Effects of heat stress and local human disturbance on the structure of coral reef ecosystems at multiple scales of biological organization

by

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BSc, Carleton University, 2015

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Abstract

The world's coral reefs are being impacted by myriad disturbances, from localized overfishing and nutrient pollution to global climate change-induced temperature increases and ocean acidification. Conservation of coral reefs in the face of increasing variability and uncertainty requires an understanding of the interacting effects of multiple stressors on the diverse components of these vital ecosystems. In this thesis, I use data from reefs around Kiritimati atoll (Republic of Kiribati) in the central equatorial Pacific Ocean to examine the effects of a severe pulse heat stress event and local human disturbance on two important components of the coral reef ecosystem – three-dimensional (3D) structural complexity and reef fish assemblages. Using 3D reef models constructed through structure-from-motion photogrammetry, I examined changes in reef structural complexity in the year following the 2015-2016 El Niño and mass coral bleaching event. I found that exposure to prolonged thermal stress and subsequent coral mortality resulted in declines in reef structural complexity, particularly reef surface rugosity and terrain ruggedness. Baseline levels of structural complexity were also negatively influenced by local human disturbance, while complexity was positively related to the densities of branching and massive coral growth forms. These findings have important implications for the maintenance of healthy reef ecosystems, as high levels of structural complexity are important for supporting diverse reef-associated fish assemblages. Next, using underwater visual censuses of reef fish assemblages, I quantified fish abundance, biomass, species richness, and assemblage structure before, during, and after the 2015-2016 El Niño. Total reef fish abundance, biomass, and species richness declined during the El Niño, suggesting that pulse heat stress events may have short-term, negative consequences for reef fish. Although these metrics did not vary substantially across the local human disturbance gradient, recovery of assemblages following the heat stress event was impeded by higher levels of local human disturbance. Reef fish assemblage structure was influenced by a more diverse array of factors, showing significant shifts in response to heat stress, human disturbance, and net primary productivity. Given the many important roles that fish play on coral reefs, declines such as those observed here may impair the ecological functioning of these ecosystems. Together, my results highlight the negative impacts of heat stress and local human disturbance on coral reefs, demonstrating ways in which these stressors may interact to limit reef resilience in the face of increasing anthropogenic pressures.

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Dedication

To Eric and Karen,
for giving me the world
and encouraging me
to explore it.

Chapter 1 – Introduction

Coral reefs are one of our planet's most productive and biodiverse natural habitats (Reaka-Kudla 1997), despite covering less than 1% of the ocean floor (Burke et al. 2011). Coral reefs are home to over 900 species of coral, 5000 species of fish, and even greater numbers of marine invertebrates (Fisher et al. 2015), supporting up to one quarter of all marine species (Spalding et al. 2001). In addition to their biological diversity, coral reef ecosystems provide essential goods and services to millions of people around the world (Moberg and Folke 1999; Burke et al. 2011). Reef fish serve as a vital source of protein for many small island nations and developing countries (Burke et al. 2011), while coral reef tourism alone has an estimated global value of US $36 billion annually (Spalding et al. 2017). The physical structure of coral reefs also provides coastal protection to over 100 countries worldwide, mitigating shoreline erosion, reducing wave damage during storms, and protecting other important coastal ecosystems such as mangroves and seagrass beds (Moberg and Folke 1999; Ferrario et al. 2014). However, despite their ecological and economic importance, coral reefs are also one of the world's most highly threatened marine ecosystems (Halpern et al. 2007; Hoegh-Guldberg 2011).

Coral reefs are currently being impacted at multiple spatial scales by a combination of local and global stressors. Localized fishing pressure and other human disturbances have been shown to alter reef fish size spectra (Graham et al. 2005; Robinson et al. 2017) and lead to decreases in the abundance and biomass of higher trophic level fishes (Mora 2008; Williams et al. 2011; MacNeil et al. 2015). Nutrient pollution can promote macroalgal growth (Schaffelke and Klumpp 1998; Fabricius 2005) and heighten coral susceptibility to bleaching (Wiedenmann et al. 2012; Vega Thurber et al. 2014), while increased sedimentation due to coastal development can smother corals and reduce the amount of light available for photosynthesis, limiting coral growth and recruitment (Rogers 1990). Meanwhile, the global threat of ocean warming and associated coral bleaching has led to drastic declines in coral cover on reefs in several regions (Glynn 1984; Wilkinson 1998; Eakin et al. 2017) and now threatens the persistence of coral-dominated systems worldwide. Ocean acidification is also projected to worsen with global increases in carbon dioxide concentrations, and may have serious consequences for the growth and maintenance of carbonate reef structure (Hoegh-Guldberg et al. 2007). When local disturbances are considered together with climate change, approximately 75% of the world's reefs are currently classified as threatened (Burke et al. 2011). This proportion is predicted to increase to 100% by 2050 in the face of continued climate warming, prompting the need to understand the impacts of thermal stress on coral reef ecosystems.

Heat stress and associated coral bleaching are arguably the most prominent threats facing coral reefs this century (Hoegh-Guldberg 2011; Hughes et al. 2018). Over the past two decades, the world's reefs have experienced three major global coral bleaching events, the most recent of which occurred during 2015-2016 in conjunction with an extreme El Niño (Eakin et al. 2016). El Niño is one component of the El Niño Southern Oscillation (ENSO), a natural, large-scale climatic event that occurs once every ~3 to 6 years (Trenberth 1997). During the El Niño phase of ENSO, changes in atmospheric circulation and oceanic conditions lead to increases in sea surface temperatures (SSTs) in the central and eastern equatorial Pacific (Cane 1983) and alter local patterns of net primary productivity (Barber et al. 1996), with potentially severe consequences for local fauna (Barber and Chavez 1983). The 2015-2016 El Niño was the most extreme warming event to date, both in terms of its extent and the level of heat stress experienced by corals (Eakin et al. 2017; Claar et al. 2018), resulting in severe coral mortality throughout all three tropical ocean basins (Hughes et al. 2018). The frequency of extreme El

Niños such as this is projected to double in the future in response to continued climate warming (Cai et al. 2014; Wang et al. 2017), leading to more frequent and severe heat stress events, and increasing the probability that annual coral bleaching will occur within the next few decades (Hughes et al. 2018). As such, it is vital that we understand the effects of pulse heat stress events on coral reefs, and the ways in which these phenomena threaten the maintenance of healthy coral reef ecosystems.

1.1 Coral reef structural complexity

One way that heat stress threatens coral reefs – beyond the direct effects of bleaching-associated coral mortality – is through its potential impacts on the structural complexity of coral reef habitat. 'Structural complexity' is defined as the physical three-dimensional structure of an ecosystem (Graham and Nash 2013), and includes factors such as the diversity of structural elements and the size, abundance, and spatial arrangement of those elements (Tokeshi and Arakaki 2012). On coral reefs, structural complexity is provided both by the living corals themselves and by the complexity of the underlying carbonate or lithic substrate (Lewis 1997; Wilson et al. 2009). This complex structure is built up over hundreds to thousands of years through the deposition of thin layers of calcium carbonate by living scleractinian (hard) corals, cemented together by calcareous algae (Adey 1998) and augmented by the presence of other organisms such as soft corals (Ferrari 2017) and sponges (Newman et al. 2015). High levels of structural complexity in these systems can positively influence reef fish abundance and diversity (Wilson et al. 2006; Graham and Nash 2013; Alvarez-Filip et al. 2015), and may even help increase reef resilience both by minimizing the impacts of coral loss on reef fish (Emslie et al. 2014) and by promoting reef recovery following severe disturbances (Graham et al. 2015).

However, both the creation and maintenance of complex reef structure are threatened by rising ocean temperatures and heat stress-associated mass bleaching events.

Even on the healthiest of coral reefs, structure is perpetually being eroded through a combination of physical, chemical, and biological forces (Hutchings 1986). Corals may be broken by tropical storms or cyclones (Harmelin-Vivien 1994), or gradually worn down and dislodged by bioeroders. Coral reefs are home to a wide variety of bioeroding organisms (Hutchings 2011; Glynn and Manzello 2015), from sponges and other invertebrates (e.g., polychaete worms, bivalve molluscs) that bore into the reef (Hutchings 2008; Schönberg 2008) to excavating parrotfish (e.g., *Chlorurus* spp.) that remove pieces of substrate while feeding on epilithic or endolithic algae (Bellwood and Choat 1990). Under normal conditions, rates of reef erosion by the above processes are balanced or even exceeded by rates of reef accretion, allowing the reef to build and maintain its physical structure through time. However, severe heat stress and mass coral bleaching events have the capacity to alter reef carbonate budgets (Perry and Morgan 2017), limiting coral growth and shifting reefs to a state of net erosion. These effects may also be compounded by increases in ocean acidification, which can further limit carbonate accretion on coral reefs (Hoegh-Guldberg et al. 2007). As many bioeroders prefer to associate with dead coral substrate (Bromley 1978; Hutchings 2008), rates of bioerosion may also increase following a mass bleaching event due to the resulting coral mortality (Carballo et al. 2013). Despite the importance of reef structure to the maintenance of healthy fish populations and the many threats posed by heat stress and mass coral bleaching events, very few studies to date have actually quantified changes in reef structural complexity following a pulse heat stress event.

1.2 Coral reef fish assemblages

The effects of severe heat stress on tropical reef fish assemblages themselves are also of great interest, as fish comprise a significant proportion of the consumer biomass on coral reefs and play critical ecological roles that aid in the maintenance of healthy reef communities. Herbivores, such as parrotfish and surgeonfish, help to maintain reefs in a coral-dominated state (Burkepile and Hay 2008), while highly-mobile fish species play important roles in energy transfer and nutrient provisioning (Allgeier et al. 2014). Reef fish are also a vital source of income and subsistence for millions of people living in tropical coastal communities (Moberg and Folke 1999). Healthy and well-managed coral reefs can yield over 10 tonnes of fish per square kilometer annually (Jennings and Polunin 1995), comprising up to a quarter of the total fish catch in developing countries (Jameson et al. 1995). Like structural complexity, healthy reef fish assemblages are an ecologically and socioeconomically vital component of coral reef ecosystems. While ocean warming and pulse heat stress events are predicted to impact coral reefs by leading to increased incidence of severe coral bleaching over the next century (Frieler et al. 2013; van Hooidonk et al. 2016), direct effects of temperature stress on vertebrates such as reef fish are less clear.

Sea surface warming and changes in primary productivity associated with extreme El Niño events are known to result in declines in many commercially important fish species in the eastern equatorial Pacific, where waters are typically cool and nutrient-rich (Barber and Chavez 1983; Ñiquen and Bouchon 2004). These shifts have been most prominently seen in pelagic species such as anchovy (*Engraulis ringens*), which undergo drastic declines in biomass during El Niño (Ñiquen and Bouchon 2004). It is possible that El Niño may have similar effects on tropical reef fish populations, however the impacts of heat stress on these assemblages have been comparatively under-studied. Most studies on the effects of El Niño in coral reef environments have focused on the influence of heat stress on live coral cover (e.g., Glynn 1984; Wilkinson et al. 1999; Glynn et al. 2017) and the impact of subsequent benthic shifts on reef fish assemblages (e.g., Graham et al. 2006; Garpe et al. 2006; Pratchett et al. 2011). For example, declines in the abundance of obligate corallivores and other coral-dependent fishes have been documented following extensive coral mortality (Pratchett et al. 2006; Graham et al. 2009), while the number of herbivores may increase in the years following coral bleaching as algae becomes more abundant (Shibuno et al. 1999; Lindahl et al. 2001). Coral loss has also been known to lead to declines in species with no obvious reliance on corals (Jones et al. 2004; Cheal et al. 2008), highlighting the hidden associations between fish abundance and diversity and coral reef benthic composition.

Heat stress is also predicted to have direct negative impacts on reef fish assemblages, as well as additional indirect effects that are unrelated to coral cover. Compared to organisms living at higher latitudes, tropical ectotherms such as reef fish are thought to be particularly vulnerable to heat stress, as their evolutionary history has resulted in relatively narrow thermal tolerances (Tewksbury et al. 2008; Comte and Olden 2017). Many physiological processes in fish are highly sensitive to temperature, and may therefore be affected by projected increases in SSTs (Munday et al. 2008a). Negative effects of elevated water temperatures have been documented for the coral reef damselfish *Acanthochromis polyacanthus*, which experiences decreased growth (Munday et al. 2008b) and impaired reproduction (Donelson et al. 2010) at temperatures predicted to occur by the end of this century. Changes in plankton assemblages during warming events, which affect food availability for planktivorous fishes, may also be influenced by the thermal tolerances of various zooplankton species (Pörtner and Farrell 2008). Pulse heat stress events may consequently result in shifts in reef fish distribution and abundance, as fish move to new areas to escape the negative effects of ocean warming. For example, shifts in reef fish assemblage structure during a strong El Niño have previously been observed on Mexican coral reefs, with the changes largely attributed to redistribution of fish populations rather than direct mortality (López-Pérez et al. 2016). The potential for these temperature-related effects on reef fish during an El Niño has been minimally explored, but will be increasingly important to understand in the face of more frequent and severe pulse heat stress events.

1.3 Thesis research

This thesis attempts to enhance our understanding of the impacts of local and global stressors on tropical coral reef ecosystems at multiple levels of biological organization. Specifically, my collaborators and I examine the short-term, interacting effects of a severe heat stress event and local human disturbance on 1) coral reef structural complexity, and 2) tropical reef fish assemblages. We use data collected from reefs around Kiritimati (Republic of Kiribati) in the central equatorial Pacific Ocean, a coral atoll that was severely impacted by the 2015-2016 El Niño and mass coral bleaching event (Baum et al. in prep.). Given the intensity of the heat stress event on Kiritimati, I predicted that heat stress would have negative consequences for structural complexity and reef fish assemblages in the short term (i.e., <2 years after the El Niño). I also predicted that the degree of change in reef structural complexity would be influenced by the intensity of local human disturbance, as would the recovery of reef fish assemblages following the mass coral bleaching event.

In Chapter 2, I quantify the impact of the 2015-2016 El Niño and mass coral mortality event on three-dimensional (3D) reef structural complexity. Using 3D models created through structure-from-motion (SfM) photogrammetry, I examine the effects of heat stress, local human disturbance, and coral morphology on three reef complexity metrics (surface rugosity, terrain ruggedness, and absolute curvature) and habitat volume. This study provides fine-scale measures of reef structural complexity (compared to traditional ‘chain-and-tape’ linear rugosity measures) and is an advance on previous coral reef SfM studies that were conducted over smaller spatial scales. I show that levels of reef surface rugosity and terrain ruggedness declined following the heat stress event, as well as with increasing levels of local human disturbance and with decreasing densities of branching and massive corals. I also document a decline in habitat volume at the majority of sites one year after the bleaching event. These results provide quantitative evidence for declines in reef structural complexity as a consequence of severe coral bleaching, and highlight the threat of both local and global stressors to the structural foundation of coral reef ecosystems.

To provide insight into the short-term effects of heat stress on tropical coral reef fish assemblages, Chapter 3 examines changes in reef fish abundance, biomass, species richness, and assemblage structure as a result of the 2015-2016 El Niño. Using survey data collected two months into the heat stress (before the onset of severe coral bleaching and mortality), as well as one year after the mass bleaching event, I quantify the effects of heat stress, local human disturbance, and net primary productivity on reef fish assemblages. I show that severe heat stress negatively impacts reef fish abundance, biomass, and species richness, but that assemblages are capable of recovery shortly after the heat stress dissipates. However, this recovery may be impeded by higher levels of local human disturbance. I also document declines in corallivorous fish abundances following the mass bleaching event, and significant shifts in reef fish assemblage structure through time. These findings highlight the interacting effects of heat stress and local disturbance on tropical reef fish assemblages, and may foreshadow the consequences of continued climate change and increasing human population growth for coral reef ecosystems.

In sum, the results of this thesis enhance our understanding of the direct and indirect impacts of severe pulse heat stress events on coral reef ecosystems, and how these impacts vary across a gradient of local human disturbance. In the face of accelerating climate change and increasing coastal development, it is critical that we quantitatively examine the interacting effects of multiple stressors on coral reef ecosystems, particularly those components that have been hitherto understudied. Our findings add to the limited body of coral reef literature concerning the effects of thermal stress on reef structural complexity and reef fish assemblages, and support the call for action at both local and global scales to preserve the world's increasingly threatened coral reef ecosystems.

Chapter 2 – Effects of bleaching-associated mass coral mortality on reef structural complexity across a gradient of local disturbance

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2.1 Abstract

Structural complexity underpins the ecological functioning of coral reefs. However, rising ocean temperatures and associated coral bleaching threaten the structural integrity of these important ecosystems. Despite the increased frequency of coral bleaching events, few studies to date have examined changes in three-dimensional (3D) reef structural complexity following severe bleaching. The influence of local stressors on reef complexity also remains poorly understood. In the wake of the 2015-2016 El Niño-induced mass coral bleaching event, we quantified the effects of severe heat stress on 3D reef structural complexity across a gradient of local human disturbance. Using structure-from-motion photogrammetry we created 3D reconstructions of permanent reef plots and observed substantial declines in reef structural complexity (surface rugosity and terrain ruggedness), and a detectable loss of habitat volume one year after the bleaching event. 3D reef complexity also declined with increasing levels of human disturbance, and with decreasing densities of branching and massive corals. These findings improve our understanding of the effects of local and global stressors on the structural foundation of coral reef ecosystems. In the face of accelerating climate change, mitigating local stressors may increase reef structural complexity, thereby heightening reef resilience to future bleaching events.

2.2 Introduction

Habitat complexity has long been known to play an important role in structuring natural communities (MacArthur and MacArthur 1961). This is particularly true in highly-complex aquatic habitats such as coral reefs, given the unique physical challenges of the aquatic environment (Tokeshi and Arakaki 2012). The physical structure provided by living corals, and the underlying topographic complexity of the substrate itself, play a critical role in the maintenance of biodiversity in coral reef ecosystems (Graham et al. 2006; Emslie et al. 2014). Complex structure supports high reef fish abundance and diversity (Wilson et al. 2006; Graham and Nash 2013; Alvarez-Filip et al. 2015), mediates the effects of competition and predation on coral reefs (Beukers and Jones 1997), facilitates the settlement of reef fish (Coker et al. 2014), and may even make reefs more resilient to severe disturbances (Graham et al. 2015). Coral reefs also provide coastal protection in over 100 countries worldwide (Cesar et al. 2003), an ability that is intimately tied to their physical structure. However, the increasing frequency and intensity of severe heat stress and associated coral bleaching events (Cai et al. 2014) threaten the structural integrity of these vital ecosystems (Hoegh-Guldberg 2011; Hughes et al. 2018).

Under normal conditions, corals live in symbiosis with photosynthetic algae (Symbiodiniaceae) that inhabit their tissues and provide the majority of energy needed for coral metabolism (Muscatine and Porter 1977). Coral bleaching occurs when environmental stressors, such as elevated water temperatures (Heron et al. 2016; Hughes et al. 2017), disrupt the relationship between corals and their symbionts, resulting in expulsion of the algae from the coral tissue (Brown 1997) and heightening the chances of coral mortality (Eakin et al. 2010). In 2015-2016, heat stress associated with an extreme El Niño triggered the third major global coral bleaching event (Eakin et al. 2016), resulting in severe coral bleaching and mortality throughout the Pacific, Atlantic, and Indian Ocean basins (Hughes et al. 2018). Beyond impacts on live coral cover, extreme warming events such as this may also affect the three-dimensional (3D) structure of coral reef ecosystems. Mass coral bleaching can severely reduce reef carbonate budgets (Perry and Morgan 2017), shifting reefs to a state of net erosion and limiting their ability to recover lost structure. This loss is compounded by increased rates of bioerosion following mass bleaching, driven by increases in the abundance of common bioeroding organisms such as sponges (Carballo et al. 2013) and the proliferation of dead coral substrate, which is more easily eroded (Hutchings 2008). Declines in reef structural complexity were reported following the 1998 mass coral bleaching event (Sheppard et al. 2002; Graham et al. 2006, 2009), however these descriptions were primarily qualitative. To date, relatively few studies have quantified changes in 3D reef structural complexity following a severe heat stress event.

Quantitative measures of structural complexity on coral reefs have traditionally been made using the ‘chain-and-tape’ method for assessing linear rugosity (Risk 1972), however this technique is time-intensive, measures a small spatial area, and suffers from high variation due to the particular placement of the chain on the reef (Friedman et al. 2012). Recent advances in the quantification of coral reef structural complexity, most notably structure-from-motion (SfM) photogrammetry (Burns et al. 2015a; Leon et al. 2015; Ferrari et al. 2016b), enable more precise and robust measures of fine-scale complexity, including a wider array of biologically-relevant structural complexity metrics (Friedman et al. 2012; Storlazzi et al. 2016). However, the application of SfM photogrammetry to answering questions about reef structural change has so far been relatively limited (but see Burns et al. 2016; Ferrari et al. 2016a, 2017; Couch et al. 2017). The few studies that have used SfM to quantify changes in reef complexity following coral bleaching have employed these techniques within only one (Burns et al. 2016; Couch et al. 2017) to three (Ferrari et al. 2016a) reef plots, limiting our ability to understand the effects of bleaching on reef structure at a wider scale. Gaining a comprehensive understanding of the effects of bleaching-associated coral mortality on the physical structure of reefs and associated ecological processes will require quantification of these changes across environmental gradients and levels of human impact (Mumby 2017) (e.g., from fishing (Hughes et al. 2007) or nutrient enrichment (Wiedenmann et al. 2012; Vega Thurber et al. 2014), which can influence coral reef resilience and recovery from bleaching), using modern techniques capable of capturing fine-scale structural changes.

This study capitalized on a severe pulse heat stress event to examine the effects of bleaching-associated mass coral mortality on 3D reef structural complexity and the influence of underlying local human disturbance on these changes. During the 2015-2016 El Niño, coral reefs around Kiritimati (Republic of Kiribati) in the central equatorial Pacific Ocean were subjected to globally unprecedented levels of heat stress and suffered over 80% loss of coral cover by the end of the bleaching event (Baum, unpublished data). Kiritimati also presents the opportunity to examine the effects of local stressors on coral reef structural complexity: the atoll is characterized by a gradient of local human disturbance with the majority of its population concentrated on the northwest side of the island (Watson et al. 2016; Fig. 2.1), resulting in a diverse spectrum of reef states ranging from highly-degraded sites near the villages to near-pristine ones on the eastern side of the island (Fig. 2.2). Within the context of this ecosystem-scale natural experiment, we used photogrammetric techniques to quantify fine-scale reef structural complexity across the atoll’s disturbance gradient over the course of the bleaching event. Specifically, we aimed to 1) quantify the change in 3D reef structural complexity on Kiritimati resulting from the 2015-2016 El Niño, 2) determine the effect of local anthropogenic stressors on levels of structural complexity and the degree of structural change, and 3) examine the relationship between shifts in benthic composition and changes in coral reef structural complexity.

2.3 Methods

2.3.1 Study site and design

To examine changes in 3D reef structure following the 2015-2016 El Niño-induced mass coral bleaching event, we surveyed nine forereef sites around Kiritimati (Christmas Island, Republic of Kiribati) in the central equatorial Pacific Ocean (01°52’N 157°24’W, Fig. 2.1) in May 2015, before the onset of the El Niño, and again in July 2017, approximately 14 months after the end of the heat stress. Each site was assigned to one of three human disturbance levels (low, medium, high) based on the intensity of fishing pressure (Watson et al. 2016) and proximity to local villages (Baum et al. unpublished data). Prior to this study, three 4 m x 4 m permanent photoquadrats (PPQs) were established along the 10-12 m isobath at each site to document temporal changes in coral assemblage composition and reef structure. Stainless steel stakes were installed to demarcate each of the PPQs’ corners at all sites, and PPQs were spaced approximately 10 m apart from each other. We surveyed all three PPQs at each site in both time points, except at one low disturbance site (where inclement weather conditions only permitted sampling two PPQs in the first time point), for a total of 26 PPQs.

2.3.2 Photographic surveys

We captured images of the reef substrate in each PPQ using SfM photogrammetry techniques for modelling coral reef habitats, described by Burns et al. (2015a). Ground control points (GCPs) were placed at each corner of the plot at known depths and locations to enable accurate orthorectification of the resulting 3D models. A calibration grid and scale bar were also placed along the margin of the PPQ to validate the spatial accuracy of the 3D models. Photographs of the benthic substrate were collected while swimming in a boustrophedonic pattern approximately 3 m above the substrate. All images had 70-80% overlap and were taken from both planar and oblique angles. All photos were taken using a Nikon D750 digital SLR camera with a 24 mm lens (Nikon Canada Inc., Mississauga, Canada) and an Ikelite housing with an 8-inch hemispheric dome port (Ikelite Underwater Systems, Indianapolis, USA).

2.3.3 Three-dimensional model generation

We used Agisoft PhotoScan software (Agisoft LLC., St. Petersburg, Russia) to process the images and produce spatially accurate 3D reconstructions and 2D orthophotomosaics of the surveyed PPQs. The 3D reconstruction workflow used photogrammetric techniques to produce a dense 3D point cloud, which represents the structure of the PPQ using data points in three-dimensional space, and a digital elevation model (DEM), which is a raster representing the 3D elevation of the reef substrate as a grid of squares. The orthophotomosaics are orthorectified, high-resolution images created using the source photos. The mosaics and DEMs are projected using the same local coordinate system, so they can be layered to perform identification and measurement of individual coral colonies (Burns et al. 2015a). See Burns et al. (2015a) for a detailed description of the model construction process.

2.3.4 Quantification of complexity metrics and habitat volume

We quantified three structural complexity metrics using the 3D analyst and spatial analyst tools in ArcMap (ArcGIS 10.5, Environmental Systems Resource Institute, Redlands, USA). These geospatial metrics were specifically selected to capture variability in topographic complexity that is known to affect the biodiversity and abundance of marine organisms (Burns et al. 2015a, 2016; Ferrari et al. 2016a, 2016b; Storlazzi et al. 2016). For each PPQ, the DEM was layered with the accompanying orthophoto and the area of the PPQ was digitized using the editor function in ArcMap. DEM cell size was set to 1.0 cm to capture fine-scale changes in the 3D physical structure of the reef. First, we quantified surface rugosity (Figueira et al. 2015; Ferrari et al. 2016b) by using the ‘add surface information’ tool to quantify the ratio of 3D to 2D surface area for each PPQ. This metric is related to the traditional measure of linear reef rugosity but uses the ratio of 3D to 2D surface area rather than the ratio of contour to linear distance. Second, we used the ‘benthic terrain modeler’ toolbox to obtain a measure of terrain ruggedness for each PPQ, using a vector ruggedness measure. This metric quantifies surface complexity by measuring the three-dimensional dispersion of vectors orthogonal to the surface of the DEM. Vectors orthogonal to each grid cell are decomposed into their *x*, *y,* and *z* components, and a resultant vector is calculated within a 3 x 3 cell window centered on each cell. Larger values indicate areas of highly complex terrain. This metric simultaneously captures variation in both slope and aspect, and produces a measure of terrain ruggedness that is not strongly correlated with slope (Sappington et al. 2007). Third, we used the ‘curvature’ tool to quantify curvature values across the surface of each DEM. Curvature is measured by calculating the second derivative of the surface for each cell within a 3 x 3 window composed of the focal cell and its eight surrounding neighbours. This metric is a quantitative representation of convexities and concavities, which enables the identification of distinct topographic features such as peaks, ridges, channels, and planar regions (Pittman et al. 2009; de Smith et al. 2015). Positive and negative curvature values represent upwardly concave or upwardly convex surfaces, respectively. Because both positive and negative values can correspond to high structural complexity, we used absolute values of curvature for our analysis.

To calculate volumetric change, we compared the 2015 and 2017 3D point clouds for each PPQ using the open-source software CloudCompare (v. 2.9.1, 2017). We aligned point clouds from the same PPQ by performing a rough alignment using the point pairs picking tool to select at least four matching pairs of points in each cloud, followed by a fine registration using the Iterative Closest Point (ICP) algorithm modified to allow for adjusted scaling of the source cloud to the reference cloud. Four permanent pins were installed at the corners of each 4 m x 4 m PPQ prior to this study. The pins from each PPQ were used as matching pairs to ensure the co-registration between point clouds was performed with invariant features that would not confound the temporal analysis. We then computed the volumetric change between the 2015 and 2017 point clouds using the 2.5D volume calculation tool, allowing us to quantify how much the volume of available reef habitat changed over time.

2.3.5 Benthic composition

To quantify changes in benthic composition, we imported the two-dimensional orthophotomosaics of each PPQ into ArcMap for benthic analysis. For each PPQ, we identified all non-encrusting, intact hard coral colonies >5 cm in diameter to the lowest possible taxonomic level and assigned them a unique label so that the status of each colony could be tracked through time. In total, we enumerated 6655 individual coral colonies. To examine the relationship between the prevalence of different coral morphologies and levels of structural complexity, we also assigned each coral taxon to one of three coral growth forms (branching, plating, or massive; Table A2.1) based on the Coral Traits Database (https://coraltraits.org/) and Veron (2000). For each PPQ, we calculated the density of each of these three coral growth forms (corals m^{-2}) by dividing the abundance of each growth form by the area of the PPQ, to account for variation in PPQ size. We also measured the maximum diameter of each coral colony using the ‘measure’ tool and used these measurements to calculate ‘coral cover’ for each growth form in each PPQ. However, we found that coral abundance, coral density, and coral cover were highly correlated ($r = 0.83 – 0.99$) for each growth form, so we proceeded with a single metric (coral density) for statistical modelling.

2.3.6 Statistical analyses

We conducted all statistical analyses using the statistical software R version 3.3.1 (R Core Team 2016). For our analysis, we used model selection and multi-model inference (Burnham and Anderson 2002) to examine the influence of local and global stressors on coral reef surface rugosity, terrain ruggedness, and absolute curvature. For each structural complexity metric, we fit linear mixed-effects models with heat stress, local human disturbance, and the density of each coral growth form as fixed effects, and site as a random effect (to account for non-independence amongst PPQs at the same site). Heat stress was modelled as a categorical variable with two levels (‘before’, ‘after’), because *in situ* temperature loggers (SBE-56, Sea-Bird Electronics, Bellevue, USA) deployed at sites around Kiritimati indicated a consistent change in water temperature around the atoll throughout the heat stress event (Fig. A2.1). Local human disturbance was also modelled as a categorical variable with three levels (‘low’, ‘medium’, ‘high’), while the densities of each coral growth form were modelled as continuous variables. Prior to analysis, all 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 and Su 2018), to allow for direct comparison of the effect sizes of different variable types (Gelman 2008). We also explored the possibility of including wave energy as a fixed effect, however this was ultimately deemed to be unnecessary because of minimal variability across the sampled sites (Appendix A).

To account for unequal variance in the residuals of our full model, we also employed residual variance structures. Variance structures provide a means of modelling identifiable structure in the residuals without the penalty of adding additional parameters to the model (Zuur et al. 2009). We used AIC corrected for small sample sizes (AIC_c; Hurvich and Tsai 1989) to compare models with and without residual variance structures, and identify metrics for which inclusion of a variance structure improved model fit. For the surface rugosity and absolute curvature models, we applied a varIdent residual variance structure to account for unequal variance between time points (before vs. after) in the full model. The same variance structure was tested for terrain ruggedness but did not improve model fit.

For each structural complexity metric, we evaluated 40 models by fitting every combination of variables, including a two-way interaction between heat stress and local human disturbance. To perform model selection, we used AIC_c to compare models and produce a top model set comprised of all models within 4 ΔAIC_c of the best model. Within this top model set, we calculated multi-model-averaged parameter estimates and 95% confidence intervals for each predictor variable. We also determined the relative variable importance (RVI) for each predictor retained in the top model set, calculated as the sum of Akaike weights across all models containing that variable. RVI is a metric that allows for the ranking of predictor variables, with the most important variable having a maximum possible value of 1.0 (Burnham and Anderson 2002). Assumptions of normality and homogeneity of variance were evaluated graphically for all models retained in the top model set, and in each case appeared to be reasonable fits. Models were fit using the R package *nlme* (Pinheiro et al. 2017), and model selection was performed using the package *MuMIn* (Bartoń 2016).

2.4 Results

2.4.1 Structural complexity metrics

Our models indicated that reef structural complexity was determined by a combination of local human disturbance, heat stress, and the densities of branching and massive corals.

However, the strongest predictors varied between surface rugosity, terrain ruggedness, and absolute curvature, and no predictor consistently explained 3D reef structural complexity across all three metrics. While the interaction between heat stress and local human disturbance appeared in the top model sets for both surface rugosity and terrain ruggedness, the effect of this predictor was fairly weak (maximum relative variable importance of 0.43; Table 2.1), suggesting that local stressors do not strongly influence patterns of structural change on coral reefs following a heat stress event.

Reef surface rugosity was heavily influenced by both local human disturbance and heat stress. Disturbance was the strongest predictor, with a relative variable importance of 0.94 across all models (Table 2.1). Surface rugosity was highest at sites with low local human disturbance and declined as disturbance increased (Fig. 2.3b). Rugosity was also negatively impacted by heat stress (Fig. 2.4a). All 26 PPQs experienced declines in surface rugosity following the mass coral bleaching and mortality event, with mean values of rugosity across all sites declining from 2.189 ± 0.452 to 1.730 ± 0.268 (mean ± standard deviation [SD], Fig. 2.3a). Massive and branching corals positively influenced reef rugosity, although morphologies had less influence than either disturbance or heat stress (Table 2.1, Fig. 2.4a).

Terrain ruggedness was predicted by local human disturbance, the densities of both branching and massive corals, and heat stress, all of which had a relative variable importance ≥ 0.90 (Table 2.1). Like surface rugosity, ruggedness was highest at low disturbance sites and declined as disturbance increased (Fig. 2.3d). Ruggedness was also positively related to the densities of branching and massive corals (Fig. 2.4b). Although slightly weaker than the effect of local disturbance, heat stress still had a negative effect on terrain ruggedness (Fig. 2.4b). As with rugosity, all 26 PPQs showed declines in terrain ruggedness one year after the mass coral bleaching event, from a mean value of 0.081 ± 0.021 in 2015 to 0.053 ± 0.013 in 2017 (Fig. 2.3c).

Massive coral density was the only important predictor of absolute curvature, having a relative variable importance of 0.84 across all models (Table 2.1). Curvature was higher in PPQs with greater densities of massive corals (Fig. 2.4c). Unlike terrain ruggedness and surface rugosity, which peaked under low levels of disturbance, curvature appeared to be slightly higher at intermediate levels of human disturbance (Fig. 2.3f). Following the heat stress event, only 15 out of 26 PPQs suffered declines in absolute curvature, with the remaining 11 PPQs experiencing increases in curvature. As such, absolute curvature values remained relatively stable (15.07 ± 8.35 prior to the heat stress event vs. 13.32 ± 14.83 afterward; Fig. 2.3e).

2.4.2 Habitat volume

Habitat volume declined in 19 out of 26 PPQs following the heat stress event, with sites at low and high levels of local human disturbance suffering a greater loss in habitat volume than those at medium disturbance (Fig. 2.5). The PPQ experiencing the greatest decline in habitat volume (a net loss of 0.990 m^3 of reef substrate) was located at one of the low disturbance sites (Fig. 2.6). All PPQs exhibited areas of both loss (red) and gain (blue) of habitat volume through time. However, on average, individual PPQs suffered a net loss in habitat volume of 0.204 ± 0.283 m^3 of substrate within one year of the severe heat stress event.

2.5 Discussion

Given the importance of 3D structural complexity in mediating the responses of reefs to disturbances such as coral bleaching (Graham et al. 2015), understanding the drivers of reef complexity will be critical for the preservation of reefs under future scenarios of climate change.

Here, we examined three different metrics of coral reef structural complexity (surface rugosity, terrain ruggedness, and absolute curvature), and found that declines in both rugosity and terrain ruggedness were detectable only a year after the 2015-2016 El Niño and mass coral bleaching event, with some PPQs losing close to 1 m^3 of reef substrate (Figs. 2.3-2.5). The declines in surface rugosity that we observed corroborate the findings of Burns et al. (2016) and Couch et al. (2017), who used SfM techniques to document changes in reef complexity on a smaller number of plots within one year of severe bleaching events in the Hawaiian Islands. Conversely, our results suggest that curvature was not substantially affected by the heat stress event, which is also consistent with the findings of Burns et al. (2016). Additionally, we provide what is, to the best of our knowledge, the first evidence that terrain ruggedness is negatively impacted by heat stress in coral reef ecosystems. Although we did not find strong evidence for an interaction between heat stress and local human disturbance, we did observe a decrease in variance around the mean values of surface rugosity and terrain ruggedness from before to after the heat stress event. This suggests that the declines in reef structure measured here are leading to a homogenization of structural complexity values, with sites across the human disturbance gradient becoming increasingly similar in their levels of structural complexity.

Despite the influence of baseline levels of structural complexity on reef resilience and recovery capacity (Graham et al. 2015), few studies to date have examined the effects of local anthropogenic stressors on 3D reef structure. Our results suggest that 3D reef complexity declines with increasing levels of local human disturbance. Reefs exposed to intermediate to high levels of local disturbance due to stressors such as fishing, pollution, and coastal development had substantially lower levels of structural complexity compared to reefs with very little local human disturbance. However, because our human disturbance metric is based on a combination of fishing pressure and proximity to local villages (which may serve as a proxy for stressors such as pollution and sedimentation), we are unable to pinpoint the precise mechanism behind this pattern. Possible drivers include high levels of sedimentation associated with coastal development that limit coral recruitment (Erftemeijer et al. 2012), overfishing of important functional groups such as herbivores that help to maintain the reef in a coral-dominated state (Hughes 1994), and direct physical damage to coral structure by fishing gear (Mangi and Roberts 2006) or boat anchors. However, more research will be needed in the future to tease apart and test the impacts of each of these factors on reef structural complexity.

The abundance of particular coral growth forms (e.g., complex branching corals) is also thought to be an important factor driving levels of 3D structural complexity on coral reefs. Here, we found evidence that levels of reef structural complexity are heavily influenced by the densities of both branching and massive corals (Table 2.1, Fig. 2.4). We found that branching coral density had a positive impact on all three structural complexity metrics, with this effect being particularly strong for terrain ruggedness. While a small number of previous studies have found negative associations between the abundance of branching corals and structural complexity (e.g., Darling et al. 2017), quantification of reef complexity in these studies was done using visual assessments, which may not be suitable for capturing the fine-scale structure provided by many branching corals. Massive coral density was also positively related to all three structural complexity metrics, with the strongest effects for terrain ruggedness and curvature. This strong influence of massive coral density on reef structural complexity may seem counterintuitive, given the domed structure of many massive coral genera. However, the massive coral assemblage on Kiritimati includes corals with a variety of finer-scale morphologies that may contribute to increased structural complexity. For example, certain submassive coral species such as *Favites pentagona* and *Goniastrea stelligera* can take on columnar forms, while *Pavona duerdeni* may produce ridge-like structures. The contribution of massive corals to measures of reef complexity may also depend both on the scale at which complexity is measured and the particular metrics that are quantified. For example, massive corals, with their rounded surfaces, may achieve higher values for metrics based on vector dispersion (e.g., terrain ruggedness) or changes in slope (e.g., curvature) compared to plating corals, which have large planar surfaces. These predictions reflect the findings of previous research on reef structure suggesting that complexity is higher for large massive and branching coral colonies than for plating colonies (Burns et al. 2015b; Figueira et al. 2015).

The lack of a relationship between plating coral density and reef structural complexity is nevertheless surprising, given the recognized role of tabular corals as “keystone structures” on coral reefs (Kerry and Bellwood 2015) and the high surface-area-to-volume ratio of these species, which would be expected to contribute to high levels of surface rugosity. However, our results may be an artifact of the type of 3D model used in our analysis. While digital elevation models (DEMs) are commonly used in photogrammetry to represent 3D surfaces, including in other coral reef studies (e.g., Burns et al. 2015a, 2015b, 2016; Couch et al. 2017), DEMs are projected from one planar angle and thus not truly three-dimensional, since they cannot model multiple z points at a single (x,y) coordinate (Kemp 2008). Given that the structural function of plating corals relies largely on the existence of sheltered spaces beneath the coral plates (Goatley and Bellwood 2011), analyzing reef structure from 2.5D DEM projections may underestimate the complexity of foliose and tabulate coral morphologies compared to other coral growth forms (Figueira et al. 2015). These effects may be especially severe in areas where plating corals form complex, multi-tiered structures. As such, we suggest that future studies work towards developing methods to extract complexity data from true 3D digital surface models.

The strong dependence of 3D reef structural complexity on the presence of branching corals has implications for the maintenance of reef structure under future climate change. Branching corals, such as acroporids and pocilloporids, are highly susceptible to heat stress and bleaching-associated mortality (Marshall and Baird 2000) as well as physical damage from storms (Harmelin-Vivien 1994). Based on our PPQ benthic data, the density of live branching corals on Kiritimati declined by 95% following the mass coral bleaching event. Although many dead branching coral skeletons remain and continue to provide structure to the reef, it is likely that these structures will soon erode, resulting in further declines in reef complexity. While our results, and those of previous studies (Alvarez-Filip et al. 2011), suggest that massive corals may play an important structural role on coral reefs, it remains to be seen how the increased dominance of this coral growth form will affect the ecological functioning of the reefs around Kiritimati. Shifts in coral assemblages from complex reef-building species to smaller, weedy coral species have previously been shown to result in substantial declines in coral reef calcification rates and linear rugosity values (Alvarez-Filip et al. 2013). Continued monitoring of the reef system will be necessary to determine the magnitude of the shift in benthic composition following the mass coral mortality event, and how this change impacts both the physical structure and ecological function of the reef over the long term.

Given the many important ecological processes and ecosystem services facilitated by coral reef structural complexity, the loss of reef structure has negative implications for both marine organisms and human coastal communities. Declines in reef complexity are expected to compromise coral reef fisheries, potentially leading to up to a three-fold decline in fisheries productivity in severe cases (Rogers et al. 2014). This problem is of particular concern for local communities on small, isolated islands such as Kiritimati, where the majority of people depend on reef fisheries for income and subsistence and opportunities for alternative livelihoods are scarce (Burke et al. 2011; Watson et al. 2016). A key question for future research will be to determine how levels of structural decline similar to those observed here, as well as those occurring in subsequent years with further degradation of the reef substrate, impact the structure of reef fish assemblages and populations of other ecologically and socioeconomically-important reef organisms.

Prior to the advent of SfM photogrammetry techniques, studies documenting bleaching-induced changes in reef complexity using conventional methods usually took place several years after the end of a severe disturbance event, and documented the extreme and highly-visible collapse of reef structure (e.g., Sheppard et al. 2002; Graham et al. 2006, 2009). While it is vital to understand the effects of severe levels of reef degradation on coral reef communities, studying multiple points along the trajectory of reef degradation will allow us to gain a better understanding of the rates and impacts of fine-scale structural change, and detect threshold levels of structural complexity below which the ecological functioning of the reef is impaired. As such, it is vital that coral reef monitoring programs incorporate modern methods for quantifying structural complexity into their standard reef monitoring protocols. Photogrammetry techniques provide a time- and cost-effective approach that can be used to this end to objectively quantify multiple measures of fine-scale structural complexity on coral reefs.

Coral reefs are currently being impacted at multiple spatial scales by a suite of natural and anthropogenic disturbances. In this study we have shown that levels of 3D structural complexity, a vital component of healthy coral reef ecosystems, are impacted by both local and global stressors. Our finding that local human disturbance is a strong predictor of structural complexity suggests that chronic local stressors may have indirect impacts on reef recovery potential through their influence on reef structure. As such, management should focus on mitigating local stressors in order to maintain reefs at ecologically functional levels of structural complexity. However, action at the local level will also need to be accompanied by policy changes at the global scale. Recent research suggests that limiting global warming to 2°C, the upper limit of the recent Paris Agreement, will still result in annual severe bleaching on the majority of coral reefs within the next few decades (van Hooidonk et al. 2016). Our results provide further evidence for the negative effects of ocean warming on coral reef ecosystems, demonstrating the need for drastic reductions in greenhouse gas emissions and support for the development of sustainable low-carbon infrastructure.

Table 2.1. Top models describing three distinct components of coral reef structural complexity: surface rugosity (a), terrain ruggedness (b), and absolute curvature (c). Plus signs indicate the presence of variables within each model in the top model set.

Rank	**Heat**	**Dist.**	**Branching**	**Plating**	**Massive**	**Heat*Dist.**	***df***	**AIC$_c$**	**ΔAIC$_c$**	***w***	**R^2**
a) Surface rugosity											
1	+	+			+		8	14.89	0.00	0.17	0.54
2	+	+	+		+		9	15.11	0.22	0.16	0.59
3	+	+			+	+	10	16.05	1.16	0.10	0.63
4	+	+					7	16.13	1.24	0.09	0.50
5	+	+	+				8	16.27	1.38	0.09	0.55
6	+	+	+		+	+	11	16.82	1.93	0.07	0.65
7		+	+		+		8	17.16	2.27	0.06	0.57
8	+	+		+	+		9	17.32	2.42	0.05	0.56
9	+	+	+	+	+		10	18.19	3.29	0.03	0.59
10	+	+		+			8	18.66	3.76	0.03	0.51
RVI	**0.92**	**0.94**	0.49	0.20	0.72	0.22					
b) Terrain ruggedness											
1	+	+	+		+		8	-304.36	0.00	0.32	0.80
2	+	+	+		+	+	10	-303.18	1.18	0.18	0.83
3	+	+	+	+	+		9	-303.11	1.24	0.17	0.80
4	+	+	+	+	+	+	11	-301.32	3.04	0.07	0.83
5	+	+	+				7	-301.08	3.27	0.06	0.76
6		+	+	+	+		8	-300.69	3.67	0.05	0.77
RVI	**0.92**	**0.96**	**0.95**	0.36	**0.90**	0.28					
c) Absolute curvature											
1					+		5	397.40	0.00	0.27	0.23
2			+		+		6	398.94	1.54	0.13	0.27
3				+	+		6	399.34	1.94	0.10	0.25
4	+				+		6	399.73	2.32	0.09	0.22
5		+					6	400.32	2.92	0.06	0.26
6		+			+		7	400.55	3.14	0.06	0.28
7	+		+		+		7	400.66	3.25	0.05	0.25
8	+			+	+		7	401.39	3.99	0.04	0.24
RVI	0.25	0.25	0.30	0.24	**0.84**	0.00					

Heat = heat stress; Dist. = local human disturbance; Branching = branching coral density; Plating = plating coral density; Massive = massive coral density; Heat*Dist. = interaction between heat stress and local human disturbance; *df* = degrees of freedom; AIC_c = AIC corrected for small sample sizes; ΔAIC_c = difference from the lowest AIC_c value, all models within ΔAIC_c of 4 are shown; w = model weight; R^2 = conditional R^2 (proportion of variance explained by both fixed and random effects); RVI = relative variable importance.

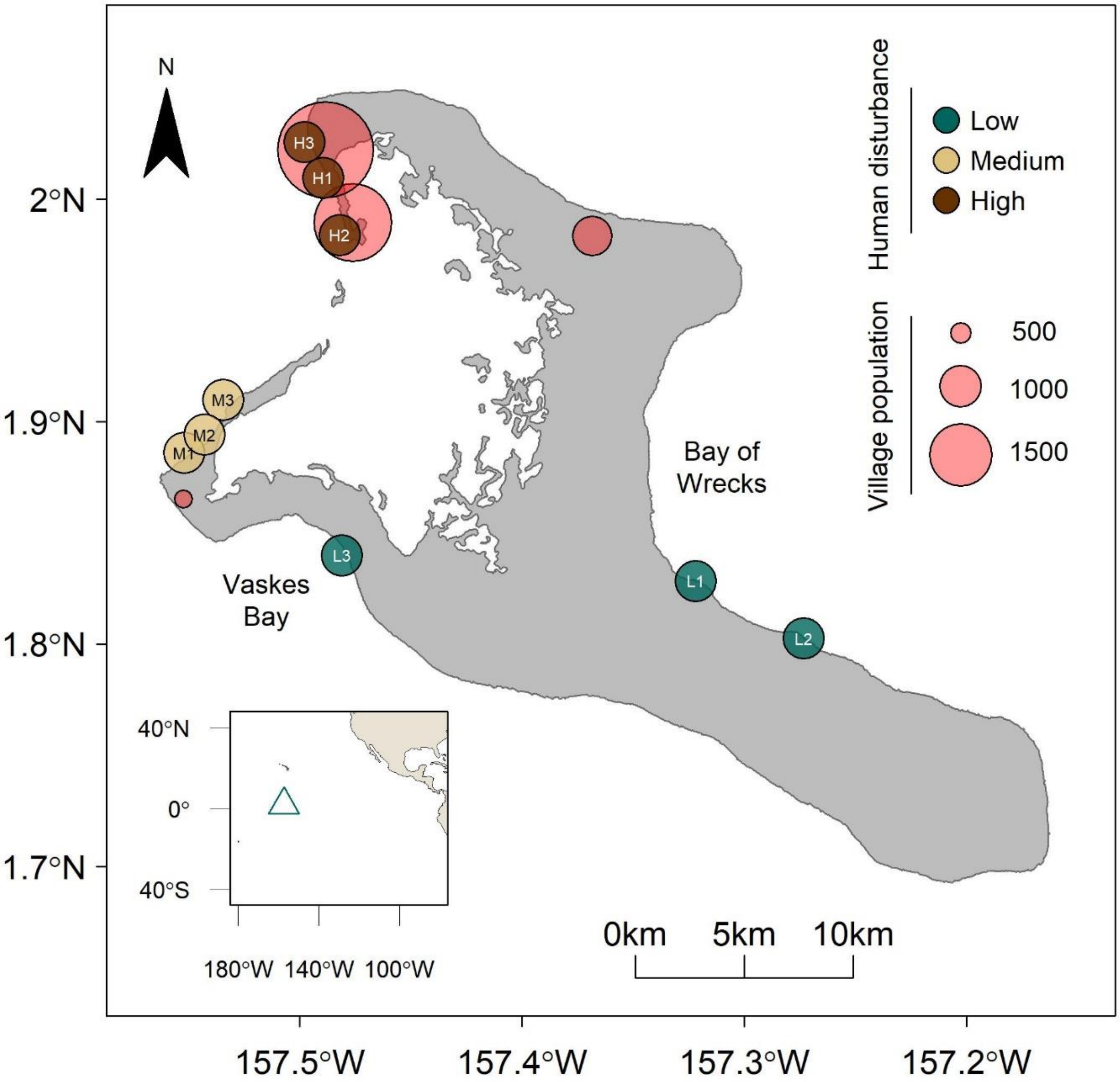

Figure 2.1. Map of forereef study sites and villages on Kiritimati, Republic of Kiribati. Sites are divided into three levels of local human disturbance, and villages (red circles) are scaled to human population size. Inset shows Kiritimati's location in the central equatorial Pacific Ocean.

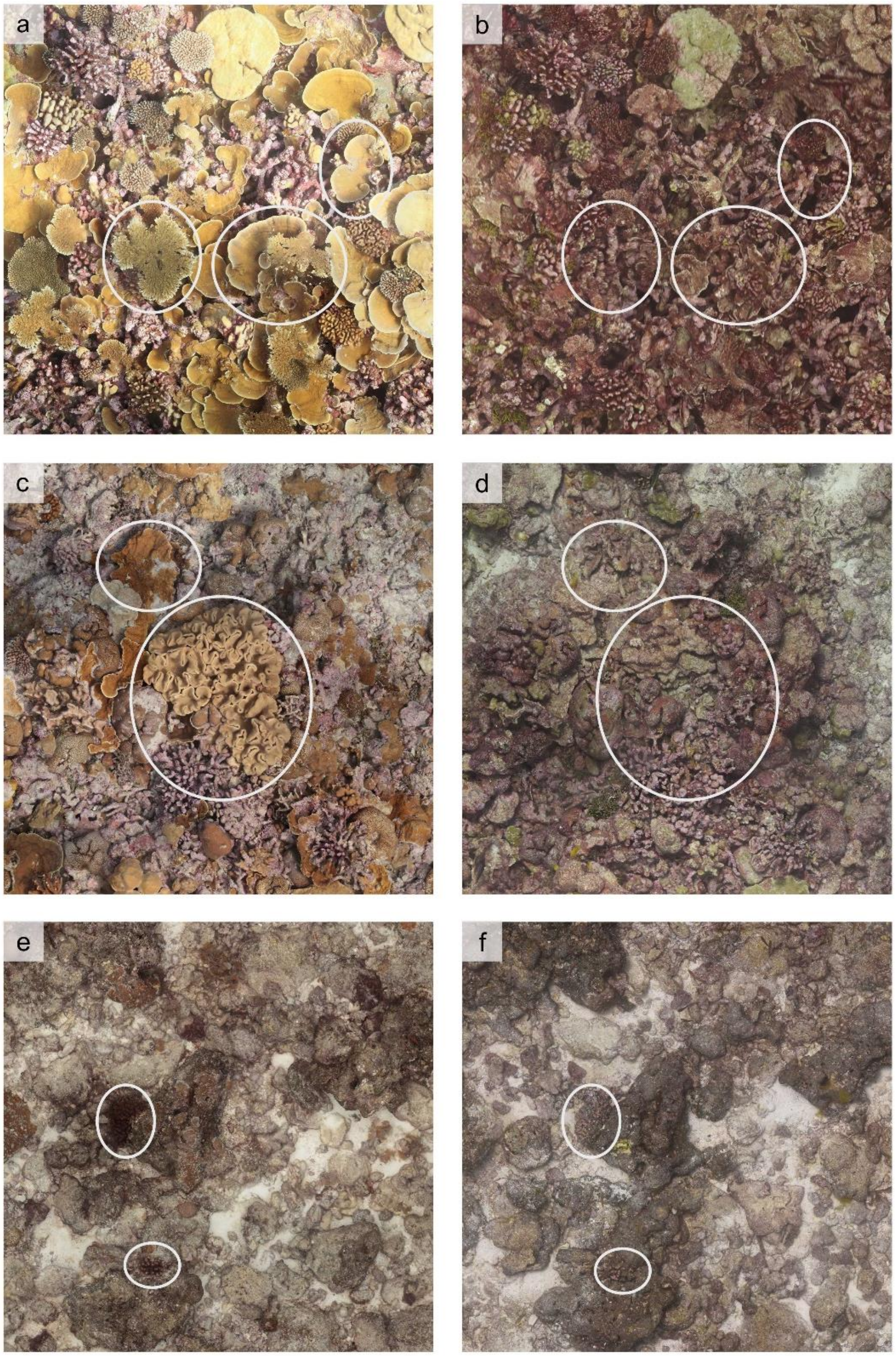

Figure 2.2. Photos of three permanent photoquadrats (PPQs) on Kiritimati, one from each of the low (a,b), medium (c,d), and high (e,f) human disturbance levels. Photos show the reef before (left) and one year after (right) the 2015-2016 El Niño and mass coral mortality event and represent approximately 2 m x 2 m sections of each PPQ. The exact same area of each PPQ is shown, with ellipses highlighting examples of visible changes in reef structure over time.

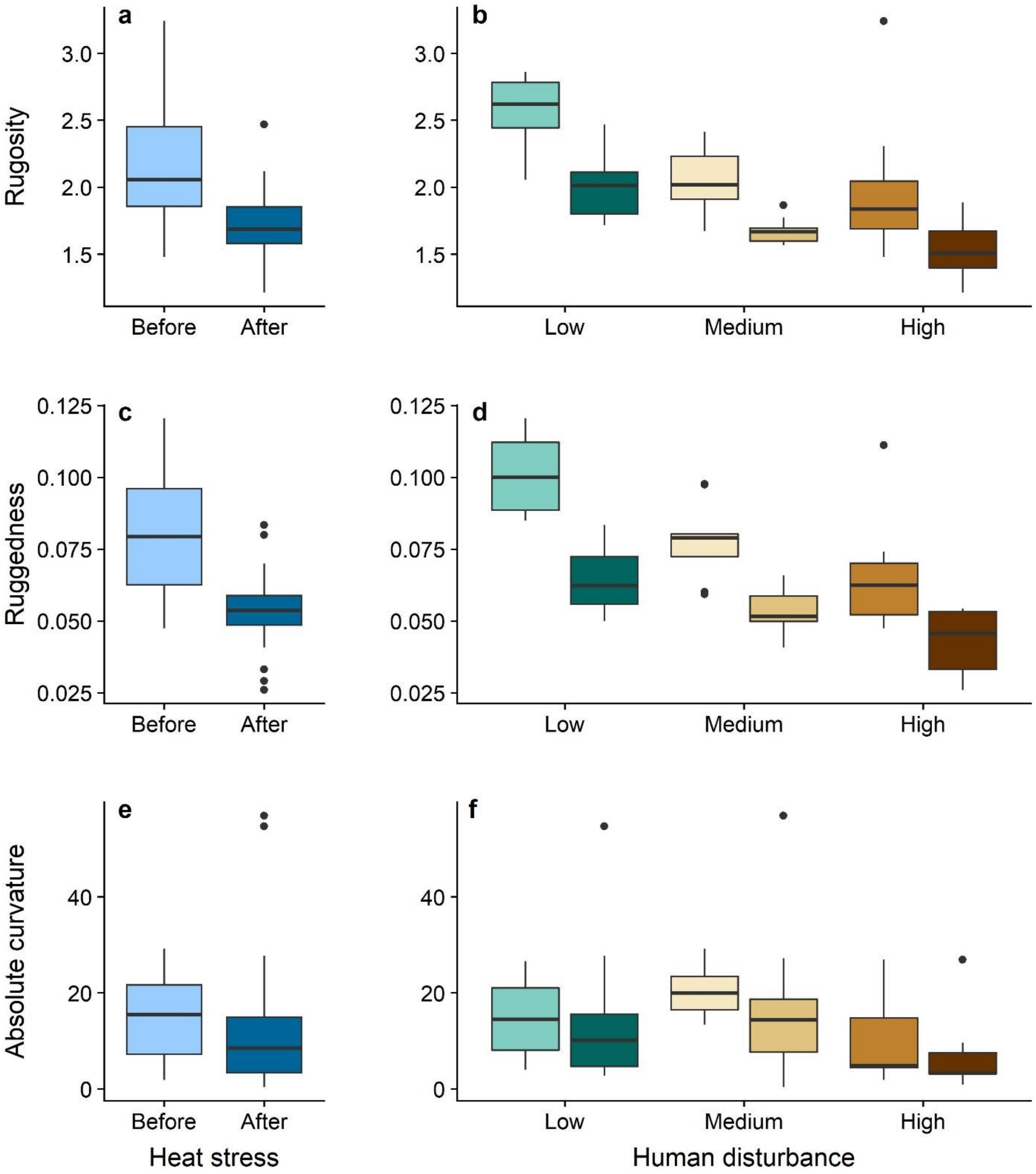

Figure 2.3. Levels of coral reef surface rugosity (a,b), terrain ruggedness (c,d), and absolute curvature (e,f) before and after the 2015-2016 heat stress event. Plots represent changes in each metric on the atoll overall (left) and across the human disturbance gradient (right). For each disturbance level, lighter boxes indicate 2015 values and darker boxes indicate 2017 values.

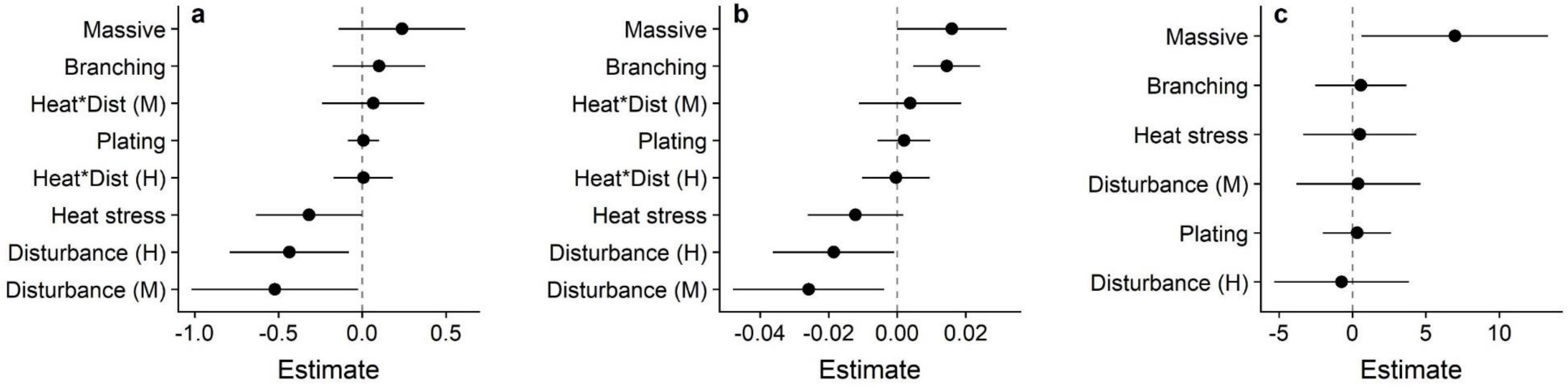

Figure 2.4. Multi-model-averaged parameter estimates and 95% confidence intervals for surface rugosity (a), terrain ruggedness (b), and absolute curvature (c). Heat*Dist refers to the interaction between heat stress and local human disturbance (M = medium disturbance, H = high disturbance).

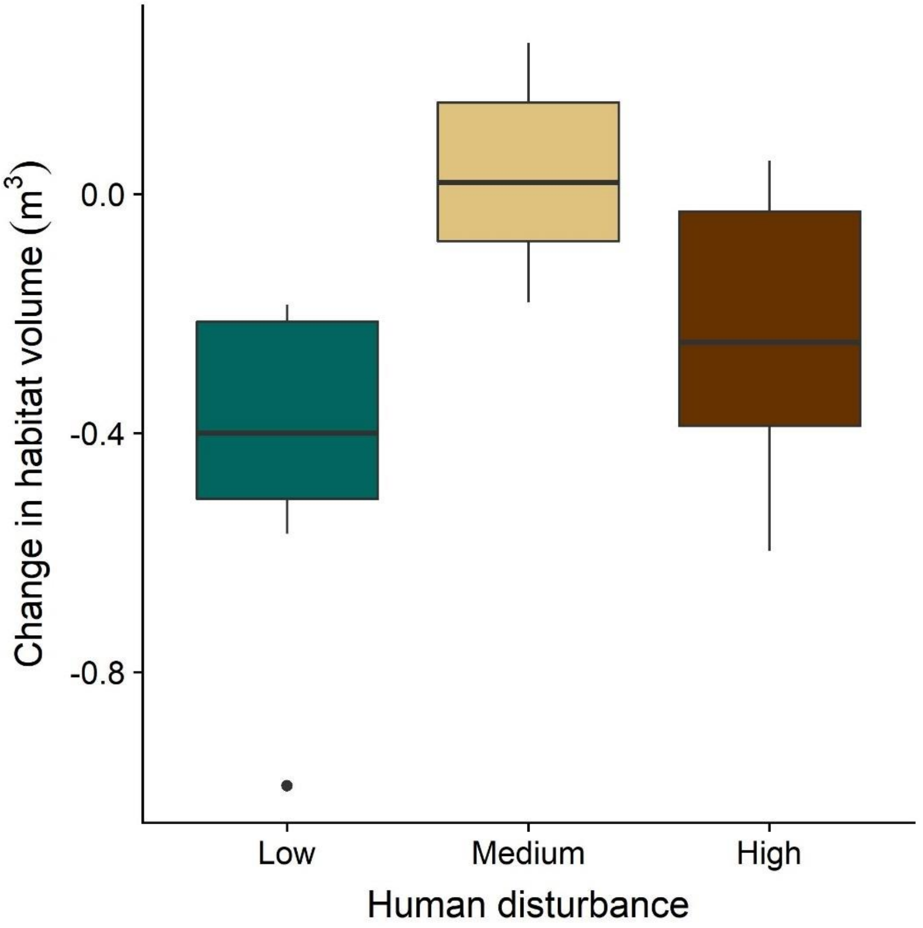

Figure 2.5. Net change in habitat volume (m^3) within individual 4 m x 4 m PPQs across the local human disturbance gradient. Changes occurred over an approximately two-year period (May 2015 to July 2017), during and after the 2015-2016 heat stress event.

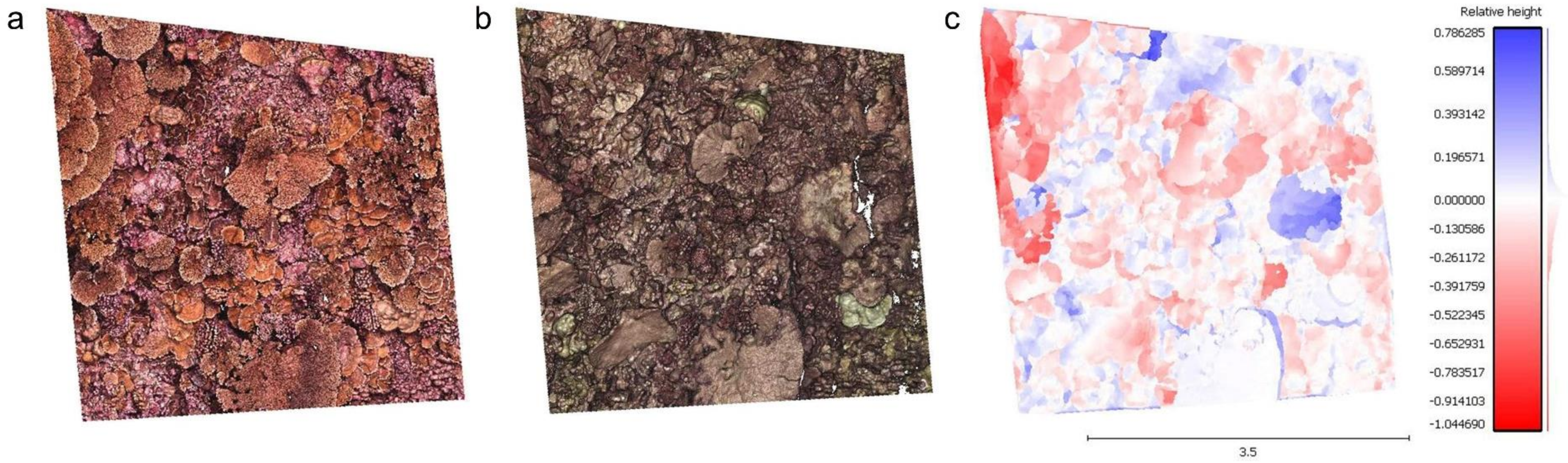

Figure 2.6. Comparison of 3D point clouds from before (a) and after (b) the 2015-2016 El Niño for the PPQ experiencing the greatest decline in habitat volume. The CloudCompare 2.5D volume calculation tool calculates the difference in height (m) between each point in the 'before' and 'after' point clouds, and depicts the loss (red) and gain (blue) of reef substrate over time (c).

Chapter 3 – Interacting effects of heat stress and local human disturbance on tropical coral reef fish assemblages

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3.1 Abstract

Heat stress and associated mass bleaching events are impacting coral reef ecosystems at multiple scales of biological organization, threatening species at all levels of the coral reef food web. While much focus has been placed on the effects of heat stress on scleractinian corals, consequences for vertebrates such as reef fish are less well understood. In this study, we quantify the immediate impacts of a severe pulse heat stress event on reef fish assemblages from Kiritimati (Republic of Kiribati) in the central equatorial Pacific Ocean, and examine the influence of local human disturbance on subsequent short-term fish assemblage recovery. Underwater visual census (UVC) surveys were conducted before, during, and after the 2015-2016 El Niño and mass coral bleaching event, at nine sites across Kiritimati's local human disturbance gradient. We found that total reef fish abundance, biomass, and species richness were all lower while subjected to heat stress, but had returned to – or exceeded – pre-disturbance levels two years later. However, the abundance of corallivores declined significantly in the two years following severe coral loss, and reefs exposed to higher levels of local human disturbance showed impaired recovery following the heat stress. We also document a significant shift in reef fish assemblage structure through time, driven mainly by decreases in the abundance of planktivorous species. These findings enhance understanding of the projected impacts of climate change-associated temperature increases on tropical reef fishes, and highlight the interacting effects of local and global stressors on this vital component of coral reef ecosystems.

3.2 Introduction

Severe heat stress and mass coral bleaching have moved to the forefront of scientific research on coral reefs over the past two decades, and are now recognized as the most prominent threats facing tropical coral reefs this century (Hoegh-Guldberg 2011; Hughes et al. 2018). El Niño-associated heat stress has precipitated several mass coral bleaching events over the past 30 years (Heron et al. 2016), leading to widespread bleaching and mass coral mortality throughout the Pacific, Indian, and Atlantic Oceans (Wilkinson 1998; Eakin et al. 2010; Hughes et al. 2017). Most recently, coral reefs around the world were impacted by the 2015-2016 El Niño, the most extreme warming event to date (Claar et al. 2018). Beyond effects on the corals themselves, changes in benthic composition resulting from such events have several implications for reef-associated fishes. Loss of live coral has been shown to trigger short-term declines in local reef fish abundance and diversity (Wilson et al. 2006; Pratchett et al. 2011), often characterized by decreases in corallivores and small-bodied, coral-dwelling species (Pratchett et al. 2006; Wilson et al. 2006). Such changes in benthic structure may also lead to long-term shifts in the structure of reef fish assemblages (Bellwood et al. 2006a, 2012a; Graham et al. 2015). These indirect effects of ocean warming on reef fish, mediated by changes in benthic composition, have been well-documented. However, there has been very little research to date examining the direct effects of ocean warming, and pulse heat stress events in particular, on tropical reef fish assemblages (but see López-Pérez et al. 2016).

Climate change is metered out in the ocean through both gradual temperature increases and short-lived temperature anomalies, such as El Niño. Pulse heat stress events occurring in conjunction with extreme El Niños may serve as ‘natural experiments,’ allowing us to examine the direct effects of heat stress on reef fish assemblages and gain insight into the potential long-term effects of climate change on these organisms. The projected impacts of climate change on fish distribution and abundance (Cheung et al. 2009, 2010) are primarily expected to manifest through effects on fish physiology – specifically, through the oxygen limitation of thermal tolerance (Pörtner and Knust 2007; Farrell 2016). A fish’s capacity to perform aerobic activity (i.e., its aerobic scope) is highly temperature-dependent, as increases in temperature lead to an increase in oxygen demand within bodily tissues (Fry 1947). A fish’s ability to tolerate thermal extremes therefore hinges on its capacity to supply oxygen to the tissues to meet this demand – a capacity that is maximized within its optimal thermal window. Beyond the upper limit of this window (at the upper pejus temperature), the capacity for oxygen supply is reduced and the fish’s aerobic scope declines (Pörtner and Knust 2007; Farrell 2016), leading to hypoxaemia (Pörtner and Farrell 2008). In addition to increasing oxygen demand, ocean warming may also enhance oxygen limitation by decreasing oxygen solubility within the water, leading to the emergence of synergistic stressors such as hypoxia that can further narrow thermal tolerance windows (Pörtner and Farrell 2008). The resulting temperature-induced declines in aerobic performance impact higher-level functions such as survival, growth and reproduction, influencing the abundance of marine species (Pörtner and Knust 2007) and making the internal effects of thermal stress visible at the population level.

The effects of future ocean warming on fish physiology are predicted to be particularly severe for tropical reef fishes (Comte and Olden 2017). Having evolved in relatively constant, aseasonal environments, tropical ectotherms such as reef fish have narrower thermal tolerances than temperate organisms (Tewksbury et al. 2008; Comte and Olden 2017), meaning there is a smaller range of temperatures over which they are able to perform aerobic activity. Several species of reef fish already appear to be living close to – or even above – their thermal optima (Rummer et al. 2014), suggesting that even small increases in sea surface temperatures (SSTs) may result in decreased performance. For example, increases in water temperature of 2-3°C above present-day values have already been shown to have direct negative impacts on the growth and reproduction of the coral reef damselfish *Acanthochromis polyacanthus* (Munday et al. 2008b; Donelson et al. 2010). To avoid supra-optimal temperatures, fish may seek out cooler waters during periods of warming, resulting in changes in fish distribution and abundance. This has previously been documented in pelagic fish communities of the eastern tropical Pacific (Barber and Chavez 1983; Ñiquen and Bouchon 2004), and it is suspected that mobile reef fish species also seek out more favourable habitat to escape the effects of severe disturbances (Wilson et al. 2006).

In addition to direct, temperature-driven physiological effects, fish may also be affected indirectly by oceanographic changes that occur during El Niño. Changes in water temperature, stratification, and circulation during El Niño have been shown to alter patterns of primary productivity in several regions of the Pacific Ocean, including the eastern equatorial (Barber et al. 1996), central equatorial (Heenan et al. 2018), and South Pacific (Lo-Yat et al. 2011). These changes have been associated with declines in both phytoplankton (Barber and Chavez 1983; Avaria and Muñoz 1987; Strutton and Chavez 2000) and zooplankton populations (Carrasco and Santander 1987). Declines in planktonic food sources may further exacerbate the effects of elevated SSTs on reef fish physiology (Donelson et al. 2010). Changes in local primary productivity and plankton assemblages have largely been recorded in the eastern Pacific, as a result of altered oceanographic conditions (i.e., upwelling). A small number of studies conducted in the central Pacific (e.g., Strutton and Chavez 2000; Heenan et al. 2018) suggest that tropical reef fish populations may be similarly affected, although it remains to be seen whether changes in productivity in this region result primarily from oceanographic or physiological influences.

Understanding the effects of pulse heat stress events on reef fish assemblages has both social and ecological implications. Fish comprise a large proportion of the consumer biomass on coral reefs, and play a number of important ecological roles. Herbivores exert pressure on competitive macroalgae, helping to maintain the reef in a coral-dominated state (Burkepile and Hay 2008) and facilitating coral recruitment (Mumby et al. 2007). Mobile fish species also play key roles in energy transfer and nutrient provisioning to coral reefs, helping these systems to thrive in nutrient-poor waters (Meyer et al. 1983; Allgeier et al. 2014, 2017). In addition, reef fish serve as an important source of food and income for coastal communities in many developing countries. Worldwide, coral reef fisheries are valued at over US $6.8 billion annually, and are an invaluable resource for many small island states in the Pacific and Caribbean (Burke et al. 2011). Studying the impacts of present-day pulse heat stress events on the abundance and diversity of reef fish could serve as a window into the future, foreshadowing the potential long-term consequences of climate change for both coral reef ecosystems and tropical coastal communities. Knowledge of the short-term impacts of these events will also be highly relevant over the next few decades, in light of projected increases in marine heat stress. Marine heat waves have increased in frequency, duration, extent, and intensity over the past several decades (Frölicher et al. 2018; Oliver et al. 2018) and will continue to do so under future global warming. To inform reef fish conservation and management under these changing conditions, it is increasingly important that we understand the impacts of pulse heat stress events on reef fish populations.

The 2015-2016 El Niño event impacted coral reefs worldwide, and provides a valuable opportunity to study the effects of severe heat stress on reef fish populations. Reefs around Kiritimati (Republic of Kiribati) in the central Pacific Ocean were subjected to unprecedented levels of heat stress during the 2015-2016 El Niño, with SST anomalies exceeding 1°C above Kiritimati's historical maximum monthly temperature for nine months (Fig. 3.1). Here, we use underwater surveys conducted across Kiritimati's gradient of local human disturbance to examine the effects of a severe heat stress event on the abundance, biomass, species richness, and assemblage structure of tropical reef fish assemblages. To the best of our knowledge, this study is one of the first to examine the direct effects of pulse heat stress events on tropical coral reef fishes. Our specific objectives were to 1) assess changes in reef fish assemblages both during the heat stress itself (i.e., prior to major changes in coral cover) and after the mass coral bleaching event, and 2) investigate the effect of local human disturbance on the response of reef fish assemblages to the heat stress event. We hypothesized that anomalously high water temperatures would negatively impact fish species across the atoll resulting in declines in total fish abundance, biomass, and species richness, potentially due to the movement of fish to more preferred thermal environments (e.g., deeper, cooler waters). However, we also expected that some species and functional groups would respond more strongly to the elevated water temperatures, leading to shifts in reef fish assemblage structure. Moreover, we predicted that severe declines in coral cover would be followed by decreases in corallivore abundance and concomitant increases in herbivore abundance, due to changes in their preferred food sources. Finally, we hypothesized that reef fish assemblages at all levels of human disturbance would be negatively impacted by the heat stress event, but those subjected to minimal disturbance would show the greatest recovery following the heat stress.

3.3 Methods

3.3.1 Study site and design

We surveyed reef fish assemblages before, during, and after the 2015-2016 El Niño at nine forereef sites around Kiritimati (Christmas Island, Republic of Kiribati). Located in the central equatorial Pacific Ocean (01°52’N 157°24’W, Fig. 3.2), Kiritimati is the world’s largest coral atoll by land mass. Kiritimati supports a population of approximately 6500 people (Kiribati National Statistics Office 2016), the vast majority of which are highly dependent on reef resources for income and subsistence given the atoll’s geographic isolation and lack of alternate livelihoods (Burke et al. 2011; Watson et al. 2016). Reef fish in particular are a vital resource, with over 95% of households on Kiritimati actively engaged in fishing activities (Watson et al. 2016). Concentration of the local population on the northwest side of the island has resulted in a spatial gradient of local human disturbance across the surrounding reefs. Following this gradient, each survey site was assigned to one of three human disturbance levels (low, medium, high) based on a combination of fishing pressure (Watson et al. 2016) and proximity to local villages (Baum et al., unpublished data). Surveys were conducted in July and August 2013 (two years prior to the 2015-2016 El Niño), July 2015 (two months into the warming event), and July 2017 (one year after the end of the El Niño). Each site was surveyed one to two times per survey year, with the majority of sites being surveyed twice in 2013 and once in 2017 (Table B3.1).

3.3.2 Reef fish assemblages

Underwater visual census (UVC) surveys of the reef fish assemblages were conducted using standard belt transect methods, following Sandin et al. (2008). At each site, reef fish size (to the nearest cm), abundance, and species identification were recorded by a pair of trained scientific divers swimming in tandem along a belt transect. Three 25 m transects laid along the 10-12 m isobath were surveyed each dive, with adjacent transects separated by 10 m. For each transect, divers first counted fishes ≥ 20 cm total length in an 8 m wide strip while the transect was being laid, then counted fishes < 20 cm total length in a 4 m wide strip while swimming in the reverse direction. Following this, divers also conducted presence/absence surveys by swimming in a zig-zag pattern in a 30 m wide strip along the transect and noting any additional species that were not observed during the UVCs. All surveys took place during daytime, between 0800 and 1800 hrs. Surveys were conducted by a total of four divers, with the same two individuals conducting all surveys within a given year. Scientific divers were highly experienced, and also spent one to two days on Kiritimati prior to commencing the surveys re-familiarizing themselves with the atoll's fish species and underwater size estimation. Size estimation accuracy was checked using PVC objects of known length (Bell et al. 1985), until divers could consistently estimate fish lengths to the nearest 2 cm.

Prior to analysis, we standardized the sampling area for each UVC by doubling the number of small fishes recorded on each transect. Length estimates for each fish were converted to body mass (grams) using published species-specific length-weight relationships (Kulbicki et al. 2005). In cases where individuals could not be identified to species level, or higher-level length-weight relationships were not available, we calculated mean length-weight parameters based on species from the same genus or family. To minimize inflation of biomass estimates we also excluded all sharks and jacks from our analyses (MacNeil et al. 2015; Williams et al. 2015b; Robinson et al. 2017), as the abundance of these highly-mobile species may be over-estimated in non-instantaneous UVCs (Ward-Paige et al. 2010).

To assess changes in reef fish assemblage structure, we assigned each fish species to one of eight trophic groups (corallivore [C], detritivore [D], generalist carnivore [GC], herbivore [H], invertivore [In], omnivore [Om], piscivore [Pi], and planktivore [Pl]) based on their dietary preferences (Yeager et al. 2017a). For each site we then calculated total fish abundance, total fish biomass, and species richness, and the abundance of each trophic group. Species richness was defined as the total number of unique species observed at each site.

3.3.3 Statistical analyses

All statistical analyses were conducted using R version 3.3.1 (R Core Team 2016). To examine the combined effects of local and global disturbances on reef fish abundance, biomass, and species richness, we fit generalized linear mixed-effects models (GLMMs) for each fish metric using the packages *glmmADMB* (Fournier et al. 2012; Skaug et al. 2016) and *lme4* (Bates et al. 2015). In all models, year and human disturbance were included as fixed effects, as well as their interaction (to account for effects across years potentially differing by disturbance level). We also included net primary productivity (Table B3.2) as a fixed effect, using a filtered remotely-sensed data product extracted from the SESYNC Marine Socio-Environmental Covariates data set (https://shiny.sesync.org/apps/msec/; Yeager et al. 2017b). This data product is calculated over a 2.5 arcmin grid based on data from NOAA CoastWatch, which models net primary productivity using satellite-derived measures of photosynthetically-available radiation, SST, and chlorophyll-*a* concentrations. We also included site and observer nested within year as random effects in all models, the latter to account for variation among observers as well as differences within the same observer between years. Prior to 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 and Su 2018).

We modelled total fish abundance and the abundance of each trophic group using a negative binomial distribution, which is appropriate for overdispersed data; total fish biomass using a Gamma distribution, which is appropriate for positive continuous data; and species richness using a Poisson distribution, which is appropriate for count data that is not overdispersed (McCullagh and Nelder 1989; Zuur et al. 2009). All models were fit with a ‘log’ link function. For each trophic group that contained more than 5% zeroes, we also fit zero-inflated negative binomial models and compared these to the non-zero-inflated models using AIC (Warton 2005). The zero-inflated model was found to provide a better fit only for detritivore abundance, and so was used as the final model for this group.

To examine changes in reef fish assemblage structure, we used multivariate statistical and ordination techniques implemented through the R package *vegan* (Oksanen et al. 2018). First, we performed a multivariate ordination (principal coordinates analysis; PCoA) using the ‘betadisper’ function to visualize differences in reef fish assemblage structure 1) among time points, and 2) across the local human disturbance gradient. Next, to test for significant differences in fish assemblage structure, we conducted permutational multivariate analysis of variance (PERMANOVA) tests with 999 permutations and Bray-Curtis distances using the ‘adonis’ function. Site x species matrices were created for the entire reef fish assemblage and for each individual trophic group using measures of species abundances (rather than biomass). Heat stress, human disturbance, and primary productivity were included as fixed effects in each model, while site was incorporated as a blocking factor using the ‘strata’ term in ‘adonis’. Finally, to determine the species responsible for driving any observed differences in assemblage structure, we used the ‘simper’ (similarity percentages) function to identify influential species both among time points and across the human disturbance gradient.

3.4 Results

3.4.1 Abundance

Total fish abundance, as well as the abundance of each trophic group, was influenced by a combination of the heat stress event, local human disturbance, and net primary productivity (Table 3.1, Fig. 3.3). Total fish abundance was significantly lower while subject to heat stress, relative to conditions before and after the event ($z = -2.09$, $p = 0.036$). Mean fish abundance per site was 2367 ± 342 (mean ± standard error of the mean [SEM]) in 2013, which declined by over 50% to a mean of 1085 ± 124 fish per site in 2015 (Fig. 3.4a). However, total abundance had returned to pre-disturbance levels (1895 ± 156 fish per site) two years later. All eight trophic groups also exhibited declines in abundance during the El Niño, however this pattern was only significant for the detritivores ($z = -2.76$, $p = 0.006$) and planktivores ($z = -2.21$, $p = 0.027$). Following the heat stress-induced mass coral bleaching event, the abundance of corallivores ($z = -6.36$, $p < 0.001$) also declined, whereas the two groups exhibiting significant shifts during the heat stress both returned to pre-disturbance levels.

Total fish abundance also varied across the human disturbance gradient, with significantly lower abundance at the medium disturbance sites ($z = -2.15$, $p = 0.031$). In addition, individual trophic groups exhibited different responses to human disturbance (Table 3.1, Fig. 3.3): corallivore, generalist carnivore, and herbivore abundances were negatively impacted by higher levels of disturbance, while abundances of detritivores and invertivores were significantly greater at highly-disturbed sites. Total fish abundance was also positively associated with levels of primary productivity ($z = 3.57$, $p < 0.001$), as were the abundances of generalist carnivores ($z = 4.87$, $p < 0.001$), herbivores ($z = 4.22$, $p < 0.001$), invertivores ($z = 2.51$, $p = 0.012$), and planktivores ($z = 2.49$, $p = 0.013$).

Finally, local disturbance also interacted with heat stress to influence the response of the reef fish assemblage to the El Niño event (Table 3.1, Fig. 3.3). During the El Niño, total fish abundance was significantly higher at the medium disturbance sites ($z = 2.87$, $p = 0.004$). However, following the heat stress event, total abundance was significantly lower at the high disturbance level ($z = -4.15$, $p < 0.001$). Significant interactions between heat stress and local disturbance were also present for several trophic groups, although the effects varied by group (Table 3.1). For example, corallivore abundance was negatively impacted by high levels of disturbance during the heat stress event (z = -2.69, p = 0.007), but was greater at the high disturbance level in 2017 (z = 2.18, p = 0.029). Conversely, the abundances of detritivores (z = -4.38, $p < 0.001$), invertivores (z = -4.82, $p < 0.001$), and planktivores (z = -4.31, $p < 0.001$) were all significantly lower at the high disturbance level after the El Niño.

3.4.2 Biomass

Total reef fish biomass decreased significantly during the El Niño event (t = -2.66, p = 0.008), from a mean value of 113.1 ± 14.1 g m^{-2} in 2013 to just 48.5 ± 6.2 g m^{-2} in 2015 (Fig. 3.4b). However, overall fish biomass had increased to an average of 139.5 ± 26.5 g m^{-2} two years later, which was significantly higher than pre-disturbance levels (t = 2.73, p = 0.006). Unlike abundance, total reef fish biomass was not significantly impacted by local disturbance or levels of net primary productivity (Table 3.1). However, there was a significant interaction between heat stress and human disturbance following the heat stress event – biomass was significantly lower at the medium (t = -3.10, p = 0.002) and high (t = -2.88, p = 0.004) disturbance levels after the El Niño, compared to low disturbance sites.

3.4.3 Species richness

Total reef fish species richness decreased significantly during the El Niño (Table 3.1), from a mean value of 44 ± 2 species per site in 2013 to 36 ± 2 species per site in 2015 (z = -2.36, p = 0.018; Fig. 3.4c). Nine species from five different trophic groups were not observed at any of the included study sites during the El Niño (Table 3.2): *Ctenochaetus hawaiiensis* [D], *Pseudocheilinus evanidus* [GC], *Acanthurus leucocheilus* [H], *Apogon kallopterus* [In], *Cheilinus undulatus* [In], *Pseudocheilinus tetrataenia* [In], *Chromis weberi* [Pl], *Heteropriacanthus cruentatus* [Pl], and *Pseudanthias pascalus* [Pl]. Of these, the only two species that appear to have returned following the heat stress are *A. leucocheilus* and *C. undulatus*. However, several species also appeared at the beginning of the heat stress that were not observed in 2013 (Table 3.3).

Following the El Niño, reef fish species richness appears to have increased significantly (relative to pre-disturbance levels) to a mean value of 48 ± 2 species per site ($z = 2.16$, $p = 0.031$). While some species seem to have persisted through the heat stress only to disappear by 2017, there were also 13 species that appeared at our study sites only after the end of the heat stress and mass coral bleaching event: *Labrichthys unilineatus* [C], *Bothus pantherinus* [GC], *Gymnothorax thyrsoideus* [GC], *Acanthurus guttatus* [H], *Cirripectes variolosus* [H], *Kyphosus cinerascens* [H], *Scarus festivus* [H], *Canthigaster amboinensis* [Om], *Gnatholepis anjerensis* [Om], *Rhinecanthus rectangulus* [Om], *Acanthurus albipectoralis* [Pl], *Eviota albolineata* [Pl], and *Myripristis kuntee* [Pl].

Similar to biomass, reef fish species richness was not strongly impacted by local human disturbance. However, there was a significant positive relationship between species richness and levels of net primary productivity ($z = 2.04$, $p = 0.041$). Species richness was also influenced by the interaction between heat stress and local human disturbance; the mean number of species at each site was significantly lower at high human disturbance following the El Niño ($z = -2.88$, $p = 0.004$), compared to both the low and medium disturbance levels.

3.4.4 Assemblage structure

Reef fish assemblage structure was influenced by a combination of heat stress, local human disturbance, and net primary productivity (Table 3.4). The structure of the reef fish assemblage as a whole varied significantly throughout the heat stress event (pseudo F = 3.57, R^2

= 0.09, *p* = 0.001; Fig. 3.5a). Over 70% of the variation in assemblage structure during the heat stress was attributable to changes in the abundance of ten planktivorous species (primarily *Chromis* spp. and *Pseudanthias* spp.) and one facultative corallivore (*Plectroglyphidodon dickii*), all of which declined in abundance during the El Niño (Table 3.5). These same ten planktivorous species were also responsible for most of the variation in assemblage structure after the heat stress event (compared to pre-disturbance composition). However, two species that had declined during the heat stress (*Chromis vanderbilti* and *Pomacentrus coelestis*) increased in abundance after the El Niño (Table 3.6). The structure of each individual trophic group, with the exception of the omnivores, was also significantly influenced by the heat stress event (Table 3.4, Fig. 3.5). These changes in assemblage structure during the El Niño were primarily the result of species declines for all groups (Table 3.5). Conversely, influential species in several trophic groups experienced increases in abundance following the El Niño (Table 3.6).

Overall reef fish assemblage structure was also significantly different across the local human disturbance gradient (pseudo F = 7.14, R^2 = 0.18, *p* = 0.001; Fig. 3.6a). Over 70% of the variation in assemblage structure between the low and medium disturbance levels was attributable to seven planktivorous species (primarily *Chromis* spp. and *Pseudanthias* spp.) as well as *P. dickii* (Table 3.7). Similarly, the majority of the variation in assemblage structure between the low and high disturbance levels was attributable to nine planktivorous species and *P. dickii*, as well as one invertivore (*Lutjanus kasmira*; Table 3.8). Of the above species, three were most abundant at the low disturbance sites (*C. vanderbilti*, *P. dickii*, and *Pterocaesio tile*), four were most abundant at the medium disturbance sites (*Chromis margaritifer, Pseudanthias dispar*, *Pseudanthias olivaceus,* and *Thalassoma amblycephalum*), and five were most abundant at the high disturbance sites (*Pseudanthias bartlettorum, Pseudanthias cooperi, Ostorhinchus apogonoides, P. coelestis*, and *L. kasmira*).

Net primary productivity also had a significant effect on overall reef fish assemblage structure (pseudo F = 14.40, R^2 = 0.19, *p* = 0.001), and on the structure of all individual trophic groups except for the generalist carnivores and omnivores (Table 3.4). However, as this is a continuous variable it could not be included in the simper analysis. There was also a significant interaction between heat stress and local human disturbance for the reef fish assemblage as a whole (pseudo F = 1.87, R^2 = 0.10, *p* = 0.001), which suggests that the effect of heat stress on assemblage structure is influenced by the intensity of local human disturbance. This effect was also present for the majority of trophic groups, excluding the generalist carnivores, omnivores, and piscivores (Table 3.4).

3.5 Discussion

Understanding how coral reef fishes respond to ocean warming, and the direct vs. indirect effects of pulse heat stress events on reef fish assemblages, are two of the major unanswered questions facing coral reef ecologists today (Wilson et al. 2010). Although El Niño-associated heat stress events tend to be relatively short-lived (<1 year in duration), studying the effects of such events on reef fish assemblages may foreshadow the more serious long-term consequences of future ocean warming for both coral reef ecosystems and the coastal communities that depend on them. Here, we document significant changes in reef fish abundance, biomass, species richness, and assemblage structure in direct response to a severe pulse heat stress event, patterns that have been largely overlooked by the majority of previous studies which have focused on reef fish responses to shifts in benthic composition (i.e., the indirect effects of heat stress).

3.5.1 Abundance

Consistent with our predictions, total fish abundance declined significantly during the heat stress event, but had recovered to pre-disturbance levels two years later. This initial decline occurred fairly quickly, with abundance dropping by more than 50% just two months after the start of the heat stress. As coral bleaching was minimal at this time, this suggests that the observed declines resulted from increased water temperatures or other changes directly associated with El Niño, rather than bleaching-induced shifts in benthic composition. At the time of the 2015 surveys, water temperatures exceeded Kiritimati's historical maximum monthly temperature by more than 1°C, which may have had several negative implications for local reef fish populations. When water temperatures exceed a species' thermal optimum, the capacity for oxygen supply to the tissues is reduced (Pörtner and Knust 2007; Farrell 2016). Depending on the degree of warming, increased water temperatures may negatively affect reef fish growth and reproduction (Munday et al. 2008b; Donelson et al. 2010) or directly impact survival (Rummer et al. 2014). If thermal refugia exist, fish may move to areas with more preferred temperatures; if not, population declines may ensue due to decreased fitness. The relatively short time frame in which the populations declined and subsequently recovered suggests that our observed changes in abundance were the result of shifts in reef fish distribution, rather than negative impacts on reef fish fitness. As Kiritimati is a highly isolated atoll (Watson et al. 2016), movement to different thermal environments would likely necessitate migration to deeper waters, rather than lateral movement to nearby reefs. However, as the present study only surveyed fish assemblages on shallow forereefs, further studies will be needed to determine the utility of deeper reefs as thermal refugia for tropical reef fish during heat stress events.

Heat stress-associated declines in abundance occurred in all trophic groups, although these changes were only significant for the detritivores and planktivores. Given that most of the variation in reef fish assemblage structure during the heat stress event was driven by planktivores (Table 3.5), it is likely that the observed decline in total fish abundance during the El Niño was also driven primarily by declines in planktivorous species. Much of the previous research on reef fish thermal tolerances has been conducted on planktivores (e.g., *Chromis* sp.; Rummer et al. 2014; Habary et al. 2017), and suggests that these fish are highly sensitive to changes in water temperature. However, this trophic group also appears to respond strongly to levels of net primary productivity (Williams et al. 2015; Table 3.1), which may be altered during El Niño (Barber et al. 1996; Lo-Yat et al. 2011). As we were unable to monitor changes in productivity throughout the heat stress event, it is not clear whether the observed declines in planktivore abundance are due to the direct physiological effects of the heat stress itself, or rather a consequence of undocumented changes in local primary productivity. Future studies examining the impacts of heat stress on reef fish assemblages should also take into account potential shifts in net primary productivity that may occur during El Niño, either as an indirect result of changes in ocean circulation or a direct result of thermal stress on plankton.

The observed decline in corallivorous fish abundance following the mass coral bleaching event is also consistent with our predictions and with the findings of several previous studies (e.g., Sano 2004; Pratchett et al. 2006, 2008; Wilson et al. 2006). Although the shift in corallivore assemblage structure was largely driven by the facultative corallivore *P. dickii*, which is known to associate closely with the coral genera *Acropora* and *Pocillopora* (Randall 2005), several obligate corallivores also experienced notable declines. In particular, the possible local extinction of the obligate corallivore *Chaetodon trifascialis*, which we documented on reefs around Kiritimati, has also been observed on reefs in Australia (Pratchett et al. 2006) and the Seychelles (Graham et al. 2009) following severe coral bleaching, and suggests that this species may be particularly vulnerable to the effects of coral loss. While past studies have reported the disappearance of this species and others within four to seven years of severe coral bleaching, our results suggest that local extinctions and declines in fish abundance following a severe heat stress event may occur more quickly than previously thought (i.e., within one year of the end of the heat stress).

Contrary to our expectations, there was no significant change in herbivorous fish abundance following the El Niño, despite increases in turf and macroalgal abundance at several sites (personal observation). This is contrary to a number of previous studies that have reported increases in herbivore abundances within one to three years of coral bleaching (Pratchett et al. 2008). For example, Lindahl et al. (2001) observed significant increases in herbivore abundance on reefs of transplanted corals six months after severe coral mortality, and Shibuno et al. (1999) reported increases in herbivores just one month after severe coral bleaching on reefs at Ishigaki Island, Japan. These changes were primarily driven by increases in parrotfish (Scaridae) and surgeonfish (Acanthuridae), the same families that dominate the herbivore assemblage on Kiritimati. However, it is possible that in some instances such short-term changes may be evident only at the species level (Spalding and Jarvis 2002), and a longer time frame may be required to see differences in abundance for the trophic group as a whole. For example, Sano (2004) also reported no change in herbivore abundances one year after the 1998 mass coral bleaching event, suggesting that a longer time frame may be needed for herbivorous fish populations to respond positively to the observed shifts in benthic composition at some sites. While relatively little is known about the effects of coral loss on groups other than corallivores (Wilson et al. 2010), our results suggest that declines in coral cover do not significantly impact most reef fish trophic groups in the short term (i.e., <2 years after a severe heat stress event).

3.5.2 Biomass

In addition to its impact on abundance, the 2015-2016 El Niño also had a significant effect on reef fish biomass. As far as we are aware, this is one of the first studies to examine changes in the biomass of tropical reef fish assemblages during an El Niño-associated heat stress event. As predicted, total reef fish biomass declined significantly during the El Niño, likely in connection with the observed changes in total fish abundance. However, unexpectedly, total biomass had recovered to be significantly greater than pre-disturbance levels just one year after the heat stress dissipated. Both the decline and subsequent increase in biomass appear to be primarily driven by changes in herbivore and planktivore biomass (Fig. 3.4b), relative to pre-disturbance levels. Although neither trophic group showed a significant increase in abundance following the El Niño, it is possible that their combined influence was enough to drive a significant increase in total fish biomass. Despite the paucity of similar studies from coral reef ecosystems, changes in fish biomass during a pulse heat stress event have previously been observed in the eastern equatorial Pacific. Here, the total biomass and catch of fisheries-targeted species typically decreases during El Niño (Barber and Chavez 1983), largely as a result of declines in planktivorous anchovy (Ñiquen and Bouchon 2004). Our results suggest that heat stress may have an effect on tropical reef fish biomass similar to those observed in the eastern equatorial Pacific, where the effects of El Niño tend to be the most pronounced.

Our data suggest that, for the sites surveyed, there was no significant difference in reef fish biomass across the local human disturbance gradient. This lies in stark contrast with the results of several other studies, which have found negative effects of local fishing pressure and human population density on tropical reef fish biomass (e.g., Mora 2008; Williams et al. 2011; Cinner et al. 2013). For example, reef fish biomass tends to be significantly higher on remote reefs compared to those near densely-populated areas (Williams et al. 2011; Cinner et al. 2013), and is usually greater within areas protected from fishing (McClanahan et al. 2007; Soler et al. 2015). Negative effects of fishing pressure on biomass have also been reported for several trophic groups commonly targeted by fishers, including large herbivores (Bellwood et al. 2012b) and piscivores (Jennings and Polunin 1997). Although we have not examined the effect of human disturbance on the biomass of individual trophic groups in the present study, our examination of the abundance data (Tables 3.7, 3.8) suggests a high abundance of two relatively large herbivorous fish species (*Acanthurus olivaceus* and *Acanthurus nigricauda*) at the highly-disturbed sites that are rarely found at lower levels of human disturbance, as well as higher abundances of several mid-sized invertivores, piscivores, and generalist carnivores at both the medium and high disturbance levels. Despite the known gradient of fishing pressure on Kiritimati (Watson et al. 2016), it is possible that the above species are not targeted by local fishers, and are contributing to the maintenance of high fish biomass in these more heavily-impacted areas. Alternatively, given the relatively small human population on the atoll, fishing pressure may not be high enough on the reefs even at our higher disturbance sites to have an appreciable effect on total reef fish biomass.

3.5.3 Species richness

Similar to the observed patterns in total fish biomass, reef fish species richness also declined during the heat stress event, but was significantly higher than pre-disturbance levels in 2017. There is limited precedent for these results in the scientific literature, and previous studies reporting changes in reef fish species richness in relation to heat stress events show conflicting results. Whereas Sano (2004) found no change in species richness on Japanese coral reefs two months into the 1998 coral bleaching event, surveys of a Mexican Pacific gillnet fishery found that fish species richness was lower during El Niño compared to La Niña conditions, but was higher during the ENSO event as a whole compared to non-anomalous years (Godínez-Domínguez et al. 2000). In the present study, disappearance of species from UVC surveys during the El Niño event (11 species; Table 3.2) was approximately balanced by the appearance of new species during this time (10 species; Table 3.3). This suggests that our observed changes in species richness may have largely been due to site-specific disappearances facilitated by the movement of persisting species to different areas, with their return after the El Niño augmented by new species that appeared after the heat stress. While some of these new species were previously observed at additional sites around Kiritimati in 2013, it is possible that others may have come from areas of the island that have not been surveyed previously. Given the unique functional roles that individual species may play in coral reef ecosystems (Bellwood et al. 2006b; Cvitanovic and Bellwood 2009; Hoey and Bellwood 2009), both local extinctions and the appearance of new species during El Niño, together with their roles in the marine food web, should be taken into consideration when predicting the impact of heat stress events on coral reef ecosystems and adjacent coastal communities.

3.5.4 Interacting effects of heat stress and local disturbance

Although total reef fish abundance, biomass, and species richness returned to – or even exceeded – pre-disturbance levels relatively quickly following the 2015-2016 El Niño, levels of recovery varied across the local human disturbance gradient. We found a significant negative interaction between heat stress and local disturbance for each metric, with significantly lower abundance, biomass, and species richness at the high disturbance sites (relative to low human disturbance) after the heat stress event. This suggests that higher levels of local disturbance may impair the ability of reef fish assemblages to recover following severe heat stress. One potential explanation for this pattern is differences in underlying levels of reef structural complexity across the human disturbance gradient. The ability of coral and reef fish assemblages to recover following a severe disturbance is strongly influenced by initial (i.e., pre-disturbance) levels of reef structural complexity (Graham et al. 2015), which tend to be inversely related to local human disturbance (Chapter 2). Although the physical structure of the reef remained largely intact following the mass coral bleaching event, lower levels of baseline structural complexity at the high disturbance sites may have limited the number of fish returning to these reefs after the El Niño. This suggests that the most important fishing sites on Kiritimati (given their proximity to the island's major villages) may be the ones to suffer the sharpest ecological impacts in the face of increasing climate change.

3.5.5 Assemblage structure

The structure of the reef fish assemblage as a whole also changed as a result of the heat stress. A significant shift in reef fish assemblage structure during a heat stress event has previously been observed on southern Mexican reefs in conjunction with a strong El Niño (López-Pérez et al. 2016). However, while the shift in assemblage structure on Kiritimati was primarily driven by changes in planktivore abundance, the shift observed by López-Pérez et al. (2016) was driven by both increases and decreases in a broader array of trophic groups, including herbivores, omnivores, piscivores, and planktivores. Short-term shifts in reef fish assemblage structure were also observed six months after the 1998 mass coral bleaching event on reefs in Tanzania (Lindahl et al. 2001). However, these shifts were primarily driven by increases in herbivorous parrotfishes and surgeonfishes, complemented by decreases in planktivores and omnivores. The dominance of planktivores in our simper analysis reflects the high abundance of these fish on Kiritimati’s reefs, compared to other survey areas. However, perhaps more importantly, the fact that our observed shifts in assemblage structure were primarily driven by declines for all trophic groups suggests the overwhelming negative impact of the 2015-2016 El Niño on Kiritimati’s reef fish assemblages.

3.5.6 Implications and future studies

The short-term shifts in reef fish assemblages documented here suggest that future studies on El Niño should focus not only on the impacts of bleaching-associated coral loss, but also the immediate impacts of elevated water temperatures on coral reef fish assemblages. In particular, the observed declines in reef fish abundance and biomass have several implications for the maintenance of healthy coral reef ecosystems in the face of increasing climate change and human coastal development. Although we are unsure of the exact mechanism behind these declines (direct physiological effects of heat stress vs. changes in primary productivity), both causes stand to negatively impact reef fish assemblages. Marine heat waves have already increased in frequency and duration over the past few decades (Oliver et al. 2018), and are projected to become even more severe with continued climate change (Frölicher et al. 2018). Ocean warming is also predicted to lead to changes in local levels of net primary productivity (Sarmiento et al. 2004; Behrenfeld et al. 2006), which may be problematic for species that are strongly influenced by this factor. Therefore, regardless of whether fish abundance and biomass declined in response to primary productivity or the direct effects of the heat stress itself, our findings still suggest negative consequences for coral reef ecosystems under future ocean warming. However, it should be noted that these observations come from the epicenter of the 2015-2016 El Niño and mass coral bleaching event. More research will be needed to better understand how both the magnitude and duration of warming impact the response of reef fish assemblages to severe heat stress events.

Although we primarily documented declines in planktivores, rather than larger fisheries-targeted species, this too may have future implications for coastal communities. Small planktivorous fishes such as damselfish and anthias are a critical component of the marine food web, serving as prey for higher trophic-level piscivores (e.g., groupers) that may be important to local fisheries (Jennings and Polunin 1995; Pet-Soede et al. 2001). Declines in planktivores may therefore have cascading effects that ripple up to higher levels of the coral reef food web and eventually to human coastal communities. Climate change is likely to have profound consequences for tropical fisheries, with maximum catch potential in the tropical Pacific projected to decline by up to 42% by 2055 (Cheung et al. 2010). These changes are predicted to occur in connection with both shifts in species distributions and changes in local net primary productivity. Knowing the responses of individual species to El Niño-associated heat stress and their place in the coral reef food web, combined with knowledge of which species are most important to local fisheries, can help us to predict and mitigate the impacts of ocean warming on small island nations that depend heavily on local reef fisheries.

3.5.7 Conclusion

Climate change impacts on coral reef ecosystems are predicted to increase substantially in the coming decades, while human populations continue to expand. In this study we document the negative effects of a severe pulse heat stress event on the tropical reef fish assemblages of an isolated coral atoll, foreshadowing the consequences of more frequent marine heat waves and continued ocean warming for coral reef ecosystems. Many small island nations, including Kiribati, are predicted to be incredibly vulnerable to the impacts of climate change on coral reefs, in large part due to their dependence on reef fish as a source of food and income (Burke et al. 2011). The results from the present study increase our understanding of the projected effects of climate change on coral reef fish, and may help managers and reef-reliant communities to better prepare for these impacts. Our finding that the recovery of reef fish assemblages is impaired by higher levels of local human disturbance also emphasizes the importance of mitigating local stressors currently impacting coral reefs. Successful preservation of our remaining coral reef ecosystems will require action at both local and global scales, to minimize the impacts of ocean warming on coral reef fishes and the millions of people who depend on them.

Table 3.1. Results (*p*-values) from generalized linear mixed-effects models describing the effects of severe heat stress, local human disturbance, and primary productivity on tropical reef fish abundance (a), biomass (b), and species richness (c). Values in bold are significantly different from baseline levels (i.e., before, low local disturbance) at α = 0.05. Red shaded boxes correspond to variables with negative parameter estimates, indicative of declines.

	Heat stress		**Local disturbance**		**Productivity**	**Heat stress x local disturbance**			
Model	**During**	**After**	**M**	**H**	**NPP**	**During:M**	**During:H**	**After:M**	**After:H**
a) Abundance									
All fish	**0.036**	0.205	**0.031**	0.914	**<0.001**	**0.004**	0.400	0.116	**<0.001**
Corallivores	0.822	**<0.001**	0.110	**0.026**	0.395	0.212	**0.007**	0.330	**0.029**
Detritivores	**0.006**	0.090	0.545	**0.047**	0.332	**0.017**	**<0.001**	0.840	**<0.001**
Gen. carnivores	0.210	0.578	**0.006**	**<0.001**	**<0.001**	0.568	0.157	0.563	0.092
Herbivores	0.054	0.780	**<0.001**	**0.002**	**<0.001**	0.352	0.975	0.113	0.860
Invertivores	0.166	0.213	0.082	**0.001**	**0.012**	0.667	**0.003**	0.522	**<0.001**
Omnivores	0.121	0.724	0.373	0.190	0.180	0.314	0.455	0.409	0.318
Piscivores	0.160	0.320	0.800	0.300	0.640	0.230	0.210	0.580	0.690
Planktivores	**0.027**	0.115	0.124	0.940	**0.013**	**<0.001**	0.520	**0.034**	**<0.001**
b) Biomass									
All fish	**0.008**	**0.006**	0.129	0.933	0.411	0.985	0.799	**0.002**	**0.004**
c) Species richness									
All fish	**0.018**	**0.031**	0.340	0.355	**0.041**	0.358	0.775	0.370	**0.004**

During = 2015, during the heat stress event; After = 2017, after the heat stress event; M = medium disturbance; H = high disturbance; NPP = net primary productivity; Heat stress x local disturbance = interaction between heat stress and local human disturbance

Table 3.2. Disappearance of species in each trophic group during and after the 2015-2016 El Niño. Values represent mean site-level abundance of each species (number of transects observed). Only species that were observed on multiple transects in at least one year are included. Green shaded boxes indicate species that were not recorded during transect surveys, but were observed during presence/absence surveys. Yellow and red shaded boxes indicate species that, although not observed at our study sites, were observed during transect surveys (yellow) or presence/absence surveys (red) at additional sites on Kiritimati.

Species	2013	2015	2017	Time of disappearance
Corallivores				
Chaetodon trifascialis	0.67 (5)	0.53 (3)	- - -	After
Chaetodon unimaculatus	0.44 (2)	0.93 (4)	🟨 - - -	After
Detritivores				
Ctenochaetus hawaiiensis	0.11 (2)	🟥 - - -	🟨 - - -	During/After
Generalist carnivores				
Epibulus insidiator	0.17 (2)	🟩 - - -	🟨 - - -	After
Pseudocheilinus evanidus	0.89 (2)	- - -	- - -	During/After
Herbivores				
Acanthurus leucocheilus	1.39 (4)	🟥 - - -	2.64 (10)	During
Acanthurus nigroris	0.28 (3)	0.13 (1)	🟨 - - -	After
Acanthurus pyroferus	2.61 (10)	0.40 (2)	- - -	After
Invertivores				
Apogon kallopterus	43.33 (10)	- - -	- - -	During/After
Cheilinus undulatus	0.33 (5)	- - -	🟩 - - -	During
Pseudocheilinus tetrataenia	1.78 (9)	🟨 - - -	- - -	During/After
Thalassoma lunare	1.78 (7)	0.93 (5)	- - -	After
Piscivores				
Cephalopholis leopardus	0.56 (5)	0.13 (1)	- - -	After
Gymnothorax breedeni	0.28 (4)	0.13 (2)	- - -	After
Planktivores				
Chromis weberi	4.89 (3)	- - -	- - -	During/After
Heteropriacanthus cruentatus	0.11 (2)	- - -	- - -	During/After
Myripristis murdjan	0.44 (2)	🟩 - - -	🟨 - - -	After
Pseudanthias pascalus	32.78 (9)	- - -	- - -	During/After

Table 3.3. Appearance of new species in each trophic group during and after the 2015-2016 El Niño. Values represent mean site-level abundance of each species (number of transects observed). Only species that were observed on multiple transects in at least one year are included. Green shaded boxes indicate species that were not recorded during transect surveys, but were observed during presence/absence surveys. Yellow and red shaded boxes indicate species that, although not observed at our study sites, were observed during transect surveys (yellow) or presence/absence surveys (red) at additional sites on Kiritimati.

Species	2013	2015	2017	Time of appearance
Corallivores				
Labrichthys unilineatus	- - -	- - -	0.50 (2)	After
Generalist carnivores				
Bothus pantherinus	- - -	- - -	0.27 (2)	After
Gymnothorax thyrsoideus	- - -	🟨 - - -	1.09 (2)	After
Herbivores				
Acanthurus guttatus	- - -	🟥 - - -	0.18 (2)	After
Acanthurus xanthopterus	🟥 - - -	0.13 (2)	🟩 - - -	During/After
Cirripectes variolosus	- - -	- - -	22.45 (36)	After
Hipposcarus longiceps	- - -	0.07 (1)	2.64 (4)	During/After
Kyphosus cinerascens	🟨 - - -	- - -	0.45 (2)	After
Naso lituratus	- - -	0.13 (2)	🟨 - - -	During
Scarus festivus	- - -	- - -	1.27 (4)	After
Invertivores				
Valenciennea helsdingenii	- - -	1.87 (4)	- - -	During
Omnivores				
Canthigaster amboinensis	- - -	- - -	1.82 (4)	After
Gnatholepis anjerensis	- - -	- - -	3.09 (8)	After
Pomacanthus imperator	- - -	🟩 - - -	0.18 (2)	During/After
Rhinecanthus rectangulus	- - -	- - -	0.64 (2)	After
Piscivores				
Epinephelus macrospilos	- - -	0.07 (1)	0.55 (5)	During/After
Epinephelus polyphekadion	- - -	0.07 (1)	0.18 (2)	During/After
Gymnothorax meleagris	- - -	🟩 - - -	0.18 (2)	During/After
Planktivores				
Acanthurus albipectoralis	- - -	- - -	1.09 (4)	After
Cirrhilabrus exquisitus	- - -	0.80 (2)	0.91 (4)	During/After
Eviota albolineata	- - -	- - -	4.00 (4)	After
Luzonichthys whitleyi	- - -	17.33 (5)	🟨 - - -	During
Myripristis kuntee	- - -	- - -	0.91 (3)	After
Naso annulatus	- - -	0.80 (2)	0.27 (1)	During/After
Priacanthus hamrur	- - -	0.33 (2)	0.09 (1)	During/After

Table 3.4. Results of permutational multivariate analysis of variance (PERMANOVA) tests examining the effects of heat stress, local human disturbance, and net primary productivity on reef fish assemblage structure. Shaded boxes indicate non-significant results. Note that the F value reported in the table is a pseudo F statistic.

	Heat stress	**Local disturbance**	**Productivity**	**Heat stress x local disturbance**
All fish	F = 3.57 $R^2 = 0.09$ $p = 0.001$	F = 7.14 $R^2 = 0.18$ $p = 0.001$	F = 14.40 $R^2 = 0.19$ $p = 0.001$	F = 1.87 $R^2 = 0.10$ $p = 0.001$
Corallivores	F = 5.54 $R^2 = 0.16$ $p = 0.001$	F = 4.49 $R^2 = 0.13$ $p = 0.001$	F = 10.15 $R^2 = 0.14$ $p = 0.001$	F = 1.70 $R^2 = 0.10$ $p = 0.025$
Detritivores	F = 1.63 $R^2 = 0.07$ $p = 0.016$	F = 1.38 $R^2 = 0.06$ $p = 0.011$	F = 4.49 $R^2 = 0.09$ $p = 0.005$	F = 1.39 $R^2 = 0.11$ $p = 0.016$
Generalist carnivores	F = 1.53 $R^2 = 0.05$ $p = 0.044$	F = 6.19 $R^2 = 0.19$ $p = 0.039$	F = 10.86 $R^2 = 0.17$ $p = 0.074$	F = 0.88 $R^2 = 0.06$ $p = 0.277$
Herbivores	F = 2.98 $R^2 = 0.08$ $p = 0.001$	F = 8.95 $R^2 = 0.24$ $p = 0.001$	F = 11.69 $R^2 = 0.16$ $p = 0.001$	F = 1.40 $R^2 = 0.07$ $p = 0.003$
Invertivores	F = 4.59 $R^2 = 0.13$ $p = 0.001$	F = 5.50 $R^2 = 0.16$ $p = 0.001$	F = 8.42 $R^2 = 0.12$ $p = 0.001$	F = 2.02 $R^2 = 0.11$ $p = 0.001$
Omnivores	F = 1.19 $R^2 = 0.04$ $p = 0.230$	F = 4.52 $R^2 = 0.15$ $p = 0.145$	F = 13.45 $R^2 = 0.22$ $p = 0.202$	F = 1.02 $R^2 = 0.07$ $p = 0.278$
Piscivores	F = 3.19 $R^2 = 0.10$ $p = 0.001$	F = 5.16 $R^2 = 0.16$ $p = 0.002$	F = 7.20 $R^2 = 0.11$ $p = 0.001$	F = 1.26 $R^2 = 0.08$ $p = 0.135$
Planktivores	F = 3.44 $R^2 = 0.09$ $p = 0.001$	F = 7.41 $R^2 = 0.19$ $p = 0.001$	F = 15.56 $R^2 = 0.20$ $p = 0.001$	F = 1.96 $R^2 = 0.10$ $p = 0.003$

Table 3.5. Species contributing to 70% of the variation in reef fish assemblage structure during the 2015-2016 El Niño (compared to pre-disturbance composition) for all fish (a) and individual trophic groups (b-i). Mean site-level abundances for each time point are given, as well as the cumulative contribution of each species to overall assemblage dissimilarity.

Species	Change (+/-)	2013	2015	Cumulative sum
a) All fish				
Chromis vanderbilti	-	650.22	228.40	0.144
Chromis margaritifer	-	600.33	483.87	0.243
Pseudanthias cooperi	-	509.22	18.80	0.329
Pseudanthias dispar	-	380.11	112.67	0.412
Pomacentrus coelestis	-	254.22	137.47	0.472
Pseudanthias bartlettorum	-	181.00	180.67	0.530
Thalassoma amblycephalum	-	205.72	195.33	0.857
Pterocaesio tile	-	277.11	8.00	0.628
Pseudanthias olivaceus	-	166.67	100.93	0.665
Ostorhinchus apogonoides	-	284.33	3.73	0.697
Plectroglyphidodon dickii	-	80.00	61.87	0.718
b) Corallivores				
Plectroglyphidodon dickii	-	80.00	61.87	0.445
Plectroglyphidodon johnstonianus	-	58.78	23.33	0.760
c) Detritivores				
Ctenochaetus marginatus	-	21.06	18.00	0.390
Ctenochaetus cyanocheilus	+	16.44	24.12	0.589
Ctenochaetus binotatus	+	5.22	47.14	0.743
d) Generalist carnivores				
Cephalopholis urodeta	-	54.28	29.93	0.345
Gomphosus varius	-	22.28	18.80	0.569
Lutjanus gibbus	+	12.61	39.47	0.760
e) Herbivores				
Acanthurus olivaceus	-	30.67	17.00	0.148
Stegastes aureus	-	30.11	29.20	0.283
Stegastes fasciolatus	-	23.78	13.33	0.407
Centropyge flavissima	-	23.11	16.27	0.502
Acanthurus nigricans	-	20.39	7.33	0.578
Acanthurus nigricauda	-	15.06	11.40	0.651
Cirripectes stigmaticus	-	10.44	4.00	0.694
Chlorurus sordidus	-	7.50	6.60	0.731
f) Invertivores				
Lutjanus kasmira	-	127.89	12.00	0.167
Parupeneus multifasciatus	-	40.61	10.27	0.266
Coris centralis	-	23.00	10.40	0.343

Pseudocheilinus hexataenia	+	12.67	16.53	0.407
Labroides dimidiatus	-	27.56	21.07	0.467
Halichoeres ornatissimus	-	13.56	13.07	0.524
Pseudocheilinus octoaenia	-	13.00	10.27	0.578
Stethojulis bandanensis	-	14.33	9.20	0.626
Apogon kallopterus	-	43.33	0.00	0.668
Valenciennea strigata	-	10.78	4.13	0.705
g) Omnivores				
Canthigaster solandri	+	5.60	12.27	0.479
Melichthys niger	+	2.27	2.53	0.652
Sufflamen bursa	-	2.27	1.47	0.774
h) Piscivores				
Cirrhitichthys oxycephalus	-	43.11	14.67	0.466
Epinephelus fasciatus	-	4.00	0.93	0.539
Plagiotremus tapeinosoma	-	3.44	0.80	0.600
Aphareus furca	+	0.67	1.60	0.647
Cephalopholis argus	-	1.67	1.07	0.689
Lutjanus bohar	-	1.89	0.60	0.731
i) Planktivores				
Chromis vanderbilti	-	650.22	228.40	0.197
Chromis margaritifer	-	600.33	483.87	0.329
Pseudanthias cooperi	-	509.22	18.80	0.441
Pseudanthias dispar	-	380.11	112.67	0.548
Pomacentrus coelestis	-	254.22	137.47	0.632
Thalassoma ambycephalum	-	205.72	195.33	0.708

Table 3.6. Species contributing to 70% of the variation in reef fish assemblage structure after the 2015-2016 El Niño (compared to pre-disturbance composition) for all fish (a) and individual trophic groups (b-i). Mean site-level abundances for each time point are given, as well as the cumulative contribution of each species to overall assemblage dissimilarity.

Species	Change (+/-)	2013	2017	Cumulative sum
a) All fish				
Chromis vanderbilti	+	650.22	1091.00	0.177
Chromis margaritifer	-	600.33	596.40	0.276
Pseudanthias cooperi	-	509.22	123.60	0.353
Pomacentrus coelestis	+	254.22	322.70	0.445
Pseudanthias dispar	-	380.11	234.90	0.514
Pterocaesio tile	-	277.11	84.45	0.558
Pseudanthias bartlettorum	-	181.00	157.10	0.602
Pseudanthias olivaceus	-	166.67	163.10	0.640
Thalassoma amblycephalum	-	205.72	106.90	0.672
Ostorhinchus apogonoides		284.33	8.54	0.702
b) Corallivores				
Plectroglyphidodon dickii	-	80.00	14.55	0.389
Plectroglyphidodon johnstonianus	-	58.78	1.10	0.741
c) Detritivores				
Ctenochaetus marginatus	-	21.06	15.36	0.398
Ctenochaetus striatus	+	4.00	18.55	0.689
Ctenochaetus cyanocheilus	-	16.44	4.55	0.889
d) Generalist carnivores				
Cephalopholis urodeta	-	54.28	24.82	0.372
Gomphosus varius	-	22.28	17.36	0.613
Paracirrhites arcatus	-	10.78	4.00	0.708
e) Herbivores				
Acanthurus olivaceus	+	30.67	32.91	0.144
Stegastes aureus	-	30.11	22.36	0.243
Stegastes fasciolatus	-	23.78	14.73	0.332
Centropyge flavissima	-	23.11	23.09	0.412
Acanthurus nigricans	-	20.39	18.27	0.485
Cirripectes variolosus	+	0.00	22.45	0.553
Chlorurus sordidus	+	7.50	23.45	0.613
Acanthurus triostegus	+	4.22	18.36	0.668
Acanthurus nigricauda	-	15.06	8.91	0.718
f) Invertivores				
Lutjanus kasmira	-	127.89	1.27	0.121
Macropharyngodon meleagris	+	4.33	46.91	0.214
Stethojulis bandanensis	+	14.33	30.36	0.295

Parupeneus multifasciatus	-	40.61	4.91	0.364
Pseudocheilinus octotaenia	+	13.00	25.45	0.425
Thalassoma quinquevittatum	+	7.56	26.55	0.481
Pseudocheilinus hexataenia	+	12.67	19.82	0.532
Halichoeres margaritaceus	+	0.33	24.55	0.582
Coris centralis	-	23.00	6.91	0.630
Labroides dimidiatus	-	27.56	13.27	0.675
Gnathodentex aureolineatus	+	2.44	15.64	0.721
g) Omnivores				
Canthigaster solandri	+	5.60	10.00	0.316
Melichthys vidua	+	1.60	3.36	0.451
Melichthys niger	-	2.27	1.27	0.576
Sufflamen bursa	-	2.27	1.36	0.681
Heniochus acuminatus	+	0.80	1.36	0.738
h) Piscivores				
Cirrhitichthys oxycephalus	-	43.11	32.91	0.437
Plagiotremus tapeinosoma	+	3.44	10.36	0.549
Cephalopholis argus	+	1.67	3.45	0.606
Lutjanus bohar	+	1.89	2.00	0.661
Epinephelus fasciatus	-	4.00	0.45	0.713
i) Planktivores				
Chromis vanderbilti	+	650.22	1091.00	0.232
Chromis margaritifer	+	600.33	596.40	0.363
Pseudanthias cooperi	-	509.22	123.60	0.478
Pomacentrus coelestis	-	254.22	322.70	0.588
Pseudanthias dispar	+	380.11	234.90	0.678
Pterocaesio tile	-	277.11	84.45	0.735

Table 3.7. Species contributing to 70% of the variation in reef fish assemblage structure between the low and medium human disturbance levels for all fish (a) and individual trophic groups (b-i). Mean site-level abundances for each disturbance level are given, as well as the cumulative contribution of each species to overall assemblage dissimilarity.

Species	Low	Medium	Cumulative sum
a) All fish			
Chromis vanderbilti	1370.25	730.50	0.248
Chromis margaritifer	591.50	613.70	0.341
Pseudanthias dispar	2.75	403.40	0.434
Pterocaesio tile	366.62	0.00	0.512
Thalassoma amblycephalum	87.75	232.35	0.576
Pseudanthias olivaceus	72.00	220.30	0.627
Pseudanthias bartlettorum	0.00	166.40	0.673
Plectroglyphidodon dickii	176.75	49.60	0.715
b) Corallivores			
Plectroglyphidodon dickii	176.75	49.60	0.671
Plectroglyphidodon johnstonianus	38.00	41.90	0.908
c) Detritivores			
Ctenochaetus marginatus	13.14	20.20	0.438
Ctenochaetus striatus	16.57	9.20	0.864
d) Generalist carnivores			
Gomphosus varius	64.37	14.15	0.456
Cephalopholis urodeta	7.00	55.50	0.807
e) Herbivores			
Stegastes fasciolatus	89.75	3.60	0.298
Stegastes aureus	15.25	50.80	0.434
Acanthurus nigricans	45.87	9.00	0.560
Centropyge flavissima	4.75	28.10	0.643
Cirripectes variolosus	11.00	7.75	0.694
Cirripectes stigmaticus	13.25	6.40	0.738
f) Invertivores			
Macropharyndogon meleagris	0.00	27.70	0.098
Halichoeres ornatissimus	1.50	18.90	0.193
Pseudocheilinus octotaenia	10.50	22.50	0.285
Pseudocheilinus hexataenia	18.75	24.60	0.363
Thalassoma quinquevittatum	13.25	18.70	0.440
Labroides dimidatus	19.75	17.50	0.504
Parupeneus multifasciatus	0.62	15.40	0.568
Coris centralis	0.00	13.40	0.627
Gnathodentax aureolineatus	10.00	0.50	0.674
Halichoeres margaritaceus	0.00	13.30	0.717

g) Omnivores			
Canthigaster solandri	0.00	4.32	0.279
Melichthys niger	4.14	1.37	0.536
Melichthys vidua	0.14	2.26	0.691
Sufflamen bursa	0.00	2.05	0.825
h) Piscivores			
Cirrhitichthys oxycephalus	8.50	18.50	0.342
Lutjanus bohar	7.62	0.20	0.469
Aphareus furca	4.50	0.15	0.565
Cephalopholis argus	4.62	1.50	0.656
Epinephelus fasciatus	0.00	3.95	0.710
i) Planktivores			
Chromis vanderbilti	1370.25	730.50	0.332
Chromis margaritifer	591.50	613.70	0.463
Pseudanthias dispar	2.75	403.40	0.587
Pterocaesio tile	366.62	0.00	0.688
Thalassoma amblycephalum	87.75	232.35	0.779

Table 3.8. Species contributing to 70% of the variation in reef fish assemblage structure between the low and high human disturbance levels for all fish (a) and individual trophic groups (b-i). Mean site-level abundances for each disturbance level are given, as well as the cumulative contribution of each species to overall assemblage dissimilarity.

Species	Low	High	Cumulative sum
a) All fish			
Chromis vanderbilti	1370.25	97.25	0.201
Pomacentrus coelestis	0.50	578.75	0.306
Chromis margaritifer	591.50	476.12	0.395
Pseudanthias cooperi	0.00	670.50	0.484
Pterocaesio tile	366.62	194.00	0.545
Pseudanthias bartlettorum	0.00	273.00	0.585
Plectroglyphidodon dickii	176.50	7.62	0.619
Ostorhinchus apogonoides	0.00	321.75	0.646
Pseudanthias dispar	2.75	189.12	0.671
Thalassoma amblycephalum	87.75	153.75	0.696
Lutjanus kasmira	0.00	156.00	0.714
b) Corallivores			
Plectroglyphidodon dickii	176.75	7.62	0.682
Plectroglyphidodon johnstonianus	38.00	17.37	0.836
c) Detritivores			
Ctenochaetus marginatus	13.14	19.00	0.330
Ctenochaetus striatus	16.57	3.81	0.568
Ctenochaetus cyanocheilus	1.14	38.31	0.755
d) Generalist carnivores			
Gomphosus varius	64.37	4.75	0.432
Cephalopholis urodeta	7.00	33.31	0.599
Lutjanus gibbus	0.62	49.50	0.742
e) Herbivores			
Stegastes fasciolatus	89.75	0.00	0.244
Acanthurus olivaceus	0.25	71.31	0.418
Acanthurus nigricans	45.87	8.19	0.520
Centropyge flavissima	4.75	19.62	0.571
Acanthurus nigricauda	0.00	21.37	0.623
Chlorurus sordidus	13.62	13.56	0.667
Stegastes aureus	15.25	5.50	0.707
f) Invertivores			
Lutjanus kasmira	0.00	156.00	0.175
Stethojulis bandanensis	0.25	39.00	0.290
Parupeneus multifasciatus	0.62	39.12	0.361
Coris centralis	0.00	23.62	0.428

Labroides dimidiatus	19.75	28.12	0.484
Pseudocheilinus hexataenia	18.75	3.25	0.540
Gnathodentex aureolineatus	10.00	8.00	0.587
Thalassoma quinquevittatum	13.25	1.87	0.629
Apogon kallopterus	0.00	48.75	0.670
Pseudocheilinus octotaenia	10.50	8.37	0.708
g) Omnivores			
Canthigaster solandri	0.00	19.73	0.536
Melichthys niger	4.14	2.07	0.651
Sufflamen bursa	0.00	2.13	0.722
h) Piscivores			
Cirrhitichthys oxycephalus	8.50	57.50	0.495
Lutjanus bohar	7.62	0.00	0.583
Plagiotremus tapeinosoma	0.25	8.00	0.654
Aphareus furca	4.50	0.19	0.716
i) Planktivores			
Chromis vanderbilti	1370.25	97.25	0.268
Pomacentrus coelestis	0.50	578.75	0.417
Chromis margaritifer	591.50	476.12	0.539
Pseudanthias cooperi	0.00	670.50	0.655
Pterocaesio tile	366.62	194.00	0.734

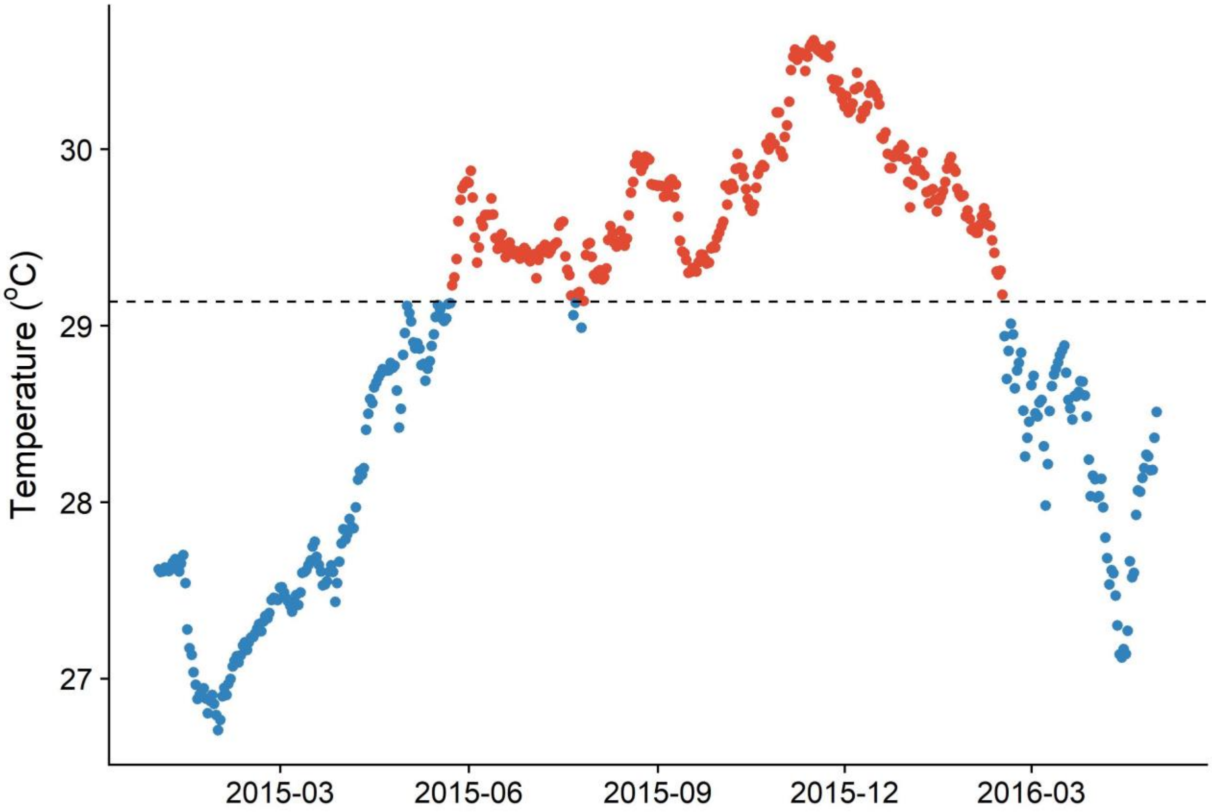

Figure 3.1. Mean daily water temperature (°C) at shallow forereef sites around Kiritimati throughout the 2015-2016 El Niño and mass coral bleaching event. The dashed line represents 1°C above Kiritimati's historical maximum monthly temperature. Points above this threshold are coloured in red, indicative of the heat stress event.

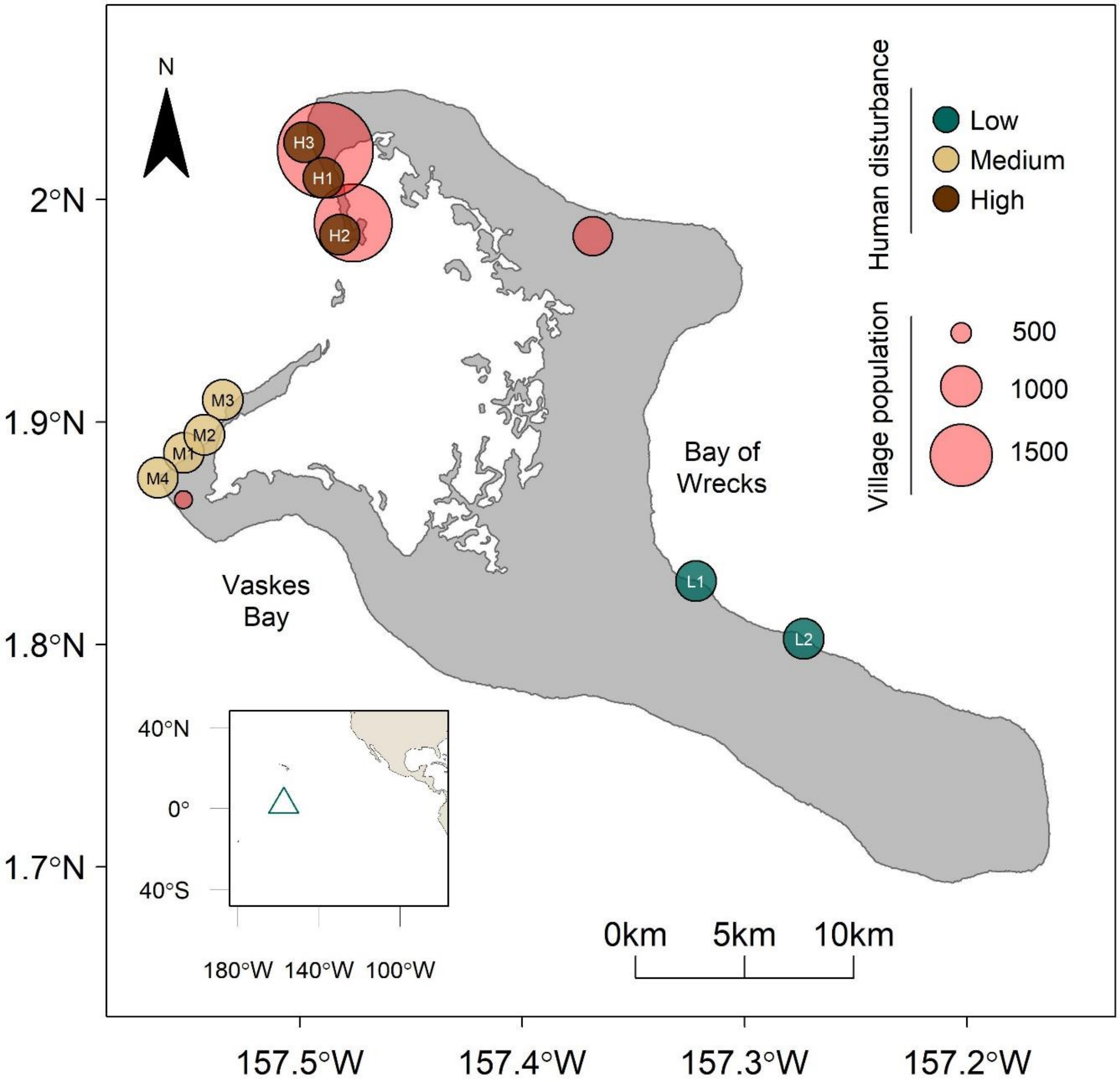

Figure 3.2. Map of forereef study sites and villages on Kiritimati, Republic of Kiribati. Sites are divided into three levels of local human disturbance, and villages (red circles) are scaled to human population size. Inset shows Kiritimati's location in the central equatorial Pacific Ocean.

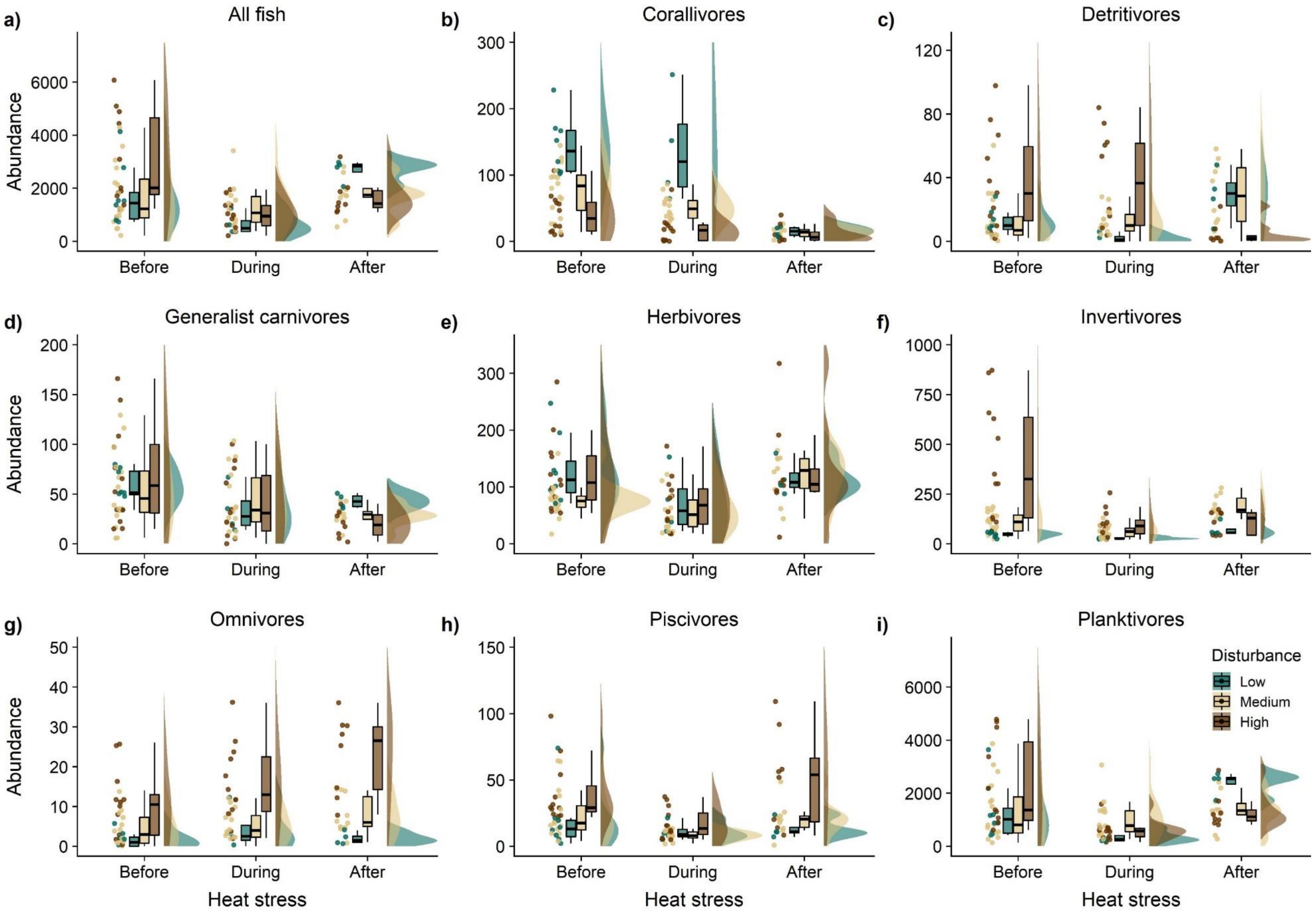
a)
All fish
Abundance
0
2000
4000
6000
Before
During
After
b)
Corallivores
0
100
200
300
Before
During
After
c)
Detritivores
0
40
80
120
Before
During
After
d)
Generalist carnivores
Abundance
0
50
100
150
200
Before
During
After
e)
Herbivores
0
100
200
300
Before
During
After
f)
Invertivores
0
250
500
750
1000
Before
During
After
g)
Omnivores
Abundance
0
10
20
30
40
50
Before
During
After
Heat stress
h)
Piscivores
0
50
100
150
Before
During
After
Heat stress
i)
Planktivores
0
2000
4000
6000
Before
During
After
Heat stress
Disturbance
Low
Medium
High

Figure 3.3. Influence of heat stress and local human disturbance on the total site-level abundance of all fish (a) and individual trophic groups (b-i). Each plot displays data as a combination of individual data points (left) showing the abundance for each site, boxplots (center), and smoothed distributions (right) showing the distribution of abundances across sites, within each disturbance level. Local disturbance levels are indicated by colour: low (blue-green), medium (beige), and high (dark brown).

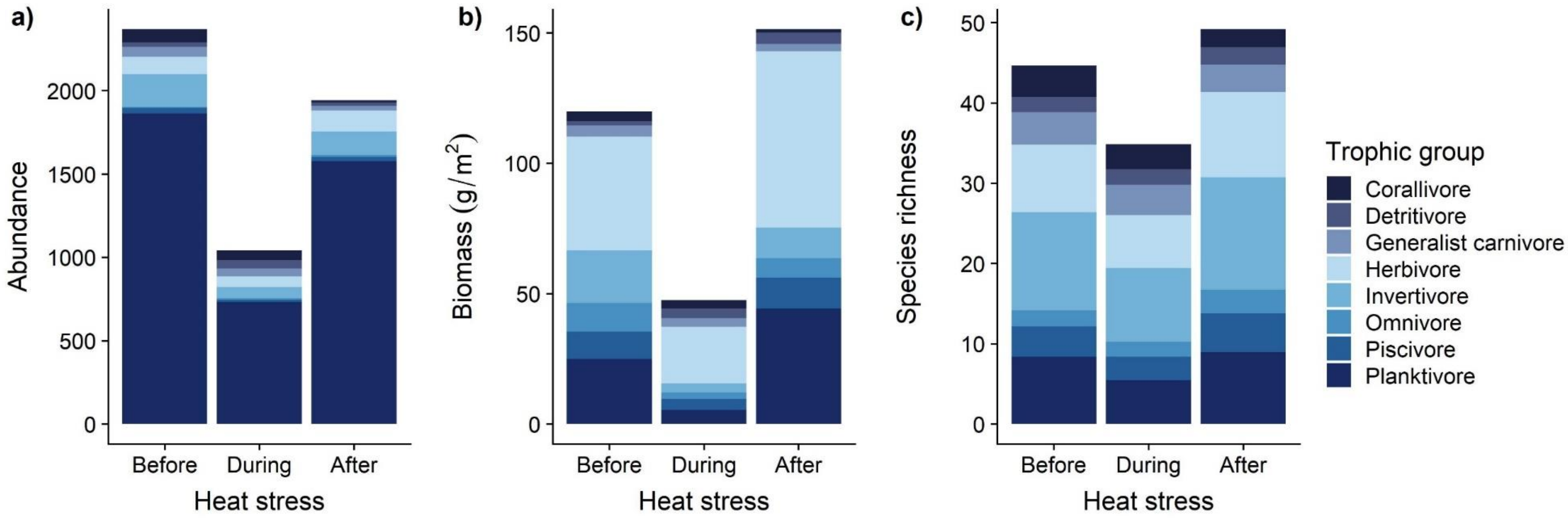

Figure 3.4. Relative contribution of individual trophic groups to total reef fish abundance (a), biomass (b), and species richness (c) at each sampling time point. Y-axes represent mean site-level values for each metric combined across all sites and disturbance levels, with corallivores at the top of each bar and planktivores at the bottom.

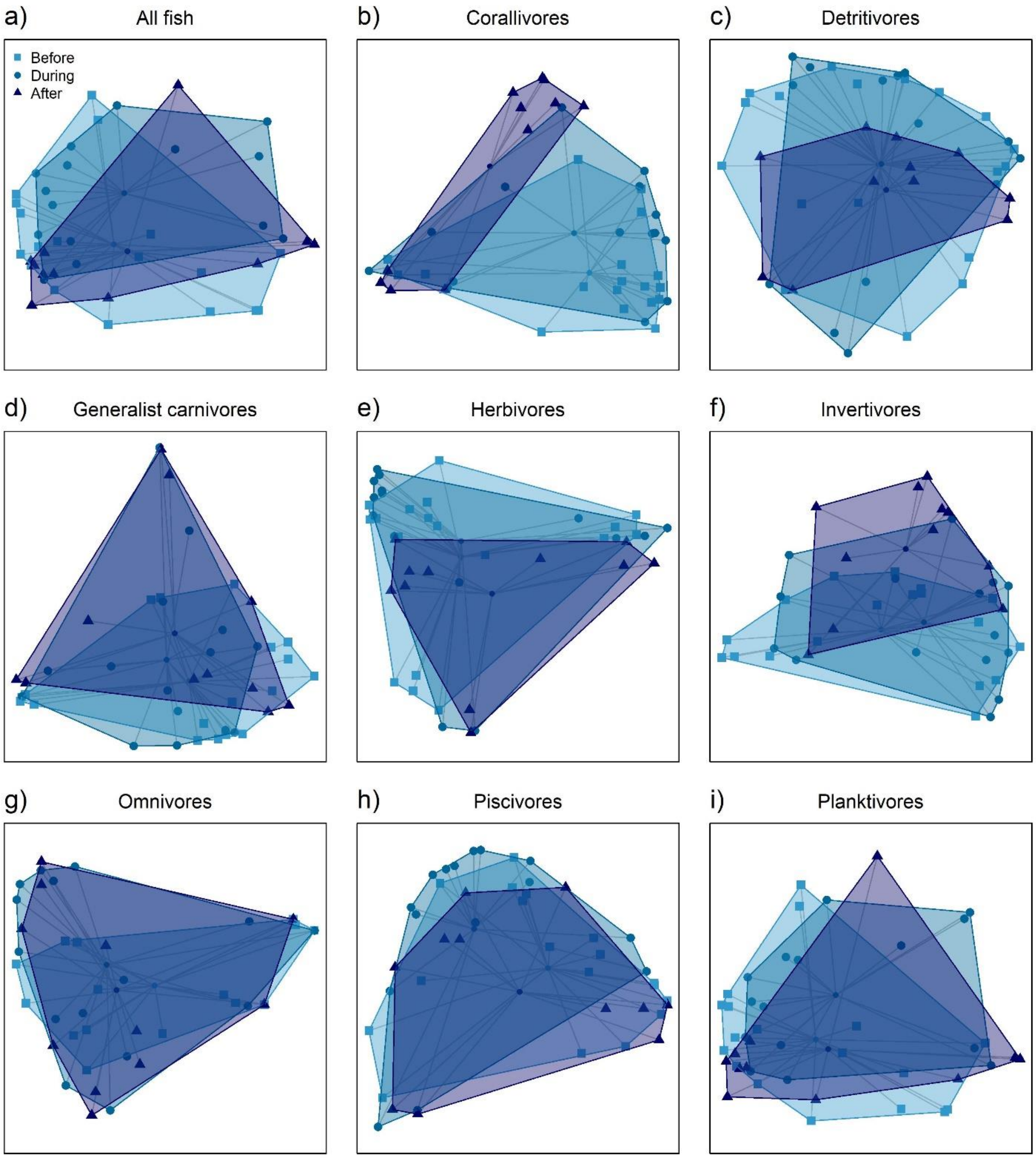

Figure 3.5. Multivariate ordination (PCoA) of reef fish assemblages, showing differences in assemblage structure through time for the entire reef fish assemblage (a) and individual trophic groups (b-i). Points represent individual sites, coloured by sampling time, and shaded polygons indicate the boundaries of observed assemblage space for each time point.

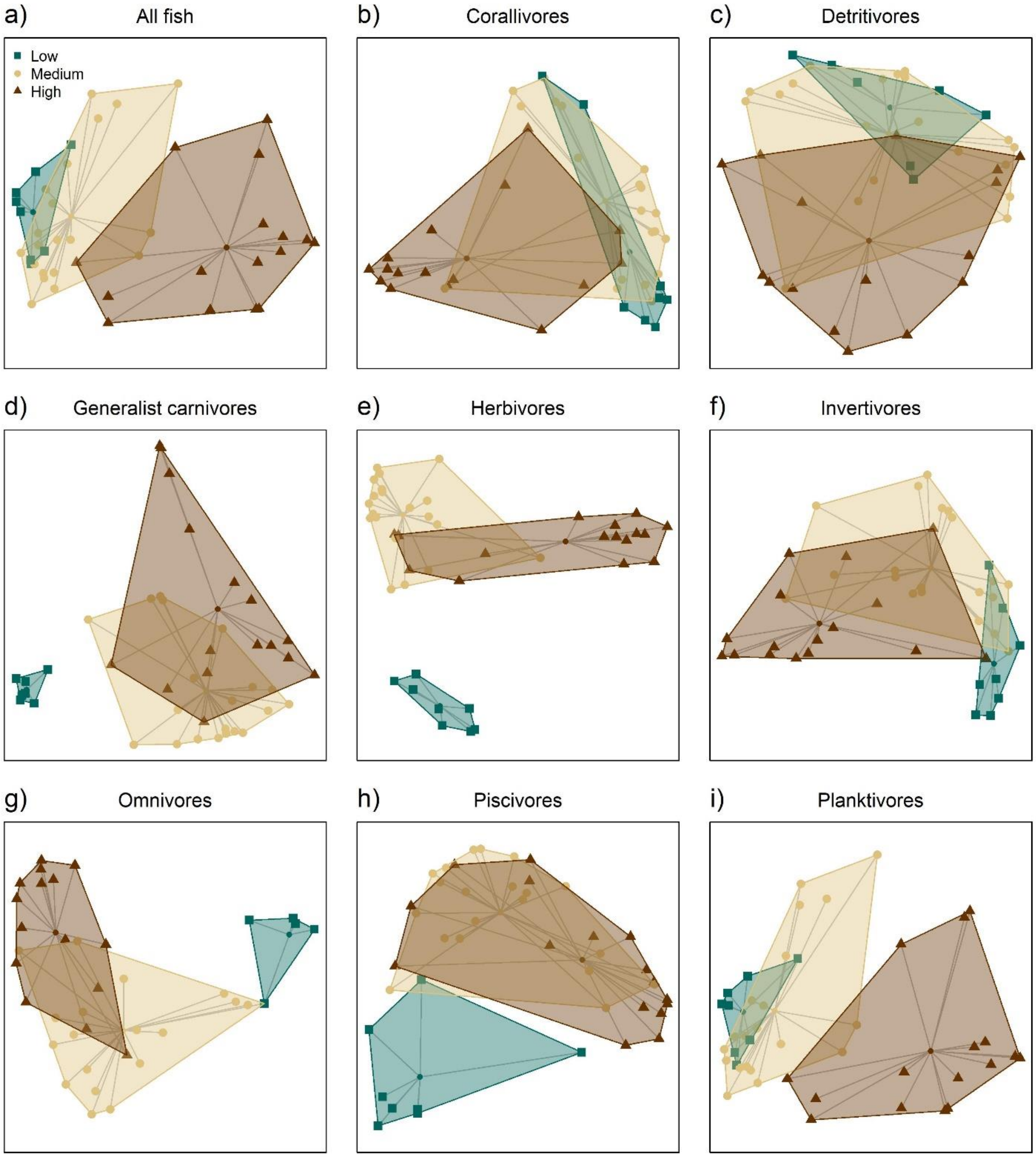

Figure 3.6. Multivariate ordination (PCoA) of reef fish assemblages, showing differences in assemblage structure across the local human disturbance gradient for the entire reef fish assemblage (a) and individual trophic groups (b-i). Points represent individual sites, coloured by human disturbance, and shaded polygons indicate the boundaries of observed assemblage space for each disturbance level.

Chapter 4 – Conclusion

Heat stress and associated coral bleaching pose a serious threat to the world’s remaining coral reef ecosystems (Hoegh-Guldberg 2011; Hughes et al. 2018). While the effects of thermal stress on live coral cover are well understood (Glynn et al. 2017), fewer studies have examined the impacts of severe pulse heat stress events on reef structural complexity or its implications for other levels of biological organization on coral reefs. The interplay between heat stress and local anthropogenic disturbances also remains uncertain. In light of the increasing threats of climate change and anthropogenic coastal development, understanding the interacting effects of local and global stressors on coral reef ecosystems is an important next step for coral reef ecologists and managers. This thesis utilizes data from reefs around Kiritimati (Republic of Kiribati) in the central equatorial Pacific Ocean, which experienced prolonged heat stress during the 2015-2016 El Niño, to examine the interacting effects of heat stress and local human disturbance on two important components of the coral reef ecosystem – three-dimensional (3D) reef structural complexity and tropical reef fish assemblages.

In Chapter 2, I examined fine-scale changes in reef structural complexity following the El Niño-induced mass coral mortality event on reefs across Kiritimati’s local human disturbance gradient. Using 3D models built through structure-from-motion photogrammetry, I documented a decrease in reef surface rugosity and terrain ruggedness less than two years after the heat stress event (Table 2.1, Figs. 2.3a,c, 2.4a,b), as well as a noticeable decline in habitat volume (Figs. 2.5, 2.6). Although there was not a strong interaction between heat stress and local disturbance, I found that levels of reef structural complexity varied across the local human disturbance gradient, with the highest levels of structural complexity occurring at sites with the lowest levels of disturbance (Table 2.1, Figs. 2.3b,d, 2.4a,b). Reef structural complexity was also strongly related to the densities of branching and massive coral growth forms (Table 2.1, Fig 2.4). These results highlight the negative impacts of local and global stressors on the structural foundation of coral reefs, and have several important implications for coral reef ecosystems under future climate change scenarios.

The abundance and diversity of coral reef fishes is known to be strongly related to levels of reef structural complexity (Wilson et al. 2006; Graham and Nash 2013). As such, declines in reef structure following mass coral bleaching may lead to subsequent declines in reef fish populations (Graham et al. 2006, 2009; Emslie et al. 2014). Although I documented declines in reef structural complexity and habitat volume following the 2015-2016 mass coral bleaching event on Kiritimati, it is unlikely that these changes were great enough to have a noticeable effect on reef fish populations less than two years after the heat stress. Mis-match between the sites visited for the structural complexity and reef fish surveys, in addition to high correlation between structural complexity and local human disturbance, also meant that we were unable to include structural complexity in our analysis of the reef fish assemblages (Chapter 3). However, we expect that accelerated structural degradation will occur over the next several years as the remaining dead coral skeletons are eroded by physical and biological forces. Continued study of the reefs around Kiritimati will be necessary to monitor the extent of future structural loss, and to examine the effects of more severe changes in reef structural complexity on the associated fish assemblages. My finding that local human disturbance negatively impacts 3D reef complexity suggests that managers should take steps to mitigate local stressors such as fishing pressure and coastal development, in order to maximize the recovery potential of reefs following severe disturbances (Graham et al. 2015). However, further research on the effects of different types of local disturbance will be needed to pinpoint the precise mechanism leading to these differences in baseline levels of structural complexity.

In Chapter 3, I examined the immediate effects of heat stress on coral reef fish assemblages by quantifying changes in fish abundance, biomass, species richness, and assemblage structure during and after the 2015-2016 El Niño. These analyses revealed that significant declines in reef fish abundance, biomass, and species richness occurred while reefs were subjected to heat stress (Table 3.1, Fig. 3.4). Although assemblages had generally recovered less than two years later, this recovery was impeded at high levels of local human disturbance. Consistent with previous studies, I also observed a significant decline in corallivore abundance after the mass coral bleaching event (Table 3.1), including the possible local extinction of the obligate corallivore *Chaetodon trifascialis* (Table 3.2). I also report significant shifts in reef fish assemblage structure through time, driven primarily by declines in the abundance of small planktivores during the heat stress event (Table 3.5, Fig. 3.5). As far as I am aware, this thesis is one of the first studies to examine changes in reef fish assemblages during a severe heat stress event, adding to our knowledge of the negative impacts of projected ocean warming on coral reef ecosystems.

In the future, this work may be expanded upon in several ways. Although I documented significant declines in reef fish abundance and biomass during the 2015-2016 El Niño, the exact cause of these changes remains uncertain. While I suspect that the observed declines were primarily due to the horizontal or vertical movement of fish rather than mortality, there is no way to be certain of this, as our surveys were limited to shallow (10-12 m depth) sites. The extent to which reef fish move during a coral bleaching event remains one of the crucial knowledge gaps facing coral reef ecologists today (Wilson et al. 2010). Future studies may work to fill this gap by surveying reef fish assemblages at multiple depths, throughout the various stages of a severe heat stress event. However, as the timing of heat stress events is somewhat unpredictable, it may be difficult for independent researchers to organize field expeditions coinciding with the early stages of heat stress. Successful resolution of this question may therefore rely on long-term coral reef monitoring programs surveying deeper reefs adjacent to already-established shallow monitoring sites.

Predicting the effects of future ocean warming on tropical coral reef fish assemblages also relies on knowledge of the physiological heat tolerances of these species. To date, very little research has been done to determine the thermal limits of reef fish and their responses to increased water temperatures, aside from a small number of studies on planktivores (e.g., Rummer et al. 2014; Habary et al. 2017). Further studies on the thermal tolerances of a greater diversity of reef fish species may help to determine the direct risk of ocean warming to other trophic groups. In order to predict the impacts of future changes in reef fish assemblages on human coastal communities, it is also necessary to know to what extent observed declines in fish abundance and biomass translate into tangible effects on local fishers. Currently, we do not know the extent to which our observed changes in reef fish assemblages impacted the local communities on Kiritimati. In the future, it would be useful to combine underwater visual census data with surveys of local fishers, to more directly quantify the effects of changes in reef fish assemblages on local reef-dependent communities.

Finally, as Kiritimati was at the epicenter of the 2015-2016 El Niño and mass coral bleaching event (Baum et al. in prep.), it is possible that our findings for both structural complexity and reef fish assemblages lie at one extreme end of the spectrum of possible results. Regardless of the level of biological organization being examined, future studies should incorporate data from reefs exposed to varying levels of heat stress, to more comprehensively examine the relationship between the degree of heat stress and impacts on coral reef ecosystems. While many unanswered questions continue to plague the realm of coral reef ecology, the results of this thesis bring us one step further towards understanding the impacts of some of the most serious local and global threats currently acting on coral reefs, which stand to influence the composition of these vital ecosystems well into the future.

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Appendices

Appendix A: Supplemental information for Chapter 2

Wave energy

The influence of physical factors such as wave energy may also impact benthic community composition and structure, and this relationship has been well-documented in coral reef ecosystems (Bradbury and Young 1981; Dollar 1982; Williams et al. 2013). As such, we also explored the possibility of incorporating wave energy in our structural complexity models. Firstly, to determine whether there was any spatial autocorrelation remaining in our models that was not accounted for by the local human disturbance variable, we plotted variograms for the full models of each structural complexity metric. Given our relatively small sample sizes, the resulting variograms exhibited considerable residual variation without any clear patterns. However, visual assessment of variance suggested that spatially clustered sites did not exhibit increased residual correlation, as they might be expected to if there was an important covariate missing from the model (Zuur et al. 2009). Furthermore, adding wave energy to the models did not appear to improve measures of variance. This suggests that the influence of spatial autocorrelation amongst our sites was already largely accounted for by the variables present in the model. While we suspect that this was mainly due to inclusion of the local human disturbance variable, some of the spatial autocorrelation may also have been accounted for by the inclusion of coral growth forms in our model, given the relationships between potentially-confounding biophysical factors such as wave energy and benthic structure (Bradbury and Young 1981).

In addition, remotely-sensed wave energy data from the Marine Socio-Environmental Covariates data set (https://shiny.sesync.org/apps/msec/; Yeager et al. 2017b) suggest that

Kiritimati experiences remarkably little variation in wave energy, with long-term mean wave energy values at our study sites only ranging from ~25-27 kW m^{-1}. In comparison, studies conducted at other locations in the Northern Line Islands, at sites comparable in depth to those surveyed here, report intra-island variations in wave energy of at least 15 kW m^{-1} (e.g., long-term mean wave energy of ~15-30 kW m^{-1} at Kingman Reef; Williams et al. 2015a). On Kingman, areas of higher wave energy are associated with lower hard coral cover, as well as lower cover of the genus *Acropora* (Williams et al. 2015a). However, the sites on Kiritimati with the highest coral cover and structural complexity (much of which is provided by Acropora) are also those with the highest mean wave energy, which contradicts the expected effects of wave energy on benthic structure. This suggests that even if the observed gradient in wave energy across our sites was sufficient to drive differences in reef structural complexity, the benthic community on Kiritimati has likely become decoupled from these natural biophysical drivers due to the presence of chronic local human disturbance (Williams et al. 2015a). Therefore, given our assessment of spatial autocorrelation in the models, the low variability in wave energy on Kiritimati, and the potential biophysical decoupling, we feel that adding wave energy to our models would not improve the analysis or interpretation of the data.

Table A2.1. Coral species (and species groups) identified from orthophotomosaics of permanent photoquadrats (PPQs), classified by growth form (branching, massive, or plating) and Family**.** Coral taxonomy and name synonymy retrieved from WoRMS (http://www.marinespecies.org/). Growth forms were assigned based on the Coral Traits Database (https://coraltraits.org) and Veron (2000).

Family	Species	Notes
	Branching corals	
Acroporidae	*Acropora* spp. (corymbose morphology)	Includes *A. rosaria* (synonym: *A. loripes*), *A. subulata*, and hybrids of these species
Acroporidae	*Acropora gemmifera*	May include *A. globiceps*
Pocilloporidae	*Pocillopora grandis*	Synonym: *Pocillopora eydouxi*
Pocilloporidae	*Pocillopora meandrina*	
Pocilloporidae	*Pocillopora* spp.	Any *Pocillopora* that could not be classified to species due to a lack of defining morphological characteristics (e.g., recruits)
	Massive corals	
Acroporidae	*Astreopora* spp.*	Includes *A. cucullata*, *A. myriophthalma*, and *A. suggesta*
Agariciidae	*Pavona duerdeni*	
Fungiidae	*Danafungia* spp., *Lithophyllon* spp., *Lobactis* spp., *Pleuractis* spp. (synonym: *Fungia* spp.)	Includes *Danafungia scruposa* (synonym: *F. corona*), *D. horrida* (synonym: *F. danai*), *Lithophyllon concinna* (synonym: *F. concinna*), *Lobactis scutaria* (synonym: *F. scutaria*), and *Pleuractis granulosa* (synonym: *F. granulosa*)
Fungiidae	*Herpolitha limax*	
Fungiidae	*Sandalolitha robusta*	
Lobophylliidae	*Lobophyllia hemprichii**	
Merulinidae	*Astrea* spp. (synonym: *Montastrea* spp.)*	May include *A. annuligera* (synonym: *M. annuligera*) and *A. curta* (synonym: *M. curta*)
Merulinidae	*Dipsastraea matthaii*	Synonym: *Favia matthaii*
Merulinidae	*Dipsastraea speciosa*	Synonym: *Favia speciosa*
Merulinidae	*Favites halicora*	
Merulinidae	*Favites pentagona**	
Merulinidae	*Goniastrea stelligera**	Synonym: *Favia stelligera*
Merulinidae	*Hydnophora microconos*	

Merulinidae	*Platygyra* spp.	Primarily *P. daedalea*; may include *P. contorta, P. ryukyuensis,* and *P. sinensis*
Poritidae	*Porites lobata*	May include *P. evermanni* and *P. lutea*
Psammocoridae	*Psammocora haimiana*	
	Plating corals	
Acroporidae	*Acropora hyacinthus*	
Acroporidae	*Montipora aequituberculata* (foliose morphology)	
Dendrophylliidae	*Turbinaria reniformis*	
Lobophylliidae	*Echinophyllia aspera**	
Merulinidae	*Hydnophora exesa**	

*Coral taxa documented as having multiple growth forms were assigned to the growth form most commonly observed on Kiritimati.

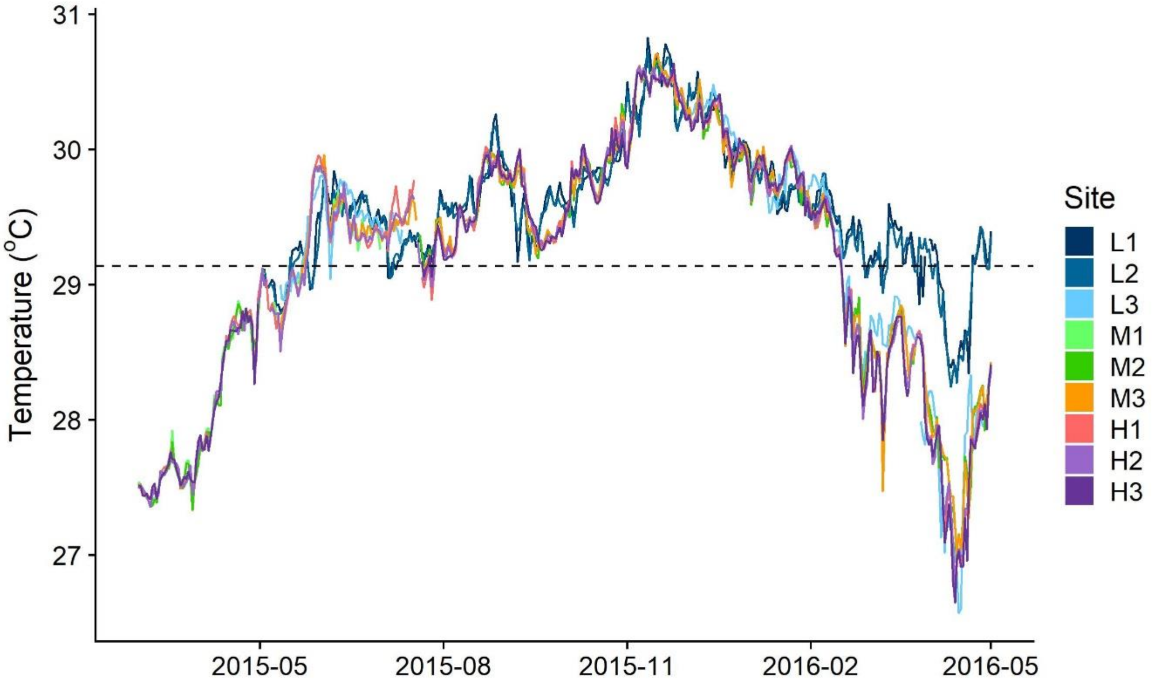

Figure A2.1. Mean daily water temperature (°C) at shallow forereef sites around Kiritimati throughout the 2015-2016 El Niño and mass coral bleaching event. Data were measured *in situ* using SBE-56 temperature loggers (Sea-Bird Electronics, Bellevue, USA). The dashed line represents 1°C above Kiritimati's historical maximum monthly temperature, indicative of the coral bleaching threshold.

Appendix B: Supplemental information for Chapter 3

Table B3.1. Number of fish surveys (n = 3 transects per survey) completed per site at each time point (Before = July/August 2013, before the El Niño; During = July 2015, two months into the El Niño; After = July 2017, one year after the end of the El Niño).

Human disturbance	**Site**	**Field Season**		
		Before	**During**	**After**
Low	L1	2	1	1
	L2	2	1	1
Medium	M1	2	2	2
	M2	2	2	1
	M3	2	2	1
	M4	2	1	1
High	H1	2	2	2
	H2	2	2	1
	H3	2	2	1

Table B3.2. Levels of net primary productivity at survey sites around Kiritimati. Data were extracted from https://shiny.sesync.org/apps/msec/, and represent a high-resolution, remotely-sensed data product averaged over the years 2003 to 2013. Maximum productivity values were used for all models.

Human disturbance	**Site**	**Net primary productivity (mg C m^{-2} day^{-1}))**		
		Min.	**Mean**	**Max.**
Low	L1	761.17	867.66	1003.66
	L2	764.79	854.64	993.43
Medium	M1	891.86	964.62	1077.88
	M2	891.86	964.62	1077.88
	M3	834.80	940.63	1070.26
	M4	944.53	963.25	984.27
High	H1	751.58	899.16	1112.00
	H2	789.72	933.08	1158.56
	H3	750.47	892.14	1097.18