Implications of heat stress and local human disturbance on early life stage corals

by

Kristina Tietjen
B.Sc., University of Hawaii at Hilo, 2013

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We acknowledge with respect the Lekwungen peoples on whose traditional territory the university stands and the Songhees, Esquimalt and W̱SÁNEĆ peoples whose historical relationships with the land continue to this day.

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Abstract

Coral reef recovery following a disturbance relies heavily on the restoration of coral cover, via growth of existing colonies and the successful recruitment of new corals. In well-connected reef networks, recruits may be sourced from neighboring reefs. In contrast, coral recruitment on geographically isolated reefs is reliant on adult corals at that location, which may limit recovery rates following mass coral mortality events. Such mortality events are increasingly caused by climate change induced temperature anomalies, which are overlaid on the local chronic human disturbances that already affect most of the world's coral reefs. In this thesis, I exploit a natural ecosystem-scale experiment to examine how multiple anthropogenic stressors impact densities of coral recruits and small corals (e.g., juveniles; ≤5 cm) on Kiritimati (Christmas Island, Republic of Kiribati), an isolated atoll in the central equatorial Pacific Ocean. Specifically, I used benthic survey videos from before, during, and one year following the 2015-2016 El Niño and coral settlement tiles deployed during the three years after the event at 22 sites across the island, to quantify small corals and coral recruits, respectively. Local chronic stress negatively impacted small corals, with densities 47% lower at sites exposed to very high levels of chronic stress prior to the heat stress. The El Niño further resulted in a 56% loss of small corals, particularly for competitive coral species. Following the event, stress tolerant small corals rebounded to pre-El Niño densities within a year, whereas competitive and small corals overall had non-significant increases. I also quantified a low recruitment rate of 8.31 recruits m^{-2} per year (± 1.9 SE) during the three years following the El Niño compared to previous studies around the Pacific; recruits were genetically identified as primarily belonging to the stress tolerant family Agariciidae and the competitive genus *Pocillopora*. Local human disturbance also impacted coral recruitment with densities significantly lower at those with the greatest local chronic disturbance, together suggesting that local disturbance impedes post-settlement survival of recruits and the resilience of young corals during acute stress events. With increased net primary productivity, densities of both small corals and recruits (non-significant) also increased, which could reflect the positive influence of coral heterotrophic nutrition supplements during and after stress events, increasing survivability. Despite very low overall coral recruitment, all island regions did have some recruits, but Vaskess Bay (a bay region on the southern part of the island) had the highest densities. Overall these results indicate the negative consequences combined chronic and acute stressors can have on coral recruits, small corals, and accompanying coral resilience. When viewed together, this work suggests how the resilience is compromised by chronic stressors on Kiritimati and that the recovery trajectory may be variable across the disturbance gradient. Thus, local reef management may provide an avenue for enhancing recovery rates as acute temperature anomalies increase in frequency under our current climate trajectory.

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Dedication

To my family, who taught me to explore the world

Chapter 1 – Introduction

Coral reefs, the world's most biologically diverse marine ecosystems, are well known for their significant benefits to the environment, economy, and society (Burke et al. 2011). Coral reefs are, however, also highly threatened: a global report on reefs in 2011 found that approximately 75% of all reefs are threatened by human activities (Burke et al. 2011). Reefs are facing numerous chronic and acute anthropogenic stressors, including the localized threats of nitrification and overfishing (Hughes et al. 2010), as well as pulse disturbances such as cyclones, ship strikes, crown-of-thorn outbreaks and diseases (Wilkinson 1999). Climate change is, however, arguably now the leading threat to coral reefs worldwide, and affects reefs through both temperature stress and ocean acidification (Hoegh-Guldberg et al. 2007; Hughes et al. 2017a).

The most recent conspicuous example of climate change impacts on coral reefs is the 2015-2016 El Niño event, which triggered the third recorded global coral bleaching event, and caused mass coral bleaching and mortality on coral reefs around the world (Eakin et al. 2016). Notably, on the Great Barrier Reef in Australia, coral cover declined by 30% over the entire area, reaching a maximum loss of 50.3% along the northern 700 km long section over the eight months of heat stress (Hughes et al. 2018). The 2015-2016 El Niño holds the record for the highest cumulative stress measured on coral reefs to date (Claar et al. 2018) and several reefs broke the "not experienced by reefs as yet" (24 degree heating weeks) barrier that Hoegh-Guldberg had described just four years prior to the event (Hoegh-Guldberg 2011; Brainard et al. 2018). There is evidence that climate change will increase the frequency and severity of El Niño warming, especially in the Pacific (Cai et al. 2014). Understanding how such pulse heat stress events interact with the aforementioned chronic and acute stressors is pivotal to protecting the resilience of coral reefs.

Coral recruitment, the settlement of new corals onto a reef, plays a vital role in maintaining a healthy coral community on a reef as living corals are the backbone of a healthy reef ecosystem. Recruitment is also essential to the recovery of coral reefs following disturbance events (Doropoulos et al. 2015; Graham et al. 2015), and recruitment rates have been identified as one of five major factors, along with initial structural complexity of the reef, water depth, herbivorous fish biomass, and nutrient conditions, that determine whether a reef will recover from stress or undergo a regime shift (Graham et al. 2015). Herein, I review the biological process of coral recruitment, natural and anthropogenic factors influencing coral recruitment, differing recruitment responses on recovering reefs, and the studies in subsequent thesis chapters.

1.1. Coral Reproduction and Recruitment

Coral recruitment occurs when a coral larva (i.e., planula) settles onto the reef and metamorphosizes into a visible new member of the community (Figure 1.1; Harrison and Wallace 1990). Corals have four basic sexual strategies: hermaphroditic (i.e., each individual contains both male and female reproductive structures) or gonochoric (i.e., each individual contains reproductive structures of only one sex), coupled with either broadcast spawning or brooding mechanisms for larval development (Harrison and Wallace 1990). Hermaphroditic broadcast spawners are the commonest (Harrison and Wallace 1990; Caley et al. 1996), but for simplicity in this thesis I focus on the two modes of larval development: broadcast spawning and brooding. Broadcast spawning corals release their gametes for external fertilization (Harrison and Wallace 1990) whereas brooding corals release mature larvae (Harrison and Wallace 1990; Doropoulos et al. 2015). Following this release, coral larvae complete their pelagic larval phase, during which they develop (some brooded planulae may be already competent to settle at release) and disperse (Figure 1.1). Finally, the coral larvae search for a settlement location, attach to the substrate, metamorphosizes, and mature into an adult coral colony. After release, coral larvae explore and test the substrate to find a suitable settlement location, and studies have shown that they have preferred substrates (reviewed in Harrison and Wallace 1990; Arnold et al. 2010). Once a larva settles and metamorphoses, it is considered a recruit (reviewed in Harrison and Wallace 1990). The outcome of each of these reproduction and settlement steps may be influenced by a number of factors, however this review will focus on large-scale processes influencing larval dispersal and the factors that directly impact recruitment.

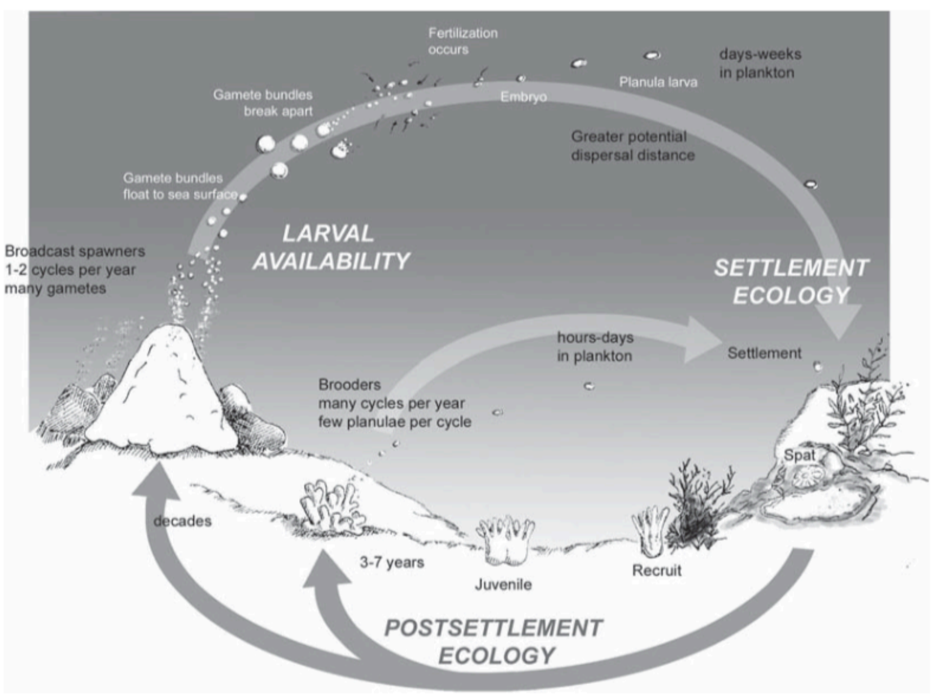

Figure 1.1. Overview of coral life history. Figure from Ritson-Willams et al. 2009; drawn by Mark Vermeij.

1.2. Oceanographic Influences on Dispersal

Hydrodynamics (e.g., wave climate, local and global currents) impact larval dispersal and thus downstream recruitment since coral planulae are weak swimmers. At the scale of an individual island, several factors, including wave energy and compass orientation of the shore, can influence the magnitude of wave exposure that a reef experiences, and thus in turn influence coral recruitment (Sammarco et al. 1991; Edmunds et al. 2010). Wave climate (i.e., seasonal variation in wave exposure and wave energy) has been found at times to be the strongest physical factor that explains the spatio-temporal variation in coral recruitment on reefs (Edmunds et al. 2010). For example, in Palau, successional communities on recovering reefs were strongly influenced by wave exposure, rather than loss of coral cover or reduction of grazing intensity (Doropoulos et al. 2016).

At larger spatial scales, currents can connect different islands and atolls creating coral meta-populations. Using modelling and genetic markers, scientists are researching the ways reefs are connected and the role that connectivity plays in reef ecology (genetics reviewed in Hellberg 2007; Ritson-Williams et al. 2009; Underwood et al. 2014; modelling see: Kojis and Quinn 2001; Treml et al. 2008; Wood et al. 2014, 2016; Monismith et al. 2018). At the regional scale, where islands are close together, there is high potential for inter-island larval dispersal (Treml et al. 2008; Wood et al. 2014). This has implications for management and may be important for mitigating the current decline of coral reefs (Kool et al. 2011). Reefs that have high interconnectedness and high recruitment such as the Great Barrier Reef may need only a limited amount of human-mediated restoration efforts (assuming some reefs remain minimally impacted to serve as recruitment sources). Conversely, isolated reefs such as those in the Commonwealth of the Northern Mariana Islands that have low to moderate recruitment rates may benefit greatly from restoration efforts (Kojis and Quinn 2001).

Scaling up to the ocean basin and global scale, currents can also play an important role in long-distance dispersal, and may connect islands to create ‘stepping stones’ between populations (Trakhtenbrot et al. 2005; Wood et al. 2014). Large-scale oceanographic models have been used to show the connectedness of islands around the world (Treml et al. 2008; Wood et al. 2014, 2016), although they do not have adequate resolution to detect smaller-scale currents and eddies that likely also affect dispersal (Treml et al. 2008; Monismith et al. 2018). For example, the widespread distribution of the genus *Porites* illustrates that there must have been historical long-distance connections amongst reefs (Glynn and Ault 2000), and that the East Pacific Barrier (i.e., over 5,000 km of open ocean which separates islands in the eastern Pacific from ones in the west) has been breached in the past. Recent biophysical dispersal models, however, reveal that the Eastern Pacific is currently isolated due to present day currents flowing east to west under normal conditions and El Niños being unable to facilitate a west to east dispersal as hypothesized (Wood et al. 2016). This supports the idea that the markedly slower reef recovery from disturbances in this area can be attributed in part to its isolation (Graham et al. 2011). Another study, which used simulated dispersal models to compare the impact of global currents on coral recruitment at three geographically isolated Pacific atolls (Johnston, Easter Island, Clipperton Atoll), suggested that only Easter Island is completely reliant on self-seeding (Figure 1.2; Wood et al. 2014). This was attributed to its position within the sluggish surface ocean currents of the South Pacific Gyre, compared to Clipperton, which lies in the strong north equatorial current. Although utilizing large-scale current models to look at connectivity can be useful, results of such studies should be viewed as upper bounds of potential recruitment. Underscoring this point, a dispersal experiment using specially designed drifters between Palau and the Philippines found that they all passed by the islands a couple of kilometers offshore despite following expected routes on the currents (Monismith et al. 2018). Thus, the larvae's limited swimming ability and local hydrodynamics (e.g., buoyancy-driven flows, wind- and wave-driven flows, or internal waves) play a vital role in connectivity, and the small-scale flows should be included in large-scale models (Monismith et al. 2018).

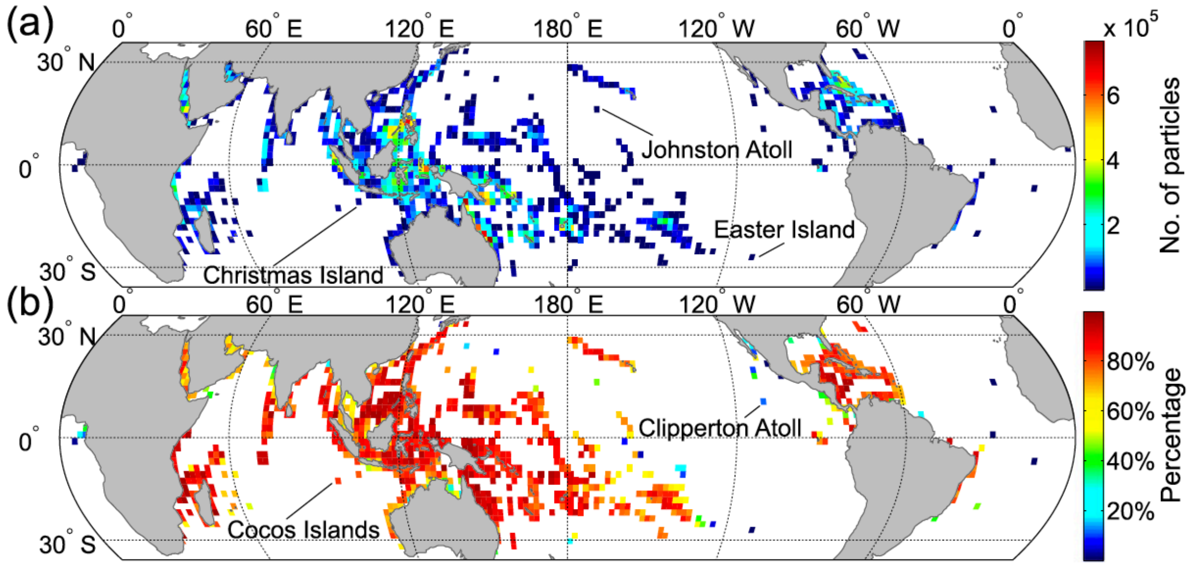

Figure 1.2. Modelled incoming particles (i.e., larvae) a) including self-seeding and b) percentage imported particles that originated from outside the cell. Figure from Wood et al. 2014.

1.3. Post-settlement Recruitment Dynamics

Density-dependence

Although larval survival is density independent during dispersal (Doropoulos et al. 2017a), density dependence can play a role in the probability and success of settlement. Negative effects arise from conspecific interactions, often in the form of competition. Conversely, high densities of adults can positively influence recruitment by leading to an increase in population-level fecundity and downstream recruitment (Bramanti and Edmunds 2016; Doropoulos et al. 2017a). The positive effect of high adult density is important for brooders, since there is a significant stock-recruitment relationship, but the same was not found for spawners as they can have more of an open population structure (Doropoulos et al. 2015). There can also be variations in the level of density dependence at the species level. On Mo'orea, French Polynesia, a positive association was found between adult cover and recruit density of *Acropora* species, while *Pocillopora* species had a negative association (Bramanti and Edmunds 2016). Three hypotheses have been suggested for this effect: 1) high densities of adult colonies might deplete the water of food which is necessary for recruits and juveniles downstream; 2) the existence of host-specific biotic interactions, such as harmful microbial flora associated with adult colonies (Marhaver et al. 2013); 3) the timing of reproduction may differ between species leading them to be exposed to variations in competition (Bramanti and Edmunds 2016). Aside from differences among species, fine-scale settlement preferences can also be impacted by density-driven mortality. One recruitment study found that corals preferably settled in crevices; however, after 30 days the density was the same in crevices and exposed surfaces (Doropoulos et al. 2017a). In fact, while gregarious settlement decreased survival in crevices, it increased it on exposed surfaces (Doropoulos et al. 2017a). Looking forward, it could be expected that density-driven mortalities will decrease as coral cover is predicted to decline with continued climate change.

Structure

Maintenance of reef structure is also important for coral recruitment because corals prefer to settle in the crevices and cryptic areas that are created by complex structure (Doropoulos et al. 2017a). However, settling on dead coral can be risky for new recruits (Loch et al. 2004; Yadav et al. 2016), as coral skeletons can be unstable due to bioerosion (Loch et al. 2004). Thus, decreases in living mature corals weakens the reef structure, which can have significant impacts on recruitment. Studies on the loss of reef structure have recently increased due to technological advances, allowing for fine-scale analyses of the 3D structure of the reef (Burns et al. 2015). In a meta-analysis of reef disturbances and recovery, maintenance of 3D structure was found to aid in the quick recovery of reefs (Graham et al. 2011), and the same study that declared coral recruitment to be one of five determining factors in reef recovery also determined that pre-disturbance structural complexity was one of two factors that could be used to accurately predict the trajectory (i.e., recover or undergo a phase shift) of the reef (Graham et al. 2015). Consequently, they found that reefs that were impacted by disturbances that leave reef structure intact, such as crown-of-thorns sea star outbreaks, had the fastest recovery time (Graham et al. 2011). At Heron Island on the Great Barrier Reef, for example, reefs recovered more slowly after acute events that damaged the structure of the reef, compared to events that simply killed corals (Connell et al. 1997).

An investigation of coral settlement on various types of reef structures revealed a preference for more stable structures, while substrates that could be classified as high risk for causing recruit mortality were generally avoided (Yadav et al. 2016). Thus, the authors of this study concluded that the relative availability and composition of settlement structures (i.e., reef platforms, dead massive corals, consolidated rubble, dead corymbose corals, dead tabular corals, and unconsolidated rubble) could be used as a rough index of the likelihood and rate of reef recovery (Yadav et al. 2016). Since stable structures are needed for recruit survival, recovery will be delayed at reefs dominated by unstable structures (Yadav et al. 2016). This effect was documented on reefs in the Maldives following the 1998 bleaching event (Loch et al. 2004) when a decrease in coral recruitment paralleled an increase in bioerosion that leveled the reef so that only the gross structure was left, creating an inhospitable settlement environment. This imbalance between constructive and destructive processes can delay reef recovery and leave the reef susceptible to further destructive processes such as storm events (Loch et al. 2004).

Biotic influences

From a community perspective, corals are secondary colonizers, meaning that they recruit to the reef after the establishment of primary successional taxa (Doropoulos et al. 2016) , including turf algae, biofilms, coralline algae, and calcareous polychaete worms (Arnold and Steneck 2011). With the exception of turf algae, these earlier successional organisms can facilitate settlement for coral recruits. In contrast, organisms later in the successional stage (e.g., encrusting sponges and bryozoans) tend to be inhibitory or harmful to coral larval settlement and survivorship, creating a race against time to find an appropriate settlement location (Arnold and Steneck 2011).

Fleshy macroalgae, one of the most studied coral competitors, use three primary strategies to compete with corals: physical, microbial, and allelopathic (Doropoulos et al. 2014). Physically, macroalgae can shade nursery microhabitats, making them hostile settlement spaces for corals (McCook et al. 2001; Arnold and Steneck 2011). Macroalgae can also cause abrasions to the coral, encroach on the coral, reduce the water flow, obstruct available settlement space (reviewed in McCook et al. 2001; Birrell et al. 2008; Ritson-Williams et al. 2009), and increase sedimentation levels by sediment entrapment (reviewed in Birrell et al. 2008). In addition to physical disturbance, macroalgae can alter coral microbial communities in the water and on the coral through contact. This is an emerging field, but early studies have shown that macroalgae increase microbial activity, triggering negative effects on the coral larvae (Smith et al. 2006; Vega Thurber et al. 2012; Doropoulos et al. 2014). The third method of macroalgal competition is the production of a secondary metabolite that is transferred to the coral. This metabolite alters vital coral processes by decreasing photosynthesis, increasing incidence of bleaching, and potentially even causing death (Rasher et al. 2011; Andras et al. 2012; Doropoulos et al. 2014).

Many other biotic and abiotic factors can influence coral recruitment, including herbivorous fish abundance (e.g., Hughes et al. 2007; Mumby et al. 2007; Arnold et al. 2010; Dixson et al. 2014; Doropoulos et al. 2017b), coral life history (e.g., Hughes et al. 1999; Vermeij 2005; Bianchi et al. 2006; Underwood et al. 2014; Doropoulos et al. 2018), fecundity of mature corals (e.g., Adjeroud et al. 2007), chemical signals (e.g., Gleason and Hofmann 2011; Dixson et al. 2014), reef sounds (reviewed in Gleason and Hofmann 2011), as well as light exposure (reviewed in Gleason and Hofmann 2011), sedimentation (e.g., Gleason and Hofmann 2011; Humanes et al. 2017), temperature (e.g., Gleason and Hofmann 2011; Figueiredo et al. 2014), and hydrostatic pressure (reviewed in Gleason and Hofmann 2011). Some of these factors, such as herbivorous fish populations, may act as top down controls (Doropoulos et al. 2016) on coral recruitment, while others that influence primary succession, like wave exposure, can have major bottom up influences on coral recruitment (Arnold and Steneck 2011). The ecological constraint from top down and bottom up influences creates a 'recruitment window' for coral by creating multiple barriers and obstacles for the recruit (Arnold and Steneck 2011) and can muddle the understanding of the intricacies of coral recruitment.

1.4. Anthropogenic Influences on Recruitment

Chronic anthropogenic stressors such as overfishing, nutrient runoff, and pollution can all decrease the health of a reef by increasing fleshy macroalgae cover (Hughes et al. 2010). Chronic stressors can also influence coral recruitment at several different stages, from the larval stage to the sources of post-settlement mortality. As previously mentioned, larvae do have some ability to search for suitable settlement substrate so the overall ‘attractiveness’ of a reef is important. Dixson and colleagues (2014) demonstrated this by showing that coral larvae preferred water from a reef inside a marine protected area (MPA) compared to water from a disturbed reef. Further tests showed that coral larvae used chemical cues in the water to detect the quality of the reef, leading them to swim towards water with coral and crustose coralline algae (CCA; a recruitment facilitator) rather than towards water with fleshy macroalgae (Dixson et al. 2014).

Fishing impacts on reefs are well studied, and there is evidence that the resulting loss of herbivorous fishes, which can exert strong top-down control on macroalgae through their grazing, may indirectly impact coral recruitment (McCook et al. 2001; Bellwood et al. 2004). This effect has principally been documented in the Caribbean (Arnold and Steneck 2011), but multiple experiments have been conducted in a variety of locations largely using caged and uncaged comparisons (caged experiments see Hughes et al. 2007; Arnold et al. 2010; Smith et al. 2010; Doropoulos et al. 2017b; other experiments see Mumby et al. 2007; Dixson et al. 2014; McManus et al. 2018). Despite variations among the experiments’ additional controlled and uncontrolled factors, these studies have tended to show that areas with low algal standing stock and high herbivory rates have higher densities of coral recruits (Hughes et al. 2007; Mumby et al. 2007; Arnold et al. 2010; Smith et al. 2010; Dixson et al. 2014; Doropoulos et al. 2017b).

The positive effect of herbivory on coral reef health and successful coral recruitment has therefore traditionally been thought of as an important consideration for management efforts. Studies have shown that marine reserves promote healthy populations of fish which facilitates high levels of herbivory, thus supporting successful coral recruitment (Mumby et al. 2007) and increased juvenile coral density but usually not adult corals or coral cover (Steneck et al. 2018). However, the effectiveness of protected areas on overall coral resilience is debated, and was recently assessed by Bruno and colleagues (2019) as being ineffective, possibly because of ineffective protected areas, uncommon macroalgae dominance, or antagonistic interactions between stressors, but seemingly largely because climate change overwhelms any positive benefits of the MPAs. The effectiveness of marine reserves are also context dependent (Bruno et al. 2019); for example in the Seychelles, it was found that whether a reef was inside or outside a no-take marine reserve had no bearing on whether a reef recovered or underwent a phase shift. This was attributed to herbivore biomass in the fished areas of the Seychelles still being sufficient to promote recovery. Thus, marine reserves may play a greater role in areas where fishing has a greater impact (Graham et al. 2015).

Successful recovery of reefs has been attributed to reduced or a lack of human-induced chronic stressors (e.g., fishing, runoff) by increasing the survival rates of recruits compared to places with chronic stress (Sheppard et al. 2008; Smith et al. 2008; Gilmour et al. 2013). Previous research supports this idea, and a meta-analysis concluded that if enough brood stock is available locally, then semi-isolated reefs with high rates of local recruitment and few chronic stressors could recovery rapidly (Graham et al. 2011). These findings emphasize the implications that local anthropogenic stressors have on coral recruitment rates and reef recovery.

1.5. Coral Recruitment During Reef Recovery

Influences of life history strategy

Corals have several different major life history strategies that also appear fundamental to coral recovery rates (Doropoulos et al. 2015). The first strategy are represented by the 'weedy' corals (e.g., branching *Porites*, some pocilloporids and faviids), which reproduce rapidly and can quickly colonize recently disturbed reefs (Darling et al. 2012). This has been recently documented on Mo'orea following a crown-of-thorns outbreak and a cyclone disturbance, where the recovery was led by a sizable increase in *Pocillopora* cover on the reefs (Edmunds 2018). While their reproduction may be quick, these corals do not have higher fecundity (eggs per polyp) which may be a result of their smaller colony sizes (Darling et al. 2012). These traits make these corals important space holders on a recovering reef.

The second life history strategy, 'competitive', includes fast-growing, broadcast spawners (e.g., *Acropora*, some *Pocillopora,* and *Montipora*), that generally have large colonies that can effectively outcompete other corals for space (Darling et al. 2012). Similar to the weedy corals, some competitive corals (e.g., *Acropora* and *Montipora*) are good colonizers, which has historically led them to be classified as weedy corals (Darling et al. 2012). These traits make these corals highly suitable competitors for opportunistic algae in competition for space (Roff and Mumby 2012). The loss of *Acropora* in the Caribbean left this functional role unfilled, severely impacting the resilience and health of the coral reefs there (Arnold and Steneck 2011; Roff and Mumby 2012).

When the early colonizer role is maintained, recovery to a coral dominated reef state is more likely. For example, the Scott Reef system, an isolated Australian reef in the Indian Ocean, experienced 70-90% coral mortality following the 1998 global bleaching event, but despite mass mortality, the reef returned to its pre-disturbance coral cover and recruitment rates within 12 years (Gilmour et al. 2013). The first six years following the mass mortality had extremely low recruitment, but this was followed by a rapid increase in *Acropora* recruitment and cover, ultimately triggering a full recovery in the following six years. Reefs in Mo'orea, French Polynesia, have also demonstrated quick recoveries following major disturbances that were driven by *Pocillopora* and *Acropora* (Bramanti and Edmunds 2016). However, the overall key to these recoveries was that, although there was a major decrease in *Acropora* and *Pocillopora* cover during the stress, adult colonies did survive to provide a source of larvae for recovery (Baker et al. 2008; Gilmour et al. 2013).

Competitive corals with high recruitment rates are important to catalyze recovery, but they can also suffer high mortality during bleaching events. In such cases other strategies, such as the ‘stress tolerant’ life history strategy, may also play an important role. Stress tolerant corals (e.g., *Porites*) are later colonists that have lower recruitment rates, but are more resistant to stress than competitive species (Adjeroud et al. 2007; Darling et al. 2012). These long-lived corals are slow growing and have longer generation times, along with several other traits that help them survive in harsh environments (Darling et al. 2012). A major advantage that stress tolerant corals have is that they can persist through decade-long periods of recruitment failure, which possibly increases their long-term survival (Hughes and Tanner 2000). Disturbed reefs often experience succession from settlement of competitive species to settlement of stress tolerant species. One such example is after the 1998 bleaching and mortality event in the Chagos Archipelago, where the first dominant recruit species were competitive corals followed by the stress tolerant corals (Sheppard et al. 2008). After five years the first competitive recruits had established themselves, prompting a loop back to the competitive *Acropora* being the dominant taxa again.

Influences of spawning mode and larval input

A coral’s mode of spawning also has an influence on recruitment and recovery following disturbances. The gametes released by broadcast spawners have a delayed competency period, during which they develop for the first part of the pelagic stage and then are competent for an average of 14 days providing the opportunity for longer dispersal (Connolly and Baird 2010). Further opportunity for long-distance dispersal exists when, in the absence of settlement substrate, some larvae can survive for 195 to 244 days in the water column (Graham et al. 2008).

In contrast, brooding corals are particularly important to local recovery since their larvae often settle in their maternal habitat due to their quick competency (Vermeij 2005; Underwood et al. 2014). In addition, the ability for some species to self-fertilize diminishes the impact a decline in adult coral abundances can have following a mortality event (Doropoulos et al. 2015). This skew towards local recovery leads to greater variation among reefs and sites with brooders and has important implications for rates of recolonization by different corals (Hughes et al. 1999). These differences between broadcast spawning and brooding corals can create ‘sources’ and ‘sinks’ for different taxonomic groups, which are important to consider for the recovery of a reef.

In addition to life history traits and spawning modes, the magnitude of larval input (i.e., supply) impacts recruitment after stress. A stressful event, such as bleaching, can cause different responses in coral reproduction. Some corals fail to complete gametogenesis, others experience a reduction in the percent of fertile polyps, number of eggs, and/or decreased sperm motility, yet others will continue business as usual (Baker et al. 2008) or even increase their reproduction (Bianchi et al. 2006). Collecting larval supply numbers is tedious and requires intense field sampling, so recruitment density is most commonly analyzed as a proxy for larval supply.

Post-disturbance recruitment rates

Most common acute disturbances result in a decrease in recruitment (Mumby 1999; Bianchi et al. 2006; Adjeroud et al. 2007; Smith et al. 2008; Rubin et al. 2008; Mallela and Crabbe 2009; Gilmour et al. 2013; Doropoulos et al. 2014; Hernández-Delgado et al. 2014; Holbrook et al. 2018; Hughes et al. 2019). As mentioned above, the Scott Reef system in the Indian Ocean failed to recruit detectably in the first year following mass coral mortality (Gilmour et al. 2013). In the following six years recruitment rates were 6% or lower compared to pre-El Niño levels, leading to the projection that the reefs would take decades to recover. However, once the early cohorts of recruits developed, reproductive output and recruitment reached similar levels compared to pre-bleaching years (Gilmour et al. 2013). Declines in recruitment have also been recorded following other stressful events such as hurricanes (Mumby 1999; Mallela and Crabbe 2009) and ship strikes (Rubin et al. 2008).

Exceptions to this observed pattern have been documented and an increase in recruitment resulted from a disturbance. In Mo'orea, the 2015-16 El Niño prompted some of the highest recruitment rates during and following the event on record (Edmunds 2017). However, relative to many reefs that exceeded eight degree heating weeks (DHW) (Eakin et al. 2016), Mo'orea had minor thermal effects from the El Niño as it did not exceed five DHW (Edmunds 2017). A DHW is a running sum of the accumulated heat stress in an area and is used to compare heat stress among reefs and put it in context of coral stress: 1-4 DHW suggests possible bleaching, at 4-8 DHW bleaching is likely, and 8 DHW and higher indicates that morality is likely (Liu et al. 2012). This lack of severe stress on the corals instead likely provided an environment that promoted coral recruitment (Edmunds 2017). Although it is hypothetically possible that recruitment was not actually related to the thermal regime, this was dismissed by the author because warmer water promotes increased growth rates which can serve to evade the high risks of remaining small (Edmunds 2017). Warmer seawater also decreases the time that the larvae spend in the water column (i.e., settle more quickly) (Harrison and Wallace 1990; Treml et al. 2012; Edmunds 2017), increasing the locality of recruitment (Harrison and Wallace 1990; Treml et al. 2012). However, if the temperature increase is extreme it can result in increased larvae mortality and decreased larval longevity (reviewed in Gleason and Hofmann 2011).

One surprising and potentially hopeful characteristic of coral recruits is that they seem to be better able to survive through bleaching and mortality events compared to their adult counterparts (Mumby 1999; Loya et al. 2001; Baker et al. 2008). In the Caribbean during the 1998 mass bleaching event, many of the coral recruits bleached, but the reefs maintained the same density of recruits (Mumby 1999). Mumby (1999), the first paper to analyze the effects of severe bleaching on coral recruit population dynamics, argued that this indicated that the severe bleaching did not induce recruit mortality, since it seemed unlikely there would have been highly successful rapid post bleaching recruitment within the month after the event. Mumby (1999) laid out four different hypotheses to explain why there was no observed mortality of recruits and low incidence of bleaching: 1) there might be a change in the bleaching susceptibility of the coral's photosynthetic endosymbionts (i.e., Symbiodiniaceae) as corals mature; 2) bleaching stress may not have been sufficient to cause mortality, but instead pushed the recruits into a dormant state; 3) coral recruits fed heterotrophically on epipelic microorganisms in the sediments to sustain their energy intake and mitigate the loss of autotrophic nutrition during bleaching (Tomascik and Sander 1987; Mumby 1999); or 4) coral recruits may have received lower levels of irradiance due to their position in cryptic habitats (Mumby 1999).

Loya and colleagues (2001) later compared the survival of *Acropora* coral recruits to the complete mortality of adult *Acropora* colonies in Japan during the 1998 mass bleaching event. They further analyzed the effect coral morphology had on the result of bleaching and discovered that corals with thick tissue and/or shapes that allow for high mass-transfer rates (i.e., flatter) were more likely to survive. While the recruits of their study species (*Acropora*) do not have thick tissue, they may remain flat for up to two years after settlement. This allows for efficient mass-transfer to eliminate the harmful photosynthesis products that are produced under stress (Loya et al. 2001).

While the mechanisms behind coral recruit survival during bleaching and mortality events remains unresolved, it seems that recruits may have better chances of surviving than adult corals. This at first sounds like good news; however, as bleaching events become more common and mortality wipes out the adult colonies, there will be a shift in the coral population age distribution towards juveniles and recruits, which may ultimately lower the fecundity and downstream recruitment rates (Baker et al. 2008).

The factors covered here and others such as settlement cues, sedimentation, and predation by fish both in the planktonic phase and when settled on the reef, combine to influence recruitment in a variety of ways across multiple scales. The importance of each individual factor varies over space and time. Since recruitment is essential to the regeneration of reefs, recovery trajectories are in turn highly variable (Baker et al. 2008). There have been significant advances in our understanding of coral recruitment, but there are still many unanswered questions that must be addressed to foster reef health and recovery.

1.6. Thesis Research

In this thesis, I sought to advance the understanding of the effects of multiple anthropogenic stressors on coral recruitment. Specifically, I analyzed the impacts of local stressors and climate change amplified heat stress on 1) coral recruitment patterns in the three years following the mass coral mortality triggered by the 2015-2016 El Niño, and 2) small coral (≤5 cm) density spanning the bleaching and mortality event. Data were collected on Kiritimati (Christmas Island), a remote coral atoll in the central Pacific Ocean. The local villages' polarity on the island has created a gradient of human disturbances on the reefs ranging from very highly impacted largely due to fishing and pollution to minimally impacted. Kiritimati was also the epicenter for the 2015-2016 El Niño, experiencing 10 months of elevated seawater temperatures culminating in a 90% decline in live coral cover. I hypothesized that human disturbance would influence the level of successful coral recruitment and the density of small corals and that the heat stress would have a negative impact on small corals. I also predicted that these effects would vary across life history strategies.

In Chapter 2, to investigate coral recruitment patterns following heat-stress induced mass coral mortality, I quantified coral recruits on Kiritimati in the three boreal summers following the 2015-2016 El Niño event. Using recruitment tiles deployed at sites around the island and Sanger sequencing, I examined the effects of heat stress, local human disturbance, and reef substrate changes on coral recruitment rates and taxa composition. I quantified low levels of recruitment compared to previous studies for the three years following the 2015-2016 El Niño. I also show local human disturbance had a predominately negative impact on successful recruitment rates, which were also significantly affected by sampling day and geographic region around the atoll. In addition, this study exposed a complete recruitment failure for the majority of surviving corals on Kiritimati as the recruit taxa was composed of corals from the family Agariciidae and one competitive coral genus, *Pocillopora*. These results provide evidence for the impact a mass coral mortality event has on coral recruitment and highlight the threats of combined acute and chronic stressors on recruitment levels and subsequent recovery of reefs.

In Chapter 3, I quantified the coupled impacts of chronic human disturbance and an acute heat stress event on small (≤5 cm) corals. Corals were counted, identified, and sized in benthic survey videos collected from across the human disturbance gradient over the course of six expeditions that spanned before, during, and after the El Niño. I show that local chronic human disturbance had a significant negative impact on densities of small corals and there was a major decline in small coral density as a result of the heat stress event. Life history strategies influenced the winners and losers and were also variably impacted by regional factors. This study provides evidence of combined effects of heat stress and local disturbance on small corals and may foreshadow the consequences of increased acute disturbance events and anthropogenic impacts on coral reef resilience.

Overall, this thesis enhances our understanding of coral recruitment rates and small coral densities on coral reefs subjected to both local and global stressors. As climate change continues to be a growing threat, coral reefs will suffer under increased stressors from the many facets that climate change impacts. To combat this and help protect reefs, we need a functional understanding of what influences coral recruitment and small coral survivorship as post disturbance reefs are heavily reliant on small corals to restore brood stock levels and on recruitment for the regeneration of reefs. This research adds to the growing body of literature focused on understanding coral reef resilience and supports the need to compile an effective action plan to protect these key ecosystems.

Chapter 2 – Coral recruitment on an isolated atoll following mass coral mortality

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2.1 Abstract

Global and local anthropogenic stressors that cause coral bleaching or mortality can also compromise the density of recruits, thus diminishing a reef's capacity for recovery following disturbance. Whereas in networks of reefs connected by patterns of seawater flow, recruits may be sourced from neighboring reefs following disturbance events that decimate adult populations, on geographically isolated reefs, recruitment is reliant on adult corals at that location or rare cases of extreme dispersal. Although recruitment under temperature stress has been well studied, the effects of combined stressors (e.g., acute El Niño events and local chronic human disturbance) on coral recruitment, and ultimately reef recovery following declines in coral cover, have received less attention. Here, we quantified coral recruitment on settlement tiles at 12 sites that span a gradient of local chronic human disturbance, on Kiritimati, a geographically isolated coral reef atoll in the central Pacific, in the three boreal summers following the 2015-2016 El Niño-induced mass coral mortality. We quantified low recruitment rates (mean = 0.2 recruits per tile (± 0.02 SE) or 8.31 recruits m^{-2} per year (± 1.9 SE); 84% of n=639 tiles had no recruits) compared to previous studies around the Pacific. Recruits, which were genetically identified to family or genus, were primarily from the families Agariciidae and Pocilloporidae. Local human disturbance significantly impaired recruitment rates (93% decline across the disturbance gradient), although the mechanism underlying this difference remains unclear. Recruitment was also significantly affected by sampling day and region of the atoll. These results suggest that local chronic stressors reduce recruitment levels and in turn, may result in variable recovery at different chronic stress levels.

2.2 Introduction

Recruitment of scleractinian corals is an important process in the maintenance of coral reef ecosystems and their recovery following acute disturbance events (Doropoulos et al. 2015; Graham et al. 2015; Edmunds 2018; Sato et al. 2018; Hughes et al. 2019). Recruitment rates have been identified as one of five major factors (along with initial reef structural complexity, water depth, herbivorous fish biomass, and nutrient conditions) that determine whether a reef will recover from acute disturbance or undergo a regime shift to algae dominance (Graham et al. 2015). Reefs today are facing many chronic and acute stressors, with the leading threats (i.e., temperature and ocean acidification) being driven by climate change (Hoegh-Guldberg et al. 2007; Hughes et al. 2017a). The 2015-2016 El Niño event triggered the third recorded global coral bleaching event and caused mass bleaching and mortality on coral reefs around the world (Eakin et al. 2016; Hughes et al. 2017b). Notably, coral cover declined by 30% over the entire Great Barrier Reef in Australia (Hughes et al. 2018) and reefs at the epicenter of the El Niño in the central Pacific lost up to 95% coral cover (Brainard et al. 2018). Evidence indicates that with continued climate change, the frequency and severity of El Niño warming events will increase (Cai et al. 2014), simultaneously increasing the threat to coral reefs and their resilience.

Successful coral recruitment in the face of acute disturbance events, such as short-term temperature anomalies, is reliant on successful gametogenesis that can result in sufficient larval supply, coupled with high settlement and post-settlement survival. Disturbance events can have negative consequences on the generation of coral larvae by causing some coral species to undergo incomplete gametogenesis or experience a reduction in fertilization success, number of eggs, and/or decreased sperm motility, while others are unaffected (Baker et al. 2008) or have increased fecundity (Bianchi et al. 2006). Disturbance events that result in the death of sexually mature corals can also reduce gamete production and impact the overall potential brood stock size (Hughes et al. 2019). If situated within a close network of reefs, local currents and wave conditions can help bolster low recruitment on an affected reef by contributing larvae from others close-by (Kojis and Quinn 2001; Graham et al. 2011; Monismith et al. 2018). However, isolated reefs that are not serviced by currents carrying larvae will have to rely on self-seeding (Wood et al. 2014) and may benefit greatly from active restoration efforts to increase local recruitment (Kojis and Quinn 2001).

Once a coral larva has settled, it undergoes metamorphosis and is subject to a variety of processes that can cause post-settlement mortality. This includes density-dependent dynamics with conspecifics and other sessile reef organisms (Bramanti and Edmunds 2016; Doropoulos et al. 2017a, 2018) and competition with algae (Arnold et al. 2010; Doropoulos et al. 2014). Abiotic and oceanographic factors can also influence post-settlement success such as smothering by sedimentation (e.g., Gleason and Hofmann 2011; Humanes et al. 2017), and plankton as an additional food source (Toh et al. 2013a). Larvae are also subject to the same stressors as adult colonies are; however, recruits can be more resilient to bleaching and mortality events compared to their adult counterparts (Mumby 1999; Loya et al. 2001; Baker et al. 2008). There are several hypotheses on why this might be the case; recruits often settle in cryptic habitats, which provide reduced exposure to irradiance compared to adults (Mumby 1999), and recruits may mitigate the loss of autotrophic nutrition by increasing heterotrophic feeding (Tomascik and Sander 1987; Mumby 1999).

Coral recruitment is primarily quantified by surveying post-settlement recruits, either through the use of recruitment tiles or *in situ* surveys, and identifying them taxonomically. The most common method of identification is by skeletal structure (e.g., Gilmour et al. 2013;

Doropoulos et al. 2014; Bramanti and Edmunds 2016). This method can reliably identify recruits to family, but only rarely to genus or species (Baird and Babcock 2000; Babcock et al. 2003). As a result, recruits are often identified as 'other' or 'unidentified' (e.g., Doropoulos et al. 2014; Elmer 2016; Hughes et al. 2019), potentially veiling key taxa. Using DNA barcoding techniques should improve the taxonomic resolution (typically to coral genus or species, e.g., Shearer and Coffroth 2006; Rubin et al. 2008; Hsu et al. 2014), which may allow for the characterization of roles that other recruit taxa not previously analyzed play in coral reef recovery and resilience. It could also help to tease apart variability within families such as the role of different life history strategies. A coral's life history strategy has been suggested to predict its response to stress events and how it may recover from acute disturbances. Both 'weedy' corals (e.g., branching *Porites*, some pocilloporids and faviids) and 'competitive' corals (e.g., *Acropora*, *Pocillopora,* and *Montipora*) are key to a recovery on a post-disturbance reef (Darling et al. 2012; Bramanti and Edmunds 2016). Weedy corals reproduce rapidly and can quickly colonize open space on a reef, while competitive corals are fast-growing broadcast spawners that generally have large colonies that can effectively outcompete competitors for space on the reef (Darling et al. 2012). Some competitive corals (e.g., *Acropora* and *Montipora*) have been documented to play a vital role in reef recovery, including in the Scott Reef System (Gilmour et al. 2013), Mo'orea (Bramanti and Edmunds 2016), and the Chagos Archipelago (Sheppard et al. 2008).

Local anthropogenic stressors such as overfishing, pollution, and coastal development can confound the natural resilience of a reef and change recovery rates or outcomes (Hughes et al. 2007; Carilli et al. 2009). These chronic, or long-term, stressors can influence coral recruitment through all stages, often by causing an increase in fleshy macroalgae cover on reefs (Hughes et al. 2010) that compete physically, microbially and allelopathically for space on the reef (Doropoulos et al. 2014). Physically, macroalgae can shade (McCook et al. 2001; Arnold and Steneck 2011), cause abrasions, encroach on the coral, reduce the water flow, obstruct available settlement space (reviewed in McCook et al. 2001; Birrell et al. 2008; Ritson-Williams et al. 2009), and increase sedimentation levels by sediment entrapment (reviewed in Birrell et al. 2008). Additionally, macroalgae can alter microbial communities in the surrounding water and within the coral through direct and indirect contact (Smith et al. 2006; Vega Thurber et al. 2012; Doropoulos et al. 2014), while the production of secondary metabolites can also transferred to the coral and alter vital biochemical processes (Rasher et al. 2011; Andras et al. 2012; Doropoulos et al. 2014). Avoiding unsuitable and stressful settlement sites is essential for post-settlement survival of coral recruits, thus using chemical cues in the water, the larvae can use its limited swimming capabilities to search for suitable settlement substrates (reviewed in Ritson-Williams et al. 2009; Gleason and Hofmann 2011).

When there is a lack of substantial human-induced chronic stressors, some reefs have recovered within 12 years from short-term, or acute impacts (Connell et al. 1997; Hughes et al. 2010; Gilmour et al. 2013). A meta-analysis conducted by Graham and colleagues (2011) showed that if there is enough brood stock available locally, then semi-isolated reefs with high rates of local recruitment and few chronic stressors could recovery rapidly. However, previous studies have only focused on either chronic or acute stress, so we have a limited understanding of the impact multiple stressors have on the reef, especially a reef in recovery. In our changing world it is essential to understand the impact of multiple stressors on recovery and resilience as they are hardly ever acting in isolation.

Here, we used settlement tiles to quantify coral recruitment rates on Kiritimati (Christmas Island), the world’s largest atoll, in the three years following the mass coral mortality induced by the 2015-2016 El Niño. Due to its geographic position, there are only rare larval connection opportunities for Kiritimati, and the islands that have the potential to supply coral larvae to Kiritimati (e.g., Jarvis and Galapagos) (Treml et al. 2008; Wood et al. 2016) have also suffered major declines in coral cover from the same El Niño event (Brainard et al. 2018; Vargas-Ángel et al. 2019). Thus, recruitment on Kiritimati is likely a result of self-seeding. The timing of coral spawning also is unknown on Kiritimati (and mostly unknown more generally on central equatorial coral reefs), such that we collected tiles annually, varying timing slightly across years to test the effects of sample timing. We took advantage of Kiritimati's gradients in local chronic disturbance gradient (Baum et al. *in prep*; Watson et al. 2016) and net primary productivity (Walsh 2011a; Magel et al. *in review*) and deployed tiles at twelve sites with high and low levels of each of these factors. We hypothesized that recruitment rates would be low around the atoll for all three years following this mortality event, but that: 1) we would still detect a negative effect of local disturbance on recruitment, potentially due to reduced numbers of reproductive adult corals at higher human disturbance levels, or differences either in the composition of the broader benthic community or the tiles themselves; 2) oceanographic productivity would enhance recruitment rates; and 3) different coral taxa would have variable recruitment rates, with fast growing weedy and competitive corals, such as *Pocillopora* and *Acropora* exhibiting greater recruitment.

2.3 Materials and Methods

2.3.1 Study area and design

We quantified coral recruitment in the three years following the 2015-2016 El Niño-induced mass coral bleaching and mortality event at twelve sites on Kiritimati (Christmas Island, Republic of Kiribati), a remote coral atoll in the central equatorial Pacific Ocean (Figure 2.1).

During this El Niño, Kiritimati's reefs experienced continuously elevated temperatures between June 2015 and April 2016, peaking at 27 Degree Heating Weeks of heat (Claar et al. 2019). This prolonged heat stress resulted in an ~90% loss of coral cover (at surveyed depths of 10-12 m) across the atoll *(Baum et al. in prep*).

Kiritimati supports approximately 6500 people (Kiribati National Statistics Office 2016), most of whom are highly dependent on reef resources for subsistence and income due to the atoll's geographic isolation and lack of alternate livelihoods (Burke et al. 2011; Watson et al. 2016). Most people live in villages on the northwest side of the atoll, which has caused a distinct spatial gradient of local chronic human disturbance across Kiritimati's reefs (Watson et al. 2016). Local disturbance at each study site has previously been quantified by combining both human population and fishing intensity data. The number of people within a 2 km radius of each site (taken from the 2015 Population and Housing Census, Kiribati National Statistics Office 2016) was used as a proxy for immediate point-source disturbances (e.g., pollution and sewage runoff) from villages into the marine environment, and spatial data on fishing intensity around the island was sourced from Watson et al. (2016) (Table A2.1; Baum et al. *in prep*; Magel et al. *in review*). We modelled local disturbance using this combined quantitative index, and for display purposes assigned study sites to local disturbance categories, by assigning all sites with an estimated local disturbance of zero as 'very low' disturbance, and other sites as medium, high or very high disturbance based on breakpoints in the quantitative disturbance levels (Table A2.1; Baum et al. *in prep*; Magel et al. *in review*). These disturbance levels should be regarded as being relative to other sites around the atoll, rather than absolute levels of human disturbance.

In addition to local human disturbance, several biotic and abiotic variables have been quantified on Kiritimati, using *in-situ* methods as part of the Baum Lab's long-term monitoring program on the atoll or through the open source data product, Marine Socio-Environmental Covariates (MSEC) (https://shiny.sesync.org/apps/msec/; Yeager et al. 2017), based upon remotely-sensed data. Wave energy, turbidity, nutrients, dissolved oxygen, and salinity do not appear to vary significantly around Kiritimati (Magel et al. 2019; Baum et al. unpublished data). Net primary productivity averaged from 2003-2013, quantified from MSEC does, however, vary around the atoll, with island-wake upwelling along the leeward (lagoon face) of the atoll (Walsh 2011; Figure A2.1).

2.3.2 Settlement tiles

We first deployed coral settlement tiles at twelve sites on Kiritimati in November 2016 (Fig 2.1). In the subsequent years from 2017 through 2019, we exchanged the deployed tiles for clean tiles during each expedition (July 14 – 30, 2017; June 14 – July 2, 2018 and July 20 – August 3, 2019), and then examined each retrieved tile for recruits (Table A2.2). We refer to tile collection/redeployment by the collection year. Due to field logistics, tiles were not seasoned prior to deployment. At each time point and site, we installed twenty to twenty-one unglazed terracotta tiles (10 cm x 10 cm x 1 cm) along a 60 m transect set on the 10 - 12 m depth isobath, with tiles placed approximately every 4 m. Each tile was deployed on the reef using a stainless-steel screw threaded through a center hole in the tile and secured with a wall anchor into the substrate in the horizontal position. A 1 cm nylon spacer was positioned on the screw between the tile and substrate to provide a cryptic space for coral recruit settlement. Inclement weather and logistical constraints prevented us from resampling all sites each year; in addition, a small proportion of tiles broke while deployed leading to a smaller sample size at some sites (Table A2.2).

After collection, tiles were transported in a cooler of seawater collected from the site with an aerator back to the lab, so as to minimize stress on any coral recruits on the tiles until processing. All collected tiles were processed the same day on which they were collected, as follows: the top and bottom of each tile was first photographed (sides of tiles were not photographed), and the tile was then systematically searched under white light and fluorescent light to locate all coral recruits present. Once a recruit was located, it was photographed using a digital microscope and a scale bar, and the 2D maximum diameter was measured using ImageJ (Abràmoff et al. 2004). The location of the recruit on the tile and the substrate it had settled on were also recorded. Recruits were then removed from the tile carefully so as to not include any substrate and preserved in 100% ethanol for molecular processing.

Coral recruits were identified to the lowest taxonomic resolution possible (family or genus) using Sanger sequencing. To do so, we extracted recruit DNA following the CTAB-chloroform protocol as described by Baker & Cunning (2016; dx.doi.org/10.17504/protocols.io.dyq7vv). PCR and Sanger Sequencing were completed on recruits collected in 2017 and 2018 by the Oceanic Institute of Hawai`i Pacific University. Sanger sequencing on scleractinian mitochondrial cytochrome *c* oxidase subunit 1 (COI) gene was used to genetically identify the coral recruits using primers described by Folmer et al. (1994) as LCO1490: 5'-GGT CAA ATC ATA AAG ATA TTG G-3' and HCO2198: 5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3'. Forward and reverse reads were assembled and trimmed at the primer site in GeneiousPrime (Biomatters), and a sequence similarity search was performed using the GenBank BLASTn plug-in (https://blast.ncbi.nlm.nih.gov/Blast.cgi). Taxonomy was assigned to genus when all BLASTn matches above 97% similarity denoted the same genus. If there was no consensus on genus, the next lowest taxonomic rank was assigned (e.g., family). Thirty-three pairs of reads were unable to form contigs, but sequence similarity searches were performed on five forward reads of high enough quality, resulting in a total of 54 identified recruits. Life history strategies were assigned to each taxa, following the Coral Trait Database (https://coraltraits.org; Darling et al. 2012).

To assess if settlement taxa on the recruitment tiles impacted recruitment or varied with the human disturbance gradient, we quantified tile community cover by identifying 100 randomly placed points on the top and bottom of each tile using CoralNet (Beijbom et al. 2012). We grouped the taxa on the tiles, according to general functional types and abundance, into the following twelve categories: coral, non-coral invertebrates (anemone, barnacle, bivalve, empty bivalve, tube worm, Tunicata, colonial tunicate, and Vermetidae), Bryozoans, crustose coralline algae (CCA), turf/cyanobacteria (Turf/cyano; turf algae and cyanobacteria algae), encrusting fleshy algae (EFA; encrusting fleshy algae and *Peyssonnelia* spp.), sediment, biofilm, bare tile, sponge, other (unknown and *Ulva* spp.), and mobile fauna.

2.3.3 Benthic Community

We also quantified site-level benthic community composition at each time point, in order to assess the influence of the adult coral community (or other benthic taxa) on coral recruitment. To do so, we used the benthic survey data collected at the time the tiles were deployed (i.e., for tiles collected in 2017 we used benthic surveys from November 2016; for 2018 collection we used benthic surveys from July 2017, and for 2019 we used benthic surveys from June 2018). In each time point, at each site, 24 – 30 1 m^2 gridded quadrats were randomly placed on the benthos and photographed along the same 60 m transect as the tiles. Due to inclement weather and logistical constraints, not all sites were surveyed at each time point. Photographs (n = 971) were analyzed in CoralNet (Beijbom et al. 2012) by manually annotating 100 random points following

Baum et al. (*in prep*) and per cent cover was calculated at site level using only points with resolved identities (e.g., did not include points that fell on a dark shadowed area). Four photos (0.42% of photos) had more than ten points that could not be annotated and were excluded from the dataset. Percent cover of hard corals was used as a proxy for abundance of adult corals. We classified coral species that comprised less than 1% of the total hard coral cover on average across the three time points as 'rare'; the exceptions were *Pocillopora grandis* and *Pocillopora meandrina*, which we retained at the species level, despite them only accounting for 0.18% and 0.27% total hard coral cover, respectively, due to their potential importance for coral reef recovery as fast initial colonizers (Darling et al. 2012; Bramanti and Edmunds 2016).

2.3.4 Statistical analyses

We first aimed to examine the influence of day of year (Julian day) sampled (due to the interannual variation in sampling dates), local human disturbance, mean annual maximum net primary productivity (NPP), and region of the atoll (as a proxy for other possible physical and oceanographic differences on the reef on different parts of the atoll aside from NPP) on coral recruitment rates (i.e., number of recruits per site per year). To do so, we used generalized linear mixed models (GLMM) with a zero-inflated negative binomial (ZINB) error structure to accommodate the large proportion of tiles with zero recruits and overdispersion in the data, in which day of the year sampled (Julian day; since collected dates varied between June 14 and August 3 across the three years, and coral spawning timing on Kiritimati is unknown), local human disturbance (continuous), NPP (continuous), and region (Figure 2.1b; categorical variable with 5 levels, following Claar et al. 2019) were included as fixed effects, and site was included as a random effect. One site (H1) stood out as an outlier, in that it had the second highest number of recruits overall (tied with VL4), despite being exposed to a high level of local disturbance

(Figure 2.2c; Table 2.1). We next present a model with all four fixed effects in which site H1 was dropped from the data set (Table 2.2).

Next, we examined how the tiles and taxa on the tiles influenced recruitment. We assessed if coral recruitment rates varied depending on tile side (i.e., top, side, or bottom) using GLMMs with a ZINB structure and site as a random effect. We then compared the tile settlement community: 1) between the tops and bottoms of tiles using a permutational multivariate analysis of variance (PERMANOVA), with site as a blocking factor (implemented using the 'strata' term in 'adonis'), and *P* values generated from 9,999 permutations based on a Bray-Curtis dissimilarity matrix; and 2) across the local human disturbance gradient, using a PERMANOVA with both local disturbance and site as factors, and *P* values generated from 9,999 permutations based on a Bray-Curtis dissimilarity matrix. We conducted separate analyses for tile tops and tile bottoms. Then, to assess if differences in coral recruitment rates across the local disturbance gradient might be determined by differences in the tile community, we grouped tile settlement organisms on each side as either coral recruitment inhibitors or facilitators, and tested the effect of local human disturbance on each side of the tile with site as a random effect, using a binomial logistical regression weighted against the total number of usable points on the tile.

To investigate whether benthic community composition had an effect on settlement we ran GLMMs with substrate percent cover and Julian day as fixed effects and site as a random effect, with a negative binomial (NB) structure. Substrates tested were hard coral, CCA, turf algae, fleshy macroalgae, all algae (turf + macroalgae), and sand/sediment. Due to the low abundance of recruits, we tested one substrate at a time. Next, influence of human disturbance on benthic community was tested using a PERMANOVA with both human disturbance and site as fixed factors. *P* values were generated from 9,999 permutations based on a Bray-Curtis dissimilarity matrix. To further test the influence of human disturbance on hard coral cover (proxy for reproductive adult abundance) we ran a binomial logistical regression with human disturbance as a fixed factor, site as a random effect, and weighted against the total number of usable points in the photoquad.

Finally, to investigate if sampling dates impacted the taxa of coral recruits on the tiles, we ran a PERMANOVA with site as a blocking factor using the 'strata' term in 'adonis' and *P* values generated from 9,999 permutations based on a Bray-Curtis dissimilarity matrix. A similar analysis was performed to explore if island region had an effect on recruit taxa.

We conducted all statistical analyses using the statistical software R v. 3.6.1 (R Core Team 2019). All GLMM and logistic regression models were run using the package *glmmADMB* (Fournier et al. 2012; Skaug et al. 2016) and PERMANOVAs were run with the *vegan* (Oksanen et al. 2016) package. Prior to analysis, the continuous independent variables (local disturbance, net primary production, Julian day) were standardized to a mean of zero and a standard deviation of 0.5 using the 'rescale' function in the *arm* package (Gelman et al. 2018).

2.4. Results

In total, we enumerated 129 coral recruits (Figure 2.2a; mean = 0.2 per tile ± 0.02 SE; 84% of tiles had 0 recruits) from 639 tiles (recruitment rate: 8.31 recruits m^{-2} per year ± 1.9 SE) deployed around Kiritimati in the three years following the 2015-2016 El Niño (2017: 60 recruits; 2018: 22 recruits; 2019: 47 recruits). Recruits ranged in size from 0.5 to 442 mm^2 and had an average area of 24 mm^2 (± 4.9 SE). We were able to genetically identify 54 recruits; the majority of these belonged to the coral family Agariciidae (47) which, on Kiritimati, have a stress tolerant life history strategy (Figure 2.3a, Table A2.3). Six recruits were *Pocillopora* sp.;

one aligned closest to *Polycyathus* (97.9% similarity); however, this coral genus is not currently known to occur in the Northern Line Islands.

Our models suggest that coral recruitment (number of recruits per site per year) was most strongly influenced by local human disturbance (Table 2.2; Figure 2.2c). Coral recruitment declined significantly across the human disturbance gradient, where recruitment was 93% lower at sites exposed to very high levels of chronic stressors compared to very low exposed sites. Coral recruitment was positively associated with sampling day (Julian day), with fewer recruits observed in June and more in mid-July and early August (Table 2.2; Figure 2.2b). The effect of region was variable between the two models. When site H1 was included, all regions were estimated to have fewer recruits than Vaskess Bay, although only South Lagoon was significant (Table 2.2). However, when site H1 was excluded, no significant differences in recruitment were detected across regions (Table 2.2). Neither sampling day (pseudo F = 0.76, R^2 = 0.016, P = 0.3062) nor region (pseudo F = 0.94, R^2 = 0.079, P = 0.432) significantly influenced the taxa of the recruits. There was a tendency for coral recruitment to increase with oceanographic productivity (NPP), but the effect was statistically non-significant.

The recruits in this study primarily settled on either CCA (47%) or bare tile (40%); the remainder settled on the red alga *Peyssonnelia* spp. (6.98%), tube worm (0.78%), barnacle (0.78%), or other substrates (8.5%). Recruit settlement substrate varied slightly amongst taxa, with Agariciidae recruits settling mainly on bare tile (47%), followed by CCA (43%) or *Peyssonnelia* (11%), and *Pocillopora* recruits settled mainly on CCA (50%), followed by bare tile (33%) or *Peyssonnelia* (17%). The *Polycyathus* sp. recruit settled on a tube worm.

Recruits settled preferentially on the bottoms of tiles (96 recruits) compared to the tops (5 recruits, z = -6.44, P < 0.001) or sides (27 recruits, z = -5.82, P < 0.001). The communities of fouling organisms on both the bottom and top of each tile were significantly different at each site (pseudo F = 480.43, $R^2 = 0.28$, $P < 0.0001$); photographs were not taken of the sides so these communities could not be assessed. The bottom of the tiles were dominated by EFA (35.54 % ± 0.87 SE), bryozoans (23.89 % ± 0.79 SE) and sponges (15.82 % ± 0.63 SE). Tile, biofilm and CCA, which are known to facilitate recruitment, accounted for only 1.14 % (± 0.14 SE), 10.55 % (± 0.42 SE), and 3.26 % (± 0.22 SE) of tile bottom communities, respectively, while turf algae and cyanobacteria made up less than 5% (4.89 % ± 0.30 SE) (Figure 2.4b). Although tile tops were also dominated by EFA (42.63 % ± 1.16 SE), the next most common substrates were recruitment inhibitors, including turf algae and cyanobacteria (22.05 % ± 0.80 SE). CCA cover was higher on tile tops (20.1 % ± 0.82 SE) than bottoms (3.26 % ± 0.22 SE) and sediment also made up a proportion of the substrate (10.4 % ± 0.70 SE) (Figure 2.4a). Bottom and top tile community each significantly differed across the continuous human disturbance gradient (Top: pseudo F = 42.32, $R^2 = 0.049$, $P < 0.0001$; Bottom: pseudo F = 115.05, $R^2 = 0.15$, $P < 0.0001$). In both cases, recruitment facilitators decreased as human disturbance increased; however only the bottom was a significant result (Top: parameter estimate = -0.8211, $z = -1.495$, $P = 0.135$; Bottom: parameter estimate = -0.9003, $z = -8.157$, $P < 0.0001$).

Hard coral cover at 10 - 12 m depth on Kiritimati averaged < 5% (4.86 % ± 0.55 SE) across sites and survey time points (n = 33; between November 2016 – June 2018) and was significantly lower at higher levels of chronic human disturbance (parameter estimate = -1.7838, $z = -3.117$, $P = 0.00183$) where sites with very high levels of exposure had an average of 3.3% (± 1.54 SE) cover and sites with very low had an average of 5.14% (± 0.39 SE). Fleshy macroalgae and turf algae averaged 13.35% (± 2.67 SE) and 27.85% ± 3.00 SE respectively across the sites and time points. The dominant substrate on the reef during this study was sand and sediment (44.05% ± 3.87 SE). CCA and *Peyssonnelia* were the rarest of the main substrate groups at 9.88% (± 1.51 SE) (Figure 5a). None of these major substrate group were found to have a significant effect on coral recruitment when tested separately (hard coral: z = 0.59, P = 0.554; macroalgae: z = -0.67, P = 0.501; turf: z = -0.58, P = 0.565; macroalgae + turf: z = -0.97, P = 0.334; sand + sediment: z = 0.34, P = 0.737; CCA: z = 1.38, P = 0.166) although, consistent with other models, Julian day was significant in all benthic substrate models. Benthic community composition varied significantly with local human disturbance (continuous) (pseudo F = 11.25, R^2 = 0.165, P = 0.0002).

2.5 Discussion

Overall, we observed very low levels of recruits at sites around Kiritimati in the three years following the 2015-2016 El Niño event. We found evidence that local disturbance impaired recruitment rates, in that this was the strongest and most significant effect in our models of recruitment. The mechanism underlying this difference remains unclear, however: benthic community composition differed significantly across the disturbance gradient, with significantly lower hard coral cover at sites with the greatest disturbance, but we did not detect an influence of hard coral cover or any other benthic substrate on coral recruitment. We speculate that this might reflect the low variability in hard coral cover across the atoll (sites ranged from 0.07% to 12.28%). Impaired coral recruitment at disturbed sites might also arise from differences in tile communities, and we did detect a significant decrease in recruitment facilitators on tile bottoms (where most recruits settled) as disturbance increased; however, we were unable to directly test the effect of tile communities on recruitment. It is possible that other factors related to local disturbance, such as habitat complexity (Graham et al. 2011; Magel et al. 2019), may underlie this observed relationship. We also quantified higher recruitment rates in July – August than in June, and the small size of recruits suggests that coral reproduction on Kiritimati may occur in late boreal spring or summer. Finally, we found evidence that NPP had a non-significant positive effect and island region (proxy for other oceanographic and abiotic conditions) was largely non-significant.

Recruitment failure, or decreased levels of recruitment, following acute disturbances have been documented previously on reefs in many parts of the world (Sheppard et al. 2008; Gilmour et al. 2013; Hughes et al. 2019). There are no recruitment tile data for Kiritimati prior to the El Niño that can be used to compare recruitment levels and assess the impact the heat stress and subsequent mass coral mortality had on recruitment rates on Kiritimati. However, there have been many recruitment studies using settlement tiles conducted in the Pacific Ocean including one on Palmyra, another atoll in the Northern Line Islands, in 2014. The recruitment rate was 92.71 recruits/m^2 (870 recruits surveyed on 391 tiles) (Elmer 2016) which is higher than the recruitment rate in this study by eleven-fold. In addition, recruitment rates on other reefs prior to acute disturbances around the Pacific Ocean were 27 to 61 times higher than levels found in the present study (Hughes et al. 1999; Edmunds et al. 2010; Cameron and Harrison 2016) indicating that recruitment on Kiritimati was considerably lower compared to healthy reefs, possibly indicating near recruitment failure. The only investigation of recruitment on Kiritimati prior to this study used different methods and measured corals roughly an order of magnitude larger (mean maximum width of recruits in this study = 4.7 mm ± 0.47 SE, surveyed recruit size range in Sandin et al. 2008 = 1-5 cm) thus was not comparable (Sandin et al. 2008).

The low recruitment levels that we observed on Kiritimati following the El Niño event were likely triggered by the mass mortality of corals across the island as a result of the extreme heat stress. The loss of adult coral can cut off the supply of recruits (Gilmour et al. 2013; Hughes et al. 2019) and, due to Kiritimati's geographical isolation, the only potential outside sources of larvae were from other reefs that also experienced mass coral loss in recent years (e.g., Jarvis Island, Galapagos) (Treml et al. 2008; Wood et al. 2016; Brainard et al. 2018; Glynn et al. 2018; Vargas-Ángel et al. 2019). Similar results were documented on the Scott Reef System, an isolated island in the Indian Ocean, which experienced complete recruitment failure within the first year following the 1998 El Niño (Gilmour et al. 2013). Recruitment rates remained below 6% for 6 years post-El Niño, but were then able to recover to pre-disturbance levels within 10 years, while subsequent coral cover, generic diversity and community structure recovered within 12 years. This fast recovery was attributed to two things 1) the recovery of *Acropora* and 2) the lack of local chronic stressors (Gilmour et al. 2013) thus there is potential for recovery on Kiritimati despite low recruitment rates.

Following acute disturbances on reefs, some weedy (e.g., *Pocillopora*) and competitive (e.g., *Acropora*) corals excel at colonizing open space (Tamelander 2002; Adjeroud et al. 2007; Gilmour et al. 2013; Edmunds 2017, 2018; Hughes et al. 2019). In some cases, shifts from previously dominant acroporid and pocilloporid recruits to agariciids have also been documented (McClanahan 2000; Zahir et al. 2002; Bianchi et al. 2006). In the present study, we similarly found the majority of recruits were from the Agariciidae family, with a lack of any acroporid recruits and only a small number of pocilloporids. Surveys from around Kiritimati have discovered that the El Niño caused the local extinction of adult *Acropora* colonies (Baum et al. *in prep*), which likely influenced the loss of acroporid larval supply (Hughes et al. 2019). In contrast, Baum et al. (*in prep*) found survival of some adult *Pocillopora* spp. colonies around the island that possibly supplied the few *Pocillopora* recruits that were found on the settlement tiles.

On Kiritimati, there were stress tolerant reef building corals including *Porites lobata*, and species from the Merulinidae family that survived the El Niño (Baum et al. *in prep*) but these corals were not represented on the tiles in 2017 or 2018. We suggest three explanations for this lack of recruits from representative surviving corals on the reef. First, adult colonies might be prioritizing their recovery (e.g., from partial mortality, lipid stores) and diverting energy away from sexual reproduction (reviewed in Harrison and Wallace 1990). Following the 1998 El Niño, reproductive output of surviving *Acropora* colonies was nearly zero on Scott Reef (Gilmour et al. 2013) and reduced gamete production in colonies that survived bleaching events has been reported across multiple regions and genera in the following year(s) (Szmant and Gassman 1990; Hirose and Hidaka 2000; Ward et al. 2000; Michalek-Wagner and Willis 2001; Mendes and Woodley 2002; Sudek et al. 2012; Howells et al. 2016). In addition to low gamete production, laboratory fertilization success following a bleaching event was either greatly reduced (Hirose and Hidaka 2000) or required at least 100 times higher sperm concentration to match fertilization levels similar to those of previous years (Omori et al. 2001). Most studies only investigated the first year after bleaching, however Michalek-Wagner (2001) reported that the soft coral, *Lobophytum compactum,* had significantly reduced egg size and fecundity for two annual spawning events after a simulated severe bleaching event. In another study, reproduction took the longest to recover after bleaching (compared to tissue depth, skeletal extension rate, and density band formation) in severely bleached colonies of *Montastraea annularis* (Mendes and Woodley 2002). They experienced reproductive failure in the first year and low reproductive output during year two despite completing gametogenesis and spawning (Mendes and Woodley

2002). The mechanisms for these results were untested but many of these papers suggested that energy levels required for reproduction had not yet recovered after depletion due to the loss of symbionts during bleaching (reviewed in Harrison and Wallace 1990). Rates of replenishing energy reserves are relatively unknown, especially following long periods of bleaching, but following a month of laboratory-induced bleaching, energy reserves and tissue biomass recovered in 8 and 1.5 months for *Porites compressa* and *Montipora capitata*, respectively (Rodrigues and Grottoli 2007). Thus, it is plausible that corals on Kiritimati that survived unprecedented levels of heat stress for 10 months (Claar et al. 2019) are not yet able to successfully reproduce.

Second, successful gametogenesis and fertilization may have occurred but resulted in incompetent larvae due to reduced resources from recovering parent colonies. While this has not been directly studied, previous research has looked at settlement success and larval competency under stressors and found that increased temperature can decrease larval survivorship and settlement success (Bassim and Sammarco 2003; Randall and Szmant 2009) and increase time spent by larvae in a swimming/searching mode (Bassim and Sammarco 2003). The same impact was found with increases in nutrients (e.g., ammonium) and sedimentation (Babcock and Smith 2000; Bassim and Sammarco 2003). Thus, in our study system we may be seeing a lag effect of the impacts of stress on *Porites* and Merulinidae larval competency.

Lastly, it is possible that the larvae did not choose to settle on the recruitment tiles. However, during a recruitment study on Palmyra, poritids were the second most common recruit (Elmer 2016), which suggests that they do not have an aversion to recruitment tiles. While it is beyond the scope of this study, we do not anticipate that there was an Allee effect due the similar spatial distribution of *Porites* and Merulinidae colonies compared to pre-El Niño distribution.

Although the surveys around the island showed a loss of adult colonies, there were a number of small corals, which most likely recruited just before or during the El Niño and survived the event (Chapter 3). Kiritimati's reefs are now reliant on those corals to reach sexual maturity and start reproducing. This delay in coral recruitment could have serious implications for the reef by allowing time for other colonizers, such as macroalgae, to take over the free reef space (Arnold and Steneck 2011) and in particular providing those algae time to gain a strong foothold on the reef making it difficult for corals to fight for space in the future. Chronic stress, such as human disturbance, can cause an initial reduction in coral cover and provide free space for algal growth (Smith et al. 2016), which may then promote a positive feedback for high algal cover within the reef ecosystem. In our study, sites exposed to medium and very high levels of local chronic stress had fewer recruits. This chronic human disturbance can influence a variety of reef traits such as increased algal cover through nutrient input and/or over-harvesting of herbivorous fish and poor water quality (Walsh 2011). These traits can decrease settlement success and, if they do settle, increase post settlement mortality (Arnold et al. 2010; Gleason and Hofmann 2011). However, in this study, no significant effect was found for any of the major benthic substrate types on recruitment, but benthic community did vary across the human disturbance gradient and hard coral was the least abundant followed by recruitment facilitators (i.e., CCA and *Peyssonnelia*). Recruitment inhibitors and abiotic substrates increased with greater human disturbance, which may limit coral settlement and increase post settlement mortality due to competition or smothering (reviewed in Ritson-Williams et al. 2009). Further, the lack of suitable substrate for settlement may force coral larvae into a longer planktonic larval stage while they search for an appropriate settlement location, causing them to deplete energy reserves and place their post-settlement survival at risk (Arnold et al. 2010).

Net primary productivity quantified from MSEC had a non-significant positive effect on recruitment. While there have been no studies on the ingestion of phytoplankton in scleractinian species, studies have shown the active removal of phytoplankton from waters above reefs suggesting that coral (along with other benthic taxa e.g., sponges and soft corals (Fabricius and Klumpp 1995)) ingest phytoplankton (reviewed in Houlbrèque and Ferrier-Pagès 2009). NPP could also be used as a proxy for other particulate loading in the water which could be beneficial for corals as they can feed on a wide range of particulates including zooplankton, dissolved and particulate organic matter, and picoplankton (reviewed in Houlbrèque and Ferrier-Pagès 2009). The majority of studies on the heterotrophic feeding of corals has been on adult colonies, however three coral species: *Pocillopora damicornis*, *Acropora hyacinthus*, and *Seriatopora caliendrum*, were able to heterotrophically feed within 8 days of settlement (Cumbo et al. 2012; Toh et al. 2013b, 2013a). This ability of coral recruits to supplement their supply of energy has been suggested to increase survivorship rates (Toh et al. 2013a), consequently future studies should investigate if increased natural levels of NPP (or other suspended material) influences survivorship of recruits.

Abiotic factors such as local currents and water movement can also influence the dispersal and settlement location of larvae. Island region around Kiritimati, which was used as a proxy for oceanographic and abiotic conditions at each tile deployment site for this study, had a largely non-significant effect. Surprisingly, the Bay of Wrecks had fewer recruits than Vaskess Bay despite it having some of the highest coral cover before the El Niño (Baum et al. *in prep*), while the north and midwest coast of the island had a greater number of recruits when the anomaly site H1 was removed. Although local current patterns around Kiritimati are currently unknown, it is likely they are affecting these patterns of recruitment. Regional and oceanographic conditions such as tidal flushing and upwelling at the mouth of the lagoon may further explain why recruitment is higher than expected at site H1 and mid lagoon. Thus, future studies should investigate the influence of both local oceanographic and abiotic conditions on coral recruitment.

Caveats and Future Directions

Due to unknown spawning patterns on Kiritimati it is possible that the tiles were deployed and sampled at inopportune times to accurately capture recruitment. Most recruitment studies using settlement tiles deploy the tiles prior to coral spawning and collect them following the event (e.g., Gilmour et al. 2013; Doropoulos et al. 2014; Hughes et al. 2019), or conduct multiple samplings in a year (e.g., Edmunds 2017). Deploying tiles too far in advance of spawning events could give other colonizers time to settle on the tile and reduce the space available for recruitment (Arnold and Steneck 2011; Elmer et al. 2018). In the present study, the majority of tiles were dominated by recruitment facilitators (e.g., CCA or biofilm) even after a year of deployment, indicating the presence of suitable substrate for larvae. In addition, it seems that tile deployment and sampling are occurring around possible spawning times when compared with known spawning times on other islands in the Central Pacific or Hawaii (e.g., *Acropora* on Palmyra spawning in spring, broadcast spawning in Hawaii occurs in late spring and summer, and western Central Pacific faviid corals spawn in June and July and *Platygyra* and *Porites* spawn in July) but this should be investigated in future studies. While there is a possibility that our sampling could have been too early to capture recruits from the yearly broadcast spawning events, we found no effect of Julian day on recruitment taxa although it may be possible that during the seven to twelve months before sampling, recruits that may have settled soon after tile deployment suffered mortality. Sampling immediately following spawning events can be key for quantifying and characterizing initial recruitment, but identifying those recruits that survive past one year, such as what was done in the present study, ensures that focus remains on the contribution of recruitment to long-term reef recovery.

Using genetic barcoding to decipher the taxa of the recruits on the tiles helped to reveal the most numerous taxonomic family that recruited in the two years following the El Niño. This would not have been achieved following the most common method of recruit identification, which uses skeletal morphology for identification as described by Babcock and colleagues (2003). In this article, there is only one species from the family Agariciidae, and it is not currently known to occur on Kiritimati nor did any of the sequences align with it. This would have left the majority of the recruits labeled as unknown, veiling the lack of recruits from the major reef building corals that survived on Kiritimati. Although barcoding proved to be useful, using only the CO1 region did not allow for greater taxonomic resolution past the Agariciidae family and the *Pocillopora* genus. In the future, using multiple gene regions (e.g., Hsu et al. 2014) may allow for finer taxonomic identification that may reveal important species roles in recruitment during recovery.

Moving forward, studies should continue to quantify recruitment rates on coral reefs following acute disturbances in order to gain a comprehensive understanding of reef recovery and the factors that influence it. Efforts also should be made to enhance molecular identification of coral recruits to further understand the impact stress events have on varying taxa and how different species contribute to reef recovery.

Conclusion

Overall, our results show that reefs on Kiritimati had relatively lower coral recruitment compared to common pre-disturbance levels seen on other reefs, indicating that it may be experiencing near recruitment failure with variable recruitment rates across the island influenced by local chronic human disturbance in the two and a half years following the mass coral mortality. Recruitment failures have been documented on reefs around the world following acute disturbance events (Sheppard et al. 2008; Gilmour et al. 2013; Hughes et al. 2019), which greatly compound the resilience of coral reefs. With the expected increase in disturbance events and severity, coupled with localized chronic human disturbance, coral reefs' ability to maintain coral dominance through resistant adults and recruitment is imperative to understand and maintain.

Table 2.1. Total number of recruits and mean recruit per tile (± SE) across all three time points per site and for the island.

Site	Number of recruits	Number of sampled tiles	Mean recruit tile $^{-1}$ ± SE
VL1[1]	3	40	0.075 ± 0.0422
VL3	29	57	0.509 ± 0.029
VL4	21	56	0.375 ± 0.094
M1	13	58	0.224 ± 0.0552
M2	6	59	0.102 ± 0.046
M3	5	54	0.093 ± 0.040
M6	3	58	0.0517 ± 0.029
M9[2]	4	33	0.1212 ± 0.072
H1	21	57	0.368 ± 0.089
VH1	5	54	0.093 ± 0.048
VH2	9	52	0.173 ± 0.060
VH3	10	61	0.164 ± 0.053
Island total	129	639	0.202 ± 0.020

[1] Due to weather VL1 could not be sampled in 2019

[2] Due to weather M9 could not be sampled in 2018

Table 2.2. Model results (parameter estimates) for fixed effects from generalized linear models examining change in coral recruitment for all data (a) and for a data set with site H1 removed (b). Site (11 levels (a); 10 levels (b)) was included as a random effect for all models. Bold indicates significant difference from baseline levels (i.e., Vaskess Bay) values at $\alpha = 0.05$; asterisks indicate levels of significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Red shaded boxes denote variables with negative estimates indicating a decline compared to baseline.

	Day sampled	Region				Productivity	Human Disturbance
Model	**Julian Day**	**NL**	**ML**	**SL**	**BOW**	**NPP**	
a) All data							
Julian day + region + NPP + human disturbance	**0.612***	-0.255	-1.157	**-1.421***	-0.931	2.460	**-2.047****
b) Data set with site H1 removed							
Julian day + region + NPP + human disturbance	**0.669***	2.868	3.074	-0.9348	-1.129	2.531	**-5.103*****

Island Region: *NL* = North Lagoon, *ML* = Mid Lagoon, *SL* = South Lagoon, *BOW* = Bay of Wrecks; Productivity: *NPP* = Net Primary Productivity

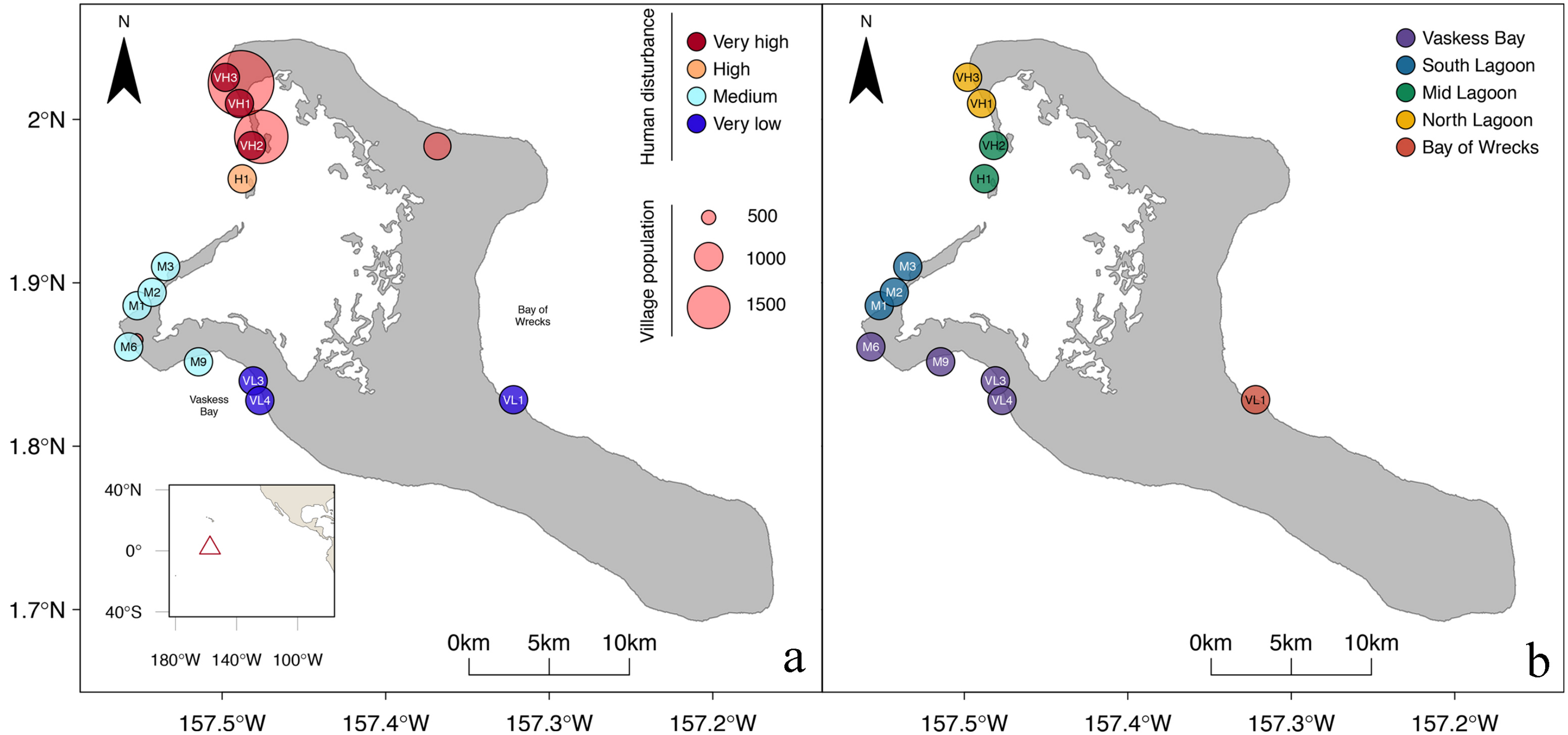

Figure 2.1. Map of Kiritimati (Christmas Island) showing coral recruitment tile deployment sites, categorized by (a) local human disturbance. Village population (red circles) is represented by bubble size. Inset shows Kiritimati's location in the equatorial central Pacific Ocean (open triangle); and b) regions of the atoll. Importantly, from a sampling perspective, sites exposed to very high, medium and very low disturbance levels each occur in two distinct regions of the atoll, helping to disentangle these two factors.

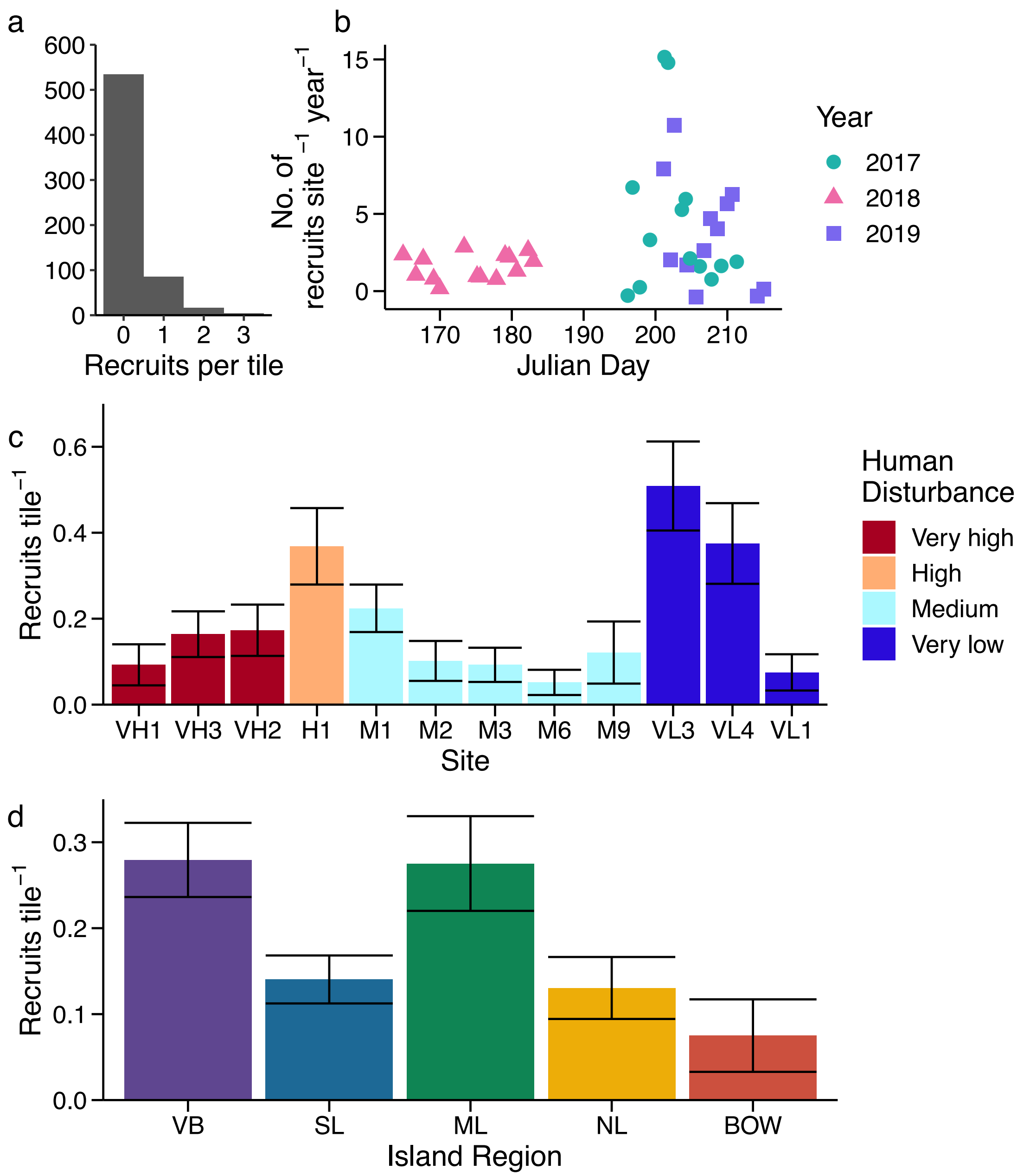

Figure 2.2. Coral recruits (a) per tile for the three years (n = 639 tiles), (b) per sampling day (Julian day) at each site, categorized by collection year, and mean (± SE) recruit per tile for each (c) site along the human disturbance gradient and (d) island region (VB = Vaskess Bay, SL = South Lagoon, ML = Mid Lagoon, NL = North Lagoon, BOW = Bay of Wrecks), over the three years. Colors in c correspond to figure 2.1a and d with figure 2.1b.

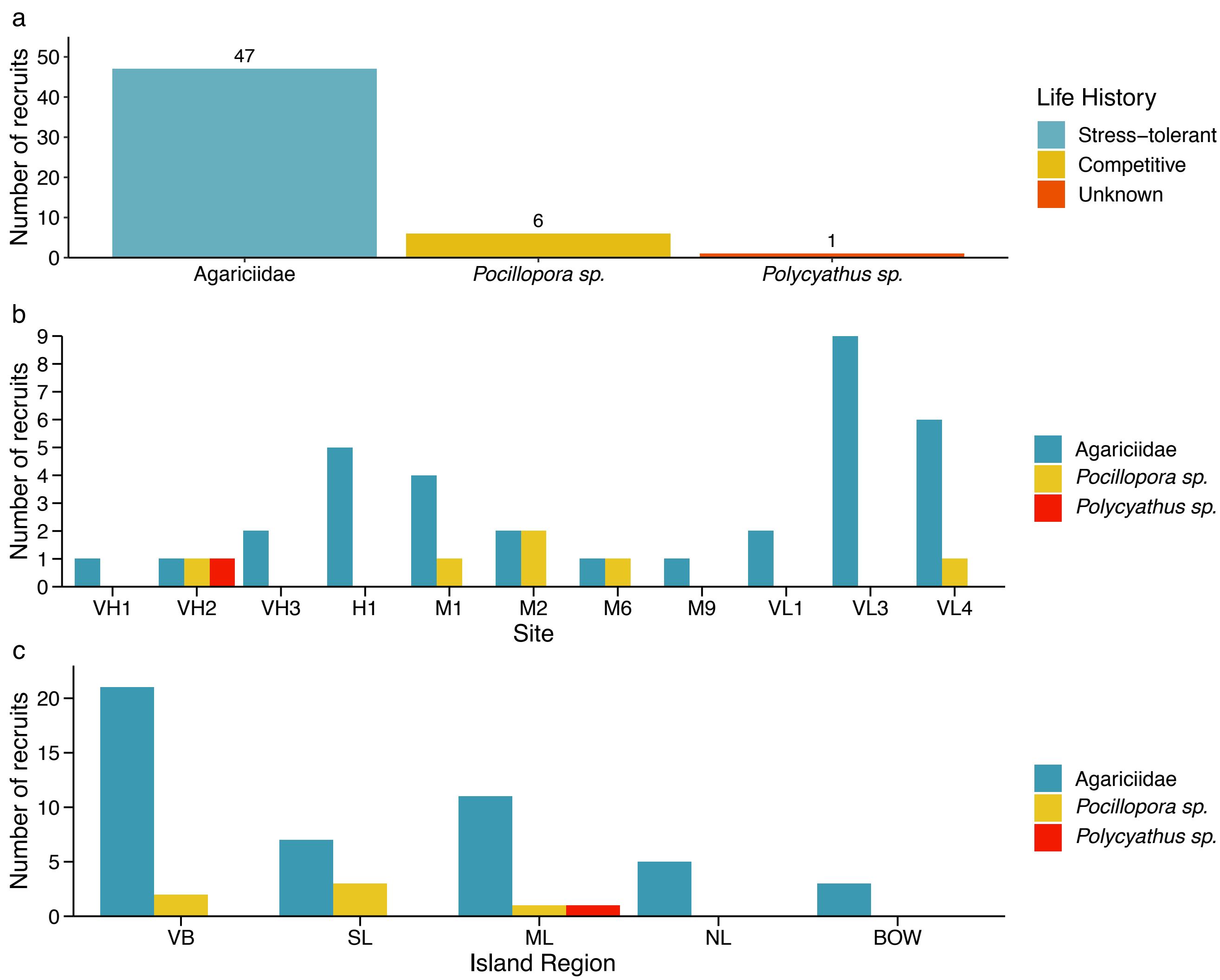

Figure 2.3. Number of recruits from recruitment tiles deployed in 2016 and 2017, that could be identified by taxon (n=54), categorized by (a) taxa and life history strategy (https://coraltraits.org), (b) sites along the human disturbance gradient (VH = very high, H = high, M = medium, VL = very low), and (c) island region (VB = Vaskess Bay, SL = South Lagoon, ML = Mid Lagoon, NL = North Lagoon, BOW = Bay of Wrecks; see Figure 2.1b).

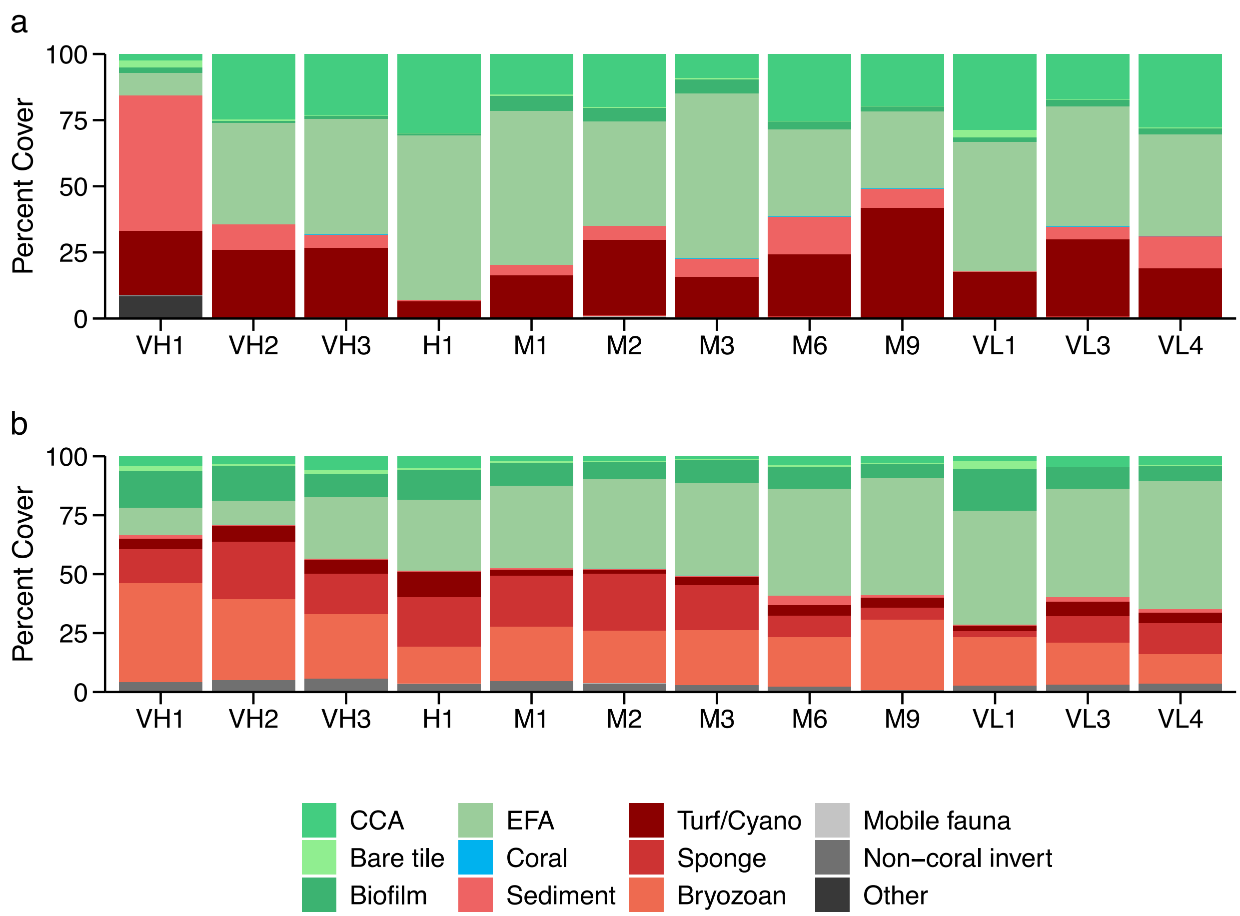

Figure 2.4. Community cover on the (a) top and (b) bottom of the recruitment tiles at twelve sites across the human disturbance gradient (VH = very high, H = high, M = medium, VL = very low), shaded by recruitment facilitators (green) and recruitment inhibitors (red); neutral substrates include coral (blue), other organisms or algae taxa (greys), and unknown substrates. EFA = encrusting fleshy algae, CCA = crustose coralline algae, Turf/Cyano = turf algae and cyanobacteria.

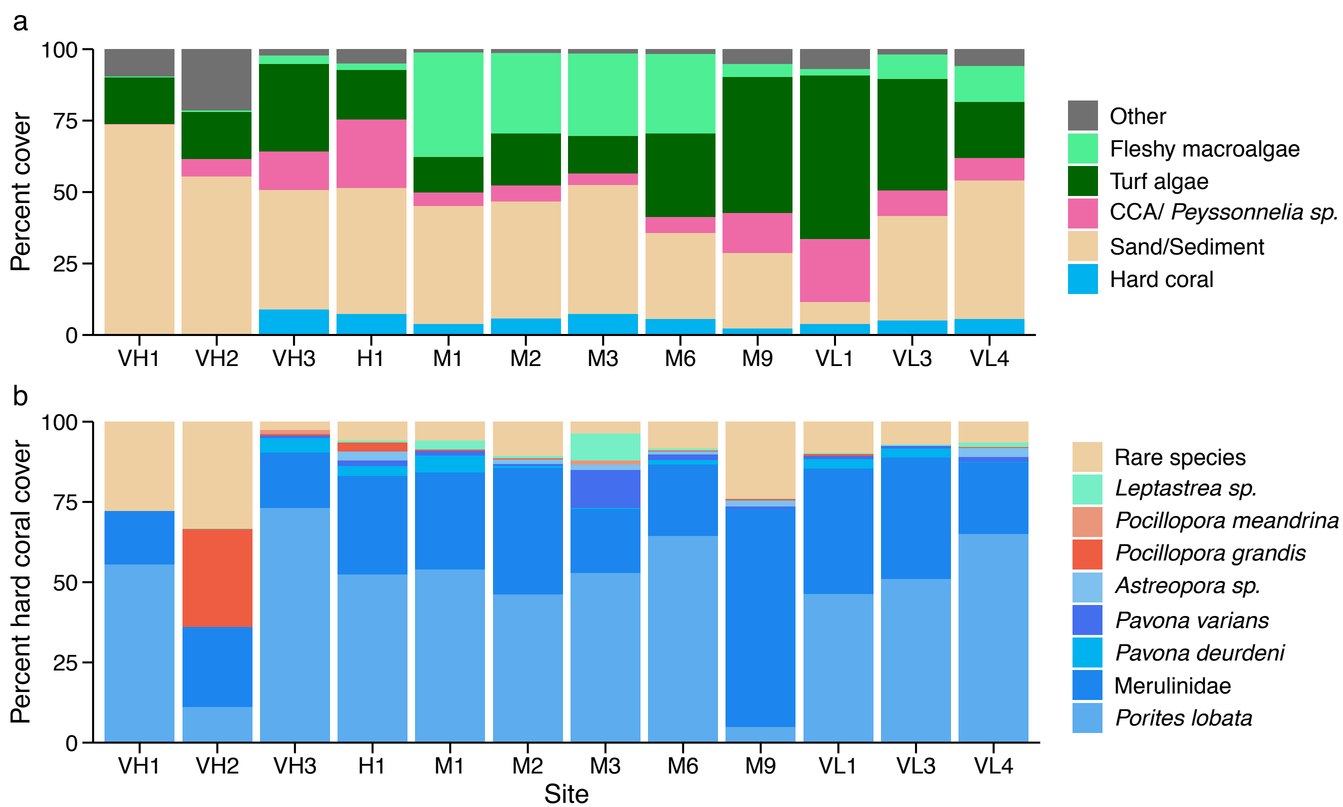

Figure 2.5. Coral reef (a) overall benthic community cover and (b) hard coral cover on Kiritimati (Christmas Island) at twelve sites across the human disturbance gradient (VH = very high, H = high, M = medium, VL = very low). In b) blue shading indicates coral taxa with stress tolerant life history traits, orange indicates competitive, and green indicates weedy. Rare species includes any coral taxa that comprised less than 1% of overall hard coral cover, with the exception of the *Pocillopora* spp. which were also less than 1% but were left out of the rare species as there were *Pocillopora* recruits.

Chapter 3 – Impacts of prolonged heat stress and local chronic disturbance on densities of small corals

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3.1 Abstract

Coral reefs are threatened by both climate change and localized chronic human disturbances. Although a few laboratory studies have investigated the effects of combined stressors, such as nutrient enrichment and heat stress, on early life stage corals growth and survival, *in situ* studies are lacking. We censused small (≤5 cm) coral densities at six time points spanning before, during, and after a prolonged heat stress event (i.e., the 2015-2016 El Niño) at 19 sites across a gradient of local chronic human disturbance on Kiritimati, a geographically isolated coral reef atoll in the central Pacific Ocean. Chronic disturbance and prolonged heat stress (i.e., 10 months of elevated seawater temperatures) did not significantly interact, but instead had an additive effect, with each having a significant negative impact on the density of small corals. Densities were 47% lower at sites exposed to very high levels of chronic stress prior to the heat stress, which then triggered a 56% island-wide decrease in densities. Small corals with a competitive life history strategy underwent a greater decline than those with a stress tolerant life history strategy. One year after the event, stress tolerant small corals had recovered to pre-El Niño densities, but competitive and overall densities had not. Our results highlight how local chronic anthropogenic and climate change combine to drive small coral densities during and after an extreme heat stress event.

3.2 Introduction

Coral reefs are increasingly impacted by the effects of climate change in conjunction with chronic regional and local scale disturbance (Hoegh-Guldberg et al. 2007; Hughes et al. 2017a). Acute disturbance events, such as El Niños, have the potential to cause the rapid loss of coral, as evidenced by mass bleaching and up to 95% mortality triggered by the 2015-2016 El Niño on coral reefs around the world (Eakin et al. 2016; Hughes et al. 2017b; Brainard et al. 2018). The persistence of coral reefs is dependent on the recovery of these corals, which can be driven by coral recruitment and the population dynamics of juvenile corals (Doropoulos et al. 2015; Graham et al. 2015). This highlights the importance of studying the effects of global and local scale disturbance on small corals.

Coral bleaching and mortality have been documented extensively in adult corals, whereas there has been comparatively less research on the effects of heat stress on small corals (most commonly termed juveniles due to small size and not maturity level; the termed used in cited studies will be used when referenced here so as to not misrepresent the authors' findings). Previous research has demonstrated that the demographics of juvenile corals can influence recovery trajectories (Miller et al. 2000; Doropoulos et al. 2015) and are one of five major factors (along with initial reef structural complexity, water depth, herbivorous fish biomass, and nutrient conditions) believed to influence a reefs response to a disturbance (Graham et al. 2015). The survival of small corals was documented in two areas in the Indian Ocean, Scott Reef off the coast of western Australia and the Maldives, following the 1998 El Niño which in turn corresponded to reef recovery within 10 – 12 years (Bianchi et al. 2006; Gilmour et al. 2013; Perry and Morgan 2017). Following a disturbance, surviving small corals rise through size classes with corresponding increases in brood stock and reproductive output (Gilmour et al.

2013) to repair stock-recruitment relationships disrupted by the loss of adult colonies (Gilmour et al. 2013; Hughes et al. 2019). This contribution to reef recovery is highly critical for isolated reefs that are reliant of self-seeding (Gilmour et al. 2013; Tsounis and Edmunds 2016).

Coral identity and life history traits appear fundamental to small coral survival during bleaching (Doropoulos et al. 2015; Álvarez-Noriega et al. 2018) and for coral reef recovery through increases in coral cover (Doropoulos et al. 2015). A study by Doropoulos and colleagues (2015) on the Great Barrier Reef, Australia found a significant stock-recruitment relationship in brooder corals but not with *Acropora* and other broadcast spawners. Corals that reproduce by brooding demonstrate a 'weedy' life history strategy (Darling et al. 2012). They have rapid generation times and excel at opportunistically colonizing recently disturbed habitats (Darling et al. 2012; Edmunds et al. 2018) yet, when reef recovery is characterized by increases in coral cover they may not contribute to reef recovery due to their small colony sizes (Darling et al. 2012; Doropoulos et al. 2015). Slow growing massive corals that have a 'stress tolerant' life history strategy and often survive disturbance events (Darling et al. 2012), also often do not contribute appreciably to increases in coral cover (Doropoulos et al. 2015). However, some corals that exhibit a 'competitive' life history strategy, such as *Acropora*, are also good at colonizing but have fast growing large colonies (Darling et al. 2012) that contribute considerably to coral cover (Doropoulos et al. 2015), and thus play a major role in reef recovery.

Although there is some evidence that juvenile corals may have greater tolerance to heat stress than their conspecific adults, the reasons underlying this remains unclear (Mumby 1999; Loya et al. 2001; Brown et al. 2002). Following the 1998 El Niño in Belize, Mumby (1999) witnessed a minor mortality of small corals compared to their adult counterparts, and while sampling design did not allow for a direct comparison he concluded that although 25% of corals

2 – 20 mm in size experienced some bleaching, it may be possible that the incidence of bleaching in these corals was less than in adults. This trend has also been documented globally on reefs in Japan, Thailand, Australia and in the Mediterranean (Loya et al. 2001; Brown et al. 2002; Shenkar et al. 2005; Álvarez-Noriega et al. 2018 respectively). Mumby (1999) also hypothesized that the higher survival could be due to reduced irradiance levels due to their cryptic microhabitats or heterotrophic feeding to replace lost autotrophic nutrition. Further research has suggested additional mechanisms based on properties such as higher concentrations of fluorescent proteins which dissipate excess light energy (Papina et al. 2002), being non-reproductive which may allow for more energy invested into maintenance (Álvarez-Noriega et al. 2018), and their relatively flat and small colonies allowing for faster elimination of toxic by-products by mass transfer (Nakamura and van Woesik 2001). In addition to exploring mechanisms for survival, studies have investigated the effects of heat stress on small corals. Two experimental laboratory studies investigated the effects of short term heat stress and found that it resulted in sub-lethal stress and negative allometric growth scaling in *Porites* (Edmunds 2008; Olsen et al. 2014), whereas another study found increases in both growth and mortality in *Acropora* after over a month of elevated temperatures (Humanes et al. 2016). A comprehensive understanding of bleaching resilience mechanisms and heat stress effects in small corals remains unresolved.

Similar to adult corals, local factors, natural and anthropogenic, can affect a small coral in several ways including growth and survival. One of the previously mentioned heat stress experiments also investigated the influence of a simulated river plume and terrestrial runoff nutrient enrichment event on juvenile corals (4-month-old corals) and found an antagonistic effect leading to reduced mortality rates (Humanes et al. 2016). This supports one of Mumby's

(1999) hypotheses as nutrients can be taken up by plankton communities which in turn are heterotrophically fed on by corals (reviewed in Houlbrèque and Ferrier-Pagès 2009), potentially supplementing reduced autotrophic nutrition that is lost during bleaching (Mumby 1999). However, in Barbados, human induced eutrophication and sedimentation resulted in decreased juvenile coral abundance compared to reefs minimally impacted (Wittenberg and Hunte 1992). The effects of macroalgae may be the most well studied on small corals and not unlike recruits or adult corals, the effects are negative and result in slowed growth and decreased survivorship (Edmunds and Carpenter 2001; Box and Mumby 2007; Olsen et al. 2014) and in turn decreases in macroalgae levels has led to increased abundances of juvenile corals (Edmunds and Carpenter 2001). Macroalgae can have negative effects on long (Edmunds and Carpenter 2001; Box and Mumby 2007) and short temporal scales (Olsen et al. 2014). One study found significant mortality of six-week-old and 1- 2-year-old corals after seven days in direct contact with, *Dictyota menstrualis*, a common macroalgae species on Caribbean coral reefs (Olsen et al. 2014). Currently there is a critical lack of research on local factors and their effects on small corals as all of the research has occurred in the Caribbean. In addition, as chronic stress is often realized as increased macroalgal cover on reefs (Smith et al. 2016), this source of stress has important implications for reef recovery. In fact, an analysis of coral reef disturbances and recoveries on the Great Barrier Reef over 30 years revealed that recovery is sensitive to chronic pressures (Ortiz et al. 2018).

Here, we aimed to fill a gap in the understanding of how multiple stressors impact the density of small corals. To do this we capitalized on a prolonged heat stress event that occurred on Kiritimati (Christmas Island) during the 2015-2016 El Niño, that overlaid the atoll's chronic disturbance gradient (Baum et al. *in prep*; Watson et al. 2016) to investigate the combined effects of heat stress and chronic stress on small corals. Kiritimati is geographically isolated, and thus is largely reliant on self-seeding for coral recruits (Treml et al. 2008; Wood et al. 2016), which helps to isolate the influences of human disturbance around Kiritimati. We censused small corals via video assay at 19 sites along the disturbance gradient before (July 2013, August/September 2014, and May 2015), during (July 2015 and March 2016), and approximately one year following (July 2017) the El Niño. This ecosystem-scale natural experiment allowed us to examine the degree of impact that severe heat stress and varying local human disturbance has on small corals with differing life history strategies, and thus its effect on an isolated island's reef recovery. Specifically, we examined variability in small coral densities and life history diversity throughout and after a temperature stress event. We hypothesized that while elevated water temperatures would lead to a significant decline in small corals, that 1) this decline would vary by human disturbance, where increased reef structure and high water quality in areas with lower human disturbance would provide more high-quality habitat suitable for recruit settlement and reduced post-settlement mortality, and thus these areas would have higher small coral densities; 2) greater oceanographic productivity would support higher densities of small corals, and 3) declines would vary among coral taxa, with a higher density of stress tolerant corals that survived the El Niño, and in the following year there would be an increase in the weedy coral densities.

3.3 Materials and Methods

3.3.1 Study area and design

To investigate patterns in small coral density across a disturbance gradient and throughout the 2015-2016 El Niño, we surveyed reefs on Kiritimati (Christmas Island, Republic of Kiribati; 01°52'N, 157°24'W), a remote coral atoll in the central equatorial Pacific Ocean

(Figure 3.1). Nineteen sites were surveyed prior to the El Niño, in 2013 (2 yrs before; 16 sites), 2014 (1 yr before; 9 sites), and May 2015 (start; 8 sites). A subset of these sites were resurveyed twice during the El Niño, 2 months (2 mo.; July 2015 – 13 sites) and 10 months (10 mo.; March 2016 – 11 sites) into the heat stress; not all sites were resampled due to inclement weather conditions. Sites were then resurveyed approximately 14 months after the end of the heat stress (1 yr after; July 2017 – 18 sites; Figure S3.1, Table B3.1). Local chronic disturbance around the island was previously quantified (Baum et al. *in prep*; Chapter 2) by combining both human population within 2 km radius (Kiribati National Statistics Office 2016) of each site and fishing intensity data (Watson et al. 2016). We modelled local disturbance using this continuous combined quantitative index and for display purposes used previously assigned local disturbance categories which should be regarded as being relative to other sites rather than absolute levels of human disturbance (Baum et al. *in prep*; Magel et al. *in review*; Chapter 2). Thermal stress in degree heating weeks was quantified using *in-situ* temperature loggers (SBE 56, Sea-Bird Scientific ± 0.001°C precision) deployed around the island, with at least one logger in each of the disturbance levels (further details in Claar et al. 2019). The heat stress from the 2015-2016 El Niño peaked at 27 Degree Heating Weeks on Kiritimati and temperatures were continuously elevated between June 2015 and April 2016 (Claar et al. 2019). This prolonged heat stress resulted in an ~90% loss of coral cover across the atoll (Baum et al. *in prep*).

Multiple other environmental parameters (e.g., primary productivity and wave energy) have been quantified around Kiritimati, either using *in-situ* methods or through the use of satellite data such as the Marine Socio-Environmental Covariates (MSEC) open source data product (https://shiny.sesync.org/apps/msec/; Yeager et al. 2017). Wave energy, turbidity, nutrients, dissolved oxygen, and salinity do not appear to vary significantly around Kiritimati

(Baum et al. *in prep*; Magel et al. 2019). However, net primary productivity (NPP) averaged from 2003-2013 in the MSEC dataset exhibited variation around the island arising from island-wake upwelling (Walsh 2011; Magel et al. *in review*; Chapter 2), so it was included in all models.

3.3.2 Small coral census

To enumerate small corals on the reef, we surveyed two 25 m transects set along the 10-12 m isobath at each site. Up to ten 1 m^2 gridded quadrats were set at predetermined random points along the transects, and were filmed following the protocol in Mumby and colleagues (2007) with the modification of 10 cm swaths instead of 20 cm (n = 757 videos total, Table B3.1). Videos were randomly analyzed by one of three trained individuals, who identified each coral to the lowest possible taxonomic unit and measured its 2D horizontal size (i.e., widest width) using the software Tracker (https://www.physlets.org/tracker/; Brown 2018). A small coral was distinguished as being a new colony—rather than a fragment of a colony that experienced partial mortality—by inconsistencies with the surrounding area (i.e., dead skeleton). Small corals (SC) were defined as corals ≤5 cm maximum width. While this size classification is arbitrary in regards to maturity of corals, this is a commonly used size classification in juvenile and young coral studies (presented in Roth and Knowlton 2009). Due to the difficulties of working underwater, some census videos had corals that were unable to be measured in the Tracker software and thus were not included in this analysis. Corals that were not fully inside a quadrat were removed from the dataset. When available, life history traits for identified corals were assigned following Baum et al. (*in prep*), which used the Coral Trait Database (https://coraltraits.org; Darling et al. 2012) to classify species found in the database, and extracted life histories for other species based on the family (Table B3.2). Three coral taxa (n =

42) could not be assigned a life history strategy and thus were removed from statistical analysis. In addition, corals with unresolved identifications or life history assignments (e.g., when coral could only be identified to family and a life history could not be assigned to the family due to multiple strategies within the family) were removed from statistical analysis (n = 331; 4.2% of the data). Generalists (n = 5) and soft corals (n = 38) were excluded from our statistical analysis due to low abundances.

3.3.3 Statistical analyses

We tested the effects of heat stress and local disturbance on small coral (SC) abundance using generalized linear mixed models (GLMMs) with a negative binomial error structure (to accommodate overdispersion in the data), and site as a random effect. Heat stress was modelled as a categorical variable with six levels (2 years before El Niño, 1 year before, at the start, 2 months and 10 months into the El Niño, and 14 months after the El Niño) denoting the sampling time in relation to the El Niño event; local disturbance was modelled as a continuous variable. Additionally, we included three other fixed effects: life history strategies (three levels: stress tolerant, competitive, and weedy); island region, as a proxy for possible physical and oceanographic differences on the reef around the island (seven levels: Bay of Wrecks, North Shore, North Lagoon, Mid Lagoon, South Lagoon, South Shore, and Vaskess Bay; Figure 3.1b); and mean annual maximum NPP (continuous). We also incorporated an offset to account for differences in the total number of census videos at each site. First, we tested the interaction between heat stress and local disturbance (model a) but there were no significant interactions so we proceeded without including an interaction (model b). To investigate the impacts of these factors on each life history strategy, model b was run for each life history type (stress tolerant =

model c, competitive = model d, weedy = model e) with the modification that life history was not included as a fixed effect. Thus, the models were as follows:

(a) SC count ~ Heat Stress * Local Disturbance + Life History Strategy + Island Region + NPP + (1|Site) + offset(Number of Quadrats per Site)

(b) SC count ~ Heat Stress + Local Disturbance + Life History Strategy + Island Region + NPP + (1|Site) + offset(Number of Quadrats per Site)

(c) Stress tolerant SC count ~ Heat Stress + Local Disturbance + Island Region + NPP + (1|Site) + offset(Number of Quadrats per Site)

(d) Competitive SC count ~ Heat Stress + Local Disturbance + Island Region + NPP + (1|Site) + offset(Number of Quadrats per Site)

(e) Weedy SC count ~ Heat Stress + Local Disturbance + Island Region + NPP + (1|Site) + offset(Number of Quadrats per Site)

All statistical analyses were conducted in R v.3.6.1 (R Core Team 2019). GLMMs were tested using the package *glmmADMB* (Fournier et al. 2012; Skaug et al. 2016) and model estimate plots were made using *coefplot2* (Bolker and Yu-Sung 2011). Prior to analysis, continuous input variables, local human disturbance and net primary production, were standardized to a mean of zero and a standard deviation of 0.5 using the 'rescale' function in the *arm* package (Gelman et al. 2018).

3.4. Results

In total, we enumerated 7939 small soft and hard corals on Kiritimati from 757 census videos (54 of these videos had 0 small corals) collected around Kiritimati over six time points before (2 yrs before = 10.6 corals m^{-2} per site ± 1.65 SE, 1 yr before = 13.8 corals m^{-2} per site ± 1.9, start = 11.1 corals m^{-2} per site ± 2), during (2 mo. = 13.9 corals m^{-2} per site ± 2.1, 10 mo. =

5.4 corals m^{-2} per site ± 1.2), and after the 2015-2016 El Niño (1 yr after = 9.6 corals m^{-2} per site ± 1.1) (Figure 3.2a). The mean width of the censused corals was 2.29 cm (± 0.01 SE). In total, 45 species from 13 different families were surveyed, however over 80% of the small corals belonged to just four families: Agariciidae (n = 2863), Merulinidae (n = 1911), Acroporidae (n = 911), or Poritidae (n = 794). Overall the majority of the corals had a stress tolerant life history (n = 5856), while 1094 corals were competitive, 559 weedy, and 5 generalists. At all time points, stress tolerant small corals had the highest densities relative to the other life history strategies: before (2 yrs before = 8.20 corals m^{-2} per site ± 1.06 SE; 1 yr before = 10.8 corals m^{-2} per site ± 1.57; Start = 6.49 corals m^{-2} per site ± 1.26 SE), during (2 months = 9.49 corals m^{-2} per site ± 1.43 SE; 10 months = 4.17 corals m^{-2} per site ± 0.954 SE) and after the El Niño (1 yr after = 8.05 corals m^{-2} per site ± 0.994 SE). The mid lagoon region had the lowest densities throughout this study with the exception of after 10 months of heat stress (Figure 3.2).

3.4.1 Overall Models

Our models suggest that 10 months of elevated seawater temperatures had a significant negative impact on small coral densities compared to 2 years before the El Niño (parameter estimate = -0.8826, z = -4.20, $P < 0.0001$; Figure 3.2a and 3.4a), that resulted in a loss of half of the small corals. Approximately 1 year after the El Niño small corals were still significantly reduced but the effect was lessened (parameter estimate = -0.4712, z = -2.72, $P = 0.0066$; Figure 3.2a) and, although not significant, densities increased relative to densities at 10 months of heat stress (Figure 3.2a and 3.4a). Local human disturbance had a negative impact on small coral abundance (parameter estimate = -1.3990, z = -5.39, $P < 0.0001$; Figure 3.2b). Life history strategies had the largest effect on small coral densities: compared to the stress tolerant life history strategy, there were fewer small corals of both the weedy (parameter estimate = -2.3540, z = -16.64, $P < 0.0001$) and competitive (parameter estimate = -1.9085, z = -13.54, $P < 0.0001$; Figure 3.3a and c) life history strategies. Small corals increased significantly with NPP (parameter estimate = 0.6872, z = 2.25, $P = 0.0242$), while island region (modelled as a proxy for other oceanographic and abiotic differences) had no significant effect (Figure 3.2a). There was no significant interaction between heat stress and local disturbance.

3.4.2 Life History Models

Prolonged heat stress significantly negatively impacted densities of both stress tolerant (parameter estimate = -0.70944, z = -4.64, $P < 0.0001$; Figure 3.3a and 3.4b) and competitive small corals (parameter estimate = -2.397, z = -6.48, $P < 0.0001$; Figure 3.3d and 3.4c), whereas for weedy corals the effect was not significant (parameter estimate = -0.0731, z = -0.24, P = 0.80904; Figure 3.4d). In the following year, stress tolerant corals recovered to pre-El Niño densities (parameter estimate = -0.08206, z = -0.67, $P = 0.50352$; Figure 3.3a and 3.4b), while competitive corals increased only slightly and non-significantly (parameter estimate = -1.754, z = -7.19, $P < 0.0001$; Figure 3.3d and 3.4c). The densities of weedy corals did not significantly vary except for two months into the El Niño when they increased (parameter estimate = 0.05881, z = 2.07, $P = 0.03810$; Figure 3.4d) but this may be due to the overall low densities of these corals.

As in the overall model, small corals of all three life history strategies were significantly negatively impacted by local chronic disturbance, which had the biggest impact on competitive small corals (stress tolerant: parameter estimate = -0.93565, z = -3.50, $P = 0.00046$; competitive: parameter estimate = -1.687, z = -4.57, $P < 0.0001$; weedy: parameter estimate = -1.1927, z = -3.66, $P = 0.00025$; Figure 3.3b, e and 3.4b, c, and d), and positively influenced by NPP but it was only significant for the stress tolerant and competitive life histories (stress tolerant: parameter estimate = 0.85361, z = 2.54, P = 0.01095; competitive: parameter estimate = 1.138, z = 2.56, P = 0.01034; weedy: parameter estimate = 0.2035, z = 0.51, P = 0.61120) (Figure 3.4b, c, and d).

Unlike the overall model, however, the effect of island region was significant and varied across life histories (Figure 3.4b, c, and d). Stress tolerant and competitive corals had significantly lower densities in the mid lagoon compared to the Bay of Wrecks (stress tolerant: parameter estimate = -1.053, z = -2.00, P = 0.04599; Figure 3.3c and 3.4b; competitive: parameter estimate = -2.131, z = -2.96, P = 0.00308; Figure 3.3f and 3.4c). In addition, densities of competitive corals were significantly lower in the south lagoon (parameter estimate = -0.992, z = -2.75, P = 0.00595; Figure 3.4c). Weedy small coral densities were higher in all regions compared to Bay of Wrecks (Figure 3.4d).

3.5. Discussion

As predicted, severe heat stress caused a decline in the density of small corals; however the effect of local chronic stress was greater overall. Since there were no significant interactions between heat stress and local disturbance and both stressors had a negative impact, this suggests that these stressors were additive (Côté et al. 2016). Overall there was a small but nonsignificant increase in small coral density a year after the heat stress but only stress tolerant corals recovered among the different life history strategies. Corals with a stress tolerant life history strategy dominated the small coral assemblage at all time points. Competitive corals were the most impacted by both heat stress and local chronic stress. Net primary production had a positive influence in all models whereas island region, as a proxy for other abiotic and biotic regional and oceanographic factors, varied among life history strategies but averaged minimal nonsignificant effects in the overall model. These results highlight the impact of heat stress in conjunction with local chronic stressors on small coral densities.

The local chronic human disturbance on Kiritimati influenced an overall decrease in small coral densities with increased disturbance. This is in accordance with previous studies that have documented the negative effects a single anthropogenic stressor has on small corals (Wittenberg and Hunte 1992; Humanes et al. 2016, 2017) and it is reasonable to expect that multiple chronic stressors would continue to have a negative impact as they does in adult and recruit life stages (Baum et al. *in prep*; Smith et al. 2016). The influence of the local chronic stress on Kiritimati may have caused the discrepancy between small corals censused on Kiritimati in 2005 with densities recorded in this study before the El Niño. Sandin and colleagues (2008) sampled only the leeward side of the island which coincides with the highest levels of human disturbance. Thus, our higher density of small corals may be bolstered by the higher densities in areas of lower human disturbance.

In contrast to local human disturbance, net primary productivity positively influenced small coral densities. While there have been no studies on the ingestion of phytoplankton by corals, it has been hypothesized to exist (reviewed in Houlbrèque and Ferrier-Pagès 2009). In addition, NPP can be used as a proxy for other particulate loading in the water such as zooplankton, picoplankton, and dissolved organic matter, which corals are known to heterotrophically feed upon (reviewed in Houlbrèque and Ferrier-Pagès 2009). The presence of additional food, particularly during a heat stress when corals lose autotrophic nutrition, could bolster survival rates as previously hypothesized by Mumby (1999). Aside from NPP, island region used as a proxy for other abiotic and biotic regional and oceanographic conditions across sites had varied significance among the three life history strategies. The mid lagoon had fewer stress tolerant and competitive corals compared to the Bay of Wrecks. This region is at the mouth of the lagoon and encompasses one of the most disturbed sites; however it is also centered on the island-wake upwelling. This could suggest that while NPP has a positive effect on small corals, the effect of human disturbance was stronger on stress tolerant and competitive corals. It is also possible that there is some other factor (e.g., tidal flushing or currents) that is beyond the scope of this study that drove this trend and thus future studies should incorporate additional oceanographic factors. Interestingly, all regions had significantly more weedy corals than the Bay of Wrecks. Again, oceanographic factors may have driven this, but it may be due to the intrinsic properties of the weedy life history strategy as they are known as colonizers of disturbed areas. Prior to the El Niño, the Bay of Wrecks had the highest coral cover on the island (Baum et al. *in prep*) and continues to have the lowest levels of local anthropogenic stress. This may have created an environment less suitable for weedy corals compared to other regions.

The 2015-2016 El Niño caused significant mortality of small corals on Kiritimati after 10 months but not after two months. Only one other study has directly documented small coral densities before and after a heat stress event in which the 1998 El Niño did not cause a significant change in small coral densities on a reef in Belize (Mumby 1999). However, the 1998 El Niño resulted in 3.5 months of heat stress (Mumby 1999) compared to 10 months in this study (Claar et al. 2019). This may suggest small corals' susceptibility to long-term elevated temperature conditions, similar to adult colonies (e.g., Baum et al. *in prep*; Hughes et al. 2017a, 2018). Other studies have documented the presence of small corals following heat stress events (McClanahan 2000; Edwards et al. 2001; Bianchi et al. 2006; Gilmour et al. 2013; Perry and Morgan 2017; Adjeroud et al. 2018) and evidence has demonstrated the critical role these corals play in repairing brood stock levels (e.g., Gilmour et al. 2013; Doropoulos et al. 2015). In the Pacific, only one other study has recorded small coral densities after a heat stress event (Adjeroud et al. 2018). Following the 2003 bleaching event on the reefs in Mo'orea the small coral density was similar to densities recorded in this study (~60 individuals 10 m^{-2} in 2004); however the density in 2008 after the 2007 bleaching was lower (~30 individuals 10 m^{-2}; Adjeroud et al. 2018). This second bleaching event occurred during an *Acanthaster planci* outbreak which further impacted small coral populations (Adjeroud et al. 2018). Compared to reefs in the Indian Ocean, our densities were similar to ones recorded in the Maldives following the 2016 bleaching event (2.7 ± 4.6 – 5.8 ± 12.3 individuals m^{-2} ; Perry and Morgan 2017). However, as mentioned by Perry and Morgan (2017), in the context of densities reported after the 1998 El Niño (McClanahan 2000; Edwards et al. 2001), these are very low. A recovery trajectory may still be conserved notwithstanding these low densities as evidenced by the ability of reefs on Mo'orea to recover despite multiple acute disturbances and low small coral densities (Adjeroud et al. 2018).

Corals with a stress tolerant life history continued to be dominant throughout and after the heat stress event. This aligns with trends documented in the adult coral community on Kiritimati, where reefs that experienced stress (e.g., reefs exposed to high levels of chronic human disturbance and reefs after the El Niño) were dominated by stress tolerant corals (Baum et al. *in prep*). This was also documented on reefs in the Maldives in the years immediately following both the 1998 (McClanahan 2000) and 2016 heat stress events (Perry and Morgan 2017). In contrast, other reefs were dominated by competitive and weedy type corals (e.g., *Acropora* and *Pocillopora*) that colonize open space on reefs ; however the timescale varies globally, likely due to differences in community dynamics and severity of disturbances. This study only extended one year past the El Niño and there was no detected significant increase in weedy and competitive corals compared to stress tolerant corals. This might suggest that recovery will be suppressed until these corals can contribute significantly to recruitment, as documented on other reefs that were severely impacted (Bianchi et al. 2006; Sheppard et al. 2008; Gilmour et al. 2013; Perry and Morgan 2017) compared to reefs less impacted by extreme heat stress events (Adjeroud et al. 2018; Edmunds 2018). Thus, with more studies, it may be possible to roughly calculate recovery times using the severity of the disturbance.

Overall, our study demonstrates the negative impact that a prolonged heat stress event and localized chronic anthropogenic stress can have on small corals that are critical for reef recovery. This study also highlights differences in impacts among life history strategies. We do acknowledge that these results require cautious interpretation as corals in this study were smaller than or equal to the general escapement size (Doropoulos et al. 2015) and thus additionally influenced by post settlement mortality factors not accounted for. While the design of this study did not allow for the determination of the mechanism for these results it provides a critical understanding of how two major sources of disturbance on coral reefs impacted small corals and what that might mean for recovery.

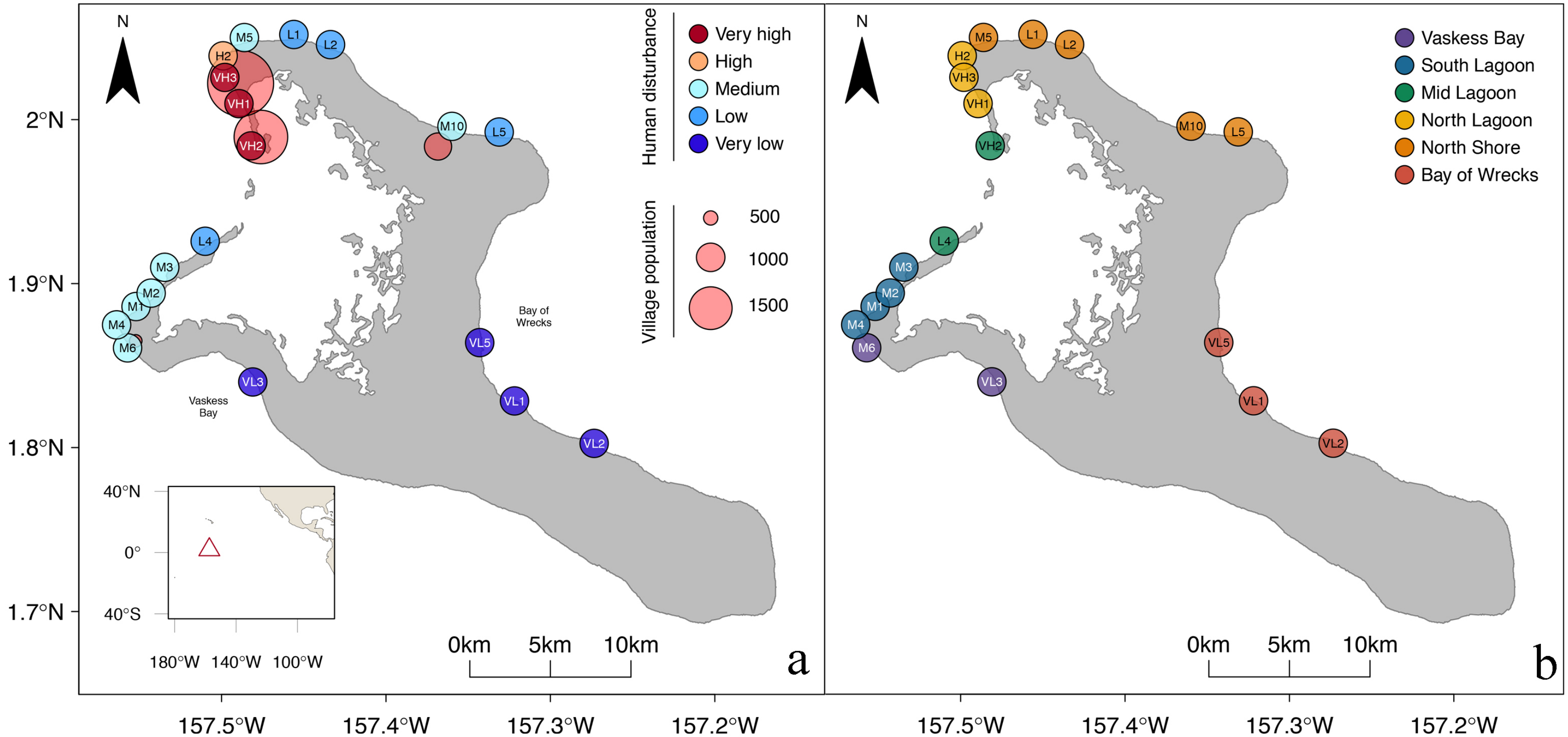


Figure 3.1. Map of reef study sites on Kiritimati (Christmas Island) categorized by (a) local human disturbance and (b) island region. Importantly, from a sampling perspective, sites within one region may be exposed to differing levels of local human disturbance. Village population (red circles) is represented by bubble size in a. Inset in (a) shows Kiritimati's location in the equatorial central Pacific Ocean (open triangle).

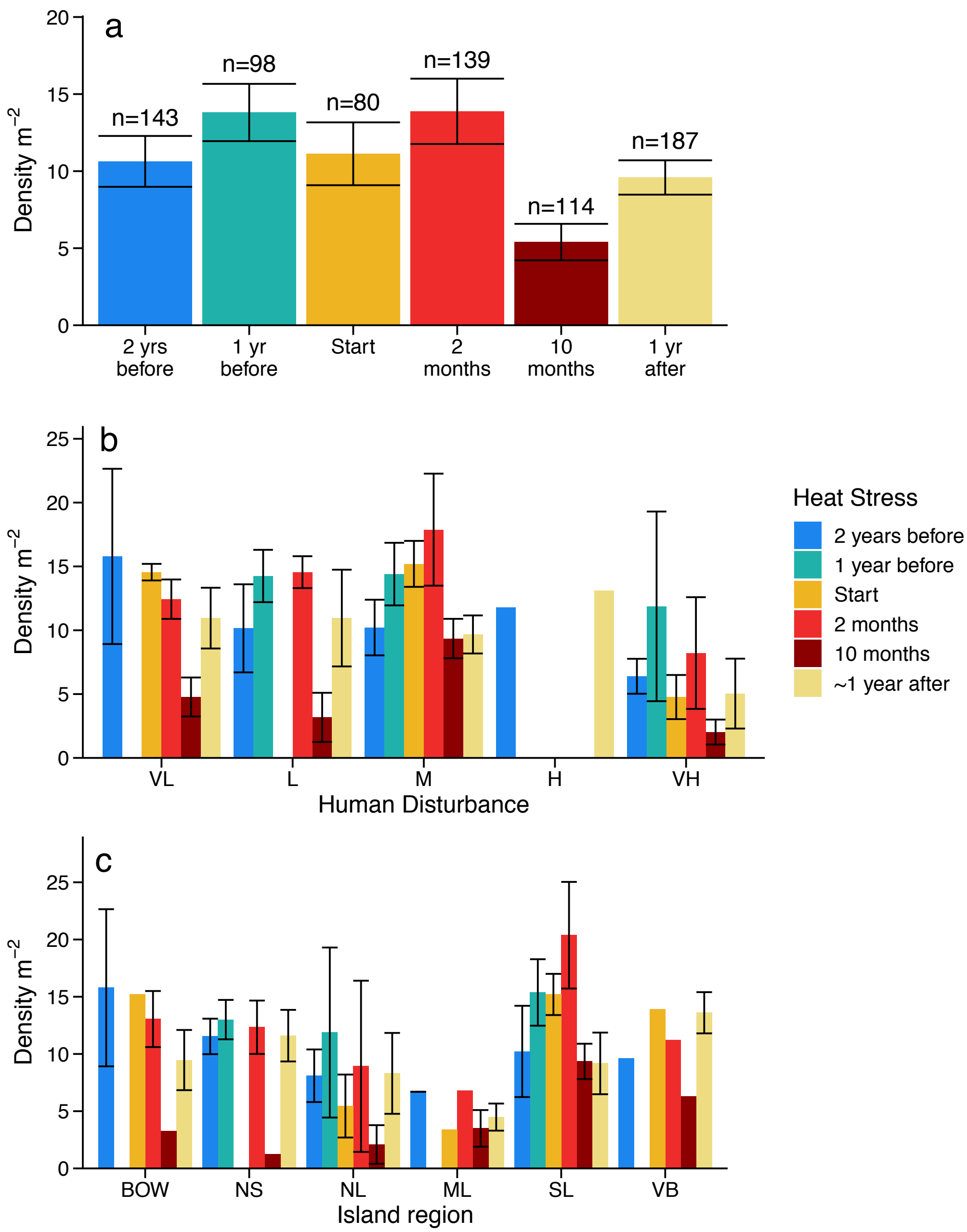


Figure 3.2. Density (± SE) of small (≤5 cm) corals at forereef sites on Kiritimati (Christmas Island) across the heat stress temporal scale (2 yrs before = summer 2013, 1 yr before = summer 2014, Start = April/May 2015, 2 months = July 2015, 10 months = March 2016, and ~1 yr after = summer 2017) for: a) entire island (19 sites; n = the number of census videos per time point), b) across the local human disturbance gradient (VL = very low, L = low, M = medium, H = high,

and VH = very high), and c) around the island regions (BOW = Bay of Wrecks, NS = North Shore, NL = North Lagoon, ML = Mid Lagoon, SL = South Lagoon, VB = Vaskess Bay). Note: Not all sites could be sampled in each time point. Y-axis scale varies among panels.

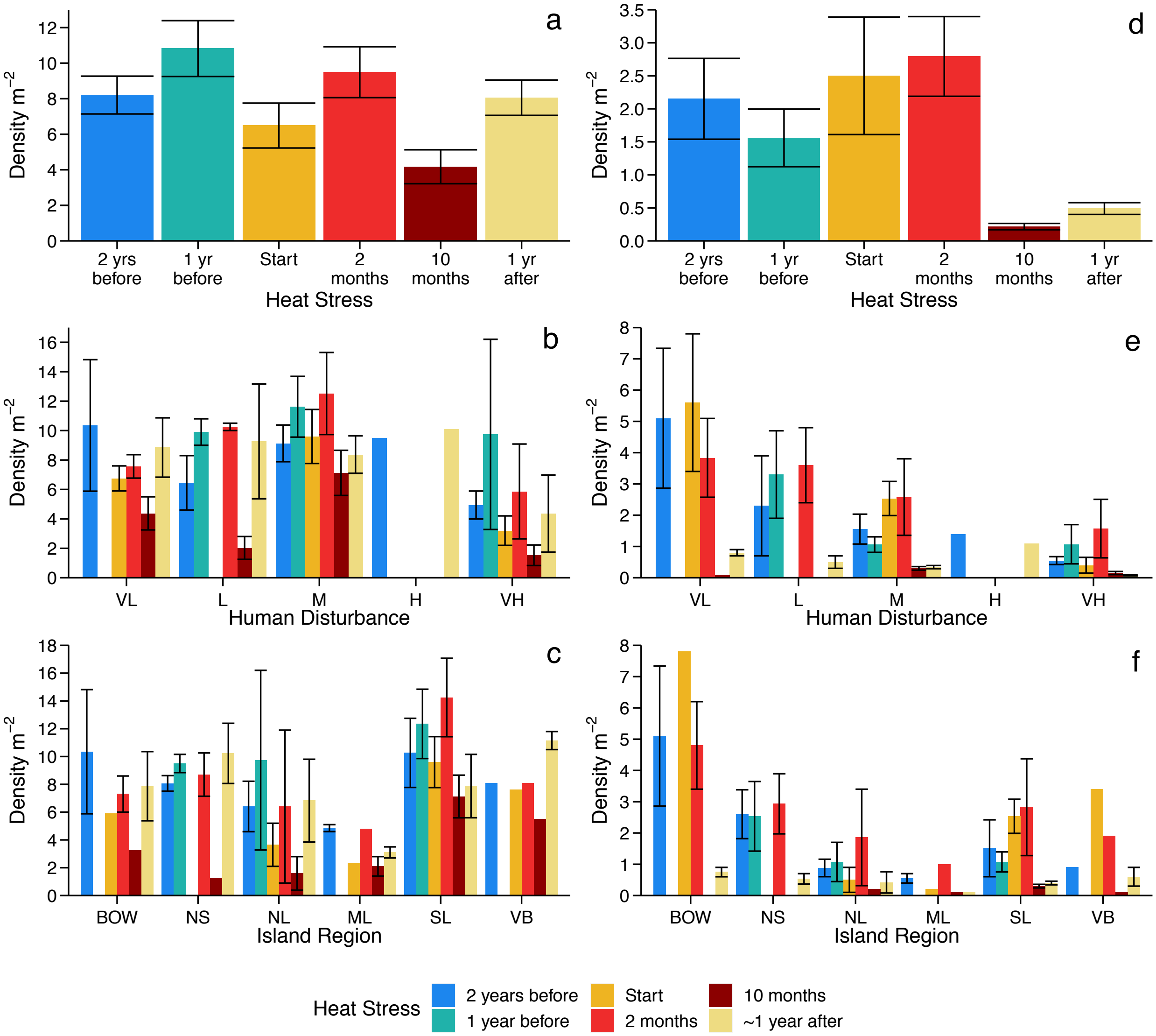
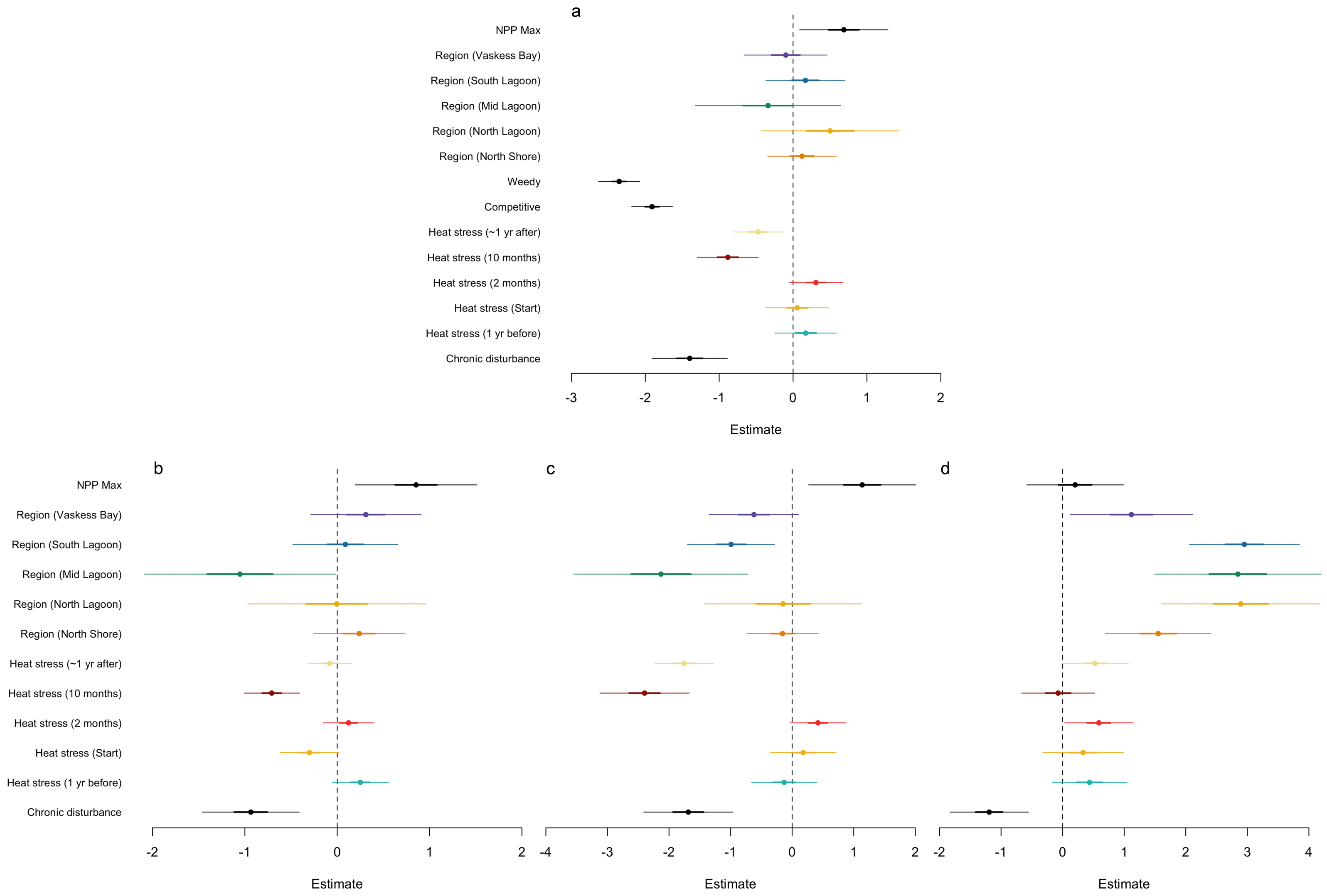


Figure 3.3. Density (± SE) of stress tolerant (a, b, c) and competitive (d, e, f) small (≤5 cm) corals on Kiritimati (Christmas Island) across the heat stress temporal scale (2 yrs before = summer 2013, 1 yr before = summer 2014, Start = April/May 2015, 2 months = July 2015, 10 months = March 2016, and ~1 yr after = summer 2017) for the entire island (a, d), across the local human disturbance gradient (b, e; VL = very low, L = low, M = medium, H = high, and VH = very high), and island region (c, f; BOW = Bay of Wrecks, NS = North Shore, NL = North Lagoon, ML = Mid Lagoon, SL = South Lagoon, VB = Vaskess Bay). Y-axis scale varies among panels.



a
NPP Max
Region (Vaskess Bay)
Region (South Lagoon)
Region (Mid Lagoon)
Region (North Lagoon)
Region (North Shore)
Weedy
Competitive
Heat stress (~1 yr after)
Heat stress (10 months)
Heat stress (2 months)
Heat stress (Start)
Heat stress (1 yr before)
Chronic disturbance
-3
-2
-1
0
1
2
Estimate
b
c
d
NPP Max
Region (Vaskess Bay)
Region (South Lagoon)
Region (Mid Lagoon)
Region (North Lagoon)
Region (North Shore)
Heat stress (~1 yr after)
Heat stress (10 months)
Heat stress (2 months)
Heat stress (Start)
Heat stress (1 yr before)
Chronic disturbance
-2
-1
0
1
2
Estimate
-4
-3
-2
-1
0
1
2
Estimate
-2
-1
0
1
2
3
4
Estimate

Figure 3.4. Generalized linear mixed model predictor coefficient effect size estimates and 95% confidence intervals for the (a) overall dataset and each tested life history strategy: (b) stress tolerant, (c) competitive, and (d) weedy. Heat stress colors correspond with figures 3.2 and 3.3 and region colors correspond with figure 3.1b. X-axis scale varies among panels. Baseline levels: region = Bay of Wrecks; Heat stress = 2 years before (2013).

Chapter 4 – Conclusion

Coral reefs are being pushed to their limits of resilience by climate change and local stressors (Hoegh-Guldberg 2011; Hughes et al. 2018), thus understanding what drives recovery and resilience is imperative. While it is understood that coral recruitment and the survival of small corals are crucial for reef recovery (Graham et al. 2015; Hughes et al. 2017b, 2019; Perry and Morgan 2017), few studies have empirically examined the effect of heat stress in conjunction with chronic stress on these aspects. Investigating these combined effects is an important next step in gaining a full understanding of reef resilience. In this thesis, I used data from Kiritimati (Republic of Kiribati), a geographically isolated atoll in the central equatorial Pacific Ocean that has a spatial gradient of chronic human disturbance, which suffered a 90% coral mortality induced by the 2015-2016 El Niño, to examine the effects of heat stress and mass coral mortality on two important components of reef recovery – coral recruitment and small coral densities.

In Chapter 2, I quantified coral recruitment in the three years following the 2015-2016 El Niño-induced mass coral mortality, across the local human disturbance gradient. Using settlement tiles deployed at 12 sites around the island, I documented very low recruitment rates compared to other Pacific reefs in each of the three years (4.58 – 10.96 recruits m^{-2}). Genetic identification revealed that the recruits were primarily from the families Agariciidae and Pocilloporidae (Figure 2.3), despite surviving adult corals largely belonging to other families (Figure 2.5b). I also found that local human disturbance curbed recruitment rates with fewer recruits at sites exposed to greater disturbance (Table 2.2, Figure 2.2c). In contrast, net primary productivity was positively correlated with recruitment suggesting the benefits that increased heterotrophic nutrition may have on recruit survival (Table 2.2). Although spawning timing is currently unknown on Kiritimati, I documented a greater number of recruits during July and August than in June, suggesting that spawning might occur in late boreal spring and summer on Kiritimati (Table 2.2, Figure 2.2b). Overall, these results suggest that local chronic stress hampers coral recruitment and thus coral reef resilience.

Small corals are vital in increasing brood stock levels that were reduced by disturbances (Doropoulos et al. 2015; Graham et al. 2015; Perry and Morgan 2017) and in Chapter 3 I examined the combined impacts of the severe heat stress from the 2015-2016 El Niño and local chronic stress on small corals. At sites spanning the local disturbance gradient, I censused small corals (≤5 cm) from benthic videos from before, during, and after the heat stress event. These analyses revealed significant declines in small corals after prolonged heat stress (i.e., 10 months of elevated seawater temperatures) (Figure 3.2a), particularly for competitive corals (Figure 3.3a and d, 3.4). Although overall there was a nonsignificant increase in small corals one year after the heat stress event (Figure 3.2a, 3.4a), this increase was minimal for competitive corals which are essential for recovery (Figure 3.3a and d, 3.4c and d). Similar to coral recruits, small coral densities were regulated by local human disturbance (Figure 3.2b, 3.3b and e, 3.4) but bolstered by net primary productivity (Figure 3.4). Regional oceanographic and abiotic factors had inconsistent effects among the three different life history strategies where the largest effects occurred in the mid lagoon region which is centered at the lagoon mouth and in the island-wake upwelling zone. Both stress tolerant and competitive small corals had significantly fewer corals in this leeward region compared to the windward Bay of Wrecks (Figure 3.3c and f, 3.4b and c); in contrast, densities of small corals with a weedy life history strategy were lowest in the Bay of Wrecks and highest along the leeward side (Figure 3.4d). Few studies have focused on small size classes of corals and as far as I am aware, this thesis was the first to examine the effects of an acute heat stress event combined with local chronic human disturbance in a natural experiment setting, adding to our understanding of the negative impacts to the resilience of coral reefs.

Together these studies suggest that recovery rates on Kiritimati may be variable across the disturbance gradient. Following acute disturbance events, surviving small corals grow to replace lost adult colonies and their reproductive output (Gilmour et al. 2013), and due to their opportunistic and fast growing traits, competitive (i.e., *Acropora* and some *Pocillopora*) and weedy species are crucial for a recovery trajectory (Darling et al. 2012; Gilmour et al. 2013; Bramanti and Edmunds 2016). The recovery of weedy and competitive corals starts to restore brood stock levels and repair stock-recruitment relationships disrupted by the loss of adult corals (Gilmour et al. 2013; Hughes et al. 2019) and the growth of *Acropora* species can contribute significantly to increases in coral cover (Doropoulos et al. 2015). However, of the surviving small corals on Kiritimati, the majority are slow growing stress tolerant species, whereas weedy and competitive coral densities are depressed, particularly at sites exposed to high levels of chronic stressors. In addition, only six of the recruits in the two years following the El Niño were competitive *Pocillopora* species and there were no *Acropora* recruits. This lack of recruits and low densities of critical *Acropora* species has the potential to suppress recovery until *Acropora* recruitment and cover increase considerably. On a similarly isolated and self-seeding reef system in the Indian Ocean, the rejuvenation of *Acropora* occurred about six years after the 1998 El Niño and full reef recovery followed within 12 years; however that was free of chronic stressors (Gilmour et al. 2013). My findings that local human disturbance on Kiritimati decreased recruitment rates and small coral densities suggests that recovery may be hindered at exposed sites which could reduce the potential for full recovery. In addition, as Kiritimati is primarily reliant of self-seeding, this may in turn impact recruitment at other sites and downstream recovery across the island.

In addition, the apparent contradiction between very low levels of coral recruitment (Chapter 2) and increases in small corals only one year following the heat stress event (Chapter 3) indirectly suggests that coral recruits are able to survive marine heat wave events. Due to the severity of the heat stress, it seems improbable that surviving adult corals would have reproduced in the following spawning season (i.e., summer 2016 – only ~2-4 months after the end of the El Niño); these corals might have still had limited reproduction in subsequent years, thus explaining the low recruitment in 2017 – 2019. Instead, previous research (see: Mumby 1999; Loya et al. 2001; Brown et al. 2002; Bianchi et al. 2006; Perry and Morgan 2017) suggests that it is more likely that new corals, produced in the summer of 2015 (at the start of the heat stress event), were able to survive the El Niño using one or several of the suggested mechanisms by Mumby (1999), and that these recruits then grew to become the juveniles recorded in 2017 (Chapter 3). Without the capacity for recruits and small corals to survive heat stress events, recovery on reefs would be delayed possibly causing a failure to recover.

Coral reef ecology would benefit from the continued monitoring of coral recruitment rates and reef recovery on Kiritimati. The work presented in this thesis only focused on the immediate effects of heat stress on coral reef resilience, but reef recovery occurs on longer time scales. Gaining an understanding of how multiple stressors influences reef recovery is imperative to understand in the face of projected climate change and increased human populations.

This work can be further expanded on in several ways. As discussed in Chapter 2, through the use of molecular sequencing, I was able to gain further insight into the identification of recruits on Kiritimati compared to skeletal morphology, but there were limitations to the genetic resolution. Thus, enhancing this method will continue to increase the resolution which has the potential to reveal important patterns in recruitment. Future research on Kiritimati would further benefit from identifying spawning patterns and times which would further clarify patterns in recruitment. In addition, little is known about length of recovery trajectories in surviving adult colonies post heat stress and particularly in reference to reproduction and the viability of any larvae produced. Future studies may work to fill this gap as surviving adult colonies, in addition to juveniles, are important for restoring brood stock levels on reefs and delayed adult recoveries can result in prolonged depressed recruitment rates and failures.

Finally, as ecology progresses, the inclusion of multiple predictor variables has increased and in turn increases our understanding of ecosystem function. While, in addition to the primary factors, I did include other potential predictors such as net primary productivity, I was unable to include water flow or current data in this study as they are currently unknown on Kiritimati. Local currents and water movement have the potential to greatly influence recruitment patterns such as transporting larvae across the reef (Sammarco et al. 1991; Edmunds et al. 2010; Monismith et al. 2018), muddling recruitment patterns and site scaled adult-recruit relationships when unaccounted for. Thus, successful resolution of influences on recruitment relies on the inclusion of water flow data, therefore future studies should include this variable. In addition, future research would benefit from further investigations into the positive influence that net primary productivity and other oceanographic factors such as lagoon tidal flushing may have on corals as my findings may suggest their ability to subdue chronic stressors.

As climate change progresses and previously uncrossed limits are crossed, coral reefs will be pushed further from their natural capacity to be resilient (Hughes et al. 2017a). Thus, the future of coral reefs relies on a resolved understanding of what drives resilience and the impact multiple stressors have on corals, of which coral reef ecologist and managers can act on to safeguard the continuation of coral reefs. While there are still many unanswered questions, this thesis contributes to the overall understanding of reef recovery driven by coral recruitment and the survival of small corals on reefs subjected to local and global stressors.

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Appendices

Appendix A: Supplemental information for Chapter 2

Table A2.1. Local chronic human disturbance at each tile deployment site on Kiritimati. Population is the number of people residing within 2 km of the site. Fishing pressure is the extracted value from a kernel density function of fishing pressure from Watson et al. (2016) and standardized to the maximum population size. Combined metric is the sum of population and fishing pressure. Site numbers and disturbance level colors match those on Figure 2.1a. Adapted from Baum et al. (*in prep*).

Site	Population	Fishing pressure	Combined metric	Disturbance Category
VH1	4042	3234	7276	Very High
VH2	1223	3638	4861	Very High
VH3	3065	2021	5086	Very High
H1	0	2425	2425	High
M3	0	1213	1213	Medium
M2	0	1213	1213	Medium
M1	0	1213	1213	Medium
M6	351	1213	1564	Medium
M9	0	1213	1213	Medium
VL3	0	0	0	Very Low
VL4	0	0	0	Very Low
VL1	0	0	0	Very Low

Table A2.2. Number of settlement tiles deployed and retrieved at twelve sites around Kiritimati (Christmas Island) from November 2016 to summer 2019. Sites are ordered first by decreasing levels of local chronic human disturbance (Figure 2.1a) then by island region (Figure 2.1b).

Site		**VH3**	**VH1**	**VH2**	**H1**	**M3**	**M2**	**M1**	**M6**	**M9**	**VL3**	**VL4**	**VL1**	**Total for year**
Human Disturbance Level		Very high	Very high	Very high	High	Medium	Medium	Medium	Medium	Medium	Very low	Very low	Very low	
Island Region		NL	NL	ML	ML	SL	SL	SL	VB	VB	VB	VB	BOW	
Nov. 2016	Deployed	20	20	20	20	20	20	20	20	20	20	20	20	
July 2017	Retrieved	20	19	20	19	20	19	18	19	15	19	20	20	228
	Deployed	21	20	20	20	20	21	20	21	20	20	20	20	
June 2018	Retrieved	20	18	16	19	17	19	17	20	NS*	20	16	20	202
	Deployed	21	18	19	21	19	21	18	19	NS*	18	16	20	
July – Aug. 2019	Retrieved	21	17	16	19	17	22	22	19	18	18	20	NS*	209

Island region: *NL* = North Lagoon, *ML* = Mid Lagoon, *SL* = South Lagoon, *BOW* = Bay of Wrecks, *VB* = Vaskess Bay

*NS = Not Sampled due to inclement weather

Table A2.3. Sequencing similarity search results from GenBank BLASTn (https://blast.ncbi.nlm.nih.gov/Blast.cgi) from recruits sampled in 2017 and 2018. Taxonomy was assigned to genus when all BLASTn matches above 97% similarity denoted the same genus. If there was no consensus on genus, the next lowest taxonomic rank was assigned (e.g., family). Of the 60 recruits from 2017, 32 formed contigs and of the 22 recruits from 2018, 17 formed contigs. Thirty-three pairs (28 from 2017, 5 from 2018) of reads were unable to form contigs, but sequence similarity searches were performed on five (4 from 2017, 1 from 2018) forward reads of high enough quality. In total, 54 of the 82 recruits were genetically identified.

Year	Site	Recruit #	Aligned Taxa ID	Accepted Taxa ID	Matching GenBank Accession #	Percentage similarity
2017	H1	1	*Pavona decussata*	Agariciidae	KP231535	99.7%
2017	H1	2	Poor quality			
2017	H1	3	*Pavona decussata*	Agariciidae	KP231535	99.4%
2017	H1	4	*Pavona decussata*	Agariciidae	KP231535	99.4%
2017	H1	5	Poor quality			
2017	H1	6	*Pavona decussata*	Agariciidae	KP231535	99.7%
2017	H1	7	*Pavona decussata* *Leptoseris foliosa* *Gardineroseris planulata* *Pavona cactus*	Agariciidae	KP231535 HE978506 AB441218 AB441217	99.6%
2017	VH2	8	*Pavona decussata*	Agariciidae	KP231535	99.9%
2017	VH2	9	Poor quality			
2017	VH2	10	Poor quality			
2017	VL3	11	Poor quality			
2017	VL3	12	*Pavona decussata* *Leptoseris foliosa*	Agariciidae	KP231535 HE978506	99.8%
2017	VL3	13	*Pavona decussata*	Agariciidae	KP231535	100%
2017	VL3	14	Poor quality			
2017	VL3	15	Poor quality			
2017	VL3	16	*Pavona decussata* & *Leptoseris foliosa* & *Gardineroseris planulata* & *Pavona cactus* (forward read only)	Agariciidae	KP231535 HE978506 AB441218 AB441217	99.2%
2017	VL3	17	*Pavona decussata*	Agariciidae	KP231535	99.6%
2017	VL3	18	*Pavona decussata*	Agariciidae	KP231535	99.7%
2017	VL3	19	Poor quality			
2017	VL3	20	Poor quality			
2017	VL3	21	Poor quality			
2017	VL3	22	*Pavona decussata*	Agariciidae	KP231535	99.5%
2017	VL3	23	*Pavona decussata*	Agariciidae	KP231535	99.9%

Year	Site	Recruit #	Aligned Taxa ID	Accepted Taxa ID	Matching GenBank Accession #	Percentage similarity
2017	VL3	24	*Pavona decussata* *Leptoseris foliosa*	Agariciidae	KP231535 HE978507 HE978506	99.5%
2017	VL3	25	*Pavona decussata* *Leptoseris foliosa*	Agariciidae	KP231535 HE978506	99.7%
2017	VL4	26	*Pavona decussata* (forward read only)	Agariciidae	KP231535	99.4%
2017	VL4	27	Poor quality			
2017	VL4	28	*Pocillopora damicornis*	*Pocillopora* sp.	KF194196	97.6%
2017	VL4	29	*Pavona decussata* *Leptoseris foliosa*	Agariciidae	KP231535 HE978506	99.7%
2017	VL4	30	Poor quality			
2017	VL4	31	*Pavona decussata* *Leptoseris foliosa*	Agariciidae	KP231535 HE978506	99.7%
2017	VL4	32	Poor quality			
2017	VL4	33	*Pavona decussata*	Agariciidae	KP231535	99.9%
2017	VL4	34	Poor quality			
2017	VL4	35	*Pavona decussata*	Agariciidae	KP231535	99.9%
2017	VL4	36	Poor quality			
2017	VL4	37	*Pavona decussata* *Leptoseris foliosa*	Agariciidae	KP231535 HE978507 HE978506	99.8%
2017	VL4	38	Poor quality			
2017	M1	39	*Pavona decussata* *Leptoseris foliosa*	Agariciidae	KP231535 HE978506	99.9%
2017	M1	40	*Pavona decussata* (forward read only)	Agariciidae	KP231535	99.7%
2017	VL4	41	Poor quality			
2017	VL4	42	Poor quality			
2017	M1	43	*Pavona clavus* *Pavona decussata* (forward read only)	Agariciidae	DQ643836 KP231535	99.3%
2017	M1	44	*Pavona decussata*	Agariciidae	KP231535	99.8%
2017	M1	45	Poor quality			
2017	M2	46	Poor quality			
2017	M2	47	Poor quality			
2017	M2	48	*Pocillopora damicornis* (x48) *Pocillopora eydouxi* (x2) *Pocillopora verrucose (x2)*	*Pocillopora* sp.	48 x *P. damicornis* KY887487 EF526303 AY139812 AB441230	98.9%
2017	M2	49	*Pavona decussata* *Leptoseris foliosa* *Pavona cactus*	Agariciidae	KP231535 HE978506 AB441217	99.6%
2017	M2	50	*Pavona decussata*	Agariciidae	KP231535	99.3%

Year	Site	Recruit #	Aligned Taxa ID	Accepted Taxa ID	Matching GenBank Accession #	Percentage similarity
2017	M2	51	*Pocillopora damicornis* (x50) *Pocillopora eydouxi* (x2) *Pocillopora verrucosa* (x2)	*Pocillopora* sp.	50 x *P. damicornis* KY887487 EF526303 AY139812 AB441230	97.8%
2017	M3	52	Poor quality			
2017	M3	53	Poor quality			
2017	M9	54	Poor quality			
2017	M9	55	*Pavona decussata*	Agariciidae	KP231535	99.6%
2017	M6	56	*Pavona decussata*	Agariciidae	KP231535	100%
2017	VH3	57	*Pavona decussata*	Agariciidae	KP231535	99.6%
2017	VH3	58	*Pavona decussata*	Agariciidae	KP231535	99.6%
2017	VL1	59	*Pavona decussata* *Leptoseris foliosa*	Agariciidae	KP231535 HE978507 HE978506	99.3%
2017	VL1	60	*Pavona decussata* *Leptoseris foliosa* *Pavona cactus*	Agariciidae	KP231535 HE978506 AB441217	99.7%
2018	H1	1	*Pavona decussata* *Leptoseris foliosa* *Gardineroseris planulata* *Pavona cactus*	Agariciidae	KP231535 HE978506 AB441218 AB441217	99.7%
2018	H1	2	*Pavona decussata* *Leptoseris foliosa* *Gardineroseris planulata* *Pavona cactus* (forward read only)	Agariciidae	KP231535 HE978506 AB441218 AB441217	99.4%
2018	VH1	3	*Pavona decussata* & *Leptoseris foliosa*	Agariciidae	KP231535 HE978506	100%
2018	VL3	4	*Pavona decussata* & *Leptoseris foliosa*	Agariciidae	KP231535 HE978506	99.6%
2018	VL3	5	*Pavona clavus* & *Pavona decussata*	Agariciidae	DG643836 KP231535	99.2%
2018	H1	6	*Pavona decussata* & *Leptoseris foliosa* (x2) & *Pavona calvus* & *Gardineroseris planulata* & *Pavona cactus* (x2)	Agariciidae	KP231535 HE978507 HE978506 DQ643836 AB441218 AB441217 AB441216	99.1%
2018	VH2	7	*Pocillopora damicornis* (x38) & *Pocillopora eydouxi* (x2) & *Pocillopora verrucosa*	*Pocillopora* sp.	38 x *P. damicornis* KY997487 EF526303 AY139812	100%
2018	VH2	8	*Pavona decussata*	Agariciidae	KP231535	99.8%

Year	Site	Recruit #	Aligned Taxa ID	Accepted Taxa ID	Matching GenBank Accession #	Percentage similarity
2018	VH2	9	*Polycyathus* sp.	*Polycyathus* sp.	JF825140	97.9%
2018	VH3	10	*Pavona decussata* & *Leptoseris foliosa*	Agariciidae	KP231535 HE978506	99.4%
2018	VL1	11	*Pavona decussata* & *Leptoseris foliosa* & *Pavona cactus*	Agariciidae	KP231535 HE978506 AB441217	99.6%
2018	M3	12	Poor quality			
2018	M1	13	*Pavona decussata*	Agariciidae	KP231535	98.8%
2018	M1	14	*Pocillopora damicornis* & *Pocillopora eydouxi* & *Pocillopora verrucosa*	*Pocillopora* sp.	46 *P. damicornis* KY887487 EF526303 AY139812 AB441230	99.8%
2018	M6	15	*Pavona decussata*	Agariciidae	KP231535	99.8%
2018	M6	16	*Pocillopora damicornis* & *Pocillopora verrucose* & *Pocillopora eydouxi (x2)*	*Pocillopora* sp.	47 x *P. damicornis* AY139812 KY887487 EF526303	99.8%
2018	VL3	17	*Pavona decussata*	Agariciidae	KP231535	99.5%
2018	H1	18	*Pavona decussata* & *Leptoseris foliosa (x2)* & *Pavona cactus*	Agariciidae	KP231535 HE978506 HE978507 AB441217	99.7%
2018	H1	19	Poor quality			
2018	H1	20	Poor quality			
2018	VH3	21	Poor quality			
2018	VH3	22	*Pavona decussata* & *Leptoseris foliosa*	Agariciidae	KP231535 HE978506	99.2%

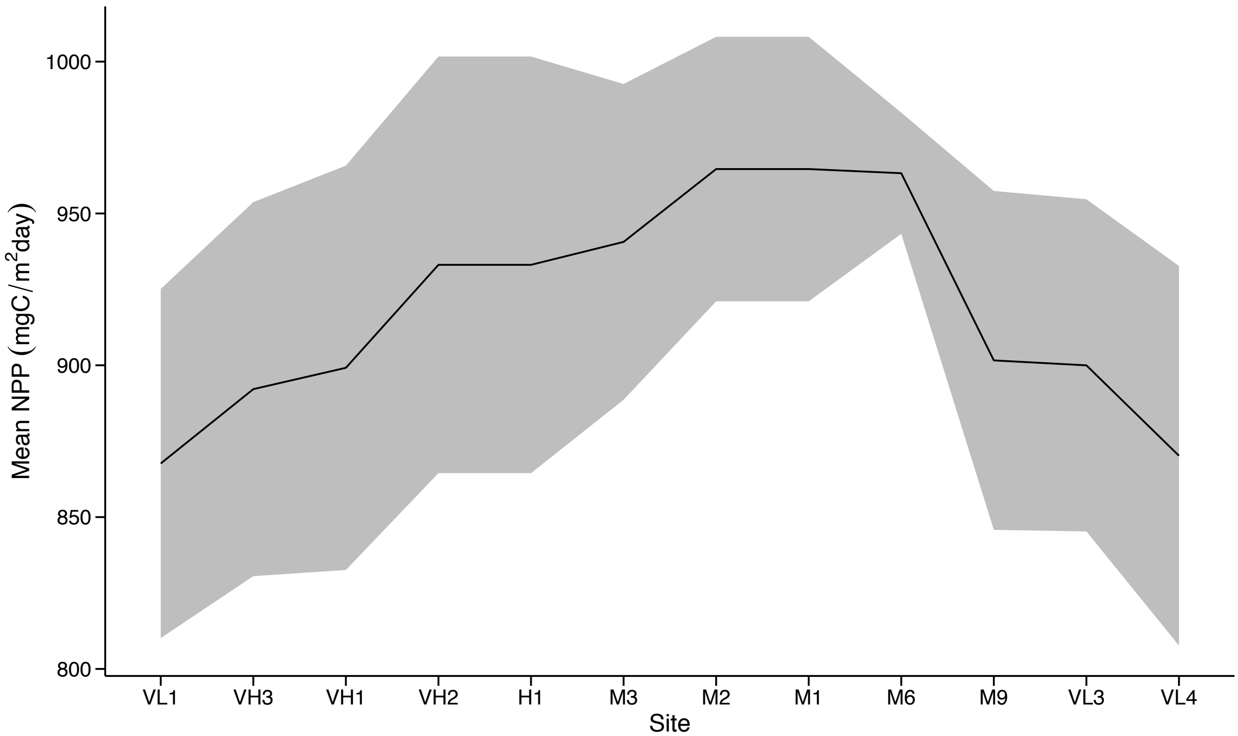

Figure A2.1. Mean (± SD, grey shading) net primary productivity at sites around Kiritimati from the Marine Socio-Environmental Covariates open source data product (https://shiny.sesync.org/apps/msec/; Yeager et al. 2017). Sites are ordered counterclockwise from the Bay of Wrecks to Vaskess Bay.

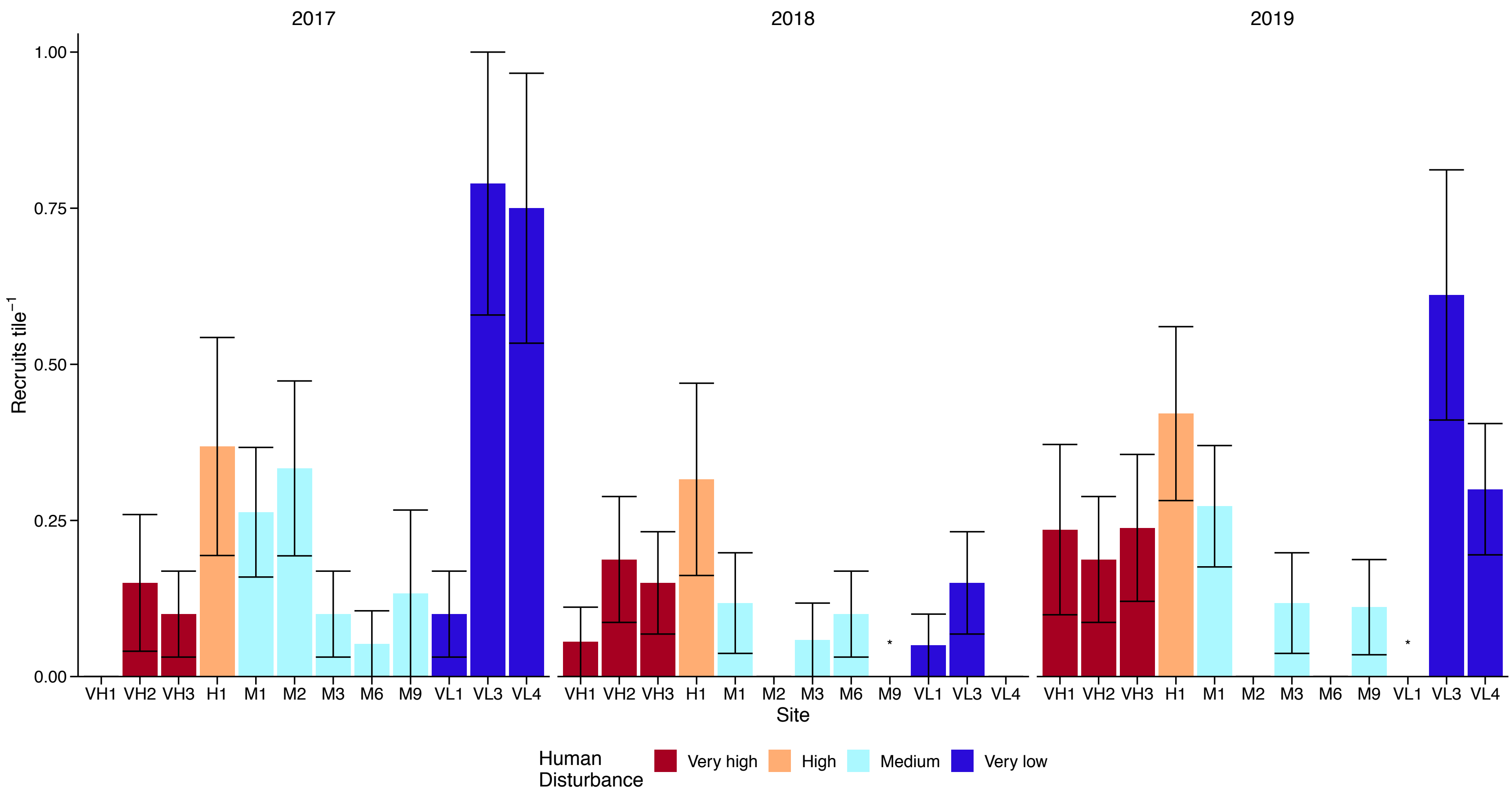

Figure A2.2. Mean (± SE) coral recruits per tile for each site along the human disturbance gradient categorized by year. * denotes that site was not sampled during that time point. Colors correspond with figure 2.1a.

Appendix B: Supplemental information for Chapter 3

Table B3.1. Video assays at 19 sites around Kiritimati. Sites are ordered first by decreasing levels of local chronic human disturbance (Figure 3.1a) then by island region (Figure 3.1b).

Site	**VH3**	**VH1[1]**	**VH2**	**H2**	**M1**	**M2**	**M3**	**M4**	**M6**	**M5**	**M10**	**L1**	**L2**	**L5**	**L4**	**VL1**	**VL2**	**VL5**	**VL3**	**Total for time point**
Human Disturbance Level	**VH**	**VH**	**VH**	**H**	**M**	**M**	**M**	**M**	**M**	**M**	**M**	**L**	**L**	**L**	**L**	**VL**	**VL**	**VL**	**VL**	
Island Region	**NL**	**NL**	**ML**	**NL**	**SL**	**SL**	**SL**	**SL**	**VB**	**NS**	**NS**	**NS**	**NS**	**NS**	**ML**	**BOW**	**BOW**	**BOW**	**VB**	
2013	10	9	10	10	10	10	9	1	10	10	10	N	N	10	10	10	4	10	N	143
2014	10	18	N	N	10	10	10	10	N	10	N	10	10	N	N	N	N	N	N	98
May 2015	10	10	10	N	10	10	10	N	N	N	N	N	N	N	N	10	N	N	10	80
July 2015	10	18	10	N	10	10	10	10	N	10	N	10	10	N	N	10	10	N	10	138
2016	9	25	10	N	10	10	10	10	N	N	N	N	4	N	10	4	N	N	10	112
2017	10	16	10	10	10	10	10	10	10	10	10	10	N	10	10	10	10	10	10	186

[1]More than 10 videos are done for site H1 since it is not uncommon for there to be videos of all sand from that highly degraded site.

N = Not Sampled due to inclement weather; Human disturbance: *VH* = Very High, *H* = High, *M* = Medium, *L* = Low, *VL* = Very Low; Island Region: *NL* = North Lagoon, *ML* = Mid Lagoon, *SL* = South Lagoon, *NS* = North Shore, BOW = Bay of Wrecks, *VB* = Vaskess Bay

Table B3.2. Life history table small coral taxa identified from video assays processed using Tracker (https://www.physlets.org/tracker/). Coral life history strategy retrieved from the Coral Traits Database (https://coraltraits.org/), unless otherwise noted. Current taxonomy (and name synonymy) retrieved from WoRMS (http://www.marinespecies.org/).

Life History	Family	Species	Notes
Competitive	Acroporidae	*Acropora* spp.	Includes: corymbose morphology (*A. loripes* (synonym: *A. rosaria, Madrepora loripes*), *A. subulata*, and hybrids of these species); tabulate morphology (*Acropora hyacinthus* synonym: *M. hyacinthus);* digitate morphology (*A. globiceps* synonym: *M. globiceps*) also includes any corals that could only be identified to genus
Competitive	Acroporidae	*Montipora aequituberculata*	*M. aequituberculata* with foliose morphology
Competitive	Acroporidae	*Montipora spp.*	*Montipora* spp. with encrusting morphology, includes *M. aequituberculata*, and a few potentially unnamed species
Competitive	Pocilloporidae	*Pocillopora* spp.	Includes: *Pocillopora grandis* (synonym: *Pocillopora eydouxi*) and *Pocillopora meandrina*; also includes any corals that could only be identified to genus
Competitive[1]	Pocilloporidae	*Pocillopora zelli*	
Competitive[2]	Dendrophylliidae	*Turbinaria reniformis*	
Stress tolerant	Acroporidae	*Astreopora* spp.	Includes *A. cucullata, A. myriophthalma*, and *A. suggesta*
Stress tolerant	Agariciidae	*Pavona duerdeni*	
Stress tolerant	Agariciidae	*Pavona varians*	
Stress tolerant	Agariciidae	*Gardineroseris planulata*	Synonym: *Agaricia planulata*, *Pavona planulata*
Stress tolerant[3]	Agariciidae	*Leptoseris mycetoseroides*	

Life History	Family	Species	Notes
Stress tolerant	Fungiidae	*Lithophyllon* sp., *Danafungia* spp., *Pleuractis* sp., and *Lobactis* sp., *Cycloseris* sp. (synonym: *Fungia* spp.)	Includes *Lithophyllon concinna* (synonym: *Fungia concinna*), *Danafungia scruposa* (synonym: *F. corona*), *D. horrida* (synonym: *F. danai*), *Pleuractis granulosa* (synonym: *F. granulosa), Lobactis scutaria* (synonym: *F. scutaria*), *C. fragilis* (synonym: *Diaseris fragilis*), and *C. tenuis* (synonym: *F. tenuis*)
Stress tolerant[4]	Fungiidae	*Herpolitha limax*	Synonym: *Madrepora limax*
Stress tolerant[5]	Fungiidae	*Sandalolitha robusta*	Synonym: *Podabacia robusta*
Stress tolerant[6]	Fungiidae	NA	Corals only identifiable to family
Stress tolerant[7]	Lobophylliidae	*Echinophyllia aspera*	Synonym: *Madrepora aspera*
Stress tolerant[8]	Lobophylliidae	*Lobophyllia hemprichii*	Synonym: *Manicina hemprichii*
Stress tolerant	Merulinidae	*Favites* spp.	Includes: *Favites pentagona* (synonym: *Madrepora pentagona*) and *Favites halicora* (synonym: *Astraea halicora*); also includes any corals that could only be identified to genus
Stress tolerant	Merulinidae	*Hydnophora microconos*	Synonym: *Monticularia microconos*
Stress tolerant	Merulinidae	*Platygyra* spp.	Includes: *P. daedalea* (synonym: *Madrepora daedalea*), *P. contorta*, *P. ryukyuensis*, and *P. sinensis* (synonym: *Astroria sinensis*); also includes any corals that could only be identified to genus
Stress tolerant	Merulinidae	*Dipsastraea* spp.	Includes: *Dipsastraea matthaii* (synonym: *Favia matthaii)* and *Dipsastraea speciose* (synonym: *Favia speciose*); also includes any corals that could only be identified to genus
Stress tolerant	Merulinidae	*Goniastrea stelligera*	Synonym: *Favia stelligera*
Stress tolerant	Merulinidae	*Astrea* spp. (synonym: *Montastraea* spp.)	May include *A. annuligera* (synonym: *Montastraea annuligera*), *A. curta* (synonym: *M. curta*); also includes any corals that could only be identified to genus
Stress tolerant[9]	Merulinidae	NA	Corals only identifiable to family

Life History	Family	Species	Notes
Stress tolerant	Poritidae	*Porites* spp.	Primarily: *Porites lobata* and may include *P. evermanni* and *P. lutea*; also includes any corals that could only be identified to genus
Weedy	*Incertae sedis* (synonym: Faviidae)	*Leptastrea* spp.	Includes *L. pruinose, L. bewickensis* and *L. purpurea* (synonym: *Astaea purpurea*); also includes any corals that could only be identified to genus
Generalist	Merulinidae	*Hydnophora exesa*	Synonym: *Madrepora exesa*
Unknown	Coscinaraeidae	*Coscinaraea* spp.	No recorded life history strategy for any species in the family
Unknown	Dendrophylliidae	*Turbinaria stellulata*	Could not be extracted from congenerics; Synonym: *Astrea stellulata*
Unknown	Psammocoridae	*Psammocora profundacella*	No recorded life history strategy for any accepted species in the family

[1] Life history strategy extracted from congeneric *Pocillopora eydouxi*

[2] Life history strategy extracted from congeneric *Turbinaria mesenterina*

[3] Life history strategy extracted from family Agariciidae (i.e., *Gardineroseris* and *Pavona*)

[4] Life history strategy extracted from family Fungiidae (i.e., *Fungia*)

[5] Life history strategy extracted from family Fungiidae (i.e., *Fungia*)

[6] All corals with a known life history in family Fungiidae on Kiritimati have the same life history strategy so extracted to the family level identifications

[7] Life history strategy extracted from congeneric *Echinophyllia orpheensis*

[8] Life history strategy extracted from congenerics *Lobophyllia corymbosa* and *Lobophyllia pachysepta*

[9] As *Hydnophora exesa*, the only non-stress tolerant species in the family Merulinidae on Kiritimati, is morphometrically distinct, corals that could only be identified to family were assigned stress tolerant due to the probably that they were not *H. exesa*

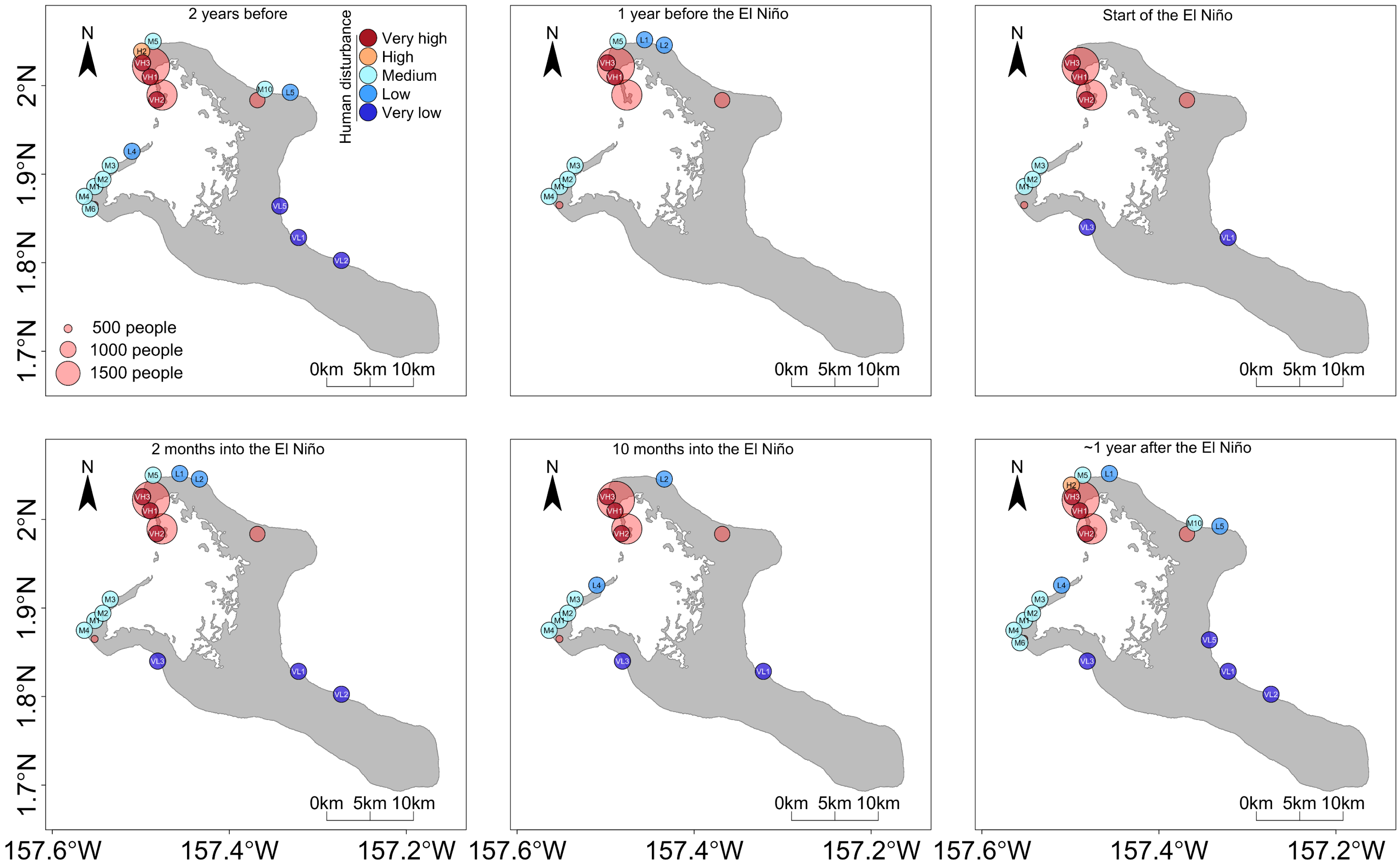

Figure B3.1. Map of reef study sites on Kiritimati (Christmas Island) sampled at each heat stress time point (2 years before = summer 2013, 1 year before = summer 2014, Start = April/May 2015, 2 months = July 2015, 10 months = March 2016, and ~1 year after = summer 2017). The sites are divided into five levels of local human disturbance. Village population (red circles) is represented by bubble size.