be investigated for future studies of coral reef acoustics. Passive acoustic monitoring has the potential to help conserve coral reefs on a global scale; however, its application depends on a foundation of field-tested methods through studies such as this one.

Table 2.1. Top models from AIC_c stepwise comparisons ($\Delta\text{AIC}_c < 6$) and results (parameter estimates) for final model fixed effects from linear mixed-effects model examining changes in low frequency SPL associated with changes in fish calls at four times of day. The intercept and all continuous main effects represent our 15:00 sampling time

Model	**K**	**AICc**	**ΔAIC**	**Adjusted R^2**	**P value**
Knocks * Hour + Herbivory + Year + Lunar Phase + Fishing Pressure	13	884.55	0.284	0.534	< 0.0001
Knocks * Hour + Herbivory + Long Calls + Year + Lunar Phase + Fishing Pressure	14	885.71	1.433	0.534	<0.0001

Parameter estimates for final model

Parameter	**Estimate**	**Std. Error**	**t value**	**P value**
(Intercept)	102.67	0.497	206.72	< 0.0001
Knocks	-1.94	1.070	-1.81	0.071
21:00	1.54	0.567	2.71	0.007
03:00	0.50	0.586	0.85	0.395
09:00	2.26	0.589	3.83	< 0.001
Herbivory	1.28	0.395	3.23	0.002
Year	3.53	0.348	10.15	< 0.0001
Lunar Phase	0.08	0.385	0.22	0.829
Fishing Pressure	-0.41	0.390	-1.05	0.293
Knocks * 21:00	2.14	1.243	1.73	0.086
Knocks * 03:00	2.31	1.216	1.90	0.059
Knocks * 09:00	7.30	1.231	5.93	< 0.0001

Table 2.2. Top models from AIC_c stepwise comparisons and results (parameter estimates) for each frequency resolution from linear mixed-effects model examining changes in low frequency ACI associated with changes in fish vocalizations. The intercept and all main effects represent our 15:00 sampling time.

Frequency Resolution	Model	K	AICc	ΔAIC	Adjusted R^2	P value
32.1 Hz	**LF ACI ~ Knocks * Hour + Herbivory + Year + Lunar Phase + Fishing Pressure**	**11**	**408.88**	**0**	**0.507**	**0.23**
15.6 Hz	LF ACI ~ Knocks * Hour + Herbivory + Year + Lunar Phase + Fishing Pressure	11	597.83	188.94	0.418	0.31
4 Hz	LF ACI ~ Knocks * Hour + Herbivory + Year + Lunar Phase + Fishing Pressure	11	745.99	337.12	0.405	0.48

Parameter estimates for final model

Parameter	Estimate	Std. Error	t value	P value
(Intercept)	20.199	0.143	141.281	< 0.0001
Knocks	0.365	0.308	1.184	0.238
21:00	-0.0482	0.163	-0.295	0.768
03:00	1.292	0.169	7.663	< 0.0001
09:00	0.397	0.170	2.344	0.020
Herbivory	0.330	0.114	2.905	0.004
Lunar Phase	-0.096	0.111	-0.862	0.495
Year (2018)	0.069	0.100	0.684	0.390
Fishing Pressure	0.593	0.112	5.280	< 0.0001
Knocks * 21:00	0.967	0.358	2.701	0.008
Knocks * 03:00	0.345	0.350	0.986	0.326
Knocks * 09:00	0.832	0.354	2.347	0.020

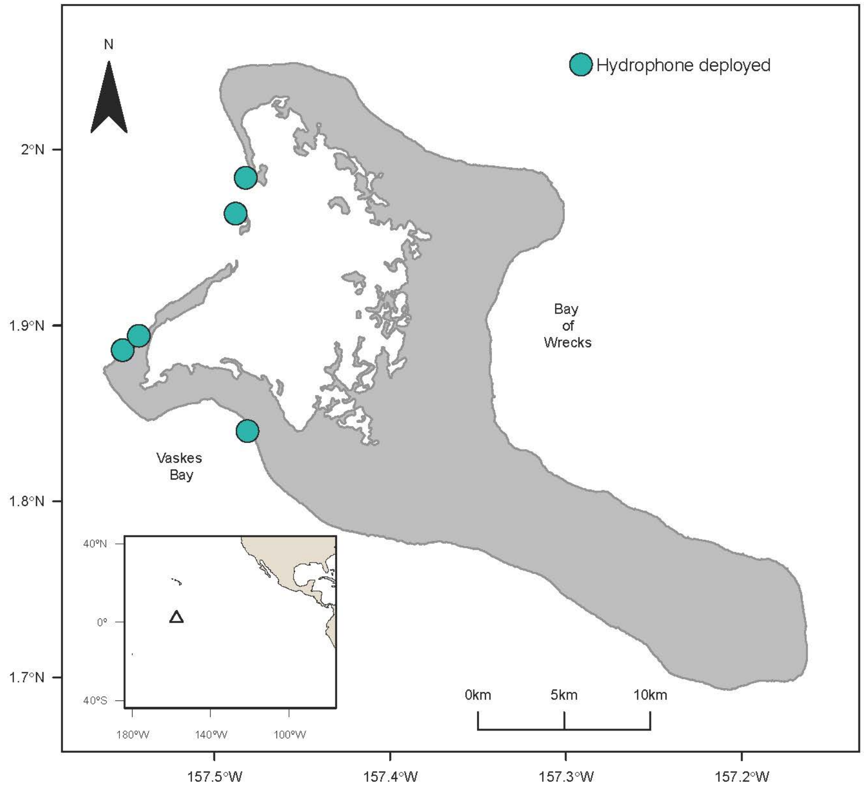

Figure 2.1. Map of Kiritimati atoll (Republic of Kiribati) with hydrophone sites marked by blue circles.

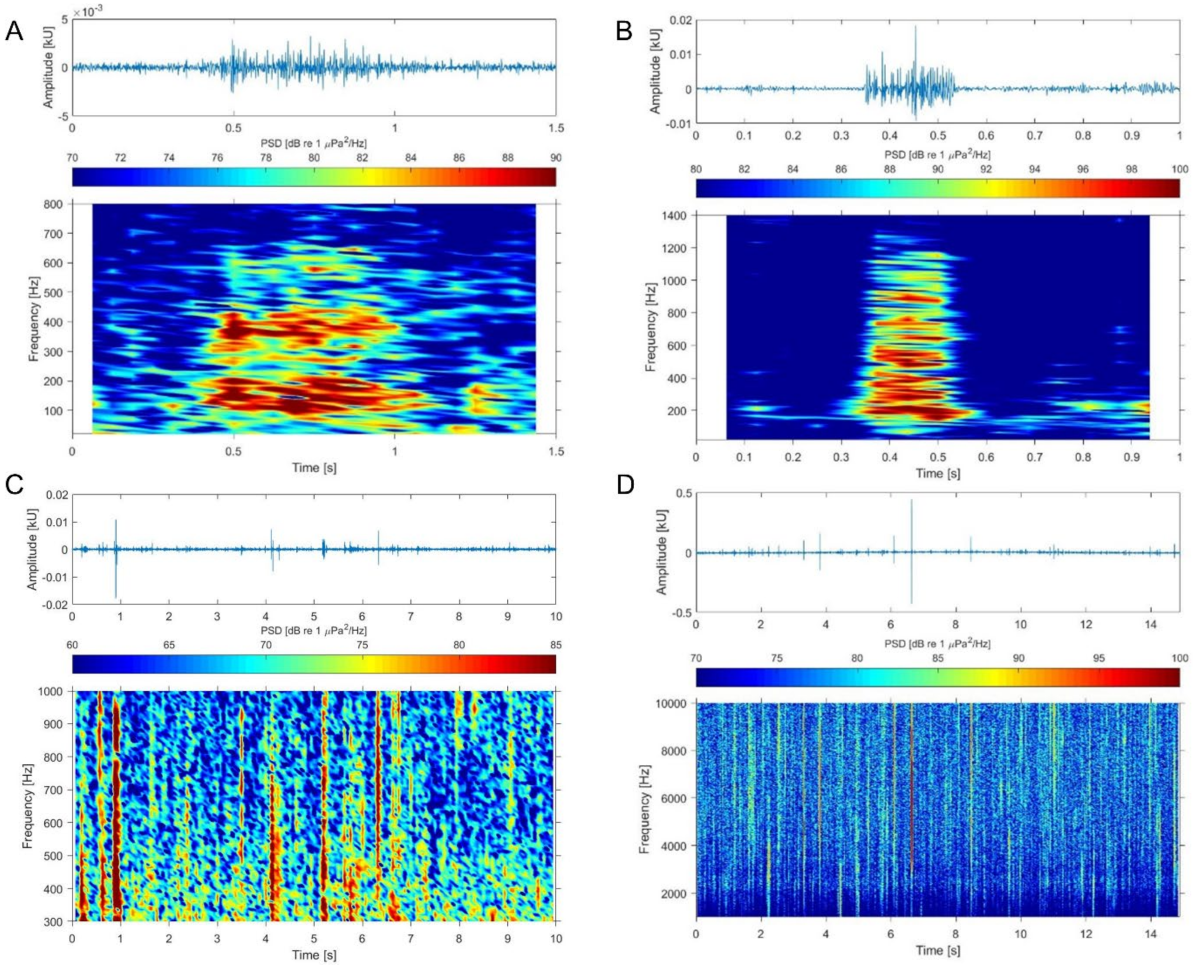

Figure 2.2. Example waveforms and spectrograms of each sound type counted: A-C in the low frequency, D in the high frequency: A) long call, B) herbivory sounds, C) fish knocks, and D) snapping shrimp snaps in the high frequency band. Spectrograms were computed with sample rate = 96 kHz, window size = 12000 samples, and using a Hanning window with 50% overlap.

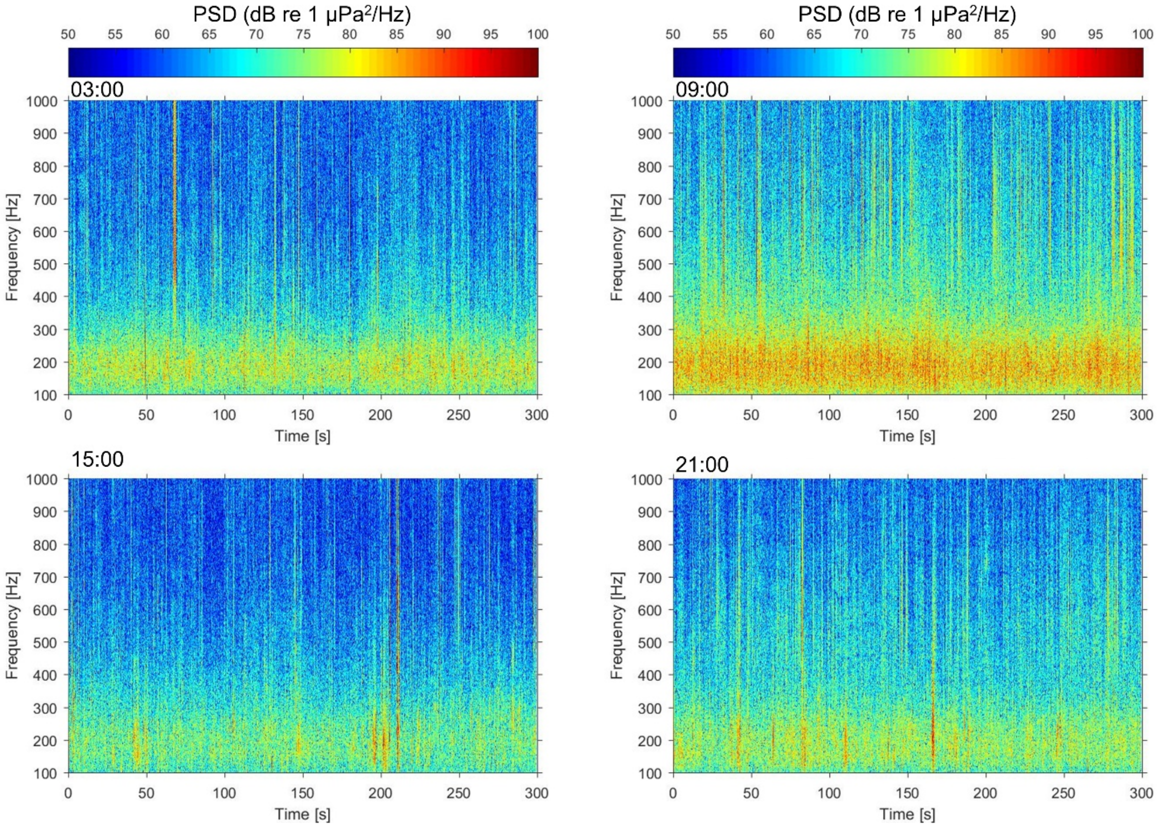

Figure 2.3. Low frequency (100-1000 Hz) spectrograms from one representative site visualizing patterns in sound production levels (SPL) among our four sampled times of day: 3:00, 9:00, 15:00, and 21:00. Spectrograms were computed with sample rate = 96 kHz, window size = 24000 samples, and using a Hanning window with 50% overlap.

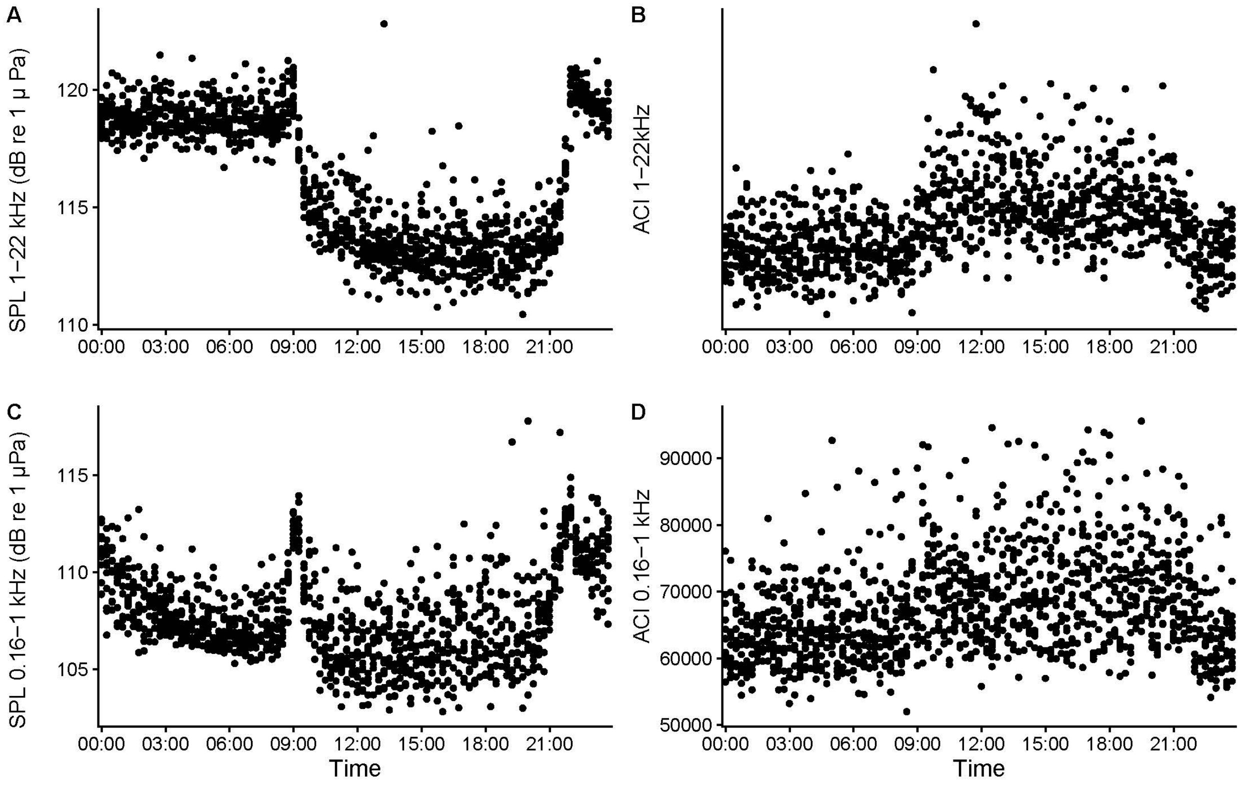

Figure 2.4. All plots collect data from the entire deployment at one site in 2018. Each plot represents a 24-hour day. A) High frequency SPL values. B) High frequency ACI values. C) Low frequency SPL values. D) Low frequency ACI values. All ACI values displayed were calculated using a 31.2 Hz frequency resolution and 0.5 s temporal resolution.

Chapter 3 – Immediate and long-term effects of a mass coral mortality event on a corallivorous fish community

Sean Dimoff[1], Julia K. Baum[1,2*]

[1]Department of Biology, University of Victoria, PO Box 1700 Station CSC, Victoria, British Columbia, V8W 2Y2, Canada

[2]Hawai‘i Institute of Marine Biology, University of Hawai‘i, 46-007 Lilipuna Road, Kāne‘ohe, Hawai‘i, 96744, USA

3.1 Abstract

Marine heatwaves and associated mass coral mortality events are threatening coral reef ecosystems, jeopardizing the survival of specialist fish species that rely on coral for food and habitat. Research into corallivorous fishes is typically focused on butterflyfishes or investigates changes to corallivores as one functional group among many. Because of this, to our knowledge no studies have provided an in-depth examination of the response of an entire corallivorous fish assemblage to a mass coral mortality event. In this study, we quantify the immediate and lagged effects of a marine heatwave on a corallivorous fish community from Kiritimati (Republic of Kiribati) in the central equatorial Pacific and investigate the role of local human disturbance in shaping their recovery. Underwater Visual Census (UVCs) were conducted across Kiritimati's local human disturbance before, during, and for three years after the 2015-2016 El Niño and mass coral mortality event. We found that trends in both obligate and facultative corallivores were influenced by the large decline in two dominant coral-associated damselfish species, *Plectroglyphidodon johnstonianus* for obligate and *Plectroglyphidodon dickii* for facultative. Obligate corallivores experienced declines in species richness and a lagged decline in abundance while facultative abundance was positively associated with human disturbance. These findings enhance our understanding of how both obligate and facultative corallivores respond to coral mortality, provide a timeline for obligate abundance decline following a coral mortality event, and highlight the interacting effects of local and global stressors on corallivorous communities.

3.2 Introduction

Coral reefs are among the most threatened ecosystems on the planet, under threat from both global and local stressors (Hoegh-Guldberg, 2011; Hoegh-Guldberg et al., 2017; Kotb et al., 2004). In particular, these ecosystems are threatened by marine heatwaves, often associated with large scale climatic events like El Niño (Holbrook et al., 2020). As these events become more frequent and intense due to climate change, their effects will continue to alter coral reef ecosystems and the diverse fish communities that they foster (Barber and Chavez, 1983; Frölicher et al., 2018). Locally, coastal development can result in increased nutrients in nearby waters (Dubinsky and Stambler, 1996) and sedimentation which can smother corals (Roy and Smith, 1971), preventing their symbiotic algae from photosynthesizing (Bellwood and Fulton, 2008). Overfishing can reduce key piscivores in fish communities, resulting in "prey release" and altered trophic dynamics in coral reef ecosystems (Advani et al., 2015; Sandin et al., 2008), or reduce herbivorous fishes that maintain top-down pressures on macro-algae (Kelly et al., 2017). Similarly, coral reef fishes are threatened by overexploitation from aquarium collectors which can significantly alter the abundances of high value species(Tissot and Hallacher, 2003).

Corallivorous fish species may be the most threatened by heatwaves and subsequent coral loss because of their reliance on live coral for food and shelter. Obligate corallivores, fishes that rely on corals for most of their diet, are threatened as they can lose their primary food source to heat stress (Graham, 2007). Facultative corallivores, fishes that consume coral as only a part of their diet, are often much less affected by the loss of live coral (Emslie et al., 2011), although they can decline as coral structure degrades following coral death (Graham et al., 2009). Obligate corallivores are also often specialists, preferentially eating only a few species of corals, which decreases their chances of survival when heat stress events decrease the abundance and diversity of available prey (Berumen and Pratchett, 2006; Graham, 2007; Pratchett et al., 2004). Therefore, as coral reefs continue to change due to both local and global stressors, coral-associated specialist species are under threat of extinction (Munday, 2004).

Most studies that have investigated the impacts of heatwaves and local stressors on coral reef fishes either split a full fish community into functional groups (Robinson et al., 2019; Shibuno et al., 1999) or highlight a few species of concern (Graham, 2007; Pratchett et al., 2013). Investigations that include a complete corallivore functional group are typically only a part of larger research questions seeking to answer questions about an entire fish community (Bargahi et al., 2020; Spalding and Jarvis, 2002) and can only inform about broad trends in corallivore assemblages. Studies directed specifically at corallivores are mostly conducted on butterflyfishes (*Chaetodontidae*), a family of fishes typically associated with corallivory (Cole et al., 2008) and rarely include other corallivorous species. These studies also only use a subset from a corallivore assemblage, selecting a few species to analyze at a time (Crosby and Reese, 2005; Pratchett et al., 2004; Zambre and Arthur, 2018) or selecting only corallivores within *Chaetodontidae* (Emslie et al., 2011; Graham et al., 2009; Pratchett et al., 2006; Pratchett et al., 2013). While some studies have investigated changes in non-butterflyfish species, they also use a subset of a few species within the corallivore functional group (Guzmán and Robertson, 1989; Jayewardene et al., 2009). Additionally, no studies to our knowledge have investigated how local human disturbance interacts with heat stress induced coral mortality to impact corallivorous fishes. Investigating how coral mortality and human proximity affect entire corallivore communities is key to understanding how corallivore communities will adapt to changing coral reefs.

In this study, we examined variability in an entire assemblage of corallivorous reef fishes over the course of a decade on the world's largest atoll to determine the lasting and lagged effects of a coral mortality event. The 2015-2016 El Niño event resulted in almost 90% coral mortality around Kiritimati, nearly eliminating a consequential diet item for an entire functional group of fishes on the surrounding coral reefs (Claar et al. 2020; J.K. Baum, *unpublished data*). Here we build from previous work by Magel et al. (2020), which investigated how each functional group around Kiritimati responded to the 2015-2016 El Niño and found that corallivorous fish biomass had declined by over 70% only one year after the heatwave. We expand on this study by adding an additional two years, including changes to the corallivore assemblage from 2018 and 2019, and by highlighting changes to both facultative and obligate corallivores and the dominant species that influence those trends. Our underwater reef fish surveys also encompassed the atoll's gradient of local human disturbance (Magel et al., 2020; Watson et al., 2016), allowing us to identify how human development can influence the impact of a marine heatwave on corallivore assemblages.

Our objectives were to (1) assess changes in individual species abundance, species richness, and assemblage structure before, during, and after the mass coral mortality event caused by the 2015-2016 El Niño for both the obligate and facultative functional groups (2) quantify how the response of dominant species in each functional group influenced group trends, (3) and to determine how human disturbance and coral cover influenced corallivore abundance spatially and temporally in the three years following the El Niño.

We hypothesized that the coral mortality event would result in significant declines in obligate corallivore abundance and species richness resulting in major shifts in their assemblage composition due to their reliance on coral as a primary component of their diet. In both obligate and facultative communities, we predicted that dominant coral-associated damselfish would be most affected due to their reliance on live coral cover for territory and reproduction. Following the mortality event, we expected obligate corallivore abundance to positively respond to coral recovery. In contrast, we anticipated that facultative corallivores would experience no immediate declines or shifts in species composition in response to the coral mortality, with lagged declines and shifts connected to structural loss on the coral reef in subsequent years. We also expected that human disturbance might modulate the effects of the coral mortality by creating corallivore communities accustomed to minimal live coral that would experience smaller changes following coral mortality than coral communities in areas of previously high coral cover.

3.3 Methods

3.3.1 Study Site and Design

We surveyed reef fish communities before, during and after the 2015-2016 El Niño at forereef sites around Kiritimati (Christmas Island, Republic of Kiritimati; Fig. 3.1). Located in the central equatorial Pacific Ocean (01°52'N 157°24'W), Kiritimati is home to approximately 6500 people (Kiribati National Statistics Office, 2016), most of whom rely on reef resources for both subsistence and income (Watson et al. 2016). Due to its geographical isolation, residents are reliant on the local fishery for protein. The local economy is also centered around fishing, as the most common source of income in 2013 was selling fish (Watson et al., 2016)

The population of Kiritimati is concentrated on the northwestern corner of the atoll (Fig. 3.1), creating in a spatial gradient of human disturbance across its surrounding reefs. This gradient has created distinct differences in the benthic communities around the atoll. All models used a continuous measure of human disturbance which combined population size, fishing pressure, and proximity to nearby population centers, following methods described in Magel et al. (2020). While fishing pressure is not a concern for the species of this study, areas of high fishing pressure are also used by aquarium collectors who target ornamental species included within our corallivore functional group. These areas are also the nearest to human population centers, presenting these sites with increased run-off and pollution (Watson et al., 2016). In order to visualize this gradient for figures, each survey site was assigned one of four human disturbance levels (very low, low, medium, or high).

Surveys were conducted at 16 sites before the El Niño (July-August 2011, and 2013), during (July 2015), and after the heat stress ended (June - August 2017) (Fig. 3.1a). The July 2015 surveys were conducted after Kiritimati's waters had experienced 15°C-week degree heating weeks (Claar and Baum, 2019). To assess how corallivore assemblages changed following the heatwave, surveys were conducted at 14 sites between June and August in 2017, 2018 and 2019 (Fig 3.1b). We conducted 168 fish surveys in total with some sites surveyed multiple times in a single year during different days. Sites were surveyed either once or twice each survey year throughout the study.

3.3.2 Fish Surveys

Underwater visual censuses (UVCs) were conducted using belt transect methods described in Sandin et al. (2008). At each site, a pair of trained divers identified, quantified, and sized all species along three separate 25 m long transects, with adjacent transects separated by 10 m. All surveys were conducted within the 10-12m isobath. For each transect, divers counted only large, mobile fish (≥ 20 cm) within an 8 m wide strip while laying out the transect, divers would then return, swimming back along the transect and counting only small, site-specific fish (< 20 cm) within a 4 m wide strip. Prior to analysis, to standardize the sampling area between small and large fish surveys, we doubled the number of small fishes observed on each transect, as described in Robinson and Baum (2016). Therefore, all abundances presented below represent a density of fishes within a 600 m^2 (3 × 25 × 8m) survey area. All surveys were conducted within day-time hours. Surveys were conducted by a total of eight divers, with the same buddy pairs conducting all surveys within a given year, except in 2019 when three divers interchanged for surveys. The two most experienced divers conducted surveys for three and four years each. Scientific divers were highly experienced and spent the first 1-2 days on Kiritimati each year re-familiarizing themselves with the atoll's diverse fish communities and underwater size estimation. To ensure accurate fish length estimation by divers, size estimation was practiced using sections of PVC pipe of predetermined lengths (Bell et al. 1985), until divers could consistently estimate lengths within 2 cm.

3.3.3 Benthic Surveys

Benthic surveys were conducted from 2017 – 2019 using 1×1m photo-quadrats taken at random points along a 100 m long transect. Following their collection, photos were analyzed using CoralNet (Beijbom et al., 2015). To provide coral cover information, CoralNet randomly overlays 100 points across the photo, the substrate underneath each point can then identified by trained technicians. Points on top of substrate that could not be identified (e.g. shadows, hardware, blurry spots) were grouped together as unidentifiable points and any quadrat that had more than 10% of its points categorized as unidentifiable was removed before analysis. Due to this, 19 quadrats were removed prior to analysis. Percent cover was calculated per quadrat using only identifiable points, site-level cover was then calculated by averaging the percent cover of each quadrat. For this study, coral cover was calculated using only points classified as "healthy" corals, therefore bleached corals were excluded.

3.3.4 Corallivore Designations

Species were first categorized into the broad trophic groups determined by Magel et al. (2020). We then conducted a literature review to classify corallivorous fishes included in our study as either facultative or obligate corallivore species. Due to the inclusion of facultative corallivores in this study, some species previously categorized as omnivores, invertivores, and generalist carnivores in Magel et al. (2020) are included here because coral has been documented in their diets. Species previously categorized as omnivores include: *Plectroglyphidodon dickii* and *Zanclus cornutus*. Species previously categorized as invertivores include *Forcipiger flavissimus* and *Balistapus undulatus*. Only one species was previously categorized as a generalist carnivore, *Sufflamen fraenatum*.

The separation between facultative and obligate corallivores is not always concrete. In their review of corallivores impact on coral reefs, Rotjan and Lewis (2008) indicated that obligate corallivores were those that ate exclusively live coral, while Pratchett et al. (2013) included only species that were dependent on coral for their survival. Some studies place a dietary threshold on their species, indicating that species whose diets are composed of > 80% coral are considered obligate corallivores (Cole et al., 2008; Emslie et al., 2011). However, these categorizations can be confounded by differences between individuals and locations, making determining the level of coral dependence difficult for many species (Cole et al., 2008; Ho et al., 2009). Facultative corallivores are similarly difficult to discern, Emslie et al. (2011) categorized facultative feeders as those whose diet consisted of 50-80% coral while other studies categorize facultative corallivores only as fishes whose diet includes coral (Berumen and Pratchett, 2006; Cole et al., 2008; Pratchett et al., 2013; Rotjan and Lewis, 2008). To address these inconsistencies, we conducted an independent review of the literature and categorized each species accordingly (Table 3.1). Following our independent review, our designations aligned with those found by Cole et al. (2008), which categorized obligate corallivores as fishes that consumed coral for more than 80% of their diet and facultative corallivores as species that had a wide range of coral dependence in their diet. We also included two species not included in their study, *Amanses scopas* and *Zanclus cornutus*, which were classified as obligate and facultative corallivores, respectively (Table 3.1).

3.3.5 Statistical Analysis

All statistical analyses were conducted using R version 3.6.1 (R Core Team, 2019). To examine the combined effects of both local and global stressors on corallivore abundance we fit generalized linear mixed-effects models (GLMMs) using the package glmmTMB (Brooks et al., 2017). Prior to each analysis, continuous input variables were standardized to a mean of zero and a standard deviation of 0.5 using the 'rescale' function in the *arm* package (Gelman et al., 2020). All analyses used abundance per transect (individuals/600 m^2) as the response variable. Analyses designated "Heat Stress Models" used sites sampled between 2011 and 2017 around Kiritimati (Fig. 3.1), while analyses designated "After-effect Models" used some overlapping and some different sites sampled from 2017 - 2019 (Fig. 3.2).

3.3.6 Heat Stress Models

Heat stress models were fit for both facultative and obligate corallivores and included surveys from before (2011 & 2013), during (2015), and after (2017) the 2015-2016 El Niño. Each model distribution was determined by its response variable. Abundance was modelled using a negative-binomial distribution, which is appropriate for overdispersed data and were fit with a 'log' link function (Bolker, 2008). Species richness was modelled using a Poisson distribution, which is appropriate for count data that are not overdispersed (Bolker, 2008). Heat stress models included heat period (before, during, and after) and human disturbance as fixed effects, as well as their interaction. We included net primary productivity as a fixed effect using a filtered remotely-sensed data product extracted from SESYNC Marine Socio-Environmental Covariates data set (https://shiny.sesync.org/apps/msec/; Yeager et al. 2017). This data product is calculated over a 2.5 arcmin grid based on data from NOAA Coastwatch, which models net primary productivity, and is modeled using satellite-derived measures of photosynthetically available radiation, SST, and chlorophyll-*a* concentrations. Sites included in these models were surveyed at least once within each heat period. We also included site and observer as random effects, observer was included to account for variation between observers as well as variation by the same observer before, during, and after the heat stress.

To assess changes in facultative and obligate assemblage structure before, during, and after the El Niño, we used multivariate statistical and ordination techniques available through the R package *vegan* (Oksanen et al., 2009). To visualize differences in corallivore assemblage structure, we began by creating a multivariate ordination (principal coordinates analysis; PCoA) using the 'betadisper' function across our different heat-periods. Site x species matrices were created for obligate and facultative communities using species abundance. To visualize variation in assemblage structure between sites within each heat stress period we also created distance-to-centroid plots. Following this, we used a permutational multivariate analysis of variance (PERMANOVA) test with 999 permutations and Bray-Curtis distances with the 'adonis' function. Heat period and human disturbance were included as well as their interaction. Primary productivity was also included as a fixed effect in each model, while site was included as a blocking factor using the 'strata' term within the 'adonis' function. To assess differences in assemblage structure between each heat stress period, pairwise comparisons were made using the 'permutest' function with 999 permutations. Finally, to determine which species were responsible for driving observed differences in assemblage structure within facultative and obligate communities, we used the 'simper' (similarity percentages) function to identify the most influential species between heat stress periods.

3.3.7 After-effect Models

To investigate how obligate and facultative corallivore abundance and species richness has changed following the 2015-2016 El Niño we designed models that included the three years sampled following the El Niño. Again, distributions depended upon the response variable. Abundance was modelled using a negative-binomial distribution, which is appropriate for overdispersion while species richness used a Poisson distribution, which is appropriate for count data that is not over dispersed (Bolker, 2008). Due to a convergence error, the facultative species richness model was fit using a Conway-Maxwell Poisson distribution as recommended by Brooks et al. (2017). We included all sites surveyed in at least two years between 2017, 2018, and 2019. This resulted in a total of 14 sites, 9 of which included fish surveys and benthic surveys in all three years. To ensure that our included sites with incomplete sampling did not change our results, we have also provided a sensitivity analysis conducted using only the 9 sites sampled every year (Table B3.1). These models included year as a categorical fixed effect and human disturbance as a continuous fixed effect, as well as their interaction. Coral cover was also included as a continuous fixed effect in these models. We also included net primary productivity, using the same data extracted from SESYNC Marine Socio-Environmental Covariates data set (https://shiny.sesync.org/apps/msec/; Yeager et al. 2017). Site and observer were included as random effects to account for variation between observers.

To assess changes to facultative and obligate corallivore abundance as they recover from the El Niño, we conducted the same multivariate and statistical methods used in our overall model. However, for this model, we substituted year for heat period as a fixed effect. Therefore, the PCoA used here visualized differences in each of the corallivore assemblages between each year. Variation between sites within each year was also visualized using distance-to-centroid plots. Additionally, this PERMANOVA test included coral cover, as well as year and human disturbance as fixed effects as well as the interaction between year and human disturbance. Primary productivity was also included as a fixed effect, and site was again included as a blocking factor using the 'strata' term within the 'adonis' function. To assess differences in assemblage structure between each year, pairwise comparisons were made using the 'permutest' function with 999 permutations. A simper analysis was used to identify which species were responsible for the observed changes in assemblage structure within facultative and obligate communities in the years following the El Niño.

3.3.8 Separation Models

To determine how the changes in the abundance of the most dominant species influenced trends in obligate and facultative corallivore abundance, we separated the dominant species from both the obligate and facultative assemblages, replicated both the heat stress and after-effect abundance models and analyzed how both the dominant species and the remaining assemblages changed. All abundance models used a negative binomial distribution to account for overdispersed data (Bolker, 2008), however, due to increased zeroes following separation we also fit zero-inflated negative binomial models and compared using AIC (Brooks et al., 2017; Warton, 2005). All models were fit with a 'log' link function. For the obligate corallivores, we separated *Plectroglyphidodon johnstonianus* from the remaining obligate assemblage and then analyzed each group independently. The zero-inflated model was found to provide a better fit only for the *P. johnstonianus* abundance in the after-effect model (2017-2019), so it was used as the final model. For the facultative corallivores, we separated *Plectroglyphidodon dickii* from the remaining facultative assemblage and analyzed each group independently. The zero-inflated model was found to provide a better fit for all separated facultative abundance models and was therefore used for the final models.

3.4 Results

3.4.1 Heat Stress

At sites sampled, before, during, and after the 2015-2016 El Niño (Fig. 3.1a), obligate corallivore abundance declined from a mean of 28.6 ± 2.8 (calculated mean from raw data ± SE) fish per site before the heat stress, to 16.3 ± 1.8 fish per site during ($z_{152} = -2.628$, $p = 0.009$), and 3.2 ± 0.9 fish per site after the heat stress ($z_{152} = -7.008$, $p < 0.001$; Table 3.2; Fig. 3.3a). However, when the dominant species was analyzed separately, the decline in abundance for the remaining obligate species was no longer significant either during or after (Table 3.2b). The abundance of *P. johnstonianus* declined from (mean ± SE) 25 ± 2.8 individuals per site before the heat stress to 13.3 ± 1.7 individuals per site during ($z_{152} = -2.154$, $p = 0.031$) and 0.91 ± 0.4 individuals per site after ($z_{152} = -5.560$, $p < 0.001$).

When considering the entire facultative corallivore assemblage, abundance significantly declined from a mean of 57.2 ± 4.7 fish per site before the heat stress to 19.1 ± 1.5 fish per site after ($z_{152} = -3.19$, $p = 0.001$; Table 3.2a), although the abundance did not significantly differ between before and during the heat stress. When *P. dickii* was analyzed separately, facultative declines were no longer significant (Table 3.2b). *P. dickii* abundance significantly declined from

46.5 ± 5.1 individuals per site before to 11 ± 1.4 individuals per site after the heat stress (z_{151} = -3.031, $p = 0.002$).

Local human disturbance significantly affected both obligate and facultative communities. Local disturbance had a significant negative effect on obligate corallivore abundance for the entire obligate functional group (z_{152} = -2.514, $p = 0.012$; Table 3.2a). However, when the obligate assemblage was analyzed separately from *P. johnstonianus*, this effect was only significant for *P. johnstonianus* (z = -3.042, $p = 0.002$; Table 3.2b). The entire facultative functional group also displayed a significant negative effect due to local human disturbance (z_{152} = -2.487, $p = 0.013$; Table 3.2a). Although, when *P. dickii* was analyzed separately, the effect of local disturbance was significant and positive for the remaining facultative assemblage (z_{151} = 6.205, $p < 0.001$; Table 3.2b), while the abundance of *P. dickii* was negatively affected by local human disturbance (z_{151} = -3.793, $p < 0.001$). The abundance of the entire facultative assemblage was also negatively associated with higher levels of primary productivity (z_{152} = -2.487, $p = 0.045$; Table 3.2a), although in the separated models *P. dickii* was not significantly affected by productivity and the remaining facultative species were positively affected (z_{151} = 3.343, $p < 0.001$).

Finally, local human disturbance amplified the response of the entire facultative functional group to heat stress. Sites with higher levels of local disturbance had significantly larger facultative corallivore abundance after the heat stress (z_{152} = 4.587, $p < 0.001$), compared to sites subject to lower levels of disturbance (Table 3.2a, Fig 3.5). However, when the facultative assemblage was separated from *P. dickii*, this trend was only significant and positive for *P. dickii* (z_{151} = 3.081, $p = 0.002$; Table 3.2b). For the obligate assemblage, this interaction was not significant in both the full assemblage and the separated models (Fig. 3.5).

3.4.2 After-effect

Following the El Niño, obligate corallivores experienced intense long-term declines in abundance that were influenced by a decline in *P. johnstonianus* abundance. At sites included in the "after" models (Fig. 3.1b), obligate corallivore abundance significantly declined from 3.33 ± 0.99 fish per site in 2017 to 0.97 ± 0.4 fish per site in 2019 ($z_{91} = -2.772$, $p = 0.006$; Table 3.3a; Fig. 3.4a). When *P. johnstonianus* was separated from the obligate functional group and analyzed separately, the remaining obligate species still experienced a significant decline in abundance between 2017 and 2019, declining from 2.5 ± 0.9 fish per site in 2017 to 0.9 ± 0.35 fish per site in 2019 ($z_{93} = -3.864$, $p = 0.004$; Table 3.3b, Fig 3.4b). *P. johnstonianus* also significantly declined between 2017 and 2019, from 0.85 ± 0.43 individuals per site in 2017 to 0.07 ± 0.07 individuals per site in 2019 ($z_{91} = -2.909$, $p = 0.004$). However, neither *P. johnstonianus* or the remaining obligate assemblage were significantly different between 2017 and 2018. Facultative corallivores significantly declined from 20.6 ± 1.5 fish per site in 2017 to 16.3 ± 2.96 fish per site in 2018 ($z_{91} = -2.980$, $p = 0.003$; Table 3.3a). Although, by 2019 facultative corallivore abundance had returned to 19.4 ± 2.8 fish per site, similar to the abundance in 2017. When *P. dickii* was separated from the rest of the facultative functional group, we did not detect any significant differences in abundance between each of the three years following the El Niño (Table 3.3b; Fig. 3.4d).

Although we could not directly compare assemblage abundance from before (2011-2013) to abundance in 2019 because different sites were sampled, we provide changes in the raw means here. *P. johnstonianus* abundance declined from 25 ± 2.8 individuals per site before the heat stress to 0.9 ± 0.35 individuals per site in 2019, at sites sampled for after-effect models. The remaining obligate species declined from 3.5 ± 0.42 fish per site before the heat stress to 0.9 ±

0.35 fish per site in 2019. *P. dickii* abundance declined from 46.5 ± 5.1 individuals per site before, to 4.4 ± 0.83 individuals per site in 2019, while the remaining facultative species abundance increased from 10.8 ± 1.46 fish per site before the heat stress to 15.0 ± 3.16 fish per site in 2019.

Coral cover also influenced obligate corallivore abundance in the three years following the El Niño. Obligate corallivore abundance was higher at areas with higher coral cover ($z_{91} = 2.668$, $p = 0.007$; Table 3.3a) When *P. johnstonianus* was analyzed separately, the abundance of the remaining obligate species was nearly significant and positively associated with coral cover ($z_{93} = 1.780$, $p = 0.0751$; Table 3.3b). *P. johnstonianus* abundance was positively associated with both coral cover ($z_{91} = 3.367$, $p < 0.001$) and primary productivity ($z_{91} = 3.694$, $p < 0.001$). The abundance of the full facultative assemblage was not significantly associated with changes in either primary productivity or coral cover (Table 3.3a). When *P. dickii* was analyzed separately, its abundance was positively associated with productivity ($z_{90} = 2.171$, $p = 0.030$; Table 3.3b), while the abundance of the remaining facultative species was not significantly associated with productivity.

Local disturbance modulated the response of both obligate and facultative corallivore abundances in the 3 years following the El Niño. For the entire obligate assemblage, in 2018 sites subject to higher local disturbance had increased abundance compared to those with lower levels of disturbance ($z_{93} = 2.430$, $p = 0.015$; Table 3.3a; Fig. 3.6). However, this interaction was only significant in 2018 and when the *P. johnstonianus* was analyzed separately, the interaction was not significant for either the remaining obligate species or *P. johnstonianus* (Table 3.3b). For the entire facultative assemblage, sites with higher local disturbance in both 2018 ($z_{91} = 4.862.$, $p < 0.001$; Table 3.3a; Fig 3.6) and 2019 ($z_{91} = 3.506$, $p < 0.001$) had increased abundance compared to those with lower disturbance. When *P. dickii* was separated from the facultative species, the interaction was still significant for the remaining facultative species in both 2018 ($z_{90} = 3.037$, $p = 0.002$) and 2019 ($z_{90} = 2.610$, $p = 0.009$), and not significant for *P. dickii* in either year (Table 3.3b).

3.4.3 Species Richness

Obligate corallivore species richness declined significantly after the El Niño, from a mean of 2.2 ± 0.1 species per site before the heat stress, to a mean of 0.95 ± 0.15 species per site after ($z_{154} = -4.601$, $p < 0.001$; Table 3.2c; Fig. 3.3). In the three years following the El Niño, obligate species richness decreased from a mean of 0.95 ± 0.16 species per site in 2017 to a mean of 0.33 ± 0.11 species per site in 2019 ($z_{92} = -3.130$, $p = 0.002$; Table 3.3c; Fig 3.4). Obligate species richness was also higher at sites with higher coral cover ($z_{92} = 2.957$, $p = 0003$). Between 2011 and 2017, there were more facultative species at sites with higher productivity ($z_{154} = 2.248$, $p = 0.025$). Between 2017 and 2019, facultative species richness was positively impacted by local human disturbance ($z_{91} = 3.525$, $p < 0.001$; Table 3.3c), productivity ($z_{91} = 2.731$, $p = 0.006$), and coral cover ($z_{91} = 2.985$, $p = 0.003$). When accounting for these covariates, facultative species richness also significantly decreased between 2017 and 2019 ($z_{91} = -2.441$, $p = 0.015$).

3.4.4 Assemblage Structure

Assemblage structure for both obligate (pseudo $F = 8.87$, $R^2 = 0.152$, $p = 0.001$; Table 3.4a; Fig. 3.7, 3.9) and facultative (pseudo $F = 9.48$, $R^2 = 0.113$, $p = 0.001$) corallivore functional groups varied significantly across heat stress periods. Obligate assemblages significantly changed between both before and after (pseudo $F = 10.73$; $p = 0.001$, 999 permutations; Table

3.6a) and during and after (pseudo $F = 10.73$; $p = 0.002$, 999 permutations) In the obligate group, 67% of the dissimilarity after the heat stress (compared to pre-heat stress assemblage structure) was due to changes in *P. johnstonianus* abundance (Table 3.8a). Obligate assemblage structure was also significantly altered by local disturbance (pseudo $F = 9.98$, $R^2 = 0.086$, $p = 0.001$; Table 3.4a) and productivity (pseudo $F = 1.45$, $R^2 = 0.013$, $p = 0.009$). However, when *P. johnstonianus* was removed from the functional group and structure was reanalyzed, assemblage structure did not significantly vary across any of the measured variables (Table 3.4b, 3.6b). For facultative corallivores, 61% of dissimilarity after the heat stress (compared to pre-heat stress assemblage structure) was due to changes in *P. dickii* abundance (Table 3.6b). The facultative corallivore assemblage structure was also significantly altered by local human disturbance (pseudo $F = 41.19$, $R^2 = 0.246$, $p = 0.001$; Table 3.4a) and productivity (pseudo $F = 3.419$, $R^2 = 0.42$, $p = 0.001$). Additionally, the interaction between heat stress and local human disturbance was significant for the facultative corallivore assemblage (pseudo $F = 3.28$, $R^2 = 0.035$, $p = 0.001$) which suggests that the effect of heat stress on facultative assemblage structure is influenced by the severity of local human disturbance. When *P. dickii* was removed and assemblage structure was reanalyzed, only heat stress (pseudo $F = 2.89$, $R^2 = 0.052$, $p = 0.001$; Table 3.4b) and productivity (pseudo $F = 2.404$, $R^2 = 0.021$, $p = 0.026$) significantly altered the remaining assemblage structure.

In the three years following the El Niño both obligate (pseudo $F = 2.69$, $R^2 = 0.111$, $p = 0.005$; Table 3.5a; Fig 3.8, 3.10) and facultative (pseudo $F = 4.097$, $R^2 = 0.065$, $p = 0.001$) assemblages continued to change. However, assemblages were less dominated by a single species. Within obligate corallivores, changes in *P. johstonianus* abundance only contributed to 22% of the dissimilarity between 2017 and 2019 (Table 3.9a). The entire obligate assemblage was only significantly altered between 2017 and 2018 (pseudo $F = 2.47$, p = 0.024, 999 permutations; Table 3.7a). In addition to year, both local disturbance (pseudo $F = 2.56$, $R^2 = 0.054$, $p = 0.020$; Table 3.5a) and productivity (pseudo $F = 1.29$, $R^2 = 0.027$, $p = 0.014$) significantly influenced obligate assemblage structure, while coral cover did not have a significant effect. When *P. johnstonianus* was removed and the functional group was reanalyzed, only year (pseudo $F = 3.57$, $R^2 = 0.159$, $p = 0.001$; Table 3.5b) and local disturbance (pseudo $F = 2.33$, $R^2 = 0.052$, $p = 0.006$) significantly altered assemblage structure. Obligate assemblages without *P. johnstonianus* significantly changed between 2017 and 2018 (pseudo $F = 1.69$, $p = 0.019$, 999 permutations; Table 3.9b) and between 2017 and 2019 (pseudo $F = 1.69$, $p = 0.007$, 999 permutations). In the facultative corallivore functional group, changes in *P. dickii* abundance only contributed to 33% of the dissimilarity between 2017 and 2019 (Table 3.9b). The facultative assemblage was also altered by local disturbance (pseudo $F = 34.53$, $R^2 = 0.272$, $p = 0.001$; Table 3.5a), while neither coral cover nor productivity had a significant effect. Similar to the heat stress model, the interaction between year and local human disturbance was significant for the facultative corallivore functional group here (pseudo $F = 3.30$, $R^2 = 0.052$, $p = 0.001$) indicating that the intensity of local human disturbance has continued to influence facultative assemblage structure year after year following the heat stress. When *P. dickii* was removed and the functional group was reanalyzed, only year (pseudo $F = 2.13$, $R^2 = 0.045$, $p = 0.008$; Table 3.5b) and the interaction between year and local disturbance (pseudo $F = 2.031$, $R^2 = 0.043$, $p = 0.001$) significantly altered assemblage structure.

3.5 Discussion

Understanding how corallivorous fishes respond to ocean warming and subsequent coral mortality becomes increasingly important in the face of continued global climate change (Chong-Seng et al., 2012). As El Niño events are predicted to become more frequent (Frölicher et al., 2018), species that rely on corals for food, including corallivorous fishes, will likely be the first and most threatened (Cole et al., 2008). Here, we document significant changes in obligate and facultative corallivore abundance, species richness, and assemblage structure in direct response to a marine heatwave and the resultant mass coral mortality. While only *P. johnstonianus* showed a marked response during the heat stress (Table 3.2b), the associated coral loss had large effects on the corallivore assemblage around Kiritimati. In addition to finding significant changes in abundance, species richness, and assemblage structure our results also incidentally provide a timeline for change in an obligate corallivore population following a major coral mortality event.

3.5.1 Abundance

Consistent with our predictions, the response of dominant coral-associated damselfish - *P. johnstonianus* and *P. dickii* – to the heat stress and coral mortality significantly influenced changes in the abundance of their associated functional groups. These results are similar to those of a recent study by Pratchett et al. (2020) which found that following a crown-of-thorns outbreak, small coral-associated damselfish vacated dead coral hosts within five days and despite some individuals recolonizing nearby live corals damselfish abundance still declined proportionally to the coral loss. These results also align with those of Wismer et al. (2019), who found that small coral-associated damselfishes drove declines in fish populations following a coral mortality event caused by the 2015-2016 El Niño on the Great Barrier Reef. While the species highlighted in their study were planktivores, the damselfish that drove changes in our study were corallivorous and thus more directly affected by the loss of coral.

In the obligate corallivore functional group, a massive decline in the abundance of the dominant species, *P. johnstonianus*, in response to the heat stress and coral mortality, significantly influenced declines in the entire functional group during and after the heat stress (Fig. 3.3). Declines during the heat stress might be explained by the direct effect of the heat stress which can limit the swimming ability and metabolic performance of damselfish (Johansen and Jones, 2011). However, it is odd that these declines would only be observed in *P. johnstonianus* and not *P. dickii*. While it is possible that some individuals migrated to deeper and cooler water as hypothesized by Magel et al. (2020), the small size and territorial behavior of these species makes that unlikely. Therefore, the immediate declines in *P. johnstonianus* abundance are likely due to mortality which was related to their reliance on *Acroporid* and *Pocilloporid* branching corals (Coker et al., 2014; Randall, 2005), some of the first and most affected by heat stress (Loya et al., 2001; Renema et al., 2016). Additionally, coral polyps are a primary component of their diet, accounting for over 90% of dietary content in Hawaii (Hobson, 1974) and Okinawa (Sano 1984). Similar declines in *P. johnstonianus* abundance following a coral mortality event were also reported in the Seychelles following the 1997-1998 El Niño (Spalding and Jarvis, 2002). Therefore, the marked declines in *P. johnstonianus* that we observed (Table 3.2; Fig. 3.3) in response to the marine heatwave were likely driven by the loss of their coral hosts.

In the three years following the heat stress, *P. johnstonianus* abundance continued to decline, although only the difference between 2017 and 2019 was significant (Table 3.3b). The decline between 2017 and 2019 was the largest decline recorded in any of the communities however, indicating a continual decline that increased three years after the coral bleaching and subsequent mortality occurred. The lag might be due to the ability of some damselfish to switch to new coral hosts in response to coral mortality (Pratchett et al., 2020; Wismer et al., 2019b). Their eventual decline, however, was likely caused by the increased susceptibility of coral dwelling fish to predation after coral bleaching and algal overgrowth (Coker et al., 2009) combined with nutrient deficiencies caused by the loss of this specialist's preferred prey (Berumen and Pratchett, 2008). When coral cover was included as a covariate, *P. johnstonianus* abundance was positively associated with live coral cover (Table 3.3b), providing further evidence that their decline was driven by mortality of their coral-hosts, which were drastically reduced by the El Niño heat stress. *P. johnstonianus* abundance was also positively associated with oceanographic productivity in the three years following the heat stress. However, as we were unable to monitor changes in productivity throughout the heat stress event or after, the mechanism behind this effect remains unclear.

In the facultative corallivore functional group, declines after the heat stress primarily reflected changes in the abundance of another coral-associated damselfish, *P. dickii* (Table 3.2d, 3.3d; Fig. 3.3, 3.4). Declines in *P. dickii* were also likely driven by the decline in live coral cover following the heat stress, as their territories are often associated with branching corals including *Acropora* and *Pocillopora* (Jones et al., 2006; Randall, 2005). Other coral-associated damselfish have been observed to evacuate their coral-hosts within 5 days of bleaching on the Great Barrier Reef (Pratchett et al., 2020). *P. dickii* maintain algal farms on small sections of their territories, which are used for food and as nest sites(Jones et al., 2006). However, they do not exclusively rely on their algal farms for food and their diet can also depend on their habitat. A study in Taiwan by Ho et al. (2009), for example, found that individuals consumed algae and coral in a coral dominated habitat and mostly sea anemones in a sea anemone dominated habitat. This ability to adapt to new habitats might also explain why *P. dickii* abundance was not associated with coral cover in our after-effect model (Table 3.3d). It is likely that the combined effects of coral mortality and subsequent macroalgal overgrowth created adverse conditions to *P. dickii* survival and reproduction, particularly in areas with previously high levels of coral cover.

Between 2017 and 2019, the obligate corallivore functional group, excluding *P. johnstonianus*, also declined in abundance (Table 3.3b; Fig. 3.4b). This decline is likely associated with the coral mortality and this timeline resembles the findings of Pratchett et al. (2006), who found that it took several years for coral depletion to be reflected in obligate corallivore populations on the Great Barrier Reef. The delayed decline might have been caused by the ability of specialist species utilizing prey-switching to survive, which can postpone the effects of prey depletion (Berumen and Pratchett, 2008; Pratchett et al., 2004). Recruitment failure might have also played a role, as obligate corallivores develop feeding specializations for scleractinian corals during settlement (Harmelin-Vivien, 1989), therefore reduced live coral cover could present serious consequences for settling juveniles. Despite the overall declining trend in obligate abundance, *Chaetodon ornatissimus* increased in abundance between 2017 and 2019 (Table 3.7). *C. ornatissimus* boasts a broad diet without any clear preferences and was one of two Chaetodon species that were observed at sites of low coral cover in Hawaii (Cox, 1994), two adaptations that likely aided its recovery following the coral mortality.

Consistent with our predictions, variation in facultative corallivore abundance, excluding *P. dickii*, was not associated with either the heat stress or year. While facultative corallivores do consume corals, they are also capable of consuming other prey items and often use them to supplement their diet (Cole et al., 2008), making them more resilient to coral depletion (Emslie et al., 2011). Facultative corallivore abundance is typically unaffected by changes in live coral cover (Glynn et al., 2014; Pratchett et al., 2006), rather declines have been connected to the loss of coral structure following a mortality event (Graham et al., 2009). However, within the timeline of our study we did not observe any decline in facultative corallivores despite there being (at least a statistically) significant loss of rugosity and habitat volume on reefs around Kiritimati following the heat stress (Magel et al., 2019). This indicates that structural declines have not been extensive enough or our study's timeline is too limited to encompass a subsequent decline in facultative corallivore abundance. Facultative corallivore abundance was also positively associated with productivity both throughout the heat stress and the recovery timelines. Again, we were unable to monitor changes in net primary productivity which changes in response to El Niño (Liao et al., 2012), and thus the mechanism behind this remains unclear.

Local human disturbance contributed to changes in *P. johnstonianus*, *P. dickii*, and facultative corallivore abundance. The negative effect of human disturbance on *P. johnstonianus* and *P. dickii* abundance is likely explained by their positive association with coral cover, as reduced coral cover has been connected to increased human populations on Kiritimati (Magel et al., 2019). Low coral cover reduces potential territory for coral-associated species like *P. johnstonianus* and *P. dickii* and would therefore diminish their populations (Jones et al., 2006). Interestingly, local disturbance had a positive effect on facultative corallivore abundance, excluding *P. dickii*, in both heat stress and after-effect periods (Nagelkerken et al. 2009). Similar to our results, studies on the Great Barrier Reef (Pratchett et al., 2006) and Chagos (Pratchett et al., 2013), found that specialist obligate species dominated areas with high coral cover. Therefore, at sites near human populations with reduced coral cover might provide increased niche space for more generalist facultative species, allowing for increased populations.

We also found a significant positive interaction between local human disturbance and year on facultative abundance in the three years following the heat stress (Table 3.5; Fig. 3.6). This indicates that areas with previously low coral cover might have sustained increased populations of facultative corallivores despite coral mortality. Despite relying on coral for a portion of their diets, facultative corallivores can display impressive diet plasticity (Nagelkerken et al., 2009) allowing them to thrive in areas with low coral cover that could not sustain large obligate corallivore populations. A study conducted by Wismer et al. (2019) found that when coral-associated damselfish were exposed to two heat stress events, they only declined in response to the first. They conclude that fish populations stabilized within 24 months because of behavioral modifications made by surviving individuals to expand their traditional habitats to include bleached and dead coral. Similarly, we might be observing adaptations by facultative populations in areas with previously low coral cover to rely on alternate food sources, providing a survival advantage following the coral mortality around the atoll. Alternatively, in areas near human populations, piscivorous predators are often reduced by fishing (Sandin et al., 2008), which might allow for populations of omnivorous fishes like facultative corallivores to thrive (Boaden and Kingsford, 2015).

3.5.2 Species Richness

Similar to the observed patterns in obligate corallivore abundance, species richness also significantly declined after the heat stress and continued to decline in the years afterwards. Previously highlighted by Magel et al. (2020), one species - *Chaetodon trifascialis* - was observed only before the heat stress, even with our extended time series, this species was not observed after the heat stress. *C. trifascialis* is a specialist species that consumes primarily *Acroporid* and *Pocilloporid* coral polyps and has shown limited ability to adapt to a diet of nonpreferred prey (Berumen and Pratchett, 2008). Specialist species, particularly corallivores, are more prone to extinction from coral bleaching and mortality than generalist species due to their reliance on a limited number of prey sources (Munday, 2004). In our results, this is reflected by the substantial change in obligate species richness after the heat stress and between 2017 and 2019, while facultative corallivores only showed a much smaller significant difference in species richness between 2017 and 2019 (Table 3.2c; Fig 3.4).

By 2019, only four species of obligate corallivores were observed: *Arothron meleagris, Chaetodon meyeri, Chaetodon ornatissimus,* and *Plectroglyphidodon johnstonianus,* compared to eleven before the heatwave. Three of these species – *A. meleagris, C. meyeri,* and *C. ornatissimus* – have each demonstrated the ability to exist in areas of low coral cover (Cox, 1994), consume a broad range of coral prey (Pratchett et al., 2013), or adapt to consume a more generalist diet (Guzmán and Robertson, 1989). *P. johnstonianus* remains an outlier, a coral-associated species that is reliant on corals for both habitat and food (Randall, 2005). However, even *P. johnstonianus* has shown the ability to modify its diet, in Taiwan following a phase-shift from a hard coral to an anemone dominated environment, individuals who continued to reside in anemone dominated habitats displayed lower coral content in their diet, supplemented with increased detritus (Ho et al., 2009).

3.5.3 Assemblage Structure

Contrary to our predictions, the structure of the obligate corallivore functional group was not significantly altered by the heat stress when *P. johnstonianus* was removed (Table 3.8c; Fig 3.7). However, significant shifts in assemblage structure were observed in the three years following the heat stress (Table 3.7c; Fig 3.8). Few studies have analyzed corallivore assemblage structure in response to coral loss, although in one recent study on the Great Barrier Reef, Richardson et al. (2018), found that fish communities contained less functional redundancy following a coral mortality event. With the loss of obligate specialists on reefs around Kiritimati, these assemblages are experiencing a similar loss in redundancy. In the three years following the El Niño, local disturbance was also responsible for dissimilarities in assemblage structure within the obligate functional group. These differences might have arisen due to distinct corallivore communities developing between areas of previously high coral cover and areas of previously low coral cover around the atoll, as Richardson et al. (2018) also found that the pre-bleaching coral assemblage was the best predictor of post-bleaching fish assemblages.

Facultative corallivore assemblage structure changed both during the heat stress and in the three years following, even after *P. dickii* was separated from the functional group (Table 3.8b, 3.9b; Fig 3.7b, 3.8b). Despite this change in assemblage structure there was no significant difference in overall facultative abundance attributed to either the heat stress or the subsequent years (Table 3.2b, 3.3b). This indicates that changes in the assemblage structure are likely the result of shifting species compositions. From before to after the heat stress, most of the change in facultative assemblage structure was attributed to declines in the abundance of 3 species – *Canthigaster solandri*, *Chaetodon kleinii*, and *Chaetodon auriga* - while *Balistapus undulatus* abundance increased (Table 3.8b). After the heat stress, in the after-effect models, most of the change was attributed to increases in two species, *Canthigaster solandri* and *Chaetodon auriga* and declines in two species, *Balistapus undulatus* and *Chaetodon vagabundus* (Table 3.9b). These shifts might be explained by changes in the abundance of non-overlapping prey as a result of thermal stress and coral loss (Nagelkerken et al., 2009). For some facultative species, live coral might also present indirect benefits and therefore its loss might have resulted in shrinking populations (Pratchett et al., 2015).

The interaction between year and local disturbance also significantly shifted facultative assemblage structure in the three years following the El Niño (Table 3.4b). This interaction indicates that local disturbance modulated assemblage structure between years although there was not a significant effect of local disturbance overall. This unique interaction might be a consequence of local shifts in facultative functional group composition following the coral loss to fill niche spaces evacuated by declining specialist obligate species (Munday, 2004) or communities shifting in response to new habitats formed by the extensive coral loss (Magel et al., 2019). It should be noted that the R^2 values for our PERMANOVA tests were quite low in the obligate and facultative communities suggesting that heat stress, year, and local disturbance explained little variation in assemblage structure. Therefore, additional research is needed to further understand the direct and lagged effects of extensive coral mortality and local disturbance on reef fish communities.

3.5.4 Implications and Future Studies

The shifts in corallivore assemblages and decline in obligate functional group abundance following a massive coral mortality event presented here provide insight into how coral loss affects an entire corallivore assemblage. Typically, species are subset from the existing assemblage and studied in isolation (Guzmán and Robertson, 1989; Reyes-Bonilla and Calderon-Aguilera, 1999). Most often these subsets consist of only species within the well-known corallivorous *Chaetodontidae* family, excluding other potentially important species (Cox, 1994; Graham, 2007; Graham et al., 2009; M. Kulbicki et al., 2005; Pratchett et al., 2006; Morgan S. Pratchett et al., 2013). Our research included the entire corallivore assemblage present on the coral reefs surrounding Kiritimati, providing insight into how coral loss affected both dominant corallivorous species and the remaining obligate and facultative corallivore communities. Our results indicate that obligate corallivores can survive for years before declining in response to a coral mortality event, a critical period of time for a population to stabilize before it collapses.

Corallivore recovery timelines might be decadal and require an extended period of time without major coral destruction, as observed in the Philippines (Russ et al., 2018). Unfortunately, our surveys only extend three years beyond the heat stress event, providing only a brief glimpse into the long-term recovery process of a coral reef. As marine heatwaves have already become more frequent and intense over the past several decades and it is predicted that this trend will only accelerate with continued climate change (Frölicher et al., 2018), lengthy recovery periods will become less common for coral reefs in the future. While some studies have already begun investigating the impacts of multiple heat stress and subsequent coral mortality events on subsets of fishes (Wismer et al., 2019b), larger studies that include more corallivorous species might reveal novel consequences or adapted resilience to repeated events. Additionally, future studies investigating the response of corallivore communities to heat stress should also consider potential temporal shifts in net primary productivity that can occur during El Niño events (Liao et al., 2012) as our study was unable to determine the mechanism connecting primary productivity to our study species. Understanding the long-term impacts of coral mortality on corallivore communities can help us predict and mitigate the effects of ocean warming on highly susceptible corallivore communities.

3.5.5 Conclusion

Climate-change induced mass coral bleaching and mortality is expected to increase the combination of rising global temperatures, ocean acidification, and increasing coastal development. In this study we examined the effects of an unprecedented coral mortality on the entire corallivore assemblage around Kiritimati and broke down the separate responses of obligate and facultative communities and their most dominant species. Corallivore communities include the fishes most closely tied to coral health and can serve as an indicator of the relationship between live coral cover and their associated fishes (Cole et al., 2008). Our results also incidentally provide a timeline for obligate corallivore abundance collapse following a coral mortality event, a vital piece of information for assisting regrowth and recovery of the functional group following these events. The success of preserving corallivore abundance and diversity in a changing world is dependent upon action at both local and global scales, which both rely on the detailed resources and timelines provided here.

Table 3.1. Functional classifications for all corallivore species encountered during underwater visual censuses (UVCs) on Kiritimati in the current study. References used for diet classifications are coded by number based on the reference list below.

Family	Species	Reference
	Obligate	
Chaetodontidae	Chaetodon bennetti	2, 14
	Chaetodon lunulatus	1, 2, 3
	Chaetodon meyeri	2, 5
	Chaetodon ornatissimus	1, 2, 3
	Chaetodon punctatofasciatus	2, 17
	Chaetodon trifascialis	2, 7
	Chaetodon unimaculatus	1, 2, 3, 17
Labridae	Labrichthys unilineatus	2
Monacanthidae	Amanses scopas	15
	Cantherhines dumerilii	2, 10
Pomacentridae	Plectroglyphidodon johnstonianus	2, 8, 9
Tetraodontidae	Arothron meleagris	2, 4, 6
	Facultative	
Balistidae	Balistapus undulatus	2, 12, 16
	Sufflamen fraenatum	11
Chaetodontidae	Chaetodon auriga	2, 5, 7
	Chaetodon citrinellus	2, 5, 7
	Chaetodon ephippium	1, 2, 7
	Chaetodon kleinii	2, 5
	Chaetodon lineolatus	2
	Chaetodon lunula	2, 5
	Chaetodon pelewensis	2
	Chaetodon quadrimaculatus	2, 7, 16
	Chaetodon ulietensis	1, 2, 7
	Chaetodon vagabundus	2, 7, 14
	Forcipiger flavissimus	2, 7, 13
	Heniochus chrysostomus	1, 2, 7, 16
Pomacentridae	Plectroglyphidodon dickii	2, 8
Tetraodontidae	Canthigaster solandri	2
Zanclidae	Zanclus cornutus	12

References: 1) Berumen and Pratchett (2006); 2) Cole et al. (2008); 3) Cox (1994); 4) Glynn et al (1972) 5) Graham et al. (2009); 6) Guzmán and Robertson (1989); 7) Harmelin-Vivien and Bouchon-Navaro (1983); 8) Ho et al. (2009); 9) Hobson (1974); 10) Jayewardene and Birkeland (2006); 11) Kulbicki et al. (2005); 12) McClanahan et al. (2005); 13) Nagelkerken et al. (2009); 14) Pratchett et al. (2006); 15) Pratchett et al. (2013b); 16) Randall (2005); 17) Sano (1989)

Table 3.2. Results (p-values) from generalized linear mixed-effects models describing the effects of heat stress, local human disturbance, and net primary productivity on obligate and facultative corallivore abundance (a), obligate and facultative corallivore communities with their most abundant species analyzed separately (b), and species richness (c) from 2011 – 2017, before, during and after the El Niño. Values in bold are significantly different from baseline levels (2011-2013) at α = 0.05, colors correspond to the value of the parameter estimate (blue = positive, red = negative).

	Heat Stress				**Heat x Disturbance**	
Model	**During**	**After**	**Local disturbance**	**Productivity**	**During**	**After**
a) Overall						
Obligate	**-0.504**	**-2.01**	**-0.991**	0.184	-0.323	0.649
Facultative	-0.006	**-0.661**	**-0.525**	**-0.36**	-0.229	**0.882**
b) Separate						
Obligate	-0.008	-0.377	0.19	0.259	-0.238	-0.238
P. johnstonianus	**-0.554**	**-2.762**	**-2.111**	0.295	-0.516	0.309
Facultative	-0.146	0.086	**1.401**	**0.644**	-0.154	-0.251
P. dickii	0.0574	**-0.793**	**-3.793**	-0.109	-0.283	**1.222**
c) Species Richness						
Obligate	-0.146	**-0.817**	-0.236	0.095	-0.026	0.039
Facultative	-0.21	-0.046	0.296	**0.291**	-0.106	0.093

Table 3.3. Results (p-values) from generalized linear mixed-effects models describing the effects of year, local human disturbance, coral cover, and net primary productivity on obligate and facultative corallivore abundance (a), obligate and facultative corallivore communities with their most abundant species analyzed separately (b), and species richness (c) from 2017-2019 following the El Niño. Values in bold are significantly different from baseline levels (2017) at α = 0.05, colors correspond to the value of the parameter estimate (blue = positive, red = negative).

	Year					**Year x Disturbance**	
Model	**2018**	**2019**	**Local disturbance**	**Productivity**	**Coral Cover**	**2018**	**2019**
a) Overall							
Obligate	-0.176	**-1.524**	-0.769	0.112	**0.17**	**1.562**	1.291
Facultative	**-0.325**	-0.26	0.23	-1.55	-0.003	**1.058**	**0.843**
b) Separate							
Obligate	0.203	**-1.42**	-0.552	-0.457	0.125	1.21	0.62
P. johnstonianus	-1.000	**-7.118**	-1.391	**1.637**	**0.438**	1.824	1.866
Facultative	-0.191	-0.136	**1.087**	**0.306**	-0.01	**0.896**	**0.78**
P. dickii	-0.324	-0.334	**-3.468**	-0.435	-0.007	0.609	-0.133
c) Species Richness							
Obligate	0.052	**-1.407**	-0.094	0.038	**0.112**	0.39	0.324
Facultative	-0.006	**-0.27**	**0.425**	**0.241**	**0.051**	0.217	0.27

Table 3.4. Results of permutational analysis of variance (PERMANOVA) tests examining the effects of heat stress, local human disturbance, and net primary productivity on reef fish assemblage structure from 2011 – 2017, before, during, and after the El Niño. Bold text indicates significant results. F value reported in the table is a pseudo F statistic.

Model	**Heat Stress**	**Local Disturbance**	**Productivity**	**Heat stress x local disturbance**
a) Obligate	**F = 8.8743** **R^2= 0.152** **p = 0.001**	**F = 9.976** **R^2= 0.086** **p = 0.001**	**F = 1.450** **R^2= 0.013** **p = 0.009**	F = 1.118 R^2= 0.0192 p = 0.436
b) Facultative	**F = 9.480** **R^2= 0.113** **p = 0.001**	**F = 41.187** **R^2= 0.246** **p = 0.001**	**F = 3.419** **R^2= 0.020** **p = 0.001**	**F = 2.944** **R^2= 0.0352** **p = 0.001**
c) Obligate (*P. johnstonianus* removed)	F = 1.709 R^2= 0.042 p = 0.060	F = 2.869 R^2= 0.035 p = 0.327	F = 1.081 R^2= 0.013 p = 0.859	F = 0.631 R^2= 0.015 p = 0.798
d) Facultative (*P. dickii* removed)	**F = 2.892** **R^2= 0.052** **p = 0.001**	F = 16.090 R^2= 0.143 p = 0.069	**F = 2.404** **R^2= 0.021** **p = 0.026**	F = 1.025 R^2= 0.018 p = 0.075

Table 3.5. Results of permutational analysis of variance (PERMANOVA) tests examining the effects of year, local human disturbance, and net primary productivity on reef fish assemblage structure from 2017-2019 following the El Niño. Bold text indicates significant results. F value reported in the table is a pseudo F statistic.

Model	**Year**	**Local Disturbance**	**Coral Cover**	**Productivity**	**Year x local disturbance**
a) Obligate	**F = 2.685**	**F = 2.560**	F = 1.738	**F = 1.293**	F = 0.734
	R^2= 0.111	**R^2= 0.054**	R^2= 0.036	**R^2= 0.027**	R^2= 0.030
	p = 0.005	**p = 0.020**	p = 0.306	**p = 0.014**	p = 0.761
b) Facultative	**F = 4.099**	**F = 34.526**	F = 4.131	F = 2.649	**F = 3.301**
	R^2= 0.065	**R^2= 0.272**	R^2= 0.033	R^2= 0.021	**R^2= 0.052**
	p = 0.001	**p = 0.001**	p = 0.587	p = 0.038	**p = 0.001**
c) Obligate (*P. johnstonianus* removed)	**F = 3.570**	**F = 2.333**	F = 1.580	F = 0.613	F = 0.540
	R^2= 0.159	**R^2= 0.052**	R^2= 0.035	R^2= 0.014	R^2= 0.024
	p = 0.001	**p = 0.006**	p = 0.390	p = 0.057	p = 0.790
d) Facultative (*P. dickii* removed)	**F = 2.127**	F = 16.954	F = 2.413	F = 0.839	**F = 2.031**
	R^2= 0.045	R^2= 0.101	R^2= 0.026	R^2= 0.009	**R^2= 0.0430**
	p = 0.008	p = 0.101	p = 0.723	p = 0.092	**p = 0.001**

Table 3.6. Pairwise comparisons (with no adjustments for multiple tests) of the corallivore assemblages between the three heat stress periods measured: before (2011 & 2013), during (2015), and after (2017). Calculated using Bray-Curtis dissimilarities and 999 permutations. F-values reported for each ANOVA-like permutation test.

Assemblage	Pairwise Comparison	F	P
a) Obligate	Before - During	10.73	0.91
	During - After		**0.002**
	Before - After		**0.001**
b) Facultative	Before - During	0.58	0.98
	During - After		0.411
	Before - After		0.32
c) Obligate (*P. johnstonianus* removed)	Before - During	2.86	0.073
	During - After		0.839
	Before - After		0.052
d) Facultative (*P. dickii* removed)	Before - During	0.84	0.202
	During - After		0.695
	Before - After		0.418

Table 3.7. Pairwise comparisons (with no adjustments for multiple tests) of the corallivore assemblages between the three years sampled after the El Niño. Calculated using Bray-Curtis dissimilarities and 999 permutations. F-values reported for each ANOVA-like permutation test.

Assemblage	**Pairwise Comparison**	**F**	**P**
a) Obligate	2017-2018	2.47	**0.024**
	2018-2019		0.904
	2017-2019		0.074
b) Facultative	2017-2018	1.69	0.48
	2018-2019		0.251
	2017-2019		0.077
c) Obligate (*P. johnstonianus* removed)	2017-2018	4.12	**0.019**
	2018-2019		0.392
	2017-2019		**0.007**
d) Facultative (*P. dickii* removed)	2017-2018	1.37	0.443
	2018-2019		0.336
	2017-2019		0.139

Table 3. 8 . Top 5 species contributing to variation in fish assemblage structure after the El Niño (compared to pre-disturbance composition) for obligate (a) and facultative (b) corallivore functional groups. Mean site-level abundances for each time point are listed, as well as the cumulative contribution of each species to the overall assemblage dissimilarity.

Species	Change (+/-)	Before	After	Cumulative sum
a) Obligate				
Plectroglyphidodon johnstonianus	-	25.47	1.95	0.67
Chaetodon meyeri	-	1.37	0.79	0.75
Chaetodon ornatissimus	-	1.66	1.11	0.82
Labrichthys unilineatus	+	0	1.95	0.87
Cantherhines dumerilii	-	0.37	0.47	0.91
b) Facultative				
Plectroglyphidodon dickii	-	45.58	11	0.61
Canthigaster solandri	-	3.13	2.91	0.69
Chaetodon kleinii	-	2.84	0.36	0.77
Balistapus undulatus	+	1.61	2.68	0.81
Chaetodon auriga	-	2.24	0.77	0.860

Table 3.9. Top 5 species contributing to variation in fish assemblage structure in 2019 (compared to assemblage composition in 2017) for obligate (a) and facultative (b) corallivore functional groups. Mean site-level abundances for each time point are listed, as well as the cumulative contribution of each species to the overall assemblage dissimilarity.

Species	Change (+/-)	2017	2019	Cumulative Sum
a) Obligate				
Chaetodon ornatissimus	+	1.19	2.67	0.323
Plectroglyphidodon johnstonianus	-	2.13	0.33	0.54
Chaetodon meyeri	-	0.94	0	0.67
Labrichthys unilineatus	-	2.31	0	0.78
Cantherhines dumerilii	-	0.5	0.5	0.87
b) Facultative				
Plectroglyphidodon dickii	-	11.1	5.13	0.33
Canthigaster solandri	+	4.25	10	0.62
Balistapus undulatus	-	2.45	1.77	0.71
Chaetodon auriga	+	1.05	1.2	0.76
Chaetodon vagabundus	-	1.05	0.8	0.81

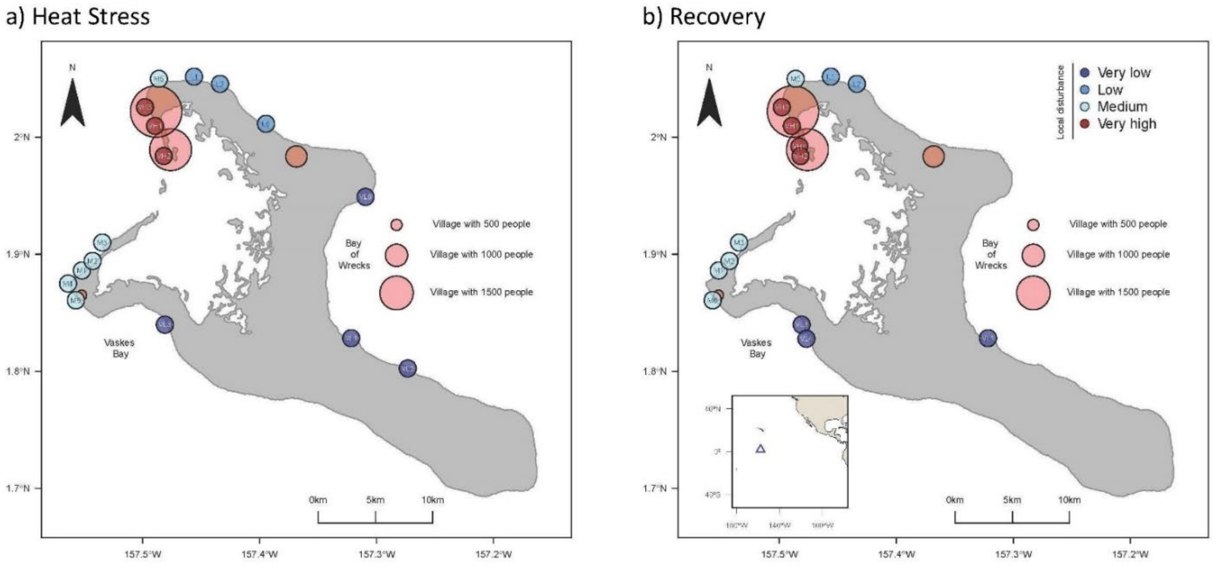

Figure 3.1. Map of the study sites surveyed for a) heat stress models (2011-2017), b) after-effect models (2017-2019), and villages on Kiritimati, Republic of Kiribati. Sites are categorized into four levels of local human disturbance, and villages (red circles) are scaled human population size. Inset shows Kiritimati's location in the central Pacific.

Figure 3.2. Representative species from both obligate and facultative functional groups included in the study. Obligate species are pictured along the left side (from top to bottom): Johnston Island damselfish (*Plectroglyphidodon johnstonianus*), ornate butterflyfish (*Chaetodon ornatissimus*), and the scrawled butterflyfish (*Chaetodon meyeri*). Facultative species are pictured along the right site (from top to bottom): Blackbar devilfish (*Plectroglyphidodon dickii*), spotted sharpnose (*Canthigaster solandri*), and the sunburst butterflyfish (*Chaetodon kleinii*). Photo credits (clockwise from top left; year provided if photos were taken on Kiritimati): [reeflifesurvey.com; Sean Dimoff (2019); Kristina Tietjen (2019); Kristina Tietjen (2016); Keoki Stender; Kristina Tietjen (2016)]

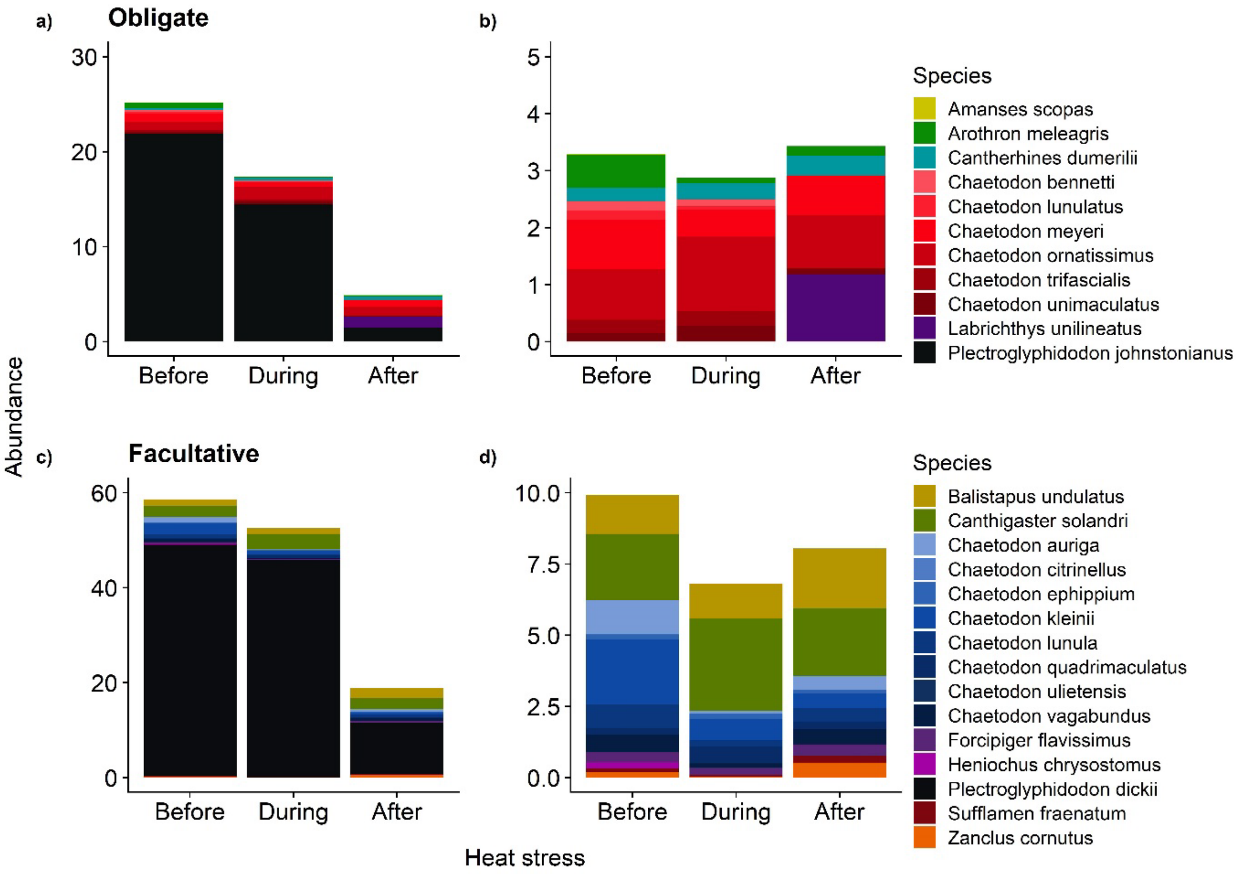

Figure 3.3. Relative contribution of obligate (a,b) and facultative (c,d) species to overall functional group abundance during each sampling period. Sampling occurred before (2011-2013), during (2015), and after (2017) the 2015-2016 El Niño. Abundance is represented by mean site-level across all sites and local disturbance levels. Plots along the left side (a, c) display all species in each corallivore functional group, while plots along the right side (b, d) have had the most abundant species in each functional group removed to make trends in other species more visible.

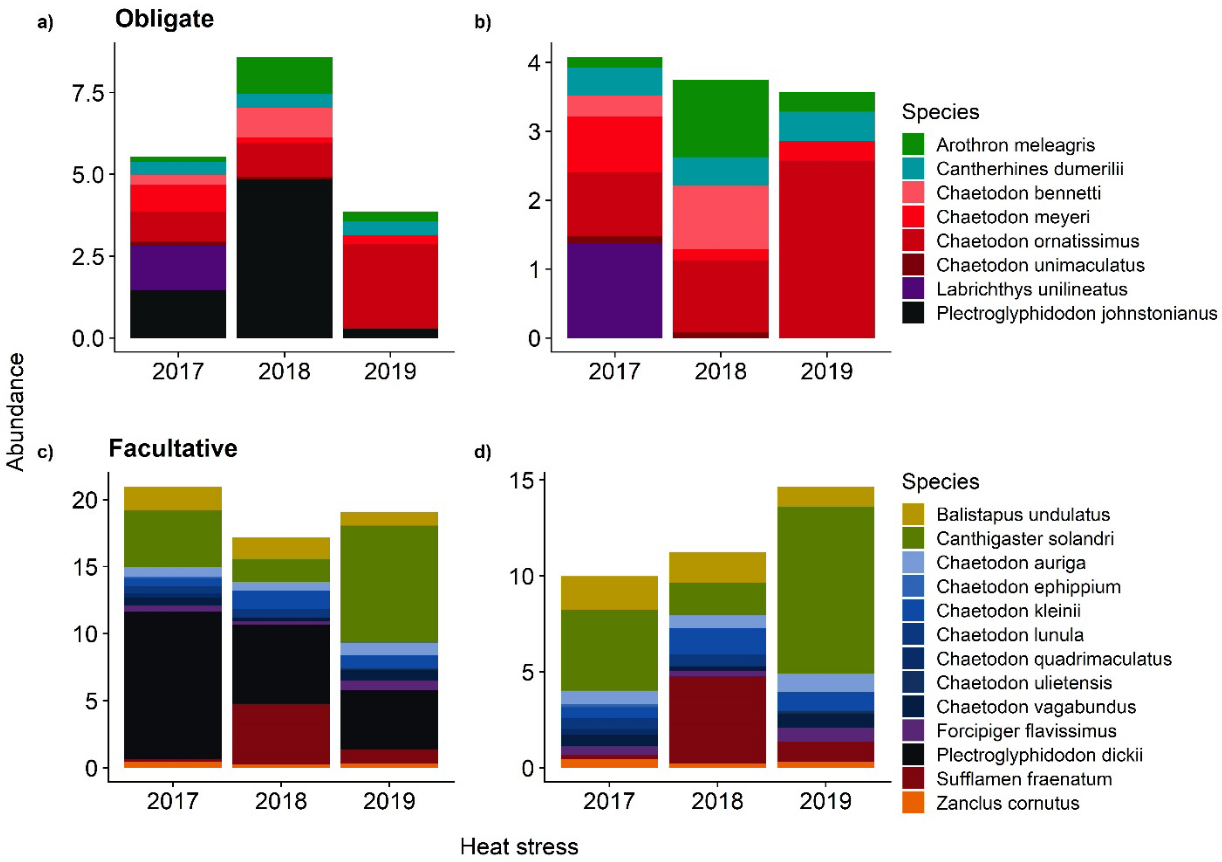

Figure 3.4. Relative contribution of obligate (a, b) and facultative (c,d) species to functional group abundance in the three years following the 2015-2016 El Niño. Abundance is represented by mean site-level across all sites and local disturbance levels.Plots along the left side (a, c) display all species in each corallivore functional group, while plots along the right side (b, d) have had the most abundant species in each functional group removed to make trends in other species more visible.

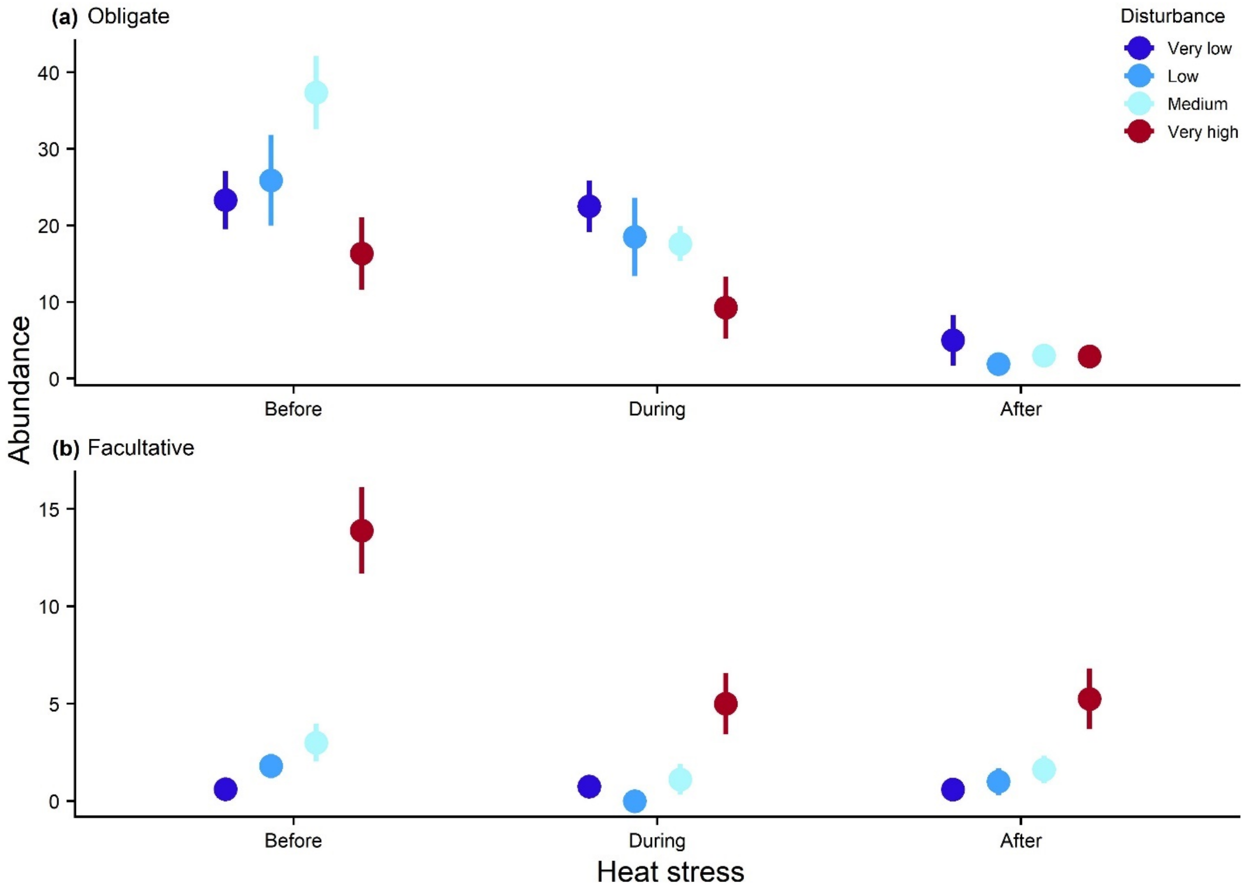

Figure 3.5. Mean site-level abundance of obligate (a) and facultative (b) corallivore functional groups at each of the four local human disturbance levels on Kiritimati before, during, and after the 2015-2016 El Niño. Dots represent the mean ± and are colored by their local disturbance category.

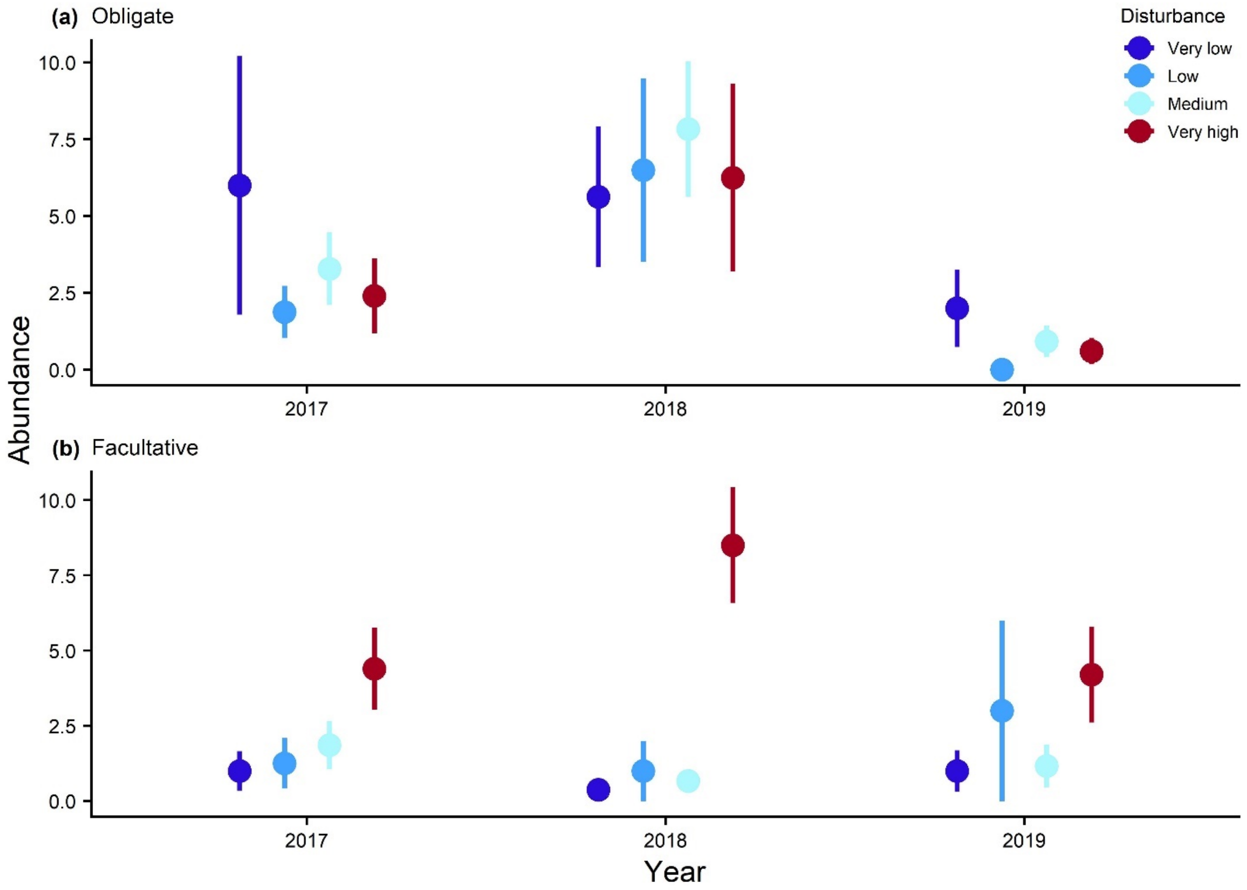

Figure 3.6. Mean site-level abundance of obligate (a) and facultative (b) corallivore functional groups at each of the four local human disturbance levels on Kiritimati in the three years following the 2015-2016 El Niño. Dots represent the mean ± and are colored by their local disturbance category.

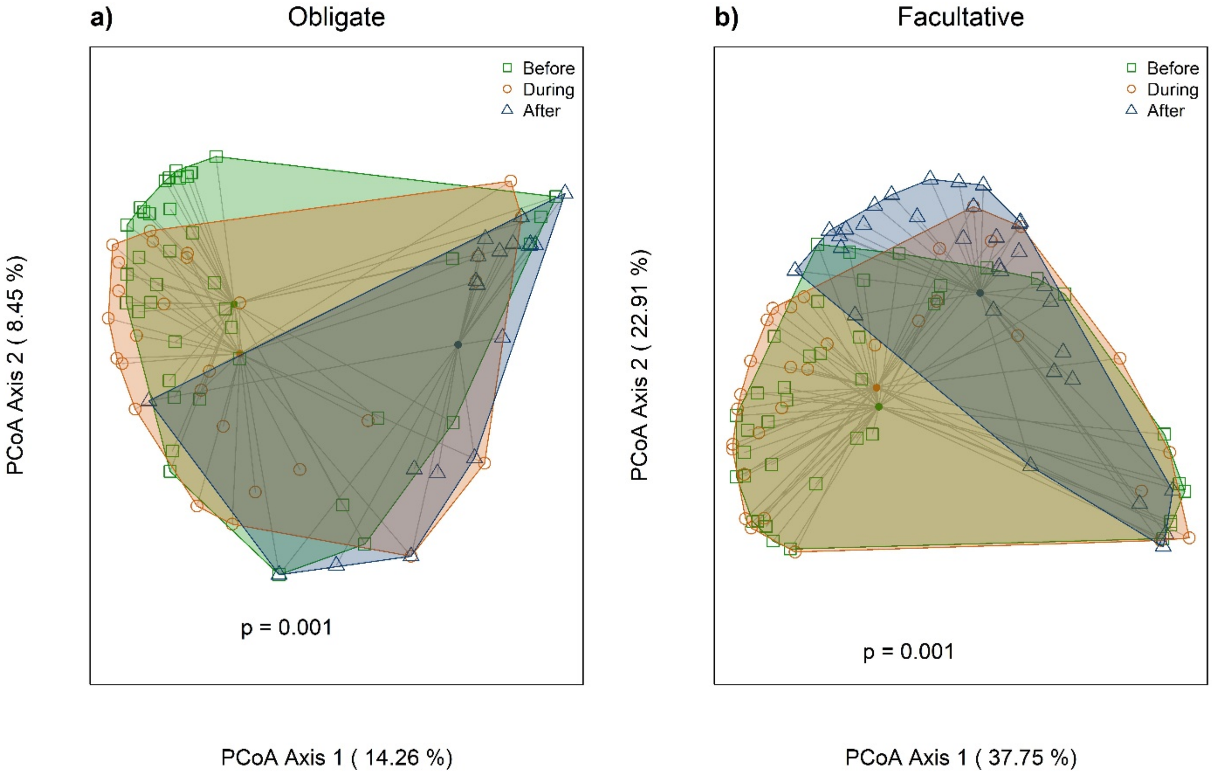

Figure 3.7. Multivariate ordination (PCoA) of obligate (a) and facultative (b) functional groups, displaying differences in assemblage structure before, during and after the 2015-2016 El Niño. Points represent individual sites, colored by sampling period, and shaded polygons indicate the boundaries of observed assemblage space for each sampling period.

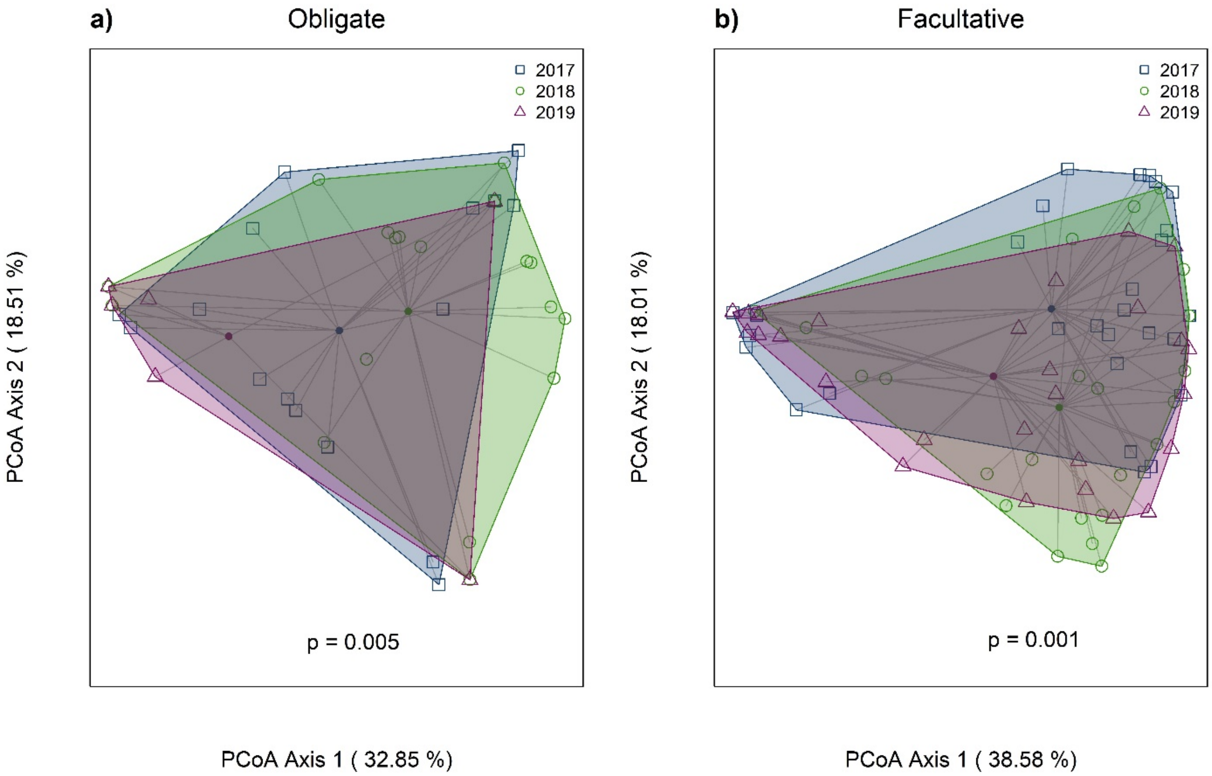

Figure 3.8. Multivariate ordination (PCoA) of obligate (a) and facultative (b) functional groups, displaying differences in assemblage structure in the three years following the 2015-2016 El Niño. Points represent individual sites, colored by sampling period, and shaded polygons indicate the boundaries of observed assemblage space for each sampling period.

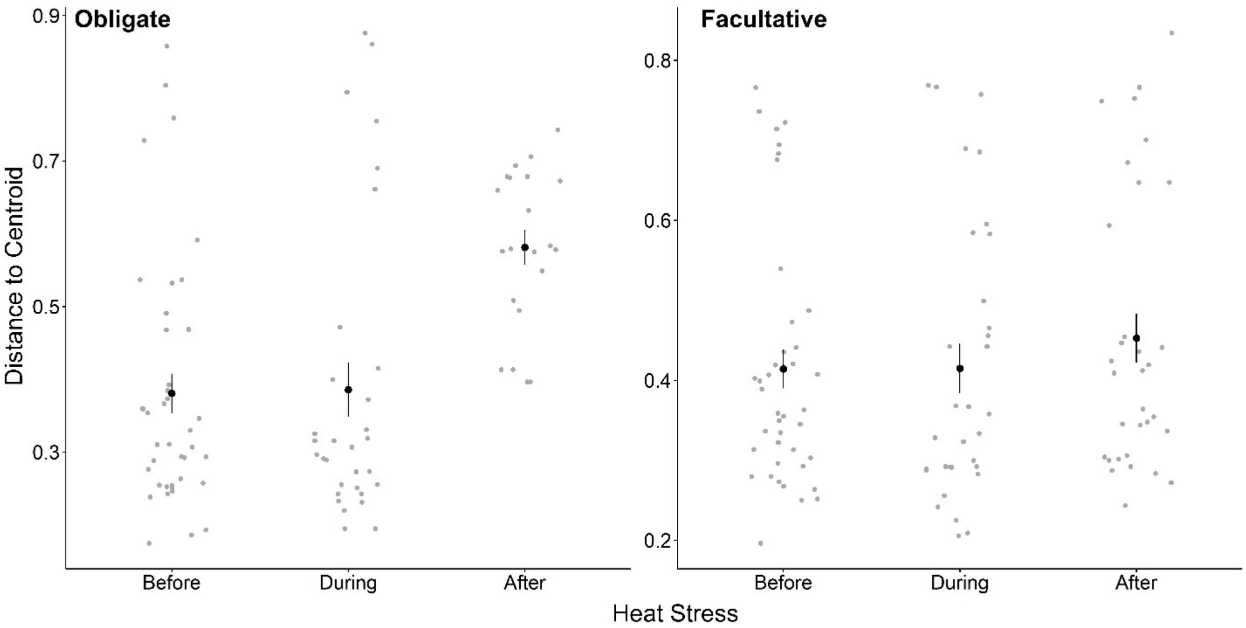

Figure 3.9. Bray-Curtis dissimilarities from individual sites in the full dimensional space to their group centroid, along with the group average ± 1 SE for assemblages observed before, during, and after the 2015-2016 El Niño.

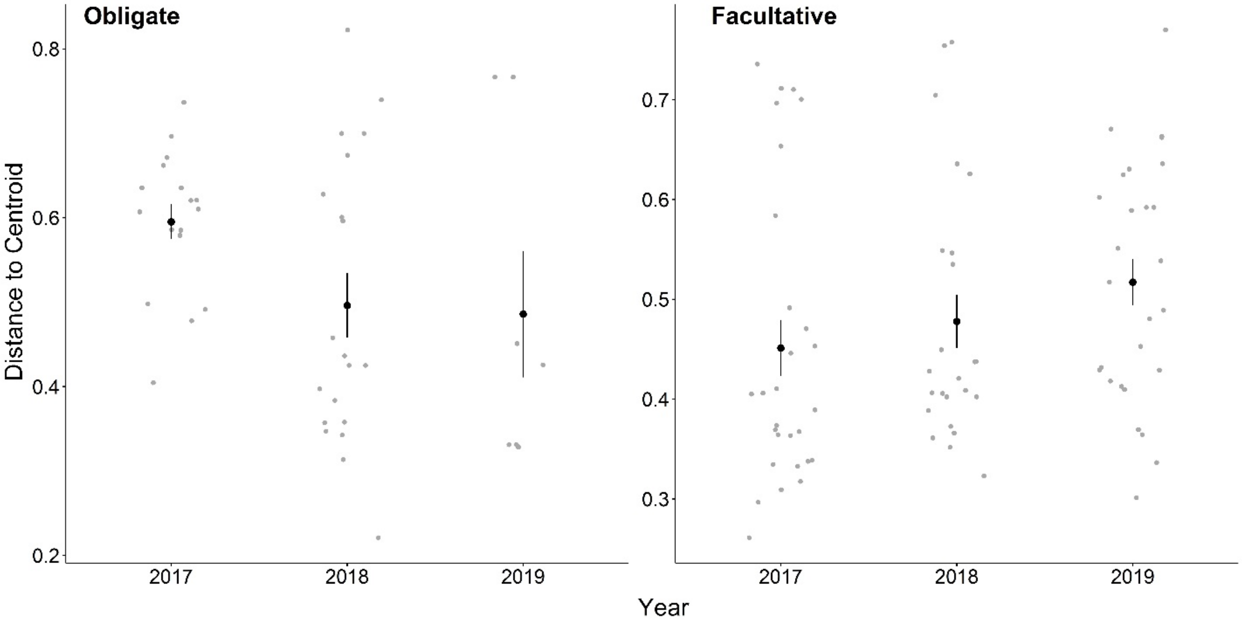

Figure 3.10. Bray-Curtis dissimilarities from individual sites in the full dimensional space to their group centroid, along with the group average ± 1 SE for assemblages observed in the three years following the 2015-2016 El Niño.

Chapter 4 – Conclusion

Coral reefs are increasingly threatened by global stressors like climate change amplified marine heatwaves and local stressors like coastal development and overfishing. The combination of these stressors reduces live coral cover (Hoegh-Guldberg, 2011) and fish abundance (Darling et al., 2017; Graham et al., 2017) which can result in novel problems for island nations and coastal communities that rely on coral reefs for food (Bell et al., 2009) and protection from storms (Ferrario et al., 2014). As coral reefs continue to change at a global scale, new monitoring technologies need to be deployed that are inexpensive but provide accurate data. One of the most promising new technologies is passive underwater acoustics (Lindseth and Lobel, 2018). However, despite these technologies, assessing changes in tropical fish communities is still typically conducted using in-person surveys, which provide un-paralleled insight into ecological processes. This thesis uses data collected from the reefs surrounding Kiritimati (Republic of Kiribati) in the central equatorial Pacific, before, during and after a prolonged heat stress event caused by the 2015-2016 El Niño, to examine the applicability of a recently adopted index in underwater acoustics on coral reefs and to determine how the corallivorous fish assemblage around Kiritimati changed in response to the coral loss following the heat stress.

In Chapter 2, I examine the applicability of a recently and prolifically adopted acoustic index to monitor coral reef ecosystems. Using data collected from hydrophones deployed on coral reefs around Kiritimati, I provide evidence that ACI results are dependent upon the frequency resolution chosen for its calculation (Table A2.2) and that in an environment with high levels of snapping shrimp snaps, ACI actually decreases with an increasing frequency of snaps (Table A2.3). I also document that changes in SPL, a more common and historically used acoustic metric, were associated with changes in both fish sounds and snapping shrimp snaps

(Table 2.1, A2.1). These results highlight the need for stringent field-testing and standardization in new acoustic metrics before they are applied to new and distinct marine ecosystems like coral reefs.

Underwater acoustics presents a globally applicable solution to ecological monitoring, if systems are thoroughly tested and supported by research conducted in the field. As new technologies are developed to extract meaningful information from acoustic data, they should always be applied with caution. The inconsistent results provided by the several studies that have applied ACI to coral reefs (Bohnenstiehl et al., 2018; Bolgan et al., 2018; Lyon et al., 2019; Staaterman et al., 2014) serve as evidence that each new index or acoustic metric should first be rigorously tested before its use. Despite these results providing evidence against the adoption of one new metric, the future of passive acoustic monitoring is bright. Growth in technologies related to computer-learning and event detection have the potential to make underwater passive acoustic monitoring more useful than ever before (Farina and Salutari, 2016; Lin et al., 2018, 2017). Therefore, labor-intensive research methods, like those used here, might become a thing of the past. While contemporary acoustic monitoring might only provide important supplementary information about underwater ecosystems, as more of these technologies become available, PAM systems will be poised to inform conservation efforts on a global scale.

In Chapter 3, I examined immediate and long-term effects of heat stress on corallivorous fish communities by quantifying changes in fish abundance, species richness and assemblage structure before, during and for three years after the 2015-2016 El Niño. These analyses revealed that significant changes in both obligate and facultative corallivore abundance were influenced by large declines in the abundance of the dominant species in each group, which were two damselfish species: *Plectroglyphidodon johnstonianus* for obligate corallivores, and

Plectroglyphidodon dickii for facultative corallivores (Table 3.2b, 3.3b; Fig. 3.3, 3.4). The remaining obligate assemblage also experienced declines in species richness immediately following and lagged declines in abundance three years after a mass coral mortality event caused by heat stress. Additionally, these results reveal that facultative species abundance is positively associated with areas of high human disturbance (Table 3.2b, 3.3b; Fig 3.5b, 3.6b) and that there was an interaction between human disturbance and year in the three years following the heat stress. While most other studies typically either categorize all corallivores together (Glynn et al., 2014; Robinson et al., 2019), or investigate only corallivores belonging to the Family *Chaetodontidae* (Graham et al., 2009; Pratchett et al., 2013), this study examines changes in an entire corallivore assemblage while describing how obligate and facultative species differ in their responses to a coral mortality event within the context of local human disturbance. As far as I know, this thesis is one of the first studies to examine how an entire corallivore assemblage is affected by a coral mortality event, adding to our knowledge of how coral reef fish communities will change with increased coral mortality.

Future studies can continue to build upon this work in several ways. Although we detected significant declines in obligate abundance three years after a massive coral mortality event, long-term studies have found that corallivore communities can stabilize following coral mortality if coral regrowth occurs (Russ and Leahy, 2017). The positive relationship between human disturbance and facultative corallivore abundance poses new questions about how certain fish communities can thrive in the novel environments being created by global and local stressors. Facultative fishes are omnivorous (Cole et al., 2008), and can consume a wide range of prey (Nagelkerken et al., 2009), inviting inquiry into how trophic relationships of these primary and secondary consumers are altered by coral mortality and subsequent benthic shifts. We do not currently know how the corallivore assemblages around Kiritimati will respond in the long term to coral regrowth or if the assemblage will be permanently altered by the 2015-2016 El Niño. Therefore, it would be useful to continue monitoring these changing reefs, analyzing how repeated events influence fish assemblages, and if even coral-specialist communities can adapt and become more resilient in an increasingly stressful environment.

As coral reefs continue to change in the wake of global and local stressors, understanding how their associated assemblages respond and change is vital to assessing and establishing conservation goals. Passive acoustic monitoring provides one new method of monitoring these ecosystems, one that has the potential to provide large-scale monitoring of a range of underwater environments. While in-person surveys can answer detailed questions about how fish communities are changing in response to coral bleaching and mortality that is becoming a global phenomenon. This thesis explores novel questions posed in both methods of monitoring, exploring the applicability of acoustics to coral reefs while utilizing in person surveys to investigate how corallivore communities are shifting in response to coral mortality. The results presented here expand our current breadth of knowledge concerning coral reefs and provide information useful to the protection of these vital ecosystems.

Bibliography

Advani, S., Rix, L.N., Aherne, D.M., Alwany, M.A., Bailey, D.M., 2015. Distance from a Fishing Community Explains Fish Abundance in a No-Take Zone with Weak Compliance. PLoS ONE 10, e0126098. https://doi.org/10.1371/journal.pone.0126098

Archer, S., Halliday, W., Riera, A., Mouy, X., Pine, M., Chu, J., Dunham, A., Juanes, F., 2018. First description of a glass sponge reef soundscape reveals fish calls and elevated sound pressure levels. Mar. Ecol. Prog. Ser. 595, 245–252. https://doi.org/10.3354/meps12572

Barber, R.T., Chavez, F.P., 1983. Biological Consequences of El Niño. Science 222, 1203–1210.

Bargahi, H.R., Shokri, M.R., Kaymaram, F., Fatemi, M.R., 2020. Changes in reef fish assemblages following multiple bleaching events in the world's warmest sea (Kish Island, the Persian Gulf). Coral Reefs 39, 603–624. https://doi.org/10.1007/s00338-020-01945-3

Beck, M.W., Losada, I.J., Menéndez, P., Reguero, B.G., Díaz-Simal, P., Fernández, F., 2018. The global flood protection savings provided by coral reefs. Nature Communications 9, 2186. https://doi.org/10.1038/s41467-018-04568-z

Beijbom, O., Edmunds, P.J., Roelfsema, C., Smith, J., Kline, D.I., Neal, B.P., Dunlap, M.J., Moriarty, V., Fan, T.-Y., Tan, C.-J., Chan, S., Treibitz, T., Gamst, A., Mitchell, B.G., Kriegman, D., 2015. Towards Automated Annotation of Benthic Survey Images: Variability of Human Experts and Operational Modes of Automation. PLoS ONE 10, e0130312. https://doi.org/10.1371/journal.pone.0130312

Bell, J.D., Craik, G.J.S., Pollard, D.A., Russell, B.C., 1985. Estimating length frequency distributions of large reef fish underwater. Coral Reefs 4, 41–44. https://doi.org/10.1007/BF00302203

Bell, J.D., Kronen, M., Vunisea, A., Nash, W.J., Keeble, G., Demmke, A., Pontifex, S., Andréfouët, S., 2009. Planning the use of fish for food security in the Pacific. Mar. Policy 33, 64–76. https://doi.org/10.1016/j.marpol.2008.04.002

Bellwood, D.R., Fulton, C.J., 2008. Sediment-mediated suppression of herbivory on coral reefs: Decreasing resilience to rising sea-levels and climate change? Limnology and Oceanography 53, 2695–2701. https://doi.org/10.4319/lo.2008.53.6.2695

Bellwood, D.R., Hoey, A.S., Ackerman, J.L., Depczynski, M., 2006. Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. Global Change Biology 12, 1587–1594. https://doi.org/10.1111/j.1365-2486.2006.01204.x

Bellwood, D.R., Pratchett, M.S., Morrison, T.H., Gurney, G.G., Hughes, T.P., Álvarez-Romero, J.G., Day, J.C., Grantham, R., Grech, A., Hoey, A.S., Jones, G.P., Pandolfi, J.M., Tebbett, S.B., Techera, E., Weeks, R., Cumming, G.S., 2019. Coral reef conservation in the Anthropocene: Confronting spatial mismatches and prioritizing functions. Biol. Conserv 236, 604–615. https://doi.org/10.1016/j.biocon.2019.05.056

Beretitenti, T., 2012. Kiritimati (Census No. 20), Republic of Kiribati Island Report Series. Office of Te Beretitenti & T'Makei Services, Tarawa, Kiribati.

Bertucci, F., Parmentier, E., Lecellier, G., Hawkins, A.D., Lecchini, D., 2016. Acoustic indices provide information on the status of coral reefs: an example from Moorea Island in the South Pacific. Sci. Rep. 6, 33326. https://doi.org/10.1038/srep33326

Berumen, M.L., Pratchett, M.S., 2008. Trade-offs associated with dietary specialization in corallivorous butterflyfishes (Chaetodontidae: Chaetodon). Behav Ecol Sociobiol 62, 989–994. https://doi.org/10.1007/s00265-007-0526-8

Berumen, M.L., Pratchett, M.S., 2006. Recovery without resilience: persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea. Coral Reefs 25, 647–653. https://doi.org/10.1007/s00338-006-0145-2

Boaden, A.E., Kingsford, M.J., 2015. Predators drive community structure in coral reef fish assemblages. Ecosphere 6, art46. https://doi.org/10.1890/ES14-00292.1

Bohnenstiehl, D.R., Lillis, A., Eggleston, D.B., 2016. The Curious Acoustic Behavior of Estuarine Snapping Shrimp: Temporal Patterns of Snapping Shrimp Sound in Sub-Tidal Oyster Reef Habitat. PLoS ONE 11, e0143691. https://doi.org/10.1371/journal.pone.0143691

Bohnenstiehl, D.R., Lyon, R.P., Caretti, O.N., Ricci, S.W., Eggleston, D.B., 2018. Investigating the utility of ecoacoustic metrics in marine soundscapes. J. Ecoacoust. 2, R1156L. https://doi.org/10.22261/JEA.R1156L

Bohnsack, J.A., Bannerot, S.P., 1986. A Stationary Visual Census Technique for Quantitatively Assessing Community Structure of Coral Reef Fishes (Technical Report No. NMFS 41). NOAA.

Bolgan, M., Amorim, M.C.P., Fonseca, P.J., Di Iorio, L., Parmentier, E., 2018. Acoustic Complexity of vocal fish communities: a field and controlled validation. Sci. Rep. 8, 10559. https://doi.org/10.1038/s41598-018-28771-6

Bolker, B.M., 2008. Ecological Models and Data in R. Princeton University Press. https://doi.org/10.2307/j.ctvcm4g37

Brandl, S.J., Emslie, M.J., Ceccarelli, D.M., Richards, Z.T., 2016. Habitat degradation increases functional originality in highly diverse coral reef fish assemblages. Ecosphere 7, e01557. https://doi.org/10.1002/ecs2.1557

Brooks, M., E., Kristensen, K., Benthem, K., J. ,van, Magnusson, A., Berg, C., W., Nielsen, A., Skaug, H., J., Mächler, M., Bolker, B., M., 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal 9, 378. https://doi.org/10.32614/RJ-2017-066

Burke, L., Reytar, K., Spalding, M., Perry, A., 2011a. Reefs at Risk Revisited.

Burke, L., Reytar, K., Spalding, M., Perry, A., 2011b. Reefs at Risk Revisited. World Resources Institute, Washington, DC.

Buscaino, G., Ceraulo, M., Pieretti, N., Corrias, V., Farina, A., Filiciotto, F., Maccarrone, V., Grammauta, R., Caruso, F., Giuseppe, A., Mazzola, S., 2016. Temporal patterns in the soundscape of the shallow waters of a Mediterranean marine protected area. Sci. Rep. 6, 34230. https://doi.org/10.1038/srep34230

Butler, J., Butler, M.J., Gaff, H., 2017. Snap, crackle, and pop: Acoustic-based model estimation of snapping shrimp populations in healthy and degraded hard-bottom habitats. Ecol. Indic. 77, 377–385. https://doi.org/10.1016/j.ecolind.2017.02.041

Butler, J., Stanley, J.A., Butler, M.J., 2016. Underwater soundscapes in near-shore tropical habitats and the effects of environmental degradation and habitat restoration. J. Exp. Mar. Biol. Ecol. 479, 89–96. https://doi.org/10.1016/j.jembe.2016.03.006

Cai, W., Borlace, S., Lengaigne, M., van Rensch, P., Collins, M., Vecchi, G., Timmermann, A., Santoso, A., McPhaden, M.J., Wu, L., England, M.H., Wang, G., Guilyardi, E., Jin, F.-F., 2014. Increasing frequency of extreme El Niño events due to greenhouse warming. Nature Climate Change 4, 111–116. https://doi.org/10.1038/nclimate2100

Chong-Seng, K.M., Mannering, T.D., Pratchett, M.S., Bellwood, D.R., Graham, N.A.J., 2012. The Influence of Coral Reef Benthic Condition on Associated Fish Assemblages. PLoS ONE 7, e42167. https://doi.org/10.1371/journal.pone.0042167

Claar, D.C., Baum, J.K., 2019. Timing matters: survey timing during extended heat stress can influence perceptions of coral susceptibility to bleaching. Coral Reefs 38, 559–565. https://doi.org/10.1007/s00338-018-01756-7

Claar, D.C., Tietjen, K.L., Cox, K.D., Gates, R.D., Baum, J.K., 2020. Chronic disturbance modulates symbiont (Symbiodiniaceae) beta diversity on a coral reef. Scientific Reports 10, 4492. https://doi.org/10.1038/s41598-020-60929-z

Coker, D.J., Pratchett, M.S., Munday, P.L., 2009. Coral bleaching and habitat degradation increase susceptibility to predation for coral-dwelling fishes. Behavioral Ecology 20, 1204–1210. https://doi.org/10.1093/beheco/arp113

Coker, D.J., Wilson, S.K., Pratchett, M.S., 2014. Importance of live coral habitat for reef fishes. Rev Fish Biol Fisheries 24, 89–126. https://doi.org/10.1007/s11160-013-9319-5

Cole, A.J., Pratchett, M.S., Jones, G.P., 2008. Diversity and functional importance of coral-feeding fishes on tropical coral reefs. Fish and Fisheries 9, 286–307. https://doi.org/10.1111/j.1467-2979.2008.00290.x

Cox, E.F., 1994. RESOURCE USE BY CORALLIVOROUS BUTTERFL YFISHES (FAMILY CHAETODONTIDAE) IN HAW All. BULLETIN OF MARINE SCIENCE 54, 11.

Cox, K., Brennan, L.P., Gerwing, T.G., Dudas, S.E., Juanes, F., 2018. Sound the alarm: A meta-analysis on the effect of aquatic noise on fish behavior and physiology. Glob. Change Biol. 24, 3105–3116. https://doi.org/10.1111/gcb.14106

Crosby, M.P., Reese, E.S., 2005. Relationship of habitat stability and intra-specific population dynamics of an obligate corallivore butterflyfish. Aquatic Conservation: Marine and Freshwater Ecosystems 15, S13–S25. https://doi.org/10.1002/aqc.697

Darling, E.S., Graham, N.A.J., Januchowski-Hartley, F.A., Nash, K.L., Pratchett, M.S., Wilson, S.K., 2017. Relationships between structural complexity, coral traits, and reef fish assemblages. Coral Reefs 36, 561–575. https://doi.org/10.1007/s00338-017-1539-z

Daw, T.M., Robinson, J., Graham, N. a. J., 2011. Perceptions of trends in Seychelles artisanal trap fisheries: comparing catch monitoring, underwater visual census and fishers' knowledge. Environmental Conservation 38, 75–88. https://doi.org/10.1017/S0376892910000901

DeMartini, E., Friedlander, A., Sandin, S., Sala, E., 2008. Differences in fish-assemblage structure between fished and unfished atolls in the northern Line Islands, central Pacific. Mar. Ecol. Prog. Ser. 365, 199–215. https://doi.org/10.3354/meps07501

Desjonquères, C., Rybak, F., Depraetere, M., Gasc, A., Le Viol, I., Pavoine, S., Sueur, J., 2015. First description of underwater acoustic diversity in three temperate ponds. PeerJ 3, e1393. https://doi.org/10.7717/peerj.1393

Doney, S.C., Fabry, V.J., Feely, R.A., Kleypas, J.A., 2009. Ocean Acidification: The Other CO2 Problem. Annual Review of Marine Science 1, 169–192. https://doi.org/10.1146/annurev.marine.010908.163834

Dubinsky, Z., Stambler, N., 1996. Marine pollution and coral reefs. Global Change Biology 2, 511–526. https://doi.org/10.1111/j.1365-2486.1996.tb00064.x

Elise, S., Bailly, A., Urbina-Barreto, I., Mou-Tham, G., Chiroleu, F., Vigliola, L., Robbins, W.D., Bruggemann, J.H., 2019. An optimised passive acoustic sampling scheme to discriminate among coral reefs' ecological states. Ecol. Indic. 107, 105627. https://doi.org/10.1016/j.ecolind.2019.105627

Emslie, M.J., Pratchett, M.S., Cheal, A.J., 2011. Effects of different disturbance types on butterflyfish communities of Australia’s Great Barrier Reef. Coral Reefs 30, 461–471. https://doi.org/10.1007/s00338-011-0730-x

Enochs, I., Toth, L., Brandtneris, V., Afflerbach, J., Manzello, D., 2011. Environmental determinants of motile cryptofauna on an eastern Pacific coral reef. Mar. Ecol. Prog. Ser. 438, 105–118. https://doi.org/10.3354/meps09259

Farina, A., James, P., 2016. The acoustic communities: Definition, description and ecological role. Biosystems 147, 11–20. https://doi.org/10.1016/j.biosystems.2016.05.011

Farina, A., Salutari, P., 2016. Applying the Ecoacoustic Event Detection and Identification (EEDI) Model to the Analysis of Acoustic Complexity. Journal of Mediterranean Ecology 14, 13–42.

Ferrario, F., Beck, M.W., Storlazzi, C.D., Shepard, C.C., Airoldi, L., 2014. The effectiveness of coral reefs for coastal hazard risk reduction and adaptation. Nature Communications 5. https://doi.org/10.1038/ncomms4794

Fish, M.P., Kelsey Jr., A.S., Mowbray, W.H., 1952. Studies on the production of underwater sound by North Atlantic coastal fishes. Journal of Marine Research 180–193.

Frölicher, T.L., Fischer, E.M., Gruber, N., 2018. Marine heatwaves under global warming. Nature 560, 360–364. https://doi.org/10.1038/s41586-018-0383-9

Garpe, K., Yahya, S., Lindahl, U., Öhman, M., 2006. Long-term effects of the 1998 coral bleaching event on reef fish assemblages. Mar. Ecol. Prog. Ser. 315, 237–247. https://doi.org/10.3354/meps315237

Gelman, A., Su, Y.-S., Yajima, M., Hill, J., Pittau, M.G., Kerman, J., Zheng, T., Dorie, V., 2020. arm: Data Analysis Using Regression and Multilevel/Hierarchical Models.

Gillis, L., Bouma, T., Jones, C., van Katwijk, M., Nagelkerken, I., Jeuken, C., Herman, P., Ziegler, A., 2014. Potential for landscape-scale positive interactions among tropical marine ecosystems. Mar. Ecol. Prog. Ser. 503, 289–303. https://doi.org/10.3354/meps10716

Glynn, P., Enochs, I., Afflerbach, J., Brandtneris, V., Serafy, J., 2014. Eastern Pacific reef fish responses to coral recovery following El Niño disturbances. Mar. Ecol. Prog. Ser. 495, 233–247. https://doi.org/10.3354/meps10594

Glynn, P.W., Stewart, R.H., McCosker, J.E., 1972. Pacific coral reefs of panamá: Structure, distribution and predators. Geol Rundsch 61, 483–519. https://doi.org/10.1007/BF01896330

Gordon, T.A.C., Radford, A.N., Davidson, I.K., Barnes, K., McCloskey, K., Nedelec, S.L., Meekan, M.G., McCormick, M.I., Simpson, S.D., 2019. Acoustic enrichment can enhance fish community development on degraded coral reef habitat. Nat. Commun. 10, 5414. https://doi.org/10.1038/s41467-019-13186-2

Graham, N.A.J., 2007. Ecological versatility and the decline of coral feeding fishes following climate driven coral mortality. Mar Biol 153, 119–127. https://doi.org/10.1007/s00227-007-0786-x

Graham, N.A.J., McClanahan, T.R., MacNeil, M.A., Wilson, S.K., Cinner, J.E., Huchery, C., Holmes, T.H., 2017. Human Disruption of Coral Reef Trophic Structure. Current Biology 27, 231–236. https://doi.org/10.1016/j.cub.2016.10.062

Graham, N.A.J., McClanahan, T.R., MacNeil, M.A., Wilson, S.K., Polunin, N.V.C., Jennings, S., Chabanet, P., Clark, S., Spalding, M.D., Letourneur, Y., Bigot, L., Galzin, R., Öhman, M.C., Garpe, K.C., Edwards, A.J., Sheppard, C.R.C., 2008. Climate Warming, Marine Protected Areas and the Ocean-Scale Integrity of Coral Reef Ecosystems. PLoS ONE 3, e3039. https://doi.org/10.1371/journal.pone.0003039

Graham, N.A.J., Wilson, S.K., Pratchett, M.S., Polunin, N.V.C., Spalding, M.D., 2009. Coral mortality versus structural collapse as drivers of corallivorous butterflyfish decline. Biodivers Conserv 18, 3325–3336. https://doi.org/10.1007/s10531-009-9633-3

Guzmán, H., Robertson, D., 1989. Population and feeding responses of the corallivorous pufferfish Arothron meleagris to coral mortality in the eastern Pacific. Mar. Ecol. Prog. Ser. 55, 121–131. https://doi.org/10.3354/meps055121

Halliday, W., Pine, M., Bose, A., Balshine, S., Juanes, F., 2018. The plainfin midshipman's soundscape at two sites around Vancouver Island, British Columbia. Mar. Ecol. Prog. Ser. 603, 189–200. https://doi.org/10.3354/meps12730

Harmelin-Vivien, M.L., 1989. Implications of feeding specialization on the recruitment processes and community structure of butterflyfishes. The butterflyfishes: success on the coral reef, Developments in environmental biology of fishes 25, 101–110. https://doi.org/10.1007/978-94-009-2325-6_7

Harmelin-Vivien, M.L., Bouchon-Navaro, Y., 1983. Feeding diets and significance of coral feeding among Chaetodontid fishes in Moorea (French Polynesia). Coral Reefs 2, 119–127. https://doi.org/10.1007/BF02395282

Herberholz, J., Schmitz, B., 1998. Role of Mechanosensory Stimuli in Intraspecific Agonistic Encounters of the Snapping Shrimp (Alpheus heterochaelis). Biological Bulletin 195, 156–167. https://doi.org/10.2307/1542823

Hill, J., Wilkinson, C., 2004. Methods for Ecological Monitoring of Coral Reefs: Version 1. Australian Institute of Marine Science, Townsville.

Hixon, M.A., Beets, J.P., 1993. Predation, Prey Refuges, and the Structure of Coral-Reef Fish Assemblages. Ecological Monographs 63, 77–101. https://doi.org/10.2307/2937124

Ho, C.-T., Fu, Y.-C., Sun, C.-L., Kao, S.-J., Jan, R.-Q., 2009. Plasticity of Feeding Habits of Two Plectroglyphidodon Damselfishes on Coral Reefs in Southern Taiwan: Evidence from Stomach Content and. Zoological Studies 8.

Hobson, E.S., 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fishery Bulletin 72, 915–1038.

Hoegh-Guldberg, O., 2011. Coral reef ecosystems and anthropogenic climate change. Reg Environ Change 11, 215–227. https://doi.org/10.1007/s10113-010-0189-2

Hoegh-Guldberg, O., Poloczanska, E.S., Skirving, W., Dove, S., 2017. Coral Reef Ecosystems under Climate Change and Ocean Acidification. Front. Mar. Sci. 4. https://doi.org/10.3389/fmars.2017.00158

Holbrook, N.J., Claar, D.C., Hobday, A.J., McInnes, K.L., Oliver, E.C.J., Gupta, A.S., Widlansky, M.J., Zhang, X., 2020. ENSO-Driven Ocean Extremes and Their Ecosystem Impacts, in: El Niño Southern Oscillation in a Changing Climate. American Geophysical Union (AGU), pp. 409–428. https://doi.org/10.1002/9781119548164.ch18

Holt, D.E., Johnston, C.E., 2014. Evidence of the Lombard effect in fishes. Behav. Ecol. 25, 819–826. https://doi.org/10.1093/beheco/aru028

Hughes, T.P., Anderson, K.D., Connolly, S.R., Heron, S.F., Kerry, J.T., Lough, J.M., Baird, A.H., Baum, J.K., Berumen, M.L., Bridge, T.C., Claar, D.C., Eakin, C.M., Gilmour, J.P., Graham, N.A.J., Harrison, H., Hobbs, J.-P.A., Hoey, A.S., Hoogenboom, M., Lowe, R.J., McCulloch, M.T., Pandolfi, J.M., Pratchett, M., Schoepf, V., Torda, G., Wilson, S.K., 2018. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359, 80–83. https://doi.org/10.1126/science.aan8048

Hughes, T.P., Kerry, J.T., Álvarez-Noriega, M., Álvarez-Romero, J.G., Anderson, K.D., Baird, A.H., Babcock, R.C., Beger, M., Bellwood, D.R., Berkelmans, R., Bridge, T.C., Butler, I.R., Byrne, M., Cantin, N.E., Comeau, S., Connolly, S.R., Cumming, G.S., Dalton, S.J., Diaz-Pulido, G., Eakin, C.M., Figueira, W.F., Gilmour, J.P., Harrison, H.B., Heron, S.F., Hoey, A.S., Hobbs, J.-P.A., Hoogenboom, M.O., Kennedy, E.V., Kuo, C., Lough, J.M., Lowe, R.J., Liu, G., McCulloch, M.T., Malcolm, H.A., McWilliam, M.J., Pandolfi, J.M., Pears, R.J., Pratchett, M.S., Schoepf, V., Simpson, T., Skirving, W.J., Sommer, B., Torda, G., Wachenfeld, D.R., Willis, B.L., Wilson, S.K., 2017. Global warming and recurrent mass bleaching of corals. Nature 543, 373–377. https://doi.org/10.1038/nature21707

Jayewardene, D., Birkeland, C., 2006. Fish predation on Hawaiian corals. Coral Reefs 25, 328–328. https://doi.org/10.1007/s00338-006-0111-z

Jayewardene, D., Donahue, M.J., Birkeland, C., 2009. Effects of frequent fish predation on corals in Hawaii. Coral Reefs 28, 499–506. https://doi.org/10.1007/s00338-009-0475-y

Johansen, J.L., Jones, G.P., 2011. Increasing ocean temperature reduces the metabolic performance and swimming ability of coral reef damselfishes. Global Change Biology 17, 2971–2979. https://doi.org/10.1111/j.1365-2486.2011.02436.x

Johnson, M.W., Everest, F.A., Young, R.W., 1947. The Role of Snapping Shrimp (Crangon and Synalpheus) in the Production of Underwater Noise in the Sea. Biol. Bull. 93, 122–138. https://doi.org/10.2307/1538284

Jones, G., Santana, L., McCook, L., McCormick, M., 2006. Resource use and impact of three herbivorous damselfishes on coral reef communities. Mar. Ecol. Prog. Ser. 328, 215–224. https://doi.org/10.3354/meps328215

Kaplan, M., Mooney, T., Partan, J., Solow, A., 2015. Coral reef species assemblages are associated with ambient soundscapes. Mar. Ecol. Prog. Ser. 533, 93–107. https://doi.org/10.3354/meps11382

Kayal, M., Vercelloni, J., Loma, T.L. de, Bosserelle, P., Chancerelle, Y., Geoffroy, S., Stievenart, C., Michonneau, F., Penin, L., Planes, S., Adjeroud, M., 2012. Predator Crown-of-Thorns Starfish (Acanthaster planci) Outbreak, Mass Mortality of Corals, and Cascading Effects on Reef Fish and Benthic Communities. PLOS ONE 7, e47363. https://doi.org/10.1371/journal.pone.0047363

Kelly, E.L.A., Eynaud, Y., Williams, I.D., Sparks, R.T., Dailer, M.L., Sandin, S.A., Smith, J.E., 2017. A budget of algal production and consumption by herbivorous fish in an herbivore fisheries management area, Maui, Hawaii. Ecosphere 8, e01899. https://doi.org/10.1002/ecs2.1899

Kiribati National Statistics Office, 2016. 2015 Population and Housing Census Volume 1. Kiribati Ministry of Finance, Bairiki, Tarawa, Kiribati.

Kotb, M., Abdulaziz, M., Al-Agwan, Z., Al, K., Al-Yami, H., Banajah, A., Devantier, L., Eisinger, M., Eltayeb, M., Hassan, M., Heiss, G., Howe, S., Kemp, J., Klaus, R., Krupp, F., Rouphael, T., Turner, J., Zajonz, U., 2004. 4. Status of coral reefs in the Red Sea and gulf of Aden in 2004, in: Status of Coral Reefs of the World: 2004. p. 18.

Kulbicki, M., Bozec, Y.M., Green, A., 2005. Implications of biogeography in the use of butterflyfishes (Chaetodontidae) as indicators for Western and Central Pacific areas. Aquatic Conservation: Marine and Freshwater Ecosystems 15(S1): S109–S126.

Kulbicki, Michel, Bozec, Y.-M., Labrosse, P., Letourneur, Y., Mou-Tham, G., Wantiez, L., 2005. Diet composition of carnivorous fishes from coral reef lagoons of New Caledonia. Aquat. Living Resour. 18, 231–250. https://doi.org/10.1051/alr:2005029

Liao, X., Ma, J., Zhan, H., 2012. Effect of different types of El Niño on primary productivity in the South China Sea. Aquatic Ecosystem Health & Management 15, 135–143. https://doi.org/10.1080/14634988.2012.687655

Lillis, A., Eggleston, D., Bohnenstiehl, D., 2014. Estuarine soundscapes: distinct acoustic characteristics of oyster reefs compared to soft-bottom habitats. Mar. Ecol. Prog. Ser. 505, 1–17. https://doi.org/10.3354/meps10805

Lillis, A., Mooney, T.A., 2018. Snapping shrimp sound production patterns on Caribbean coral reefs: relationships with celestial cycles and environmental variables. Coral Reefs 37, 597–607. https://doi.org/10.1007/s00338-018-1684-z

Lillis, A., Perelman, J.N., Panyi, A., Aran Mooney, T., 2017. Sound production patterns of big-clawed snapping shrimp (*Alpheus spp.*) are influenced by time-of-day and social context. J. Acoust. Soc. Am. 142, 3311–3320. https://doi.org/10.1121/1.5012751

Lin, T.-H., Fang, S.-H., Tsao, Y., 2017. Improving biodiversity assessment via unsupervised separation of biological sounds from long-duration recordings. Sci. Rep. 7, 4547. https://doi.org/10.1038/s41598-017-04790-7

Lin, T.-H., Tsao, Y., Akamatsu, T., 2018. Comparison of passive acoustic soniferous fish monitoring with supervised and unsupervised approaches. J. Acoust. Soc. Am. 143, EL278–EL284. https://doi.org/10.1121/1.5034169

Lindseth, A., Lobel, P., 2018. Underwater Soundscape Monitoring and Fish Bioacoustics: A Review. Fishes 3, 36. https://doi.org/10.3390/fishes3030036

Lobel, P.S., 2013. THE “CHORAL REEF”: THE ECOLOGY OF UNDERWATER SOUNDS. AAUS 179–184.

Lobel, P.S., Kaatz, I.M., Rice, A.N., 2010. Acoustical behavior of coral reef fishes., in: Reproduction and Sexuality in Marine Fishes: Patterns and Processes. University of California Press, pp. 307–386.

Locascio, J.V., Mann, D.A., 2008. Diel Periodicity of Fish Sound Production in Charlotte Harbor, Florida. T. Am. Fish. Soc. 137, 606–615. https://doi.org/10.1577/T06-069.1

Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H., Woesik, R. van, 2001. Coral bleaching: the winners and the losers. Ecology Letters 4, 122–131. https://doi.org/10.1046/j.1461-0248.2001.00203.x

Luczkovich, J.J., Krahforst, C.S., Kelly, K.E., Sprague, M.W., 2016. The Lombard effect in fishes: How boat noise impacts oyster toadfish vocalization amplitudes in natural experiments. Presented at the Fourth International Conference on the Effects of Noise on Aquatic Life, Dublin, Ireland, p. 010035. https://doi.org/10.1121/2.0000340

Lyon, R., Eggleston, D., Bohnenstiehl, D., Layman, C., Ricci, S., Allgeier, J., 2019. Fish community structure, habitat complexity, and soundscape characteristics of patch reefs in a tropical, back-reef system. Mar. Ecol. Prog. Ser. 609, 33–48. https://doi.org/10.3354/meps12829

Magel, J.M.T., Burns, J.H.R., Gates, R.D., Baum, J.K., 2019. Effects of bleaching-associated mass coral mortality on reef structural complexity across a gradient of local disturbance. Sci. Rep. 9, 2512. https://doi.org/10.1038/s41598-018-37713-1

Magel, J.M.T., Dimoff, S.A., Baum, J.K., 2020. Direct and indirect effects of climate change-amplified pulse heat stress events on coral reef fish communities. Ecol. Appl. https://doi.org/10.1002/eap.2124

McCauley, R.D., Cato, D.H., 2000. Patterns of fish calling in a nearshore environment in the Great Barrier Reef. Phil. Trans. R. Soc. Lond. B 355, 1289–1293. https://doi.org/10.1098/rstb.2000.0686

McClanahan, T.R., Maina, J., Starger, C.J., Herron-Perez, P., Dusek, E., 2005. Detriments to post-bleaching recovery of corals. Coral Reefs 24, 230–246. https://doi.org/10.1007/s00338-004-0471-1

McManus, J.W., Polsenberg, J.F., 2004. Coral–algal phase shifts on coral reefs: Ecological and environmental aspects. Progress in Oceanography, Regime shifts in the ocean. Reconciling observations and theory 60, 263–279. https://doi.org/10.1016/j.pocean.2004.02.014

McPherson, C., Martin, B., MacDonnell, J., Whitt, C., 2016. Examining the value of the Acoustic Variability Index in the characterisation of Australian marine soundscapes. Proc. Acoustics 1–13.

McWilliam, J.N., Hawkins, A.D., 2013. A comparison of inshore marine soundscapes. J. Exp. Mar. Biol. Ecol. 446, 166–176. https://doi.org/10.1016/j.jembe.2013.05.012

Moberg, F., Folke, C., 1999. Ecological goods and services of coral reef ecosystems. Ecol. Econ. 29, 215–233. https://doi.org/10.1016/S0921-8009(99)00009-9

Munday, P.L., 2004. Habitat loss, resource specialization, and extinction on coral reefs. Global Change Biology 10, 1642–1647. https://doi.org/10.1111/j.1365-2486.2004.00839.x

Nagelkerken, I., Velde, G.V.D., Wartenbergh, S.L.J., Nugues, M.M., Pratchett, M.S., 2009. Cryptic dietary components reduce dietary overlap among sympatric butterflyfishes (Chaetodontidae). Journal of Fish Biology 75, 1123–1143. https://doi.org/10.1111/j.1095-8649.2009.02303.x

Nedelec, S., Simpson, S., Holderied, M., Radford, A., Lecellier, G., Radford, C., Lecchini, D., 2015. Soundscapes and living communities in coral reefs: temporal and spatial variation. Mar. Ecol. Prog. Ser. 524, 125–135. https://doi.org/10.3354/meps11175

Nelson, H.R., Kuempel, C.D., Altieri, A.H., 2016. The resilience of reef invertebrate biodiversity to coral mortality. Ecosphere 7, e01399. https://doi.org/10.1002/ecs2.1399

Oksanen, J., Kindt, R., Legendre, P., Hara, B., Simpson, G., Solymos, P., Henry, M., Stevens, H., Maintainer, H., Oksanen@oulu, jari, 2009. The vegan Package.

Piercy, J., Codling, E., Hill, A., Smith, D., Simpson, S., 2014. Habitat quality affects sound production and likely distance of detection on coral reefs. Mar. Ecol. Prog. Ser. 516, 35–47. https://doi.org/10.3354/meps10986

Pieretti, N., Farina, A., Morri, D., 2011. A new methodology to infer the singing activity of an avian community: The Acoustic Complexity Index (ACI). Ecol. Indic. 11, 868–873. https://doi.org/10.1016/j.ecolind.2010.11.005

Prada, F., Caroselli, E., Mengoli, S., Brizi, L., Fantazzini, P., Capaccioni, B., Pasquini, L., Fabricius, K.E., Dubinsky, Z., Falini, G., Goffredo, S., 2017. Ocean warming and acidification synergistically increase coral mortality. Sci. Rep. 7, 40842. https://doi.org/10.1038/srep40842

Pratchett, M.S., Blowes, S.A., Coker, D., Kubacki, E., Nowicki, J., Hoey, A.S., 2015. Indirect benefits of high coral cover for non-corallivorous butterflyfishes. Coral Reefs 34, 665–672. https://doi.org/10.1007/s00338-014-1254-y

Pratchett, M. S., Graham, N. a. J., Cole, A.J., 2013. Specialist corallivores dominate butterflyfish assemblages in coral-dominated reef habitats. Journal of Fish Biology 82, 1177–1191. https://doi.org/10.1111/jfb.12056

Pratchett, M.S., Hoey, A.S., Cvitanovic, C., Hobbs, J.-P.A., Fulton, C.J., 2014. Abundance, diversity, and feeding behavior of coral reef butterflyfishes at Lord Howe Island. Ecology and Evolution 4, 3612–3625. https://doi.org/10.1002/ece3.1208

Pratchett, Morgan S., Hoey, A.S., Feary, D.A., Bauman, A.G., Burt, J.A., Riegl, B.M., 2013. Functional composition of Chaetodon butterflyfishes at a peripheral and extreme coral reef location, the Persian Gulf. Marine Pollution Bulletin, Coral reefs of the Gulf: Past, present and the future of a unique ecosystem 72, 333–341. https://doi.org/10.1016/j.marpolbul.2012.10.014

Pratchett, M.S., Messmer, V., Wilson, S.K., 2020. Size-specific recolonization success by coral-dwelling damselfishes moderates resilience to habitat loss. Scientific Reports 10, 17016. https://doi.org/10.1038/s41598-020-73979-0

Pratchett, M.S., Wilson, S.K., Baird, A.H., 2006. Declines in the abundance of Chaetodon butterflyfishes following extensive coral depletion. Journal of Fish Biology 69, 1269–1280. https://doi.org/10.1111/j.1095-8649.2006.01161.x

Pratchett, M.S., Wilson, S.K., Berumen, M.L., McCormick, M.I., 2004. Sublethal effects of coral bleaching on an obligate coral feeding butterflyfish? Coral Reefs 23, 352–356. https://doi.org/10.1007/s00338-004-0394-x

R Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Radford, C., Jeffs, A., Tindle, C., Montgomery, J., 2008. Resonating sea urchin skeletons create coastal choruses. Mar. Ecol. Prog. Ser. 362, 37–43. https://doi.org/10.3354/meps07444

Radford, C., Stanley, J., Jeffs, A., 2014. Adjacent coral reef habitats produce different underwater sound signatures. Mar. Ecol. Prog. Ser. 505, 19–28. https://doi.org/10.3354/meps10782

Radford, C., Stanley, J., Tindle, C., Montgomery, J., Jeffs, A., 2010. Localised coastal habitats have distinct underwater sound signatures. Mar. Ecol. Prog. Ser. 401, 21–29. https://doi.org/10.3354/meps08451

Radford, C., Tindle, C., Montgomery, J., Jeffs, A., 2011. Modelling a reef as an extended sound source increases the predicted range at which reef noise may be heard by fish larvae. Mar. Ecol. Prog. Ser. 438, 167–174. https://doi.org/10.3354/meps09312

Radford, C.A., Tindle, C.T., Montgomery, J.C., 2008. Temporal patterns in ambient noise of biological origin from a shallow water temperate reef. Oecologia 156, 921–929. https://doi.org/10.1007/s00442-008-1041-y

Randall, J.E., 2005. Reef and Shore Fishes of the South Pacific. University of Hawaii Press, Honolulu.

Renema, W., Pandolfi, J.M., Kiessling, W., Bosellini, F.R., Klaus, J.S., Korpanty, C., Rosen, B.R., Santodomingo, N., Wallace, C.C., Webster, J.M., Johnson, K.G., 2016. Are coral reefs victims of their own past success? Sci. Adv. 2, e1500850. https://doi.org/10.1126/sciadv.1500850

Reyes-Bonilla, H., Calderon-Aguilera, L.E., 1999. Population Density, Distribution and Consumption Rates of Three Corallivores at Cabo Pulmo Reef, Gulf of California, Mexico. Marine Ecology 20, 347–357. https://doi.org/10.1046/j.1439-0485.1999.2034080.x

Reyes-Bonilla, H., Carriquiry, J., Leyte-Morales, G., Cupul-Magaña, A., 2002. Effects of the El Niño-Southern Oscillation and the anti-El Niño event (1997–1999) on coral reefs of the western coast of México. Coral Reefs 21, 368–372. https://doi.org/10.1007/s00338-002-0255-4

Richardson, L.E., Graham, N.A.J., Pratchett, M.S., Eurich, J.G., Hoey, A.S., 2018. Mass coral bleaching causes biotic homogenization of reef fish assemblages. Global Change Biology 24, 3117–3129. https://doi.org/10.1111/gcb.14119

Robinson, J.P.W., Baum, J.K., 2016. Trophic roles determine coral reef fish community size structure. Can. J. Fish. Aquat. Sci. 73, 496–505. https://doi.org/10.1139/cjfas-2015-0178

Robinson, J.P.W., Wilson, S.K., Jennings, S., Graham, N.A.J., 2019. Thermal stress induces persistently altered coral reef fish assemblages. Global Change Biology 25, 2739–2750. https://doi.org/10.1111/gcb.14704

Rotjan, R., Lewis, S., 2008. Impact of coral predators on tropical reefs. Mar. Ecol. Prog. Ser. 367, 73–91. https://doi.org/10.3354/meps07531

Rountree, R.A., Gilmore, G.A., Goudey, C.A., Hawkins, A.D., Luczkovich, J.J., Mann, D.A., 2006. Listening to Fish: Applications of Passive Acoustics to Fisheries Science. Fisheries 31, 433–446.

Roy, K.J., Smith, S.V., 1971. Sedimentation and Coral Reef Development 10 Turbid Water: Fanning Lagoon. PACIFIC SCIENCE 25, 15.

Russ, G., Alcala, A., 1996. Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. Mar. Ecol. Prog. Ser. 132, 1–9. https://doi.org/10.3354/meps132001

Russ, G.R., Leahy, S.M., 2017. Rapid decline and decadal-scale recovery of corals and Chaetodon butterflyfish on Philippine coral reefs. Mar Biol 164, 29. https://doi.org/10.1007/s00227-016-3056-y

Russ, G.R., Payne, C.S., Bergseth, B.J., Rizzari, J.R., Abesamis, R.A., Alcala, A.C., 2018. Decadal-scale response of detritivorous surgeonfishes (family Acanthuridae) to no-take marine reserve protection and changes in benthic habitat. J Fish Biol 93, 887–900. https://doi.org/10.1111/jfb.13809

Sandin, Stuart A., Smith, J.E., DeMartini, E.E., Dinsdale, E.A., Donner, S.D., Friedlander, A.M., Konotchick, T., Malay, M., Maragos, J.E., Obura, D., Pantos, O., Paulay, G., Richie, M., Rohwer, F., Schroeder, R.E., Walsh, S., Jackson, J.B.C., Knowlton, N., Sala, E.,

2008. Baselines and Degradation of Coral Reefs in the Northern Line Islands. PLoS ONE 3, e1548. https://doi.org/10.1371/journal.pone.0001548

Sandin, Stuart A, Smith, J.E., DeMartini, E.E., Dinsdale, E.A., Donner, S.D., Friedlander, A.M., Konotchick, T., Malay, M., Maragos, J.E., Obura, D., Pantos, O., Paulay, G., Richie, M., Rohwer, F., Schroeder, R.E., Walsh, S., Jackson, J.B.C., Knowlton, N., Sala, E., 2008. Baselines and degradation of coral reefs in the Northern Line Islands. PLoS ONE 3, e1548. https://doi.org/10.1371/journal.pone.0001548

Sano, M., 2004. Short-term effects of a mass coral bleaching event on a reef fish assemblage at Iriomote Island, Japan. Fisheries Sci 70, 41–46. https://doi.org/10.1111/j.1444-2906.2003.00768.x

Sano, M., 1989. Feeding habits of Japanese butterfyfishes (Chaetodontidae). Environ Biol Fish 25, 195–203. https://doi.org/10.1007/BF00002212

Sano, M., 1984. Food habits of teleostean reef fishes in Okinawa Island, southern Japan. Univ Mus Univ Tokyo Bull 25, 1–128.

Shibuno, T., Hashimoto, K., Abe, O., Takada, Y., 1999. Short-term changes in the structure of a fish community following coral bleaching at Ishigaki Island, Japan. JCRS 1, 51–58.

Slabbekoorn, H., Bouton, N., van Opzeeland, I., Coers, A., Cate, C. ten, Popper, A.N., 2010. A noisy spring: the impact of globally rising underwater sound levels on fish. Trends Ecol. Evol. 25, 419–427. https://doi.org/10.1016/j.tree.2010.04.005

Slabbekoorn, H., Dooling, R.J., Popper, A.N., Fay, R.R. (Eds.), 2018. Effects of Anthropogenic Noise on Animals, Springer Handbook of Auditory Research. Springer New York, New York, NY. https://doi.org/10.1007/978-1-4939-8574-6

Spalding, M., Burke, L., Wood, S.A., Ashpole, J., Hutchison, J., zu Ermgassen, P., 2017. Mapping the global value and distribution of coral reef tourism. Marine Policy 82, 104–113. https://doi.org/10.1016/j.marpol.2017.05.014

Spalding, M.D., Jarvis, G.E., 2002. The impact of the 1998 coral mortality on reef fish communities in the Seychelles. Marine Pollution Bulletin 44, 309–321. https://doi.org/10.1016/S0025-326X(01)00281-8

Staaterman, E., Ogburn, M., Altieri, A., Brandl, S., Whippo, R., Seemann, J., Goodison, M., Duffy, J., 2017. Bioacoustic measurements complement visual biodiversity surveys: preliminary evidence from four shallow marine habitats. Mar. Ecol. Prog. Ser. 575, 207–215. https://doi.org/10.3354/meps12188

Staaterman, E., Paris, C., DeFerrari, H., Mann, D., Rice, A., D'Alessandro, E., 2014. Celestial patterns in marine soundscapes. Mar. Ecol. Prog. Ser. 508, 17–32. https://doi.org/10.3354/meps10911

Staaterman, E., Rice, A.N., Mann, D.A., Paris, C.B., 2013. Soundscapes from a Tropical Eastern Pacific reef and a Caribbean Sea reef. Coral Reefs 32, 553–557. https://doi.org/10.1007/s00338-012-1007-8

Steinberg, J.C., Cummings, W.C., Brahy, B.D., MacBain, J.Y., 1965. Further Bio-Acoustic Studies off the West Coast of North Bimini, Bahamas. B. Mar. Sci. 942–963.

Stuart-Smith, R.D., Brown, C.J., Ceccarelli, D.M., Edgar, G.J., 2018. Ecosystem restructuring along the Great Barrier Reef following mass coral bleaching. Nature 560, 92–96. https://doi.org/10.1038/s41586-018-0359-9

Sueur, J., Farina, A., Gasc, A., Pieretti, N., Pavoine, S., 2014. Acoustic Indices for Biodiversity Assessment and Landscape Investigation. Acta Acust. with Acustica 100, 772–781. https://doi.org/10.3813/AAA.918757

Tissot, B.N., Hallacher, L.E., 2003. Effects of Aquarium Collectors on Coral Reef Fishes in Kona, Hawaii. Conservation Biology 17, 1759–1768. https://doi.org/10.1111/j.1523-1739.2003.00379.x

Tricas, T., Boyle, K., 2014. Acoustic behaviors in Hawaiian coral reef fish communities. Mar. Ecol. Prog. Ser. 511, 1–16. https://doi.org/10.3354/meps10930

Versluis, M., 2000. How Snapping Shrimp Snap: Through Cavitating Bubbles. Science 289, 2114–2117. https://doi.org/10.1126/science.289.5487.2114

Viviani, J., Moritz, C., Parravicini, V., Lecchini, D., Siu, G., Galzin, R., Viriot, L., 2019. Synchrony patterns reveal different degrees of trophic guild vulnerability after disturbances in a coral reef fish community. Diversity and Distributions 25, 1210–1221. https://doi.org/10.1111/ddi.12931

Wagner, E.L.E.S., Roche, D.G., Binning, S.A., Wismer, S., Bshary, R., 2015. Temporal comparison and predictors of fish species abundance and richness on undisturbed coral reef patches. PeerJ 3, e1459. https://doi.org/10.7717/peerj.1459

Wall, C., Simard, P., Lembke, C., Mann, D., 2013. Large-scale passive acoustic monitoring of fish sound production on the West Florida Shelf. Mar. Ecol. Prog. Ser. 484, 173–188. https://doi.org/10.3354/meps10268

Warton, D.I., 2005. Many zeros does not mean zero inflation: comparing the goodness-of-fit of parametric models to multivariate abundance data. Environmetrics 16, 275–289. https://doi.org/10.1002/env.702

Watson, Maryann S., Claar, D.C., Baum, J.K., 2016. Subsistence in isolation: Fishing dependence and perceptions of change on Kiritimati, the world’s largest atoll. Ocean Coast. Manage. 123, 1–8. https://doi.org/10.1016/j.ocecoaman.2016.01.012

Watson, Maryann S, Claar, D.C., Baum, J.K., 2016. Subsistence in isolation: fishing dependence and perceptions of change on Kiritimati, the world’s largest atoll. Ocean & Coastal Management 123, 1–8.

Williams, I.D., Baum, J.K., Heenan, A., Hanson, K.M., Nadon, M.O., Brainard, R.E., 2015. Human, Oceanographic and Habitat Drivers of Central and Western Pacific Coral Reef Fish Assemblages. PLoS ONE 10, e0120516. https://doi.org/10.1371/journal.pone.0120516

Wilson, S.K., Graham, N.A.J., Pratchett, M.S., Jones, G.P., Polunin, N.V.C., 2006. Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? Global Change Biol 12, 2220–2234. https://doi.org/10.1111/j.1365-2486.2006.01252.x

Wismer, S., Tebbett, S.B., Streit, R.P., Bellwood, D.R., 2019a. Spatial mismatch in fish and coral loss following 2016 mass coral bleaching. Science of The Total Environment 650, 1487–1498. https://doi.org/10.1016/j.scitotenv.2018.09.114

Wismer, S., Tebbett, S.B., Streit, R.P., Bellwood, D.R., 2019b. Young fishes persist despite coral loss on the Great Barrier Reef. Communications Biology 2, 1–7. https://doi.org/10.1038/s42003-019-0703-0

Woodhead, A.J., Hicks, C.C., Norström, A.V., Williams, G.J., Graham, N.A.J., 2019. Coral reef ecosystem services in the Anthropocene. Functional Ecology 33, 1023–1034. https://doi.org/10.1111/1365-2435.13331

Yeager, L.A., Deith, M.C.M., McPherson, J.M., Williams, I.D., Baum, J.K., 2017. Scale dependence of environmental controls on the functional diversity of coral reef fish communities. Global Ecology and Biogeography 26, 1177–1189. https://doi.org/10.1111/geb.12628

Zambre, A.M., Arthur, R., 2018. Foraging plasticity in obligate corallivorous Melon butterflyfish across three recently bleached reefs. Ethology 124, 302–310. https://doi.org/10.1111/eth.12733

Zaneveld, J.R., Burkepile, D.E., Shantz, A.A., Pritchard, C.E., McMinds, R., Payet, J.P., Welsh, R., Correa, A.M.S., Lemoine, N.P., Rosales, S., Fuchs, C., Maynard, J.A., Thurber, R.V., 2016. Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. Nat Commun 7, 11833. https://doi.org/10.1038/ncomms11833

Appendices

Appendix A: Supplemental information for Chapter 2

Table A2.1. Top models from AIC$_c$ stepwise comparisons and results (parameter estimates) for final model fixed effects from linear mixed-effects model examining changes in high frequency SPL associated with changes in snapping shrimp snaps.

Model	K	AICc	ΔAIC	Adjusted R^2	P value
HF SPL ~ Snaps * Day/Night + Year + Lunar Phase + Fishing Pressure	8	77923.39	0	0.371	< 0.0001
HF SPL ~ Snaps + Day/Night + Year + Lunar Phase + Fishing Pressure	7	78034.51	111.11	0.367	< 0.0001
HF SPL ~ Snaps + Year + Lunar Phase + Fishing Pressure	6	79819.11	1895.72	0.292	< 0.0001

Parameter estimates for final model

Parameter	Estimate	Std. Error	t value	P value
(Intercept)	114.94	0.034	3354.404	< 0.0001
Snaps	0.87	0.059	14.696	< 0.0001
Day/Night (Night)	1.92	0.044	-8.868	< 0.0001
Snaps * Day/Night	0.21	0.045	10.652	< 0.0001
Lunar Phase	3.40	0.046	4.767	< 0.0001
Year (2018)	1.00	0.045	74.472	< 0.0001
Fishing Pressure	0.97	0.092	22.314	< 0.0001

Table A2.2. Parameter estimates for the selected low frequency ACI model calculated using a frequency resolution of 15.6 Hz. Fixed effects from linear mixed-effects model examining changes in ACI associated with changes in snapping shrimp snaps. The intercept and all main effects represent our 15:00 sampling time.

15.6 Hz Frequency Resolution Model				
LF ACI ~ Knocks * Hour + Herbivory + Year + Lunar Phase + Fishing Pressure				
Parameter estimates for final model				
Parameter	**Estimate**	**Std. Error**	**t value**	**P value**
(Intercept)	35.962	0.234	153.386	< 0.0001
Knocks	0.756	0.505	1.497	0.136
21:00	-0.161	0.268	-0.603	0.547
03:00	1.178	0.276	4.263	< 0.0001
09:00	0.038	0.278	0.136	0.892
Herbivory	0.740	0.186	3.970	0.0001
Lunar Phase	-0.058	0.182	-0.318	0.751
Year (2018)	0.216	0.164	1.315	0.190
Fishing Pressure	1.308	0.184	7.107	< 0.0001
Knocks * 21:00	1.075	0.587	1.831	0.0687
Knocks * 03:00	0.109	0.574	0.190	0.850
Knocks * 09:00	1.493	0.581	2.570	0.011

Table A2.3. Parameter estimates for the selected low frequency ACI model calculated using a frequency resolution of 4 Hz. Fixed effects from linear mixed-effects model examining changes in ACI associated with changes in snapping shrimp snaps. The intercept and all main effects represent our 15:00 sampling time.

4 Hz Frequency Resolution Model

LF ACI ~ Knocks * Hour + Herbivory + Year + Lunar Phase + Fishing Pressure

Parameter estimates for final model

Parameter	**Estimate**	**Std. Error**	**t value**	**P value**
(Intercept)	77.004	0.346	222.837	<0.0001
Knocks	0.947	0.744	1.272	0.205
21:00	-0.483	0.395	-1.223	0.223
03:00	-0.189	0.407	-0.463	0.643
09:00	-1.342	0.410	-3.276	0.001
Herbivory	1.794	0.275	6.535	< 0.0001
Lunar Phase	-0.099	0.268	-0.368	0.713
Year (2018)	0.223	0.242	0.920	0.359
Fishing Pressure	1.879	0.271	6.925	< 0.0001
Knocks * 21:00	0.319	0.865	0.369	0.713
Knocks * 03:00	-1.327	0.846	-1.569	0.119
Knocks * 09:00	1.542	0.856	1.801	0.073

Table A2.4. Top models from AIC_c stepwise comparisons and results (parameter estimates) for final model fixed effects from linear mixed-effects model examining changes in high frequency ACI associated with changes in snapping shrimp snaps. The intercept and all main effects represent our 15:00 sampling time.

Model		K	AICc	ΔAIC	Adjusted R^2	P value
31.2 Hz	**HF SPL ~ Snaps * Day/Night + Year + Lunar Phase + Fishing Pressure**	8	122047.6	0	0.3701	< 0.0001
15.6 Hz	HF SPL ~ Snaps * Day/Night + Year + Lunar Phase + Fishing Pressure	8	140954.0	18906.4	0.335	< 0.0001
4 Hz	HF SPL ~ Snaps * Day/Night + Year + Lunar Phase + Fishing Pressure	8	160751.3	38703.7	0.285	< 0.0001

Parameter estimates for final model

Parameter	Estimate	Std. Error	t value	P value
(Intercept)	-23510	376.3	-67.263	< 0.0001
Snaps	-6.829	0.242	-28.187	< 0.0001
Day/Night (Night)	-1.669	0.181	-9.212	< 0.0001
Snaps * Day/Night	0.925	0.374	2.477	< 0.0132
Lunar Phase	0.315	0.182	1.733	0.0832
Year (2018)	12.780	0.187	68.495	< 0.0001
Fishing Pressure	-8.700	0.185	-47.073	< 0.0001

Table A2.5. Parameter estimates for the selected high frequency ACI model calculated using a frequency resolution of 15.6 Hz. Fixed effects from linear mixed-effects model examining changes in ACI associated with changes in snapping shrimp snaps. The intercept and all main effects represent our 15:00 sampling time.

15.6 Hz Model				
HF SPL ~ Snaps * Day/Night + Year + Lunar Phase + Fishing Pressure				
Parameter estimates				
Parameter	**Estimate**	**Std. Error**	**t value**	**P value**
(Intercept)	-48400	682.2	-70.941	< 0.0001
Snaps	-10.49	0.4392	-23.886	< 0.0001
Day/Night (Night)	-3.753	0.328	-11.429	< 0.0001
Snaps * Day/Night	1.466	0.677	2.165	0.030
Lunar Phase	0.534	0.329	1.624	0.105
Year (2018)	24.40	0.338	72.150	< 0.0001
Fishing Pressure	-10.69	0.335	2.165	< 0.0001

Table A2.6. Parameter estimates for the selected high frequency ACI model calculated using a frequency resolution of 4 Hz. Fixed effects from linear mixed-effects model examining changes in ACI associated with changes in snapping shrimp snaps. The intercept and all main effects represent our 15:00 sampling time.

4 Hz Model				
HF SPL ~ Snaps * Day/Night + Year + Lunar Phase + Fishing Pressure				
Parameter estimates				
Parameter	**Estimate**	**Std. Error**	**t value**	**P value**
(Intercept)	-80600	1272	-63.369	< 0.0001
Snaps	-17.50	0.819	-21.370	< 0.0001
Day/Night (Night)	-7.957	0.612	-12.997	< 0.0001
Snaps * Day/Night	4.833	1.262	3.828	< 0.001
Lunar Phase	0.842	0.614	1.373	0.170
Year (2018)	40.84	0.631	64.775	< 0.0001
Fishing Pressure	-16.669	0.625	3.828	< 0.0001

Table A2.7. Model parameter estimates and statistics for a model examining the influence of time of day on the received level (dB) of individual knocks selected from the acoustic data.

Parameter	**Estimate**	**Std. Error**	**t value**	**P value**
Intercept (03:00)	111.	0.7	149.7	< 0.0001
09:00	7.7	0.9	8.1	< 0.0001
15:00	1.0	1.2	0.8	0.41
21:00	-0.2	1.1	0.1	0.89

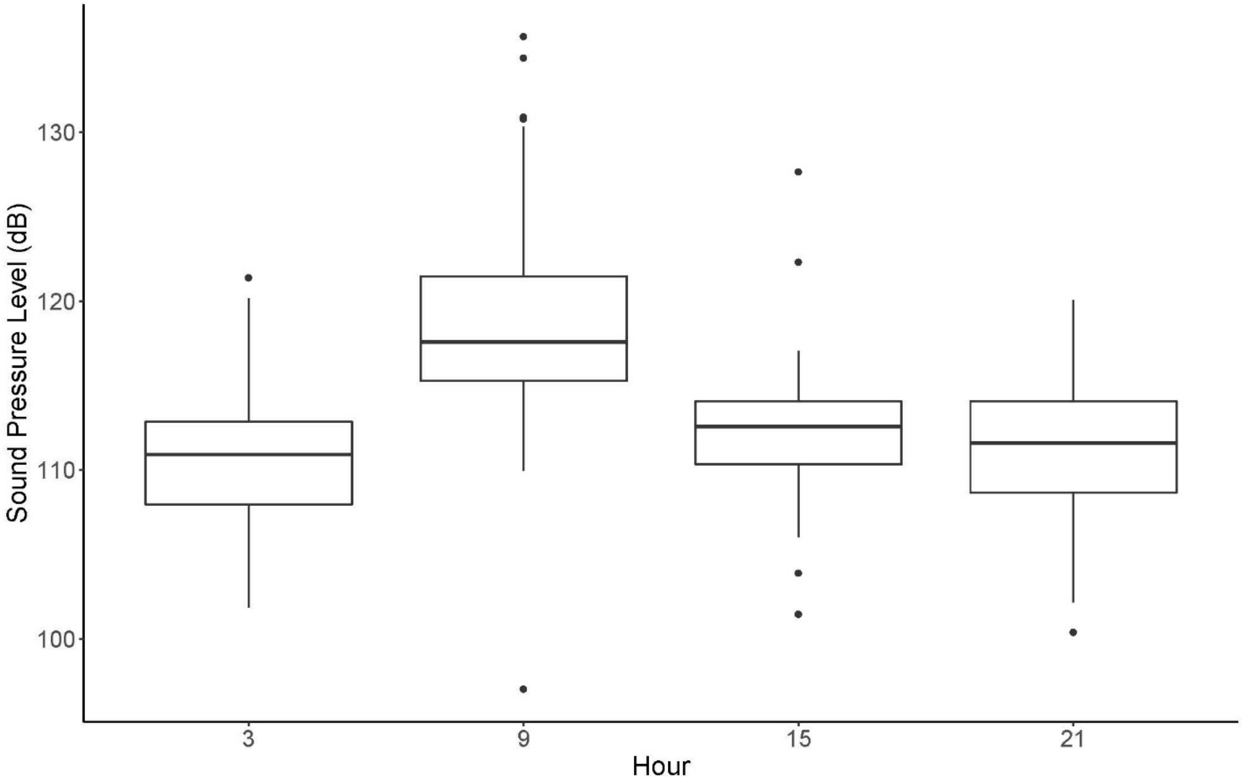

Figure A2.1. Differences in Sound Pressure Level (dB) between four sampled times of day using subsampled individually selected knocks.

Appendix B: Supplemental information for Chapter 3

Table B3.1 Results (p-values) from generalized linear mixed-effects models describing the effects of year, local human disturbance, coral cover, and net primary productivity on a) obligate and b) facultative corallivore abundance for the 9 sites sampled in all three years following the El Niño. Values in bold are significantly different from baseline levels (2017) at α = 0.05.

	Year					Year x Local Disturbance	
Model	2018	2019	Local Disturbance	Productivity	Coral Cover	2018	2019
a) Obligate	-0.096	**-1.566**	-0.817	-0.32	**0.12**	1.209	0.947
b) Facultative	**-0.329**	-0.456	0.317	-0.108	0.027	**1.052**	**0.923**

Table B3.2. Results (p-values) from generalized linear mixed-effects models describing the effects of year, local human disturbance, coral cover, and net primary productivity on a) obligate and b) facultative corallivore species richness for the 9 sites sampled in all three years following the El Niño. Values in bold are significantly different from baseline levels (2017) at α = 0.05.

	Year					Year x Local Disturbance	
Model	2018	2019	Local Disturbance	Productivity	Coral Cover	2018	2019
a) Obligate	0.129	**-1.595**	-0.258	-0.23	**0.101**	0.435	0.561
b) Facultative	-0.053	*-0.378*	**0.445**	*0.263*	**0.057**	0.224	0.36

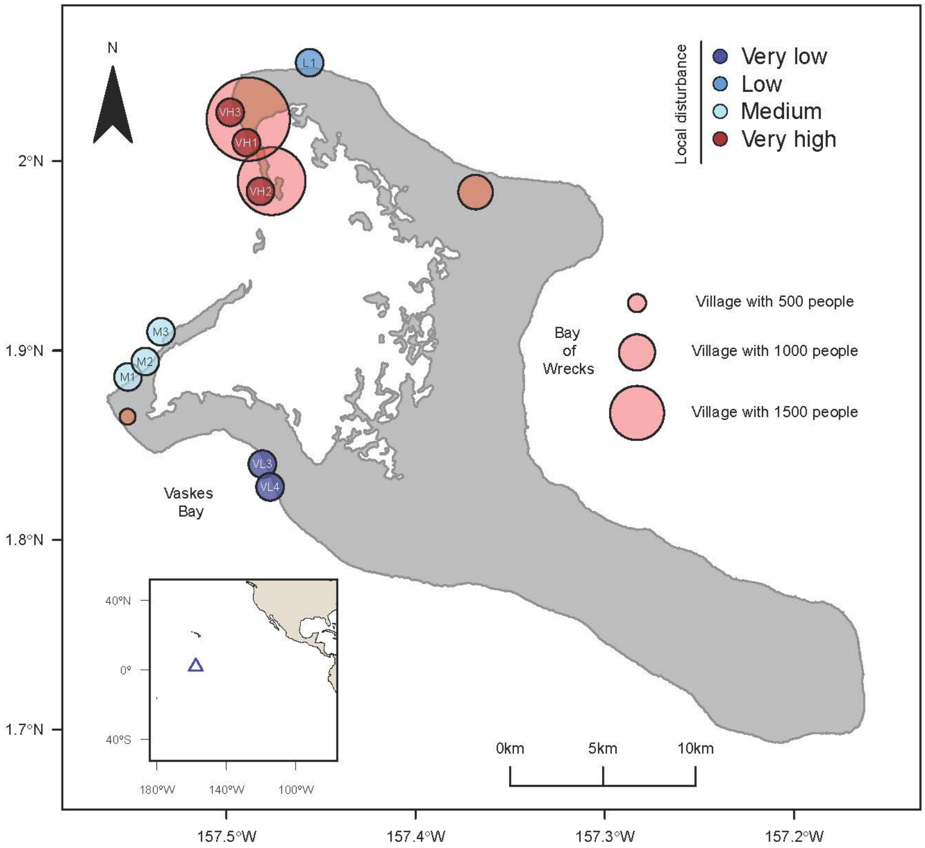

Figure B3.1. Map of the study sites used in sensitivity analyses (2017-2019), and villages on Kiritimati, Republic of Kiribati. Sites are categorized into four levels of local human disturbance, and villages (red circles) are scaled human population size. Inset shows Kiritimati's location in the central Pacific.