CALIFORNIA STATE UNIVERSITY, NORTHRIDGE

An Ecophysiological Investigation of the Effects of Macroalgae on Juvenile Corals and Larvae on Coral Reefs in the Pacific and Caribbean

A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science in Biology

By

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December 2018

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Acknowledgements

Firstly, I would like to thank my advisor, Dr. Peter Edmunds, for his guidance and the amazing opportunities I have experienced throughout my Master's degree. He is dedicated to seeing his students succeed, and I feel lucky to have been a part of the Polyp Lab for 2 years.

I would also like to thank my committee members Dr. Robert Carpenter and Dr. Chiara Pisapia. They were always available for meetings when needed and provided many valuable insights for me along the way. Additionally, Chiara has been a glowing support, not just academically, but personally as well – at CSUN and in England when we traveled for ECRS. She encouraged me when things were difficult, and her passion for the field was an inspiration.

I could not have done this research alone. In the field, I had assistance with experiment set ups, breakdowns, and the day-to-day emotional support from friends. I would like to thank Hannah Nelson and Dan Sternberg for their help and guidance during my very first week long field trip to St. John. During my longer field seasons in St. John and Moorea, I would like to thank Sigfrido Zimmermann, Ashley Potter, Jesse Bergman, Bry Wilson, Sam Gnither, Steve Doo, Hollie Putnam, Megan Williams, Griffin Srednick, Bridget Shayka, Georgios Tsounis, Lorenzo Bramanti, Jacques, and Tony, and anyone else who ever offered a kind word or assistance.

I would also like to thank Dr. Cliff Ross, who introduced me to coral research, and recommended Dr. Edmunds' lab back when I was a senior at University of North Florida. His mentorship and the research opportunities I received while in his lab as an undergrad enabled me to grow as a scientist and be competitive for a graduate degree program.

Importantly, I would also like to thank my family for their support in my move out to California, and their encouragement when the going was rough. The love and support I have received from my family, close friends, and my dog Nowda, have made the all the difference and motivated me to keep pushing forward. Special thanks to Lansing Perng, who not only was a great friend during the program, and offered help on research ponderings, but also took care of my dog while I was abroad, making the adoption a feasible option for me.

My research was made possible by financial support from CSUN's AS STAR award, CSUN Graduate Studies Travel Award, CSUN Biology Department, the National Science Foundation research support grants (OCE 16-37396, OCE 14-15268, OCE 13-50146), the Gordon and Betty Moore Foundation, and the Virgin Islands Ecological Resource Station.

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Abstract

Effects of Macroalgae on Juvenile Corals and Larvae on Coral Reefs in the Pacific and Caribbean

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On macroalgal-dominated reefs, the continuation of coral populations is dependent on successful recruitment and post-settlement success, both of which may be challenged by the presence of macroalgae. This study considers how the environment, particularly macroalgal abundance, contributes to the growth and survival of juvenile corals in two regions in the tropics: the South Pacific and the Caribbean.

To determine how juvenile corals and coral larvae are affected by macroalgae in the back reef of Moorea, surveys and manipulative experiments were used to test the hypotheses that proximity to macroalgae with and without contact, or cover of macroalgae, will impact the survival and growth of early life stages of corals. Survival of *Pocillopora damicornis* larvae did not differ when they were incubated *in situ* adjacent to coral, macroalgae, or rock. Growth of juvenile colonies of massive *Porites* spp. and *Pocillopora* spp. were unaffected by centimeter-scale proximity to macroalgae. Additionally, growth was not affected by cover of macroalgae in 4-m^2 plots, or by cages, which protected coral from macroalgal abrasion. Caged corals tended to grow faster, although this was not significant, and I hypothesize that this was related to protection from fish predation on lower cover plots, and from algae on higher cover plots.

Macroalgae may not decrease *Porites* and *Pocillopora* growth through chemical effects, but factors including macroalgal cover may have indirect effects on the fish community that adversely affect exposed coral colonies.

In St. John, US Virgin Islands, 12 sites distributed between White Point and Cabritte were selected and analyzed for benthic cover, herbivore abundance, rugosity, and rock type. Surveys of juvenile corals were conducted to determine whether the abundance and distribution of juvenile colonies within three types of microhabitats were affected by site characteristics, including macroalgae cover, and herbivore abundance. While the characteristics analyzed at the site level explained 75.9% of the variation between sites, these characteristics were not predictive of juvenile microhabitat distribution; ~ 75% of juvenile corals were found on exposed habitats at every site. While juvenile coral distribution among microhabitats was not related to site variation, survival rates within microhabitats may still vary among these sites.

Chapter 1:

General Introduction

Disturbances and Phase Shifts

Coral reefs are one of the most diverse ecosystems in the world (Hoegh-Guldberg et al., 2007) and support thousands of marine organisms (Reaka-Kudla, 1997). The number of organisms that either live on, or are supported by coral reefs (i.e. nursery areas), range from 600,000 to 9 million depending on reef location and size (Knowlton, 2001). Scleractinian corals build structurally-complex reef habitats, which provide invaluable habitat to thousands of marine organisms, and nursery areas for larger pelagic species (Idjadi and Edmunds, 2006; Hoegh-Guldberg et al., 2007; Alvarez-Filip et al., 2009; Adam et al., 2011; Roff et al., 2016). These complex coral reefs can support coastal economies through fishing, coastal storm protection, and tourism (van Oppen et al., 2015). Additionally, because corals create complex structures they act as a foundation species that encourage the settlement of other invertebrates and coral larvae, thus increasing the biodiversity and structural complexity of the reef (Idjadi and Edmunds, 2006).

However, in recent decades, coral reefs have been facing escalating effects of anthropogenic and natural stressors, which include increasing sea surface temperatures (Glynn, 1993), ocean acidification (Doney et al., 2009a, 2009b), overfishing or destructive fishing practices, and pollution (McManus, 1997). Stressors such as rising sea surface temperatures and ocean acidification have long-term ecosystem-wide effects (Connell et al., 1997; Anthony et al., 2008; Doney et al., 2009a; Koch et al., 2013). These threats have been caused by increased CO_2 output from anthropogenic sources which has

been steadily increasing since the industrial age began (Widdicombe et al., 2013), and atmospheric CO_2 levels recently exceeded 400 μatm (Mauna Loa Observatory, 2016). Rising ocean temperatures have been responsible for recent mass bleaching events (Hughes et al., 2018a, 2018b), and bleaching-related coral mortality (Anthony et al., 2007). Additionally, ocean acidification is predicted to reduce calcification in scleractinian corals and other aquatic calcifiers, although the effects of lower pH seawater differ among coral taxa (Edmunds et al., 2016). Massive *Porites* has shown 14% declines in calcification since 1990 on the Great Barrier Reef as a result of ocean acidification (De'ath et al., 2009). Due to expected slower growth rates caused by ocean acidification, and possibly dissolution, and the increasing frequency of high mortality events caused by mass thermal bleaching, many coral reefs are expected to deteriorate both structurally, and by reductions in coral cover and diversity in future elevated temperature and pCO_2 environments (Anthony et al., 2011).

In contrast, fleshy macroalgae that does not calcify, is able to survive and proliferate at elevated temperatures (Kroeker et al., 2012; Koch et al., 2013; Johnson et al., 2014; Edmunds et al., 2016). Conversely from corals, macroalgae can tolerate temperatures up to 32 ˚C and 34 ˚C for some species (Koch et al., 2013) and acidic conditions as low as pH 6.5 (Borowitzka, 1981), and will compete for space with corals (Tanner, 1995; Lirman, 2001). As herbivorous fishes are lost through overfishing, macroalgae can competitively overgrow corals (Jackson, 2001). As the extrinsic environment is changing (i.e., temperature or increased nutrient output onto the reef), many scleractinian-dominated reefs are undergoing community shifts to macroalgal dominated reefs, or phase shifts (Edmunds and Carpenter, 2001; Smith et al., 2006;

Stewart, 2008; Diaz-Pulido et al., 2009; Dudgeon et al., 2010; Fabricius et al., 2011; Bulleri et al., 2013; Enochs et al., 2015; Vieira et al., 2016b). These phase shifts are linked to a decline in reef complexity and lead to declines in the biodiversity supported by the reef (Alvarez-Filip et al., 2009; Anthony et al., 2011). Many cases of phase shifts originated in the Caribbean (Hughes, 1994; River and Edmunds, 2001; Rogers and Miller, 2006; Box and Mumby, 2007), but this downward trend in coral cover and increase in macroalgal cover is occurring on reefs worldwide (Bruno and Selig, 2007; Adjeroud et al., 2009). Cases of recovery to coral dominated states after phase shifts are rare (Edmunds and Carpenter, 2001; Idjadi et al., 2006).

The increasing prevalence of macroalgae on some coral reefs has been documented since the 1970s (Stiger and Payri, 1999; Cruz et al., 2015), and it is important because the changing abundance of macroalgae on previously scleractinian-dominated reefs can be used as a marker for assessing how the reef is affected by stressors, such as ocean acidification and climate change (Stiger and Payri, 1999; Bruno et al., 2014; Poray and Carpenter, 2014). This is because with reductions in coral cover (Gardner et al., 2003; Rogers and Miller, 2006; Bruno and Selig, 2007; Adam et al., 2011) many reefs are experiencing a loss of structural complexity (Alvarez-Filip et al., 2009; Hughes et al., 2010), which reduces the amount of biodiversity a reef can support (Idjadi and Edmunds, 2006; Alvarez-Filip et al., 2009).

Coral-Macroalgae Interactions

Increasing abundance of macroalgae on coral reefs means that competitive interactions between macroalgae and corals are becoming more common (River and Edmunds, 2001; Rasher et al., 2011). These interactions are examples of interference competition, which has been recognized in manipulating community structure for decades (Connell, 1961). Depending on the morphology of the macroalgae, some taxa produce canopies and limit light available to the coral through shading (River and Edmunds, 2001). Light reductions at 9-m depth caused by macroalgal canopies have negative effects on coral growth (Barnes and Chalker, 1990; River and Edmunds, 2001), however light reduction could be beneficial by reducing coral symbiont photoinhibition on very shallow reefs where light levels are already high (Maxwell and Johnson, 2000; Anthony and Hoegh-Guldberg, 2003). Secondly, macroalgae can abrade the coral tissue of nearby colonies (River and Edmunds, 2001), an issue which could be exacerbated in high flow environments. Reduction of understory flow by the thalli can impact growth and feeding of corals, as well as cause increased sedimentation in turbid environments (River and Edmunds, 2001; Brown and Carpenter, 2015). Free-floating macroalgae can become entangled in branching corals and smother or infect them with pathogens causing tissue necrosis in the area of contact (Nugues et al., 2004). Some macroalgal species have allelopathic or microbial effects and can limit coral growth (Thurber et al., 2012) or cause bacterial infections (Morrow et al., 2017), and sometimes transmission of bacteria to coral tissue occurs through the water column without the need for direct contact between the corals and macroalgae (Smith et al., 2006; Vieira et al., 2016a, 2016b). Ocean acidification enhanced the allelopathic effect of *Dictyota,* and thus *Dictyota* was more successful in outcompeting corals under those conditions (Del Monaco et al., 2017).

Macroalgae can also overgrow corals, which is a bigger issue for smaller or juvenile colonies which can be overgrown more rapidly than larger colonies, and have less surface area for photosynthesis and feeding (Hughes and Jackson, 1980; Zilberberg and Edmunds, 2001; Box and Mumby, 2007). Box and Mumby (2007) found that survivorship of juvenile corals (< 20-mm diameter) in the Caribbean over 14 months, was decreased to < 2% when adjacent to *Dictyota pulchella*, and to 11% when adjacent to *Lobophora variegata*. The growth of juvenile corals was also decreased by shading and abrasion, but the extent to which growth was decreased depended on which macroalgal taxa were present (Box and Mumby, 2007). A manipulative field study at 9-m depth in Jamaica between *Porites porites* fragments (3 – 6 cm tall) and *Sargassum* did not find evidence for shading reducing coral growth, but did find evidence to implicate abrasion in reducing coral growth by causing polyp retraction (River and Edmunds, 2001).

Many studies of macroalgae-coral competition have been conducted using coral fragments (River and Edmunds, 2001; Smith et al., 2006) rather than juvenile colonies, but the juvenile life stage is particularly vulnerable (Bak and Engel, 1979), and interactions between macroalgae and juveniles should be explored further. Post-settlement success, could indicate a "recruitment bottleneck" in which the decline in coral cover is related to poor recruitment (Arnold et al., 2010; Doropoulos et al., 2014; Edmunds et al., 2015). This could be related to a decline in larval survival and settlement (Olsen et al., 2015), or factors affecting the recruit and juvenile life stage (Box and Mumby, 2007).

Not only does macroalgae have effects on the closest neighboring coral (within cm), but overall reef characteristics matter as well (MPA vs. non-MPA areas). In a lab

experiment in Fiji, coral and fish larvae preferred to swim towards water sourced from MPAs, when given the choice between MPA ("healthy reef") and non-MPA ("degraded reef") water in a flow-through chamber (Dixson et al., 2014). Additionally, *Acropora* larvae swam toward water with chemical cues from many different coral taxa rather than to seawater with cues from a single conspecific coral (Dixson et al., 2014), indicating that coral larvae might prefer to settle on reefs that are already diverse with many species of corals. However, larvae face external forces (i.e., flow) that make actively swimming between water types unlikely in the natural environment (Hata et al., 2017). Flow can transfer larvae into less favorable patches (i.e., algal-dominated bommies where space to settle is limited) of reef (Oliver et al., 1992; Leichter et al., 2013). While coral larvae may not prefer more degraded reef habitats (Dixson et al., 2014), larval active swimming is weak (Hata et al., 2017), and larval settlement does occur in seawater with macroalgal signals (Edmunds et al., 2010; Dixson et al., 2014). However, it is unclear how survival of coral recruits in these environments is affected by the presence of macroalgae, and it is important to understand how presence of macroalgae may affect survival either pre- or post-settlement.

Herbivores and Microhabitats

On tropical coral reefs, the presence of herbivores can keep macroalgae abundance in check by their feeding on the algae, and prevent or reverse phase shifts (Idjadi et al., 2006). In the Caribbean, the sea urchin *Diadema antillarum* is arguably the most important herbivore for controlling macroalgal communities (Lessios et al., 1984; Levitan, 1988; Edmunds and Carpenter, 2001, 2006). Some of the dramatic phase shifts

in the Caribbean in the recent decades, including reefs in Jamaica, Mexico, Belize, and the Cayman Islands, corresponded with a disease-related mortality event of *Diadema antillarum* (Lessios et al., 1984).

Twelve years ago, Dairy Bull reef (500-m by 100-m area) in Jamaica showed evidence of a potential recovery from a coral to macroalgal phase shift due to the localized recovery of *Diadema antillarum* and structural refuges provided by *Orbicella annularis* (Edmunds and Carpenter, 2001, 2006; Idjadi et al., 2006). In this location, elevated abundances of the sea urchin were associated with higher juvenile coral abundance (2.1 times more abundant in urchin zones) and low macroalgal cover (Edmunds and Carpenter, 2001). There were approximately 10 times more *Diadema antillarum* sea urchins in the "sea urchin zones" (up to 12 urchins m^{-2}) than the macroalgal zones along the North shore of Jamaica, between 4 and 9-m depth (Edmunds and Carpenter, 2001). The recovery of a reef in Jamaica shows the importance of structural refugia and herbivores to increasing abundances of juvenile corals.

Herbivores (fishes and invertebrates) also can be responsible for accidental grazing and predation of small corals if corals are located on exposed surfaces instead of crevices (Doropoulos et al., 2016). Thus, recruitment success can be influenced by a variety of factors and the scenario for highest chance of coral recruit survival depends on a series of ecological tradeoffs (Doropoulos et al., 2016). During fish exclusion experiments in Palau, which removed both herbivores and corallivores, coral mortality was higher in crevices due to competition with macroalgae and invertebrates (i.e., sea urchins) for space and light (Doropoulos et al., 2016). However, when fish herbivores were present, mortality of coral recruits was lowest in crevices, indicating tradeoffs in

settlement location between growth, predation, and competition (Doropoulos et al., 2016). Recovery of a reef (6–8 m depth, 500 x 100-m area) in Jamaica in 2004 from ~20% coral cover to < 50% coral cover was attributed to structural refugia provided by *Orbicella annularis* (Idjadi et al., 2006). A study which deployed settlement tiles with refuges found that coral recruits were more commonly in refuges, whether the refuges were on the top or bottom of settlement tiles (Edmunds et al., 2014). Together, these studies demonstrate the importance of refuges to the settlement and survival of scleractinian recruits (Idjadi et al., 2006; Edmunds et al., 2014).

Importance of Small Corals

It is important to study how the changing community dynamics on coral reefs affect the juvenile and larval stages of corals to better predict which species will provide community structure in the future. Recruitment is an important process affecting population densities (Caley et al., 1996), and maintaining genetic diversity within a reef system (Connell and Keogh, 1985, Gaines and Bertness, 1992). It is often difficult to quantify coral recruitment, because coral larvae are difficult for human observers to follow in the field (Carlon and Olson, 1993). Instead, surviving larvae are measured more easily post-settlement when they enter the juvenile stage and can be reliably seen and measured on surveys, here defined as being at least 2-mm and <40-mm in diameter (Edmunds, 2000).

Using settlement tiles, the number of coral recruits per tile at 2-m depth in the back reef of Moorea increased from 2005-2006 to 2006-2007 during the September to January sampling period (Edmunds et al., 2010). When all coral taxa were pooled, there

was a correlation between recruitment and coral cover in the back reef (Edmunds et al., 2010). Additionally, adult coral cover in the back reef declined from ~40% to < 20% from 2005 to 2014 (Han et al., 2016). Declining adult coral cover and increased settlement of recruits over the same period may indicate that survival of the young corals is being reduced at some point in their early life stages.

Early life stages of corals, including larvae, recruits, and juveniles, are vulnerable to many factors, such as temperature (Edmunds and Gates, 2004), ocean acidification (Foster et al., 2016), predation (Penin et al., 2010), and macroalgal competition (Box and Mumby, 2007). There is strong selective pressure for young corals to grow fast to escape size-dependent mortality rates that act on smaller individuals (type III survivorship curve) (Doropoulos et al., 2012). Fast growth can make them larger and less vulnerable to processes such as corallivory, which has the potential to dislodge small colonies, and algal overgrowth, which is less likely to overgrow entire large colonies (Zilberberg and Edmunds, 2001; Doropoulos et al., 2012). Thus, faster growth rates can increase survival rates for small corals (Edmunds and Gates, 2004), making calcification an important variable to measure in small corals.

Previous studies have shown that macroalgae can impact coral growth negatively (of both juveniles and adults), even causing tissue loss in some cases (Lirman, 2001; Box and Mumby, 2007). In some cases where algae also shaded juvenile corals, growth rates were slowed by 99% compared to control corals, which were not exposed to macroalgae or shaded (Box and Mumby, 2007). Therefore, when considering how macroalgae could modulate survival of early life stages of corals, and thereby affect the future reef community structure, it is ecologically meaningful to measure growth rates of small

corals near macroalgae. It is important to determine if growth rates are impacted by proximity, cover, or physical contact with macroalgae, in order to determine if increasing abundances of macroalgae could be augmenting the mortality of small corals. In Moorea, determining how macroalgae could affect young corals can be addressed using manipulative field experiments and directly measuring coral calcification via buoyant weight technique (Jokiel et al., 1978; Davies, 1989). In St. John, to determine how macroalgae may affect juveniles, the study scope was widened to include the important Caribbean herbivore *Diadema antillarum* and a variety of site characteristics. It was hypothesized that site characteristics would affect juvenile coral distribution among microhabitats. Coral survival within each microhabitat depends on ecological tradeoffs between predation, competition, and growth and assessment of these settlement decisions in the context of the environmental conditions may allow predictions of recruit survival (Doropoulos et al., 2016).

Study locations

Moorea

The data for this thesis were collected in Moorea, French Polynesia, and St. John, U.S. Virgin Islands. Moorea is a small volcanic island in the South Pacific Ocean and the reef system is comprised of a fore reef, reef crest, back reef, lagoon, and fringing reef. My study was done in the back reef on the north shore, which receives wave-forced flow from waves breaking onto the reef crest (Hench et al., 2008). For the reefs on the north side of the island near Cook's Bay, the wave-driven flow moves seawater toward the lagoon and back out of Avaroa pass. The overall process of seawater flowing over the

reef crest and into the back reef can flush the back reef with new water within hours (Hench et al., 2008). Settlement tiles in the back reef show that coral recruitment is occurring successfully for several coral taxa (Families *Poritidae*, *Acroporidae*, and *Pocilloporidae*) despite the increasing abundance of macroalgae (Edmunds et al., 2010; Han et al., 2016). Though *Acropora* coral larvae may not swim toward water containing algal chemical cues in a laboratory flow-through experimental set up (Dixson et al., 2014), larval swimming is weak and not possible in wave-driven flow environments that exist in the back reef of Moorea (Hench et al., 2008; Leichter et al., 2013; Hata et al., 2017). Seasonal wave energy has been correlated with coral recruitment variation in the back reef, where stronger waves were correlated to increased coral recruitment (Edmunds et al., 2010; Edmunds, 2017). This wave flow over the reef crest should be supplying larvae to the back reef regardless of laboratory-based larval preference, since recruits of several different genera routinely are recorded settling on tiles in the back reef (Edmunds et al., 2010). Although coral larvae can successfully settle in the back reef (Edmunds et al., 2010), coral cover in the back reef of Moorea on all three shores has declined to ~20% since 2010 as macroalgal cover increased (Han et al., 2016). I hypothesize that macroalgal presence in the back reef of Moorea is modulating coral larvae and juvenile survival and growth and increasing their mortality. These effects may be derived from a variety of factors including proximity to macroalgal cues, abrasion, or macroalgal cover. The present study included three field manipulations over two years, and field surveys of the natural back reef environment.

St. John

St. John is an island in the Caribbean surrounded by fringe reefs and includes the Virgin Islands National Park where fishing is regulated and development is minimized (Edmunds et al., 1990). The research for the present study took place at 12 sites located on the south shore within the Virgin Islands National Park, which included sites that have been surveyed for coral recruitment and benthic cover for over 25 years (Edmunds, 2013). Choosing these 12 sites enabled the study to encompass more environmental variation among sites, including different depths and exposure regimes, which could alter community structure between sites. Besides large storm events, the water is relatively calm and does not exchange with water outside of the bays very rapidly (Edmunds, 2002), which may mean that corals might be exposed to algal exudates for longer periods. My research in St. John tested the hypothesis that macroalgal presence modulates growth and mortality of juvenile corals. Macroalgae are prevalent throughout the Caribbean, with many reefs experiencing varying levels of degradation and algal phase shifts (River and Edmunds, 2001; Gardner et al., 2003; Arnold et al., 2010; Roff and Mumby, 2012). Jamaica was also the location of the first reef (Dairy Bull reef) to show potential for recovery from a phase shift, after *Diadema antillarum* recovered and corals returned to ~57% cover at 6–8 m depth (Edmunds and Carpenter, 2001, 2006; Idjadi et al., 2006).

Thesis Objectives

The purpose of this study was to quantify how abiotic and biotic environmental variables, predominantly macroalgal cover, affect the abundance, distribution, and growth of juvenile corals in Moorea, French Polynesia, and St. John, U.S. Virgin Islands. The contrast between Moorea and St. John provided the opportunity to explore the role of

macroalgae in affecting juvenile coral growth and survival in different parts of the world with different coral and algal species, and how these impacts may affect the potential for each reef to recover from a phase shift to macroalgae.

In Chapter 2, I investigate how proximity to macroalgae affects early life stages of corals, specifically involving the freshly released larvae of *Pocillopora damicornis,* and juvenile colonies (i.e., < 4-cm diameter) of *Porites* spp. and *Pocillopora* spp. The hypothesis that proximity to macroalgae would reduce survival of coral larvae, and reduce calcification of juvenile corals, was tested with field manipulations in the back reef. I also hypothesized that coral growth would be lower in areas of higher macroalgal cover and when there was contact between corals and algae. Finally, field surveys were done to contextualize the experimental results and estimate natural juvenile coral distributions in relation to algae cover.

In Chapter 3, I investigate the effects of site characteristics (i.e., benthic cover of macroalgae and herbivore presence) on the distribution and abundance of juvenile corals among microhabitats within 12 sites on the south shore of St. John. Small corals were measured and determined to be in exposed, shallow, or protected microhabitats. I hypothesized that juvenile coral distribution within different microhabitats would be related to specific site features; for instance, in conditions of higher abundances of herbivores, and lower macroalgae cover, juvenile corals would be found more often within crevices. Further, it was hypothesized that comparing the site features to juvenile distributions within microhabitats could be used in a predictive capacity to estimate survival (i.e., juveniles would have lower survival if in exposed habitat under X conditions) based on the ecological tradeoffs described in Doropoulos et al. (2016).

Chapter 2:

Calcification responses among early life stages of corals to macroalgae in the back reef of Moorea, French Polynesia

Introduction

Many tropical reefs that formerly were dominated by scleractinians (i.e., > 50% cover) (Smith et al., 2016b) are degrading to macroalgal-dominated states due to anthropogenic and natural stressors (Edmunds and Carpenter, 2001; Smith et al., 2006; Stewart, 2008; Diaz-Pulido et al., 2009; Fabricius et al., 2011; Bulleri et al., 2013; Ainsworth and Mumby, 2015; Enochs et al., 2015; Vieira et al., 2016b). In the back reef of Moorea, corals have been declining in cover from 40% in 2010 to 20% in 2014, while macroalgal cover has increased from <1% to ~10% cover (Han et al., 2016). Settlement tiles placed in the back reef show that a variety of corals routinely recruit to this habitat (Edmunds et al., 2010), despite the ongoing decline in adult coral cover (Han et al., 2016). The combination of coral recruitment, decreasing coral cover, and increasing abundance of macroalgae may suggest that macroalgae could be having negative effects on the post-settlement success of corals. Additionally, some studies have implicated macroalgae as causal agents driving mortality of planula larvae and coral recruits (Dixson et al., 2014; Olsen et al., 2015). Juvenile corals that are small in size (i.e., ≤ 4-cm diameter) have high mortality rates defined by type III survivorship curves (Bak and Engel, 1979; Edmunds, 2000), and coral recruitment and growth may be hindered by competition with macroalgae (Box and Mumby, 2007; Doropoulos et al., 2014). Juvenile corals are vulnerable to negative impacts of macroalgae due to their small surface area and ability to be completely smothered by macroalgae (Jompa and McCook, 2002; Penin

et al., 2010). It is important to consider the vulnerability of juvenile corals because on algal-dominated reefs, growth and survival of juvenile corals is necessary to support rapid increases in coral abundance (Doropoulos et al., 2015).

As a result of shifts from scleractinian- to macroalgae-dominated reefs (Done, 1992; Hughes, 1994), interactions between corals and macroalgae have become increasingly prevalent in many coral reef habitats (River and Edmunds, 2001; Hughes et al., 2007; Rasher et al., 2011). Macroalgae can impact coral survival and physiology through shading, abrasion of tissue, reduction of flow and increased sedimentation (River and Edmunds, 2001; Brown and Carpenter, 2015), and allelopathy or microbial effects (Smith et al., 2006; Vieira et al., 2016a, 2016b). Some studies done in the lab using flow-through chambers with water sourced from macroalgae dense regions, coral conspecifics, and MPA vs. non-MPA water (Dixson et al., 2014), or using filters to separate coral from macroalgae (Smith et al., 2006), have shown that organic exudates from macroalgae can negatively affect corals without the need for direct contact between the two. Additionally, field manipulations that attached seaweeds and inert mimics to corals have determined that soluble chemicals or bacteria released from the algae reduced coral growth (Rasher and Hay, 2010; Vieira et al., 2016b). However, in these analyses, the damage caused by the algae was limited to areas of direct contact and abrasion, and did not affect the whole coral (Rasher and Hay, 2010). While these studies implicate chemicals in harming coral tissue or depressing growth (Smith et al., 2006; Rasher and Hay, 2010; Dixson et al., 2014; Vieira et al., 2016a, 2016b), some cite the need for contact (Rasher and Hay, 2010; Vieira et al., 2016b), but others do not (Smith et al., 2006). One reason the results of these studies differed could be the result of species-specific coral-macroalgal interactions

(Rasher et al., 2011), consequently, it is ecologically meaningful to test whether contact is necessary to confer negative effects between different combinations of coral-macroalgae species interactions. The purpose of this study was to identify how macroalgae common in the back reef of Moorea impact early life stages of corals *in situ*. Four hypotheses were tested: (1) that the abundance (i.e., percent cover) of macroalgae is related to the distribution of juvenile colonies of two dominant corals (*Porites* spp. and *Pocillopora* spp.) in the back reef; (2) proximity (≤ 2-cm without direct contact) to macroalgae decreases survival and settlement of coral larvae, (3) proximity (≤ 2-cm without direct contact) to macroalgae decreases calcification of juvenile colonies of *Porites* spp. and *Pocillopora* spp., and (4) calcification in juvenile corals would be reduced in areas of higher macroalgal cover, and by macroalgal abrasion. This study considers how macroalgal abundance and abrasion contribute to the growth and survival of juvenile and larval coral life stages, which could be important in predicting the future trajectory of the reef.

Materials and Methods

Study site and organisms

Sampling was conducted in April and May, in 2017 and 2018, on Moorea, French Polynesia, at the Richard B. Gump South Pacific Research Station. Field manipulations and surveys were completed along the north shore in the back reef, between Ōpūnohu Bay and Irihonu Pass. This study was conducted in two fronts: one addressed the effects of macroalgae on larvae, and the other addressed the effects of macroalgae on juveniles. To determine the effect of macroalgae on juveniles, three 3 studies were conducted using

small colonies of massive *Porites* spp. and *Pocillopora* spp. (≤ 4-cm diameter). Without a molecular approach, colonies of these taxa could not be reliably identified to species *in situ* and were therefore analyzed at the genus level, where massive *Porites* spp. included *P. lobata* and *P. lutea* (Edmunds, 2009), and *Pocillopora* spp. included *P. meandrina, P. verrucosa,* and *P. eydouxi* (Edmunds and Leichter, 2016; Tsounis and Edmunds, 2016). Henceforth, massive *Porites* spp. and *Pocillopora* spp. will be referred to throughout this paper as *Porites* and *Pocillopora,* respectively. Pocilloporidae and Poritidae corals recruit in high numbers, making up ~50-75% of recruits to the back reef of Moorea compared to other taxa (Edmunds et al., 2010) and are among the most common adult taxa in the fore reef (10-m depth) and back reef (2–3 m depth) systems of Moorea (Hench et al., 2008; Edmunds et al., 2010; Lenihan et al., 2011; Holbrook et al., 2018).

Field Surveys

Surveys were completed in the back reef (depth ~2-3 meters) to the east of Avaroa Pass (S17°28'25.80" W149°48'57.90"). Four sites were selected at four distances away from the reef crest (25 m, 50 m, 75 m, and 100 m) to sample across a gradient of varying macroalgal cover. At each site, two 15-m transects were placed parallel to the reef crest, and quadrats (0.5 x 0.5 m, n = 20) were placed at random locations along each transect. Juvenile corals were defined by size ≤ 4-cm diameter, and excluded fragments left from larger colony mortality (Edmunds, 2000, 2004; Edmunds and Carpenter, 2001). This was important because partial mortality of larger colonies can result in small corals, which are functionally different from juveniles (i.e., reproductive), although similar in size (Hughes and Jackson, 1980; Soong, 1993). All *Porites* and *Pocillopora* juveniles

were counted to test for differences in abundance and distribution between taxa and among locations. To quantify macroalgal percent cover, each quadrat was divided into 25 equal sub-squares, and each square was assigned to a dominant category (Edmunds et al., 2010).

Experiment 1

To determine how proximity to macroalgae affects settlement and survival of coral larvae in the back reef of Moorea, *Pocillopora damicornis* larvae were put in UV-transparent acrylic chambers (ACRYLITE Colorless 0070, 92% UV transmission) with mesh ends (150-µm), in situ in treatments of contrasting benthic cover differing in abundance of scleractinians, macroalgae, and bare space/carbonate rock. These benthic cover treatments (0.5 x 0.5-m area) were determined by containing dominant (> 65%) cover of macroalgae, live coral, or carbonate rock/bare space. The mesh ends on the chambers allowed sea water to flow through, while preventing larvae (~0.5 mm^2) from exiting (Putnam et al., 2010). To obtain coral larvae, twelve adult colonies (> 15-cm diameter) of the brooding coral *Pocillopora damicornis* were collected on April 26, 2017, from < 1-m depth on a fringing reef east of Cook's Bay (S17°28'50.1" W149°48'26.3"). The colonies were set up in spillover-tanks at the lab, which are tanks fitted with spouts to collect larvae in an overflow container (Putnam et al., 2010). This species was selected because of past success with larval release in the laboratory, and predictable larval release timing with the lunar cycle (Richmond and Jokiel, 1984; Jokiel et al., 1985; Edmunds et al., 2011; Putnam et al., 2013). *P. damicornis* larvae differ in size, symbiont density, and photophysiology among larval release days (Putnam et al., 2010), so to minimize potential variation in larval physiology, all larvae were collected early on the same

release morning and pooled among colonies. The larvae were pipetted into 24 acrylic chambers (n = 16 larvae chamber^{-1}) which were attached to bommies (S17°28'50.4" W149°50'46.8") in the back reef (≤ 2-m depth); 8 chambers were allocated to each benthic cover treatment, which were live coral, macroalgae, and bare carbonate rock. The chambers were 0.5-m away from one another, and distributed within a 10 x 10-m area. The larvae in the chambers were counted in situ after 48 hours and 72 hours for larval survival and settlement (Olsen et al., 2015).

Experiment 2

To determine how proximity to macroalgae affects the calcification of small corals, thirty colonies (≤ 4-cm diameter) of massive *Porites* and *Pocillopora* were collected from the back reef using a hammer and chisel (from ~3-m depth at a single site [S17°28'32.40" W149°48'57.20"]). Corals were transported to the lab in individual plastic bags in a cooler filled with seawater and shielded from the sun. On shore, they were transferred into a shallow tank with flowing filtered seawater.

To test how proximity to macroalgae (excluding direct contact between macroalgae and corals), impacted coral calcification, corals were glued to individual plastic tiles to which macroalgae also were attached outside a rigid black polypropylene cage. The cage (6 cm tall, 4 cm diameter, 0.5 cm mesh size) surrounded the coral and prevented the coral from being abraded by macroalgae, while ensuring the coral and macroalgae were ≤ 2-cm apart. To test for possible effects of the manipulation or cages, two control treatments were employed: a manipulation control (plastic base only), and a cage treatment (plastic base and cage only, no algae). To create the macroalgae treatment,

three common genera of macroalgae from the back reef were collected and bundled together for attachment to the bases. For *Turbinaria ornata* and *Sargassum* spp. 1 stipe (~20 cm long) of algae was equivalent to a wet weight of 15–20 g. The algae will be referred to by their genus name from now on. The algal treatment was composed of ~15–20 g (wet weight) each of *Dictyota*, *Turbinaria,* and *Sargassum*. These genera were selected because they are common fleshy macroalgae in the back reef of Moorea, and were found in association with juvenile corals during the field surveys (AW personal observation). Moreover, the use of three genera of algae created the opportunity for more general inferences to be made from the results of the manipulation. One algal bundle was attached to each plastic tile using plastic-coated flexible wire. Each treatment group (plastic base only, cage treatment, and algae + cage treatment) was composed of 20 corals, 10 of which were *Porites* and 10 were *Pocillopora.*

Since mortality rates are higher in small juvenile corals and fast growth is important to survival; calcification was used as the response variable to determine if macroalgae reduced growth rates, which could therefore reduce survival (Babcock, 1991; Edmunds and Gates, 2004). To measure juvenile coral calcification, buoyant weight (± 0.001 g) (Jokiel et al., 1978) was measured before and after deployment of the coral replicates to the reef. The corals were deployed in their respective treatments (i.e., control, cage control, and algae + cage) onto the carbonate rock substratum in Avaroa Pass (~3 m depth, S17°28'55.9" W149°49’25.5") on April 14, 2017. To maintain treatment conditions, algae bundles were replaced every 5 days with freshly collected algae from the back reef, and at this time the plastic tiles and cages were brushed clean to prevent build-up of turf algae on the plastic.

After 31 days (May 13, 2017), the corals in their treatment arrays were removed from the reef and brought back to the lab, where the cages and algae were removed, and the PVC bases were cleaned prior to the final buoyant weight measurement. The difference between the final and initial buoyant weights was converted to dry weight using the density of aragonite, 2.93 g cm^{-3}. To normalize the calcification per unit surface area, the corals were dried and surface area was estimated using a wax dipping technique (Stimson and Kinzie, 1991).

Experiment 3

To determine how cover of macroalgae and contact with macroalgae affect juvenile coral calcification, 120 colonies (≤ 4-cm) of massive *Porites* and *Pocillopora* (n = 60) were collected from the back reef using a hammer and chisel (from ~3-m depth at a single site [S17°28'32.40" W149°48'57.20"]). Corals were transported back to the research station and glued onto individual numbered plastic tiles. Half of the corals were protected from macroalgal contact with transparent plastic cages (Far Edge Aquatics brand; 6 cm tall, 4 cm diameter, 0.5 cm mesh size), which were attached to the plastic tiles.

Corals in their treatment arrays (i.e., cage or no cage) were deployed on the reef using hammer and nails (S17°28'28.5594" W149°48'49.1754") into one of three algal cover plots (4-m^2 area; n =40 corals per plot): high (87% cover), medium (58% cover), and low (1.6% cover). The high-cover plot was the ambient macroalgal cover at approximately 100-m from the reef crest, the medium-cover plot was created by removing macroalgae by hand, and the low-cover plot was created by removing all of the

macroalgae by hand and with an abrasive brush. The plots were located randomly along a transect parallel to the reef crest, located approximately100-m away from the reef crest. Corals remained in the field in their respective treatments for 32 days. Treatments were cleaned periodically throughout the deployment period to prevent turf build up on the plastic tiles and cages. Light reduction of the cages was measured at noon using a LI-COR Spherical Underwater Quantum Sensor ($\mu mol\ s^{-1}\ m^{-2}$) and spare cage materials.

Calcification was used as the response variable, measured using buoyant weight (Jokiel et al., 1978) before and after deployment of the juvenile corals. The difference between the initial and final buoyant weights was converted to dry weight using the density of aragonite, 2.93 $g\ cm^{-3}$. Calcification was normalized per unit surface area by drying the corals and measuring surface area using a wax dipping technique (Stimson and Kinzie, 1991).

Statistical Analysis

To determine if density of juvenile corals differed with distance from the reef crest during the field surveys, the density of juvenile corals was analyzed with a multivariate linear regression model; where the dependent variables were number of corals per each taxon, and distance from the reef crest was the independent variable. The percent cover of macroalgae at each survey site (fixed factor) was arcsine transformed and analyzed using a one-way ANOVA to determine if cover of algae changed over the distance from the reef crest. Tukeys post hoc procedure was used to determine which survey sites had different macroalgal covers. Relative flow as determined by the clod card dissolution was analyzed using a 1-way ANOVA, where the change in dry weight of

the clod cards over time was the dependent variable, and distance from the reef crest was a fixed factor. Larval settlement and post-settlement survival (both as percentages) over 72 hours were arcsine transformed, and analyzed with 1-way ANOVAs, with dominant benthic cover treatment (i.e., live coral, macroalgae, rock/bare space) as the fixed effect. To determine if the proximity to macroalgae affected juvenile calcification, a two-way ANOVA was used in which taxon and treatment (control, cage control, and algae + cage) were fixed effects. To determine if macroalgal cover or contact with macroalgae affected calcification, a two-way ANOVA was used, in which macroalgal plot and protection (i.e., cage or no cage) were fixed factors. A Tukeys post hoc procedure was used to determine which treatments had significantly different growth rates. All statistical analyses were carried out in RStudio (Version 1.1.419).

Results

Field Surveys

The back reef of Moorea was characterized by higher algal cover near the reef crest and lower algal cover closer to shore ($F = 32.92$, $df = 3, 76$, $P < 0.0001$). Mean (± SE) macroalgal cover varied from 8.4 ± 2.5% 100-m from the reef crest, to 67.4 ± 4.8% cover 25-m from the reef crest (all quadrats n = 80). Overall mean (± SE) density of juvenile corals (≤ 4-cm diameter) varied between 0.9 ± 0.3 colonies 0.25-m^{-2} and 1.6 ± 0.42 colonies 0.25-m^{-2}, and was not affected by distance from the reef crest (Fig. 2.1A; $F = 1.037$, $df = 3, 76$, $P = 0.381$). The mean (± SE) size of juvenile *Pocillopora* was 17 ± 1 mm, and for *Porites* it was 19 ± 1 mm (n = 54 and 31, respectively). Of the juvenile

corals surveyed, 51% were *Pocillopora* and 30% were *Porites* (n = 141 colonies) (Fig. 2.1B).

Although densities of all juveniles (i.e., pooled among taxa) were similar regardless of distances from the reef crest, distributions of each taxon varied in relation to distance from the reef crest. Density of *Porites* increased moving away from the reef crest, but density of *Pocillopora* remained similar (generalized linear model, *Porites: F* = 13.71, *df* = 1, 78; *P* = 0.004; *Pocillopora*: *F* = 1.222; *df* = 1, 78; *P* = 0.27). The density of juvenile *Porites* increased with distance from the reef crest, and they were more common in areas of low macroalgal cover (Fig. 2.1A). Conversely, densities of juvenile *Pocillopora* showed the opposite trend, and were more abundant closest to the reef crest, where macroalgae was most abundant (Fig. 2.1A).

Experiment 1

No changes in larval settlement or mortality occurred between the 48 and 72-hour assessment time points. Thus, the number of larvae that were swimming, settled, and missing/presumed dead were recorded at the end of 72 hours, and the chambers were removed from the reef. After 72 hours, between 20 and 30% of larvae settled on the walls of the acrylic chamber in all treatments (Fig. 2.2; *F* = 0.106, *df* = 2, 20, *P* = 0.900). Mortality of pelagic larvae was the same in all treatments (Fig. 2.2; *F* = 1.085, *df* = 2, 20, *P* = 0.357), however, mean (± SE) larval mortality was highest in chambers next to coral conspecifics (55.5 ± 12.1%), and lowest in chambers next to carbonate rock (32.0 ± 10.3%) (both n = 8).

Experiment 2

Treatment (i.e., cage + macroalgae, and cage without algae) did not affect calcification of corals over 31-days in situ (Fig 2.3D; $F = 0.011$; $df = 2, 49$; $P = 0.99$). *Porites* calcified at a rate of 2.51 ± 0.28 mg $CaCO_3$ cm^{-2} day^{-1}, and *Pocillopora* calcified at a rate of 2.18 ± 0.3 mg $CaCO_3$ cm^{-2} day^{-1} (mean ± SE, n = 30 and 23 respectively). Calcification did not differ between taxa ($F = 3.372$, $df = 1, 49$, $P = 0.068$). The interaction between taxa and treatment was not significant and was dropped from the model ($F = 0.692$, $df = 1, 4$, $P = 0.599$).

Experiment 3

Porites were, on average, 17.2 ± 0.6 mm in diameter, and calcified at 2.8 ± 0.1 mg $CaCO_3$ cm^{-2} day^{-1} (mean ± SE, n = 38). *Pocillopora* were 17.9 ± 0.6 mm in diameter, and calcified at 2.6 ± 0.5 mg $CaCO_3$ cm^{-2} day^{-1} (mean ± SE, n = 38). A split plot ANOVA was used to analyze the data, since the algal plots were not replicated, and coral individuals were nested within the plots. There were no significant interactions between macroalgal cover plots and taxa, so they were dropped from the model.

The algal plots contrasted macroalgal cover of 87.1 ± 1.0%, 58.0 ± 3.0%, and 1.6 ± 0.4% (high, medium, and low respectively). Algal cover had no effect on juvenile coral growth rates ($F = 0.314$, $df = 2, 67$, $P = 0.731$), however, growth was depressed by the presence of a cage (Fig. 2.4, $F = 9.153$, $df = 1, 67$, $P = 0.0035$). Cages reduced light at noon by 11 – 19% ($F = 69.02$, $df = 2,24$, $P < 0.0001$). Calcification did differ between taxa (Fig. 2.4, $F = 4.768$, $df = 1, 67$, $P = 0.033$).

Discussion

The effects of macroalgae on corals have been explored with increasing frequency as phase shifts from coral dominated reefs to macroalgal dominated reefs have increased (Hughes, 1994; Bruno and Selig, 2009; Diaz-Pulido et al., 2009; Vieira et al., 2016b). Phase shifts to macroalgal-dominated reefs are associated with a reduction in reef heterogeneity and decreased biodiversity supported by the reef (Alvarez-Filip et al., 2009; Ainsworth and Mumby, 2015). Phase shifts to macroalgal-dominated reefs also result in increased competition between corals and macroalgae (River and Edmunds, 2001; Jompa and McCook, 2002; Rasher et al., 2011; Vieira et al., 2016a), and although the mechanisms of competition between macroalgae and corals have been explored, many knowledge gaps continue to exist, and species-specific interactions make generalizations difficult (Koch et al., 2013; Vieira et al., 2016a). Many studies of macroalgae-coral competition have been done on coral fragments (River and Edmunds, 2001; Smith et al., 2006) rather than juveniles, but this life stage is particularly vulnerable (Bak and Engel, 1979) and was the focus of the present study.

Within the past decade, the fore reef of Moorea suffered major disturbances including an outbreak of the corallivorous crown-of-thorns sea stars, *Acanthaster planci* (2007–2009), and Cyclone Oli (2010), which left the fore reef at <5% coral cover around the island in 2010 (Holbrook et al., 2018). By 2015, coral cover recovered to pre-disturbance levels, ~ 40–50% coral cover at some sites, with sites on the north shore recovering to the highest coral cover compared to sites on the east and west shores (Holbrook et al., 2018). However, the back reef on the north shore of Moorea has much lower coral cover, which declined from ~ 40% in 2005 to < 20% in 2014, and has

remained low since (Han et al., 2016). Macroalgal cover is also higher in the back reef (some areas ~90% cover (Fig. 2.1 A, Fig. 2.4)) than the fore reef which had ≤ 15% macroalgae cover at all of the fore reef sites at 10-m depth (Holbrook et al., 2018). The present study tests the hypothesis that macroalgae in the back reef of Moorea reduces survival or growth of larval and juvenile stages of corals (*Pocillopora* and *Porites* specifically), thus preventing recovery of coral cover in the back reef.

The field surveys completed 25-m to 100-m from the reef crest found that juvenile corals were distributed evenly across this gradient. When broken down into taxa, *Porites* juveniles were more abundant further away from the reef crest, and *Pocillopora* juveniles were more abundant closer to the reef crest (Fig. 2.1 A). Macroalgae cover was also highest near the reef crest at ~70% cover in this location. If macroalgae was increasing juvenile coral mortality, I hypothesized that more corals would be found in areas of less macroalgal cover, but this trend only occurred for *Porites*, and overall abundance of juveniles didn't change with macroalgal cover (Fig. 2.1 A). Given that macroalgae did not depress coral growth in the field manipulations, it is unlikely that this pattern is due to species-specific effects of macroalgae on the juvenile corals.

One hypothesis is that this pattern could be the result of different coral recruitment patterns. *Pocillopora* is a dominant coral genus on the fore reef (Holbrook et al., 2018), and it is likely that larvae are transported over the reef crest by wave action (Tsounis and Edmunds, 2016) and would settle out, generating this distribution pattern, where *Pocillopora* juveniles are most abundant closer to the reef crest, where the larval supply is highest (Fig. 2.1 A). *Porites* is not currently a dominant space holder on the fore reef at 10-m depth (Holbrook et al., 2018), but is one of the most abundant corals in the

back reef where it forms large bommies (Lenihan et al., 2011). Both *Porites* and *Pocillopora* are broadcast spawners, meaning that they release gametes and fertilization occurs externally before larvae can settle (Oliver and Babcock, 1992; Edmunds et al., 2010). With the larval retention time of broadcast spawners, it is unclear whether *Porites* can self-seed the back reef before water flow would carry gametes and larvae out of the pass, however some of this water is redirected over the reef crest again (Hench et al., 2008), and some models have shown that self-seeding is possible to a degree (Jones et al., 2009). It is may also be that recruitment in Moorea is characteristic of an open system (Caley et al., 1996, Edmunds et al., 2010), and this variation in coral juvenile distribution could be random, or caused by an additional unconsidered factor.

The results of the field manipulation in which *Pocillopora* larvae were exposed to macroalgae, coral, or bare rock benthic treatments (Experiment 1), found that larval survival was not impacted by the adjacent (scale of 0.5-m) benthic community composition (Fig. 2.2). Settlement onto the acrylic chambers occurred at approximately the same rate in all treatments, and mortality was highest in the chambers next to live coral, though this was not significant (Fig. 2.2). Unfortunately, the sample size was limited by the number of larvae released in the aquaria, and the statistical power for observing a significant result was 52% at $\alpha = 0.5$. The lack of a significant result could therefore be due to the small sample size, or because the larvae were not affected. The latter will be discussed further.

In the Caribbean, survival of *Porites* larvae in an aquarium, was reduced by the presence of brown alga, *Dictyota* (Olsen et al., 2015). In the study by Olsen et al. (2015) *Dictyota* was placed directly within the larval chambers (scale of < 6-cm), but an algal

mimic treatment did not reduce survival at the same level as the algal treatment (Olsen et al., 2015). The present study used small acrylic chambers deployed on the back reef in the natural environment with wave-driven flow, the macroalgae was outside of the chambers, and included *Dictyota*, *Sargassum*, *Turbinaria*, and *Halimeda*. DIC, nitrate, and bacterioplankton levels are approximately the same across this region of the back reef (Leichter et al., 2013), so it may be reasonable to hypothesize that algal exudates would be distributed widely across the back reef, and the benthic treatments (0.25-m^2) do not have significant water quality differences over this scale (Leichter et al., 2013). However, Nelson et al. (2011) found that bacterioplankton and DOC concentration is variable across the back reef and lagoon areas. This field manipulation was deployed within a small region that may have been homogeneous for DOC and bacterioplankton, and thus algal exudates. Another hypothesis to explain why larvae did not have different survival rates within the benthic treatments, is that the macroalgae in the back reef of Moorea does not increase mortality of *Pocillopora damicornis* larvae prior to settlement, over a period of 72-hours. The dominant algal genera in this area were *Turbinaria* and *Sargassum,* and while there was *Dictyota* present, it did not dominate the algal cover on these benthic plots (AW, data not published). Interactions between coral and macroalgae can be species-specific (Box and Mumby, 2007; River and Edmunds, 2001), and it is possible that *Pocillopora damicornis* larvae are resilient to the potential effects of these algae.

While proximity to macroalgae didn't seem to play a large role in larval survival in Moorea (Fig. 2.2), coral larvae in the natural environment interact with macroalgae physically as well. A study on Ningaloo reef in Australia assayed recruitment of corals

with settlement tiles on the reef compared to plots that excluded herbivores (macroalgae was 40x higher on these plots), and found that macroalgae significantly reduced settlement and survival on the settlement tiles (Webster et al., 2015). Recruits in the macroalgal plots were smaller, had 75% fewer polyps, and were less abundant (Webster et al., 2015). Larval mortality due to macroalgae in Moorea is more likely to be related to access to settlement space and macroalgae and fish effects on recruits post-settlement.

If coral recruits survive long enough in macroalgae-dominated environments, they will continue competing with macroalgae as juvenile corals. Experiment 2 and 3 of the present study tested whether macroalgae affected growth of juvenile corals, using two field manipulations with *Porites* and *Pocillopora* juveniles. The first field manipulation tested the effect of a small bundle of macroalgae (~45-60 grams) on the nearest coral neighbor (≤ 2-cm distance). Growth rates were not affected over 31-days in the field, and did not differ between genera (Fig. 2.3). Power for detecting this effect was approximately 70% at $\alpha = 0.5$. Experiment 2 utilized cages to prevent contact between the macroalgae and the coral. While some macroalgae have been shown to decrease growth and survival of corals without contact (Smith et al., 2006; Vieira et al., 2016a, 2016b), other studies have found that contact between coral and macroalgae was necessary for the macroalgae to have a negative effect on the coral (Nugues et al., 2004). A possible explanation for why the macroalgae did not reduce growth in Experiment 2 is the lack of contact between coral and macroalgae, and that the cover of algae was not enough to confer any negative effects (Clements and Hay, 2015), or because the corals were allocating energy to interspecific competition rather than growth (Tanner, 1997). Additionally, it could be that algal exudates are dispersed evenly in the water throughout

the back reef and equally affected all of the treatments, and without experiments on coral-dominated reefs or in aquaria, this cannot be ruled out.

Experiment 3 was designed to address these new hypotheses that contact and abrasion between coral and macroalgae is needed to reduce growth, or that higher density of algal cover reduces growth. To test this, three macroalgal cover plots (2 x 2 m) were created on the shallow (~ 2-m depth) in the back reef to contrast algal cover at treatment levels of ~87%, 58%, and 1% cover. Corals were deployed into these plots – half with cages to protect the coral tissue from abrasion caused by macroalgae, and the other half of the juveniles on each plot had no cages. Growth was measured after 32-days in the field, and the results revealed no effect of the macroalgal cover on coral growth(Fig. 2.4). Juvenile corals within cages grew faster than those without cages, which occurred for both taxa, and all three algal treatments (Fig. 2.4). This was unlikely to be caused by shading because the cages were transparent and only reduced light by 10–19%, whereas the black cages from the first juvenile field manipulation reduced light by 48–58% and didn't affect growth (Fig. 2.3 B, D). If abrasion was the only factor in lowering growth rates of uncaged corals, I wouldn't expect to find uncaged corals growing slower on the low macroalgal cover plot where cover was 1.6 ± 0.4% and abrasion was minimal or nonexistent. Power for detecting an effect was high (~ 92% at $\alpha = 0.05$).

Manipulating macroalgal abundance on each plot had effects on the fish community, which could be associated with the trend in slower growth of uncaged individuals (AW, data not published). Herbivorous fishes remove macroalgae and can prevent their establishment on bare spaces (Han et al., 2016). In particular, *Acanthurus nigrofuscus*, visited the low-cover plot frequently and consumed turf algae off the

bommies, and cages surrounding the corals (ADW personal observation). This species of fish was not observed on either of the other two plots, but was repeatedly observed on the low-cover plot and even destroyed five cages (Supplemental Fig. 2.5).

On the medium cover algal plot, one of the corals and many of their plastic tiles had damage that appeared to be bite marks, which were likely caused by fish corallivores (Supplemental Fig. 2.6 B, C) (Grottoli-Everett and Wellington, 1997). Algal cover on the medium plot was ~60% cover, so abrasion or shading could have reduced coral growth, in addition to fish corallivory which reduced the sample size of the deployed coral juveniles. Finally, the high-cover algal plot did not seem to have any herbivore or corallivore presence and feeding activity, but abrasion of juveniles caused by the algae may have resulted in slower coral growth rates (Supplemental Fig. 2.6 A). Therefore, it seems that algal cover, even on small scales (4-m^2 area) can impact the fish community, which in turn will affect corals within that plot. Herbivorous fish do consume *Turbinaria*, which has been shown in Belize, and reefs in the Caribbean and South Pacific, despite containing phenolic compounds, which can reduce herbivory by fishes (Lewis, 1985; Steinberg, 1986). *Turbinaria* was the dominant alga in the region of the back reef where the field manipulations were deployed. It seems that once the abundance of *Turbinaria* was manipulated to create the medium and low-cover plots, the fish community changed and increased fish activity on those plots (AW, personal observation, data not published). Another study in Moorea tested a similar observation and found that fish species richness increased on coral heads where *Turbinaria* was removed (McCarthy, 2009).

Furthermore, in East Indonesia, a computer simulation of the Raja Ampat Archipelago reef was run in which different scenarios of coral reef loss, and increasing

macroalgae cover were used to calculate how fish biodiversity and fishery productivity would be affected (Ainsworth and Mumby, 2015). The simulation predicted that as coral cover declined and was replaced by macroalgal cover, small-bodied herbivorous fish density would increase, but the larger fish that were of interest to fisheries would decline (Ainsworth and Mumby, 2015). This would result in changes in the reef community structure and function, and would particularly effect coastal communities of people that rely on a piscivorous diet.

The results of the present study show that macroalgae in the back reef does not have chemical effects on *Pocillopora* larvae as well as juvenile colonies of *Porites* and *Pocillopora*. Despite these findings, macroalgae is a dominant space holder in many areas of the back reef of Moorea, which can make settlement for larvae difficult (Webster et al., 2015), and may lower juvenile coral growth via abrasion and shading. Changing densities of macroalgal cover may influence the fish community, which can be detrimental to the corals by increasing grazing and corallivory (Supplemental Fig. 2.5 and Fig. 2.6). In order to understand how changing climate (or other environmental changes) might affect coral survival and growth, it is important to consider how phase shifts may shift community structure and potentially alter future functions the reef is capable of offering (Connell et al., 1997; Bellwood et al., 2004; Ainsworth and Mumby, 2015).

Figures

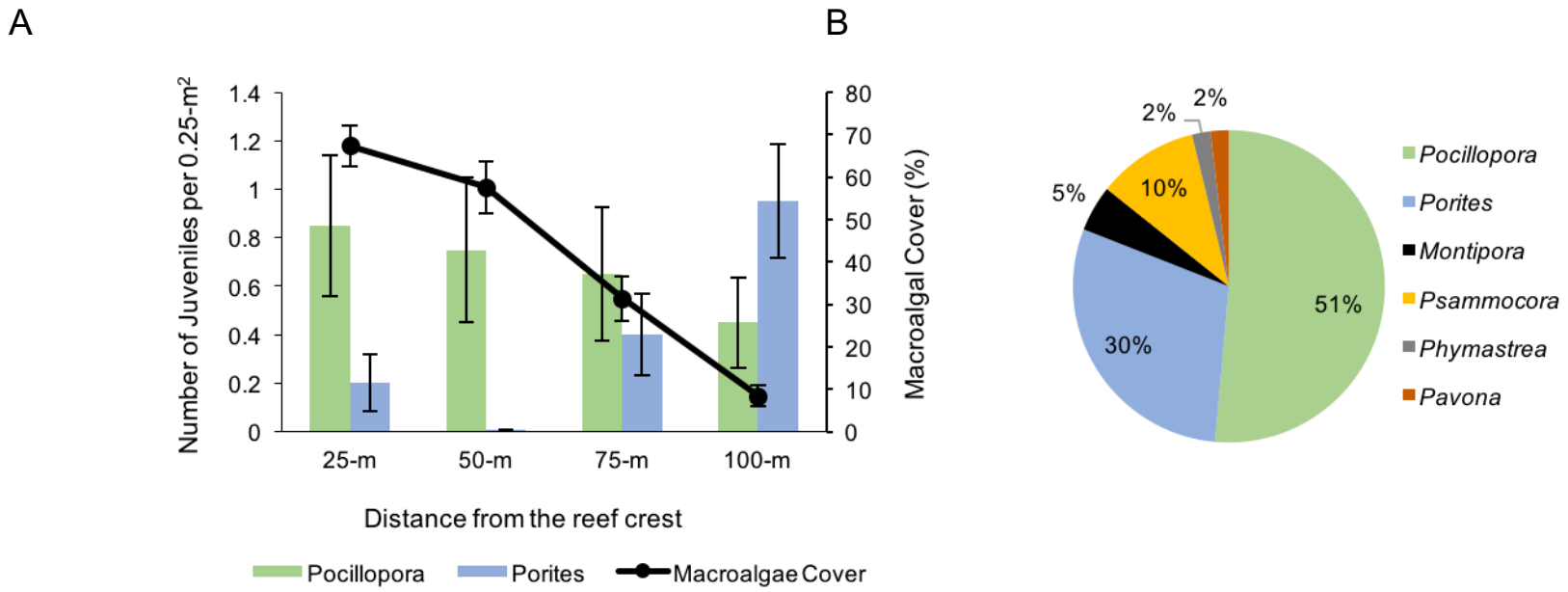


Figure 2.1 Results of field surveys showing the abundance and distribution of juvenile *Porites* and *Pocillopora* relative to distances away from the reef crest and macroalgal cover. (A) The mean density (± SE) of juvenile corals (≤ 4-cm diameter) at four distances from the reef crest (n = 20 quadrats, per distance) in the back reef of Moorea in 2017; mean (± SE) macroalgal cover (%) at each distance from the reef crest is shown on the right ordinate. (B) Pie chart showing composition of juvenile corals in the back reef of Moorea, pooled by distance from the reef crest, of which 81% were *Pocillopora* and *Porites* (n =141 colonies).

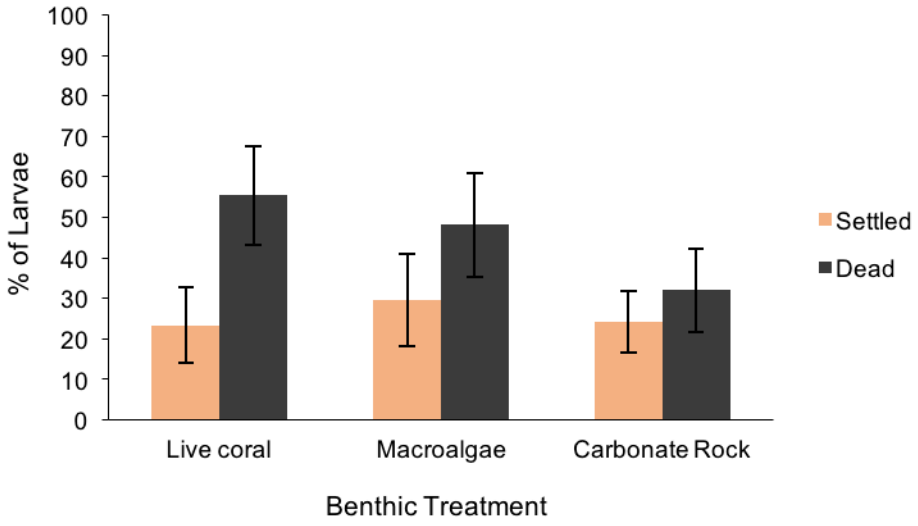


Figure 2.2 Bar graph showing the average number (± SE) of larvae (n = 8 chambers treatment^{-1}) that settled or died in the pelagic phase, in each treatment (live coral, macroalgae, and carbonate rock) over 72 hours.

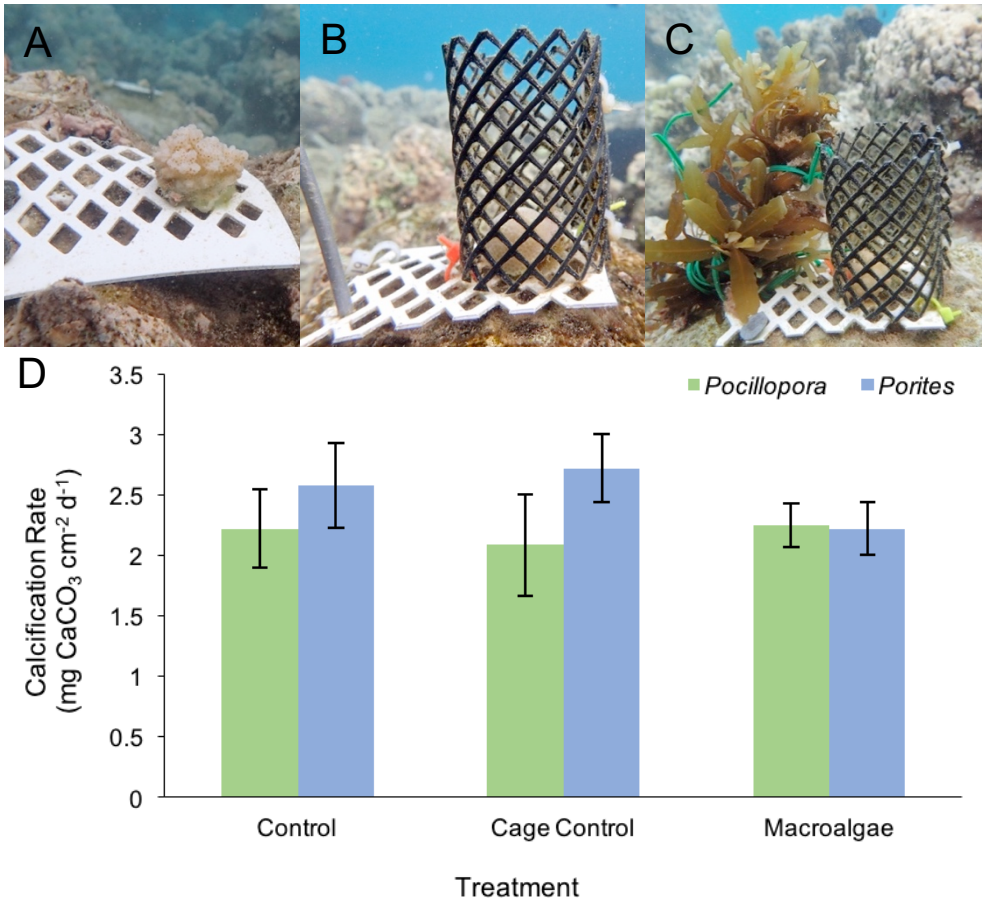


Figure 2.3 Results of manipulative experiment testing the effect of neighboring macroalgae on juvenile calcification. Photographs show the treatments used to test the hypothesis that proximity to macroalgae would decrease coral growth. (A) Control showing juvenile *Pocillopora* on the plastic tile, (B) cage control showing juvenile *Porites* on the plastic tile with cage surrounding it, and (C) macroalgal treatment showing juvenile *Pocillopora* within the cage and macroalgal bundle attached to the tile. In all cases, corals were 10–30 mm diameter. Treatments were established to test the effects of algae on the calcification rate (mean ± SE, n = 10) of juvenile corals over 31 days in the field (D).

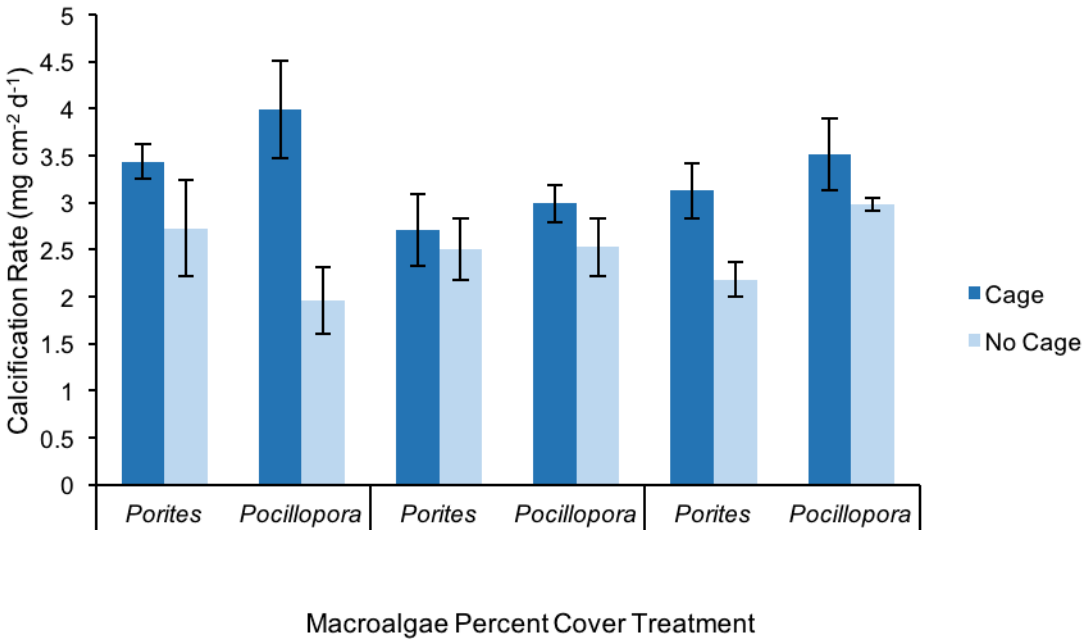
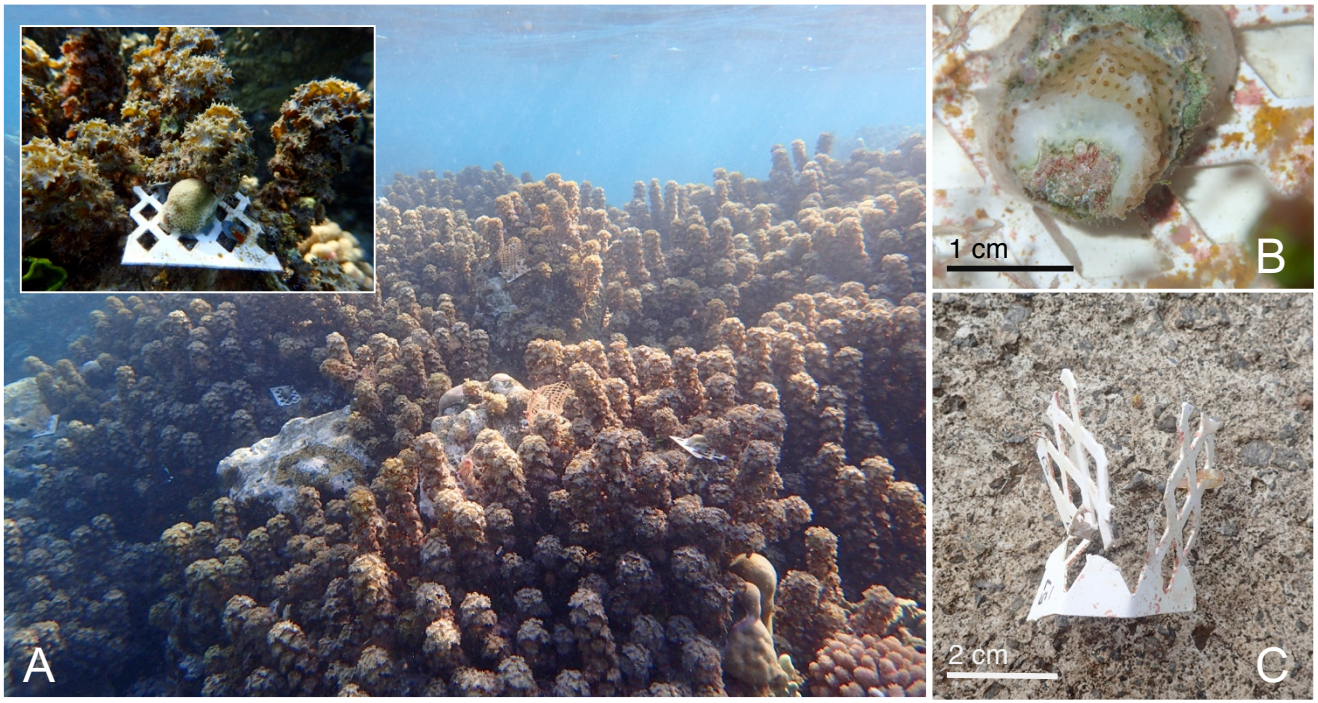


Figure 2.4 Results of manipulative experiment testing the effects of macroalgal cover in 4-m^2 plots on calcification of juvenile *Porites* and *Pocillopora* that were either protected from macroalgal abrasion with cages, or exposed. Bars show the calcification rate (mean ± SE) of juvenile corals over 32 days in the field. Sample sizes started at n = 10 and were reduced by fish activity or abrasion throughout the experiment. The final sample sizes from left to right were: *Porites* high plot n = 8, 5, *Pocillopora* high plot n = 9, 7, *Porites* medium plot n = 6, 6, *Pocillopora* medium plot n = 3, 4, *Porites* low plot n = 6, 6, and *Pocillopora* low plot n = 7, 7.

Supplemental Figures

Supplemental Figure 2.5 Image of the low-cover algal site, with herbivorous fish *Acanthurus nigrofuscus* eating turf algae off the rocks. Inset shows herbivorous fish *Acanthurus nigrofuscus. Acanthurus nigrofuscus* was observed consuming algae from the cages and causing cage breakages, sometimes followed by coral loss (indicated by the white arrow).



Supplemental Figure 2.6 (A) The high-cover macroalgal plot with an inset showing contact between a *Porites* juvenile coral and *Turbinaria* algae. On the medium algal cover plot, a *Pocillopora* juvenile had a large bite wound (B) and the plastic tiles were damaged with either bites or by suspected corallivores removing the coral juveniles (C).

Chapter 3:

The effect of environmental factors on juvenile coral abundance and microhabitat distribution in St. John, U.S. Virgin Islands

Introduction

Measuring early life stage coral survival (i.e., recruits and juveniles) is important when considering potential recovery from macroalgal-dominated to scleractinian-dominated reefs (i.e., > 50% coral cover) (Adjeroud et al., 2009; Smith et al., 2016a), as well as being integral to understanding coral reef ecology (Connell et al., 1997), particularly in a changing climate (Hughes et al., 2007). Many studies employ settlement tiles as a proxy for measuring recruitment, which can detect corals as small as 1-mm (Caley et al., 1996). Consistently, coral recruits are found most commonly on the corrugated underside of the settlement tiles (Birkeland et al., 1981; Tomascik, 1991; Edmunds et al., 2010, 2014). This may be related to the exposed surface being vulnerable to grazers or competition with macroalgae (Doropoulos et al., 2016), and sedimentation (Wittenberg and Hunte, 1992). Studies that increased the topographic complexity of the top of the settlement tiles found that the additional refuges increased settlement to the exposed surfaces of the tiles (Carleton and Sammarco, 1987; Nozawa, 2008; Edmunds et al., 2014). Early life stages of corals (i.e., larvae, recruits, and juveniles) have high mortality rates preventing many of them from reaching the adult size class (Penin et al., 2010; Doropoulos et al., 2016). Settlement choices or refuge use may play a large role in the future abundances of juvenile corals and adult corals (Edmunds et al., 2014).

On some Caribbean reefs, it has been reported that recovering populations of the sea urchin *Diadema antillarum* are associated with declines in macroalgal abundance and

subsequent increases in juvenile coral abundance, although the densities of *Diadema* observed (~ 5 m^{-2}) did not reach a level sufficient to change the whole reef (Edmunds and Carpenter, 2001). Thus, increasing abundances of *Diadema* could eventually result in reversals back to scleractinian-dominated reefs (Edmunds and Carpenter, 2001). Fish and invertebrate grazers (i.e., sea urchins) are equally effective at clearing space for coral larvae to settle, however, invertebrate grazers remove recruits from exposed surfaces more frequently than fish grazers (O'Leary et al., 2013). Tradeoffs between predation or accidental grazing, competition with macroalgae, and survival indicate that in an environment where macroalgae is prevalent but herbivores are absent, coral recruits have higher survival in an exposed habitat (Doropoulos et al., 2016). However, in an environment where herbivores are present and controlling the algal population, a coral recruit has a better chance of surviving in a crevice habitat (Doropoulos et al., 2016). This means that site characteristics, such as herbivore presence and macroalgal cover, have different effects on juvenile coral survival depending on whether the coral settled in a crevice or on an exposed surface (Doropoulos et al., 2016).

On the south shore of St. John, coral cover has been consistently low (i.e., ~8%) on random sites for 11 years (Edmunds, 2002; Rogers and Miller, 2006). Random sites were randomly chosen using GPS coordinates in 1992 as a way to expand the sampling area without introducing bias (Edmunds et al., 2002). In addition, two large reefs with permanent transects, Yawzi and Tektite, showed different trends in coral cover over 25 years (Edmunds, 2015). Yawzi experienced a loss of the structure-forming coral *Orbicella annularis* with a 75% decline in cover, and 57% decline in abundance of coral colonies over 15 years, and no signs of recovery thereafter (Edmunds and Elahi, 2006;

Edmunds, 2015). Tektite however, showed increases in *Orbicella annularis* cover from 33% to 49% from 1988 to 2002, then declined in cover to 27% by 2007, and finally stabilized at 28% cover in 2013 (Edmunds, 2015). This species is ecologically important to the Caribbean (Edmunds and Elahi, 2006), and was integral to the reversal of a macroalgal phase shift on a reef in Jamaica in 2003–2004, by providing structural refugia (Idjadi et al., 2006). The decline in *O. annularis* cover by 75% at Yawzi could be reducing the structural refugia that coral recruits tend to recruit to, whether on tiles or in the natural environment (Idjadi et al., 2006; Edmunds et al., 2014). To test how environmental variables may be affecting early coral mortality, and therefore the abundance and distribution of juvenile corals, the present study employed *in situ* surveys of juvenile corals at 12 locations on the south shore of St. John. Surveying 12 sites spread across the southern bays of St. John within the National Park enabled this study to encompass environmental variation between sites, including different depths and hydrodynamic exposure regimes which could alter community structure among sites and provide different ecological tradeoffs for juvenile corals. These surveys identify the juvenile coral's microhabitat (i.e., crevice, exposed, and the rock type the juvenile was settled on), and being a sessile organism, it informs us which habitats recruits settled in, and survived within, at least until they were 10 – 40-mm in diameter. Biotic site features such as herbivore abundance (i.e., *Diadema*) and macroalgal cover, and abiotic site characteristics such as topographic complexity (which may be correlated to the availability of refuge habitats (Zilberberg and Edmunds, 2001)), depth, and rock type, may all play a role in the distribution patterns of coral recruits. Understanding which factors are associated with juvenile coral distribution can play an important role in

understanding what is augmenting high juvenile coral mortality rates, and therefore the potential for scleractinian coral recovery following major disturbances.

Materials and Methods

Study site and organisms

Surveys were conducted in July and August 2017 on the south shore St. John, U.S. Virgin Islands, at the Virgin Islands Environmental Resource Station. This study utilized 5 sites (< 9-m depth) between Cabritte Horn and White Point that were established by Edmunds in 1992; these sites were selected randomly using GPS coordinates to expand the yearly permanent transect sampling to a larger spatial scale without bias (Edmunds et al., 2002). My surveys were also conducted at 3 additional sites: Yawzi (this site is also surveyed in the long-term studies, and is one of the sites with higher coral cover for the past few decades), East Cabritte, and West Cabritte (Edmunds et al., 2002). Sampling at East and West Cabritte, as well as the random site at Cabritte Horn, would provide a contrast between site exposure in a similar location, as each of these sites is located along Cabritte Horn which is a prominent headland within the National Park (Figure 3.1). Where possible, additional surveys were completed at 5-m depth in order to compare juvenile abundances along a depth gradient, since the herbivore *Diadema* is more abundant in shallow waters (Edmunds and Carpenter, 2001).

Surveys

At each site, the study area consisted of two parallel 15-m transects across a constant depth (~ 9-m for the deeper sites, and ~5-m for the shallow sites). Exact depth of

the surveys was recorded and used as a continuous factor in the analysis. Ten 0.25-m^2 quadrats were placed randomly along each transect. Photographs were taken of each quadrat for analysis of benthic cover and rock type, which was done by dividing the photo into 25 squares, and categorizing each square by the dominant benthic cover and dominant rock type (> 50%) (Edmunds et al., 2010). Rock type was determined based on the shape of the rocks. Igneous rock is volcanic rock, and in St. John, it was typically large flat slabs of rock and is easily identifiable. Carbonate rock is dead coral carbonate structure, and was generally smaller and more rugose, and could resemble a coral head. Within each quadrat, small corals (< 40-mm diameter) were measured, and assigned to a microhabitat type: exposed, shallow crevice, and protected crevice (Figure 3.2). Corals with fractured margins were excluded to prevent including adults that had undergone partial mortality or asexual fission products (Edmunds et al., 2007). Microhabitats were defined as the immediate area (< 6-cm) the coral was found, and included exposed habitats (flat surface for at least 4-cm), shallow crevice habitats (the coral was within a depression that was between 0.5–1 cm deep and 0.5–4 cm wide), and protected habitats (the coral was in a crevice that was > 1-cm deep and 1–4 cm across; Fig. 3.2). These definitions were established to define a protected microhabitat as providing the most protection from potential herbivore grazing (including fish and *Diadema*), and exposed habitats would provide the least (Ritson-Williams et al., 2010). In addition to categorizing the percent cover of the benthos, site characteristics were measured which included reef rugosity, or topographic complexity, which was measured using a known length of chain carefully draped along the benthic structures of the two transects for 15-m (Zilberberg and Edmunds, 2001). The length of chain used was divided by the linear

distance of the transect (15-m) to calculate the topographic complexity, where a flat reef would have a value of 1. In addition, *Diadema* surveys were conducted along the 15-m transects using 1-m wide band transects to determine the abundance per m^2 at each site.

Statistical Analysis

Pooling all sites together for the initial analysis, the average size of small corals in each microhabitat was analyzed using a one-way ANOVA, using microhabitat as a fixed factor. Tukeys post hoc procedure was used to determine which microhabitats had significantly different average coral size. A non-metric multidimensional scaling (nMDS) was performed to visualize differences between the 12 sites based on the site characteristics measured. The nMDS was completed using the R packages "vegan" and "MASS". Data were transformed to z-scores prior to the analysis so that abundance data and percent cover data were on the same scale. A cluster analysis using the library "pvclust" was done on the site characteristics data to determine which sites clustered more similarly based on the site parameters measured. The percentage of juveniles within each microhabitat was plotted separately by site, and a chi-squared test of independence was used to determine if there was an association between sites and the proportion of juveniles within each microhabitat. The chi-squared test used the average proportion of corals in each microhabitat as the expected values, so the test determined if the proportion of corals in each microhabitat at each site differed from the mean number of corals in each microhabitat across all sites. All statistical analyses were carried out in RStudio (Version 1.1.419).

Results

Overall, the average size of small corals differed between microhabitat environments ($F = 15.66$, $df = 2, 773$; $P < 0.0001$; Fig. 3.2, Fig. 3.3A) and there were differences in the average size of corals between sites ($F = 4.25$, $df = 12, 773$; $P < 0.0001$). The interaction between sites and microhabitats was not significant ($F = 0.635$, $df = 23, 773$; $P = 0.91$) and was dropped from the model. Corals in exposed microhabitats were larger, whereas corals in protected microhabitats were smallest (Fig. 3.3A). The mean size of juvenile corals (< 4-cm) in protected crevice microhabitats was 1.5 ± 0.1 cm which was smaller than corals on exposed surfaces (1.9 ± 0.03 cm) and in shallow crevice environments (1.8 ± 0.1 cm; $P < 0.0001$, $P = 0.036$ respectively; n = 811). Corals were approximately the same size among shallow crevices and exposed habitats ($P = 3.19$; Fig. 3.3A). Approximately 75% of corals (n = 811) at both depths, at all sites, were settled on exposed surfaces (Fig. 3.5), with 13–18% in protected habitats, and the rest in shallow microhabitats (Fig. 3.3B).

A hierarchical cluster analysis with multiscale bootstrap resampling and p-values was done on site characteristics (vectors on the nMDS visualization) determined that two sites were significantly different from the rest using an alpha value = 0.05; and within the other cluster of ten sites, there were two main groups (clusters indicated by ellipses, Fig. 3.4). In particular, West Cabritte and Cabritte Horn were the most similar sites, characterized by having more carbonate rock cover, Peyssonneliaceae cover, and scleractinian cover (Fig. 3.4, Supplemental Fig. 3.6). Although there were some differences in sites, juvenile corals were found more often in exposed microhabitats compared to shallow or protected crevices (Fig. 3.5) at all sites. At six of the sites, > 75%

of all juvenile corals were in exposed habitats, and the next highest percentage of juveniles was in protected habitats (Fig. 3.5). A chi-squared test of independence found that there was an association between sites and the proportion of juvenile corals within each microhabitat ($X^2 = 70.935$, $df = 22$, $P < 0.001$), meaning that the proportion of juveniles within each microhabitat was different between sites; although the pattern that most juveniles were in exposed habitats did not vary between sites.

Discussion

Early life stages of corals (i.e., larvae, recruits, and juveniles) have high mortality rates preventing many of them from reaching the adult size class (Doropoulos et al., 2016; Penin et al., 2010). Settlement choices may play a large role in survival of small corals (Edmunds et al., 2014) depending on the site characteristics and tradeoffs between competition and predation (Doropoulos et al., 2016). Juvenile corals compete with macroalgae for space and light on shallow reefs (Lirman, 2001; River and Edmunds, 2001), competition for light and space is intensified within crevices (Doropoulos et al., 2016), but in an environment with high rates of herbivory, survival of recruits and juvenile corals is highest in crevice habitats because there is less macroalgae to compete with corals, and lower risk of fish/urchin predation on corals within crevices (Doropoulos et al., 2016). The purpose of the present study was to investigate whether the meter-scale biological and physical features of 12 sites in St. John, affected the distribution and abundance of juvenile corals among three types of microhabitats categorized as exposed, shallow crevice, or protected crevice. A secondary purpose was to determine if the results

could be used in a predictive capacity to estimate juvenile coral survival, based on the ecological tradeoffs described in Doropoulos et al. (2016).

The non-metric dimensional scaling visualization of site characteristics with a cluster analysis, found that two sites (West Cabritte and Cabritte Horn) were significantly different from the rest (Fig. 3.4). The proportion of juveniles within each microhabitat was different between sites; although the pattern that most juveniles were in exposed habitats did not vary between sites. At six sites, > 75% of juvenile corals were in exposed habitats (Fig. 3.5), even though some of these sites had either higher abundance of herbivores (> 5 urchins m^{-2}, Yawzi 5-m, Fig. 3.4) or high macroalgal cover (> 50% cover, Europa 9-m, East Tektite 9-m). In higher macroalgal cover sites, a higher percentage of juveniles were predicted to be in exposed habitats to minimize competition with macroalgae, as this competition would be elevated within crevices, based on the results of Doropoulos and colleagues from Palau (Doropoulos et al., 2016). Juvenile corals were more common on exposed surfaces even on sites with higher abundances of herbivores (i.e., *Diadema*), which is contrary to predictions based on the model of ecological tradeoffs created by Doropoulos (et. al 2016), because crevices provide protection from grazing by herbivores or corallivores depending on their respective sizes (Doropoulos et al., 2016).

While all sites are spatially distributed within two bays on the south shore of St. John, the sites did show some variation in site characteristics (Fig. 3.4), and appear different from each other (Fig. 3.7). However, it is difficult to determine whether these differences are enough to be ecologically relevant for juvenile corals, which could be why the juvenile coral distribution was approximately the same across all sites. Cabritte

Horn and West Cabritte clustered closely together on the nMDS ordination for site characteristics, driven by similarities in percent cover of scleractinians, octocorals, and Peyssonneliaceae encrusting alga, and carbonate rock availability (Fig. 3.4). They also appear very similar both on a meter-scale and centimeter scale (Fig. 3.7). The other ten sites clustered on the nMDS as one large group according to the cluster analysis, however there were two distinct groupings within this. Within this larger cluster of sites, photographs of the sites show how different they appear on a meter-scale. The Yawzi 5-m site had the highest density of *Diadema* compared to any other site, was heterogeneous, and was dominated by igneous rock (Fig. 3.4, Fig. 3.7). The Europa 9-m site was mostly flat, with high macroalgal cover, and low coral cover (Fig. 3.4, Fig. 3.7). These sites appear very different from each other and from the similar sites: Cabritte Horn and West Cabritte (Fig. 3.7), and are separated on the nMDS (Fig. 3.4). This provides a ground truth for the nMDS of site characteristics and insures that it shows ecologically relevant information.

This study did not directly account for the abundance of available crevices (Doropoulos et al., 2016), which could be a factor differentiating the sites which would explain why the juvenile corals were found on exposed surfaces ~ 75% of the time. Igneous rock surfaces are generally smooth, and while crevices can be found between smooth igneous rocks, carbonate rock surfaces are created by dead scleractinian corals and provide more heterogeneous structure (Green et al., 2010). Rugosity was used as a measurement that may predict crevice availability (Zilberberg and Edmunds, 2001), however, sites with a lot of igneous rock could still rank high for rugosity if there were areas of vertical relief between rocks, but this wouldn't necessarily correspond with

crevice availability if the rocks were tall but smooth. Additionally, in St. John, rock type can influence juvenile coral growth, depending on the time of year, which may have been due to temperature changes in the rock (Green et al., 2010). Temperature of the rocks, and sea water temperature, could also be a factor that influences which microhabitat is ideal for juvenile coral growth and survival.

Previous studies using settlement tiles in the Pacific (Taiwan, Japan, and the Phillipines) and the Caribbean (St. John) have found coral recruit settlement preferences for crevice microhabitats, and elevated survival of recruits within those microhabitats (Nozawa, 2008; Edmunds et al., 2014). After one year, survival of coral recruits on settlement tiles was 0% for recruits in exposed areas of the settlement tile, but recruits in microhabitats had a 12% survival rate (Nozawa, 2008). If coral larvae show settlement preferences for crevices (Nozawa, 2008; Edmunds et al., 2014), why were 75% of the juveniles (~ 15–20 mm) in St. John found on exposed surfaces, no matter the environmental conditions? It could be survival rates in each microhabitat depend on the size of the coral. Settlement tiles assay the recruit life stage and while survival may be elevated within crevices for recruits (Nozawa, 2008), juveniles were predicted to have different survival rates in exposed and crevice microhabitats depending on the environment (Doropoulos et al., 2016). The present study brings up some interesting questions that require future investigation, potentially using tagging of juveniles, a technique which has been used successfully in St. John for many years (Edmunds, 2004; Edmunds et al., 2011). Specifically, for this study, tagging of juveniles could be used to track survival of different size classes of juveniles within different microhabitats. It is important to understand which environmental features are associated with juvenile coral

distribution and survival in order to understand what is augmenting high juvenile coral mortality rates, and therefore the reducing potential for scleractinian coral recovery.

Tables

Table 3.1 Table showing the abbreviated names (used in the PCAs) for each site, and the number of juvenile corals surveyed at each site. Depth is reported in feet so the exact depth gradient can be used in the nMDS rather than estimating to the nearest meter.

Site Name	Abbreviated Name	Depth (ft)	Sample Size
Cabritte Horn	CABHRN	36	37
East Cabritte	ECAB	30	92
East Tektite	ETEKT9	34	72
Europa 5-m	EUR5	23	112
Europa 9-m	EUR9	26	54
Tektite Cliffs	TEKCL5	23	54
West Cabritte	WCAB	35	78
West Little Lameshur	WLL	23	58
White Point 5-m	WPNT5	20	38
White Point 9-m	WPNT9	30	67
Yawzi 5-m	YAWZ5	22	88
Yawzi 9-m	YAWZ9	29	32

Figures

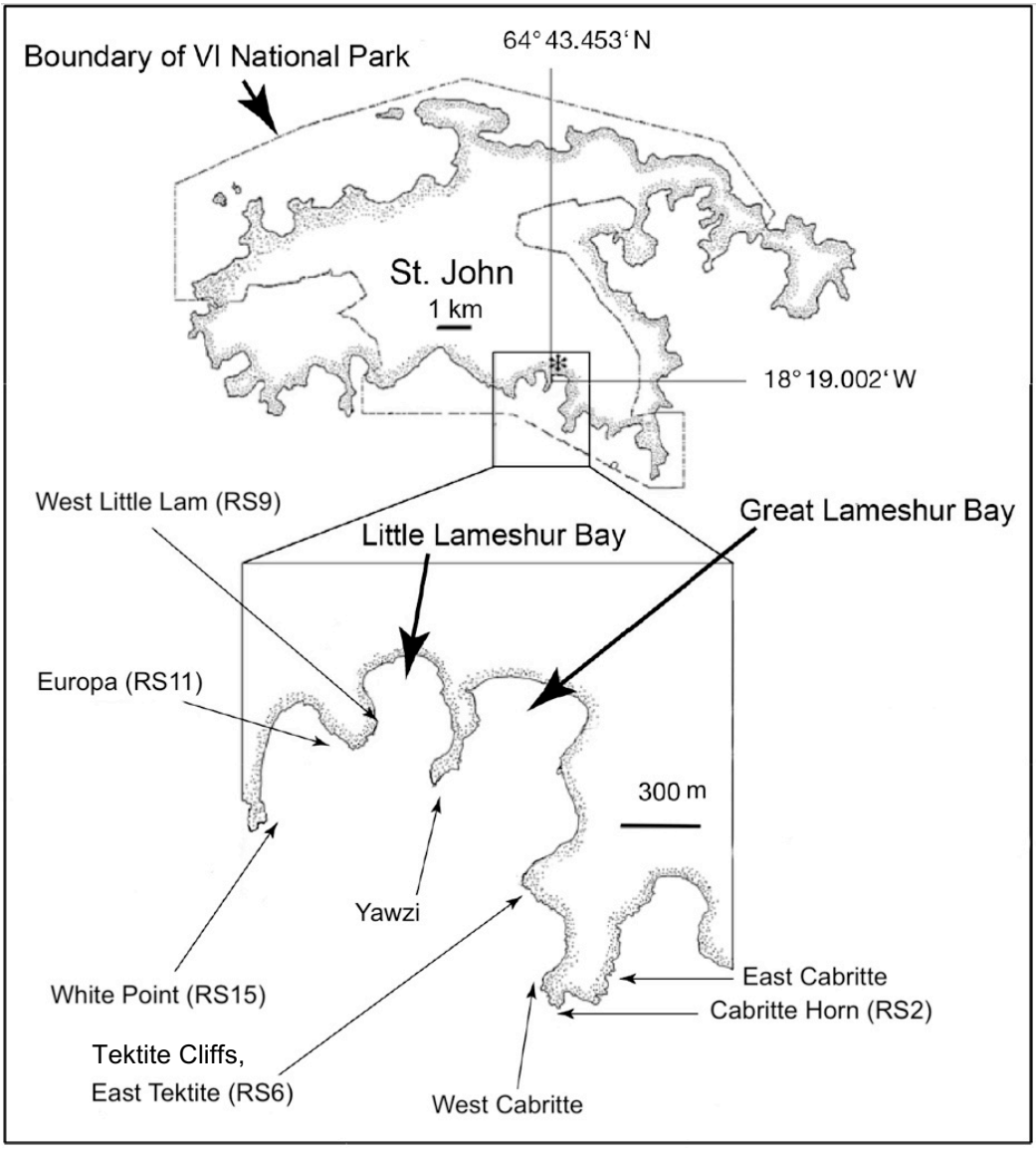


Figure 3.1 Map of St. John showing the study sites between White Point and East Cabritte, modified from (Edmunds, 2013) to include all of the sites for this study. Sites labeled with RS and a number are random sites established by Edmunds in 1992. All sites were surveyed at 7–9-m depth. White Point, Europa, Yawzi, and East Tektite had additional survey sites at 5-m depth.

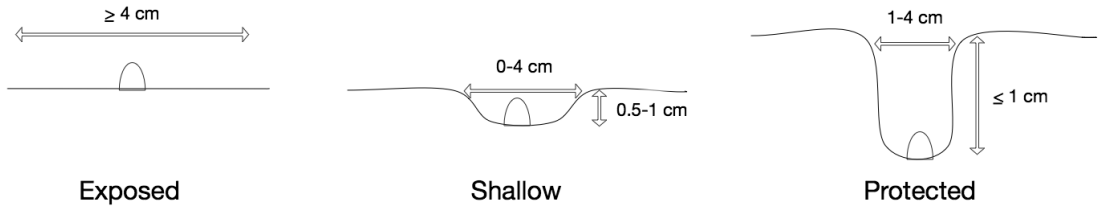


Figure 3.2 Diagram of the microhabitat definitions for this study. Protected habitats provided the most shelter from potential grazing or macroalgal interactions, whereas exposed habitats provided the least refuge.

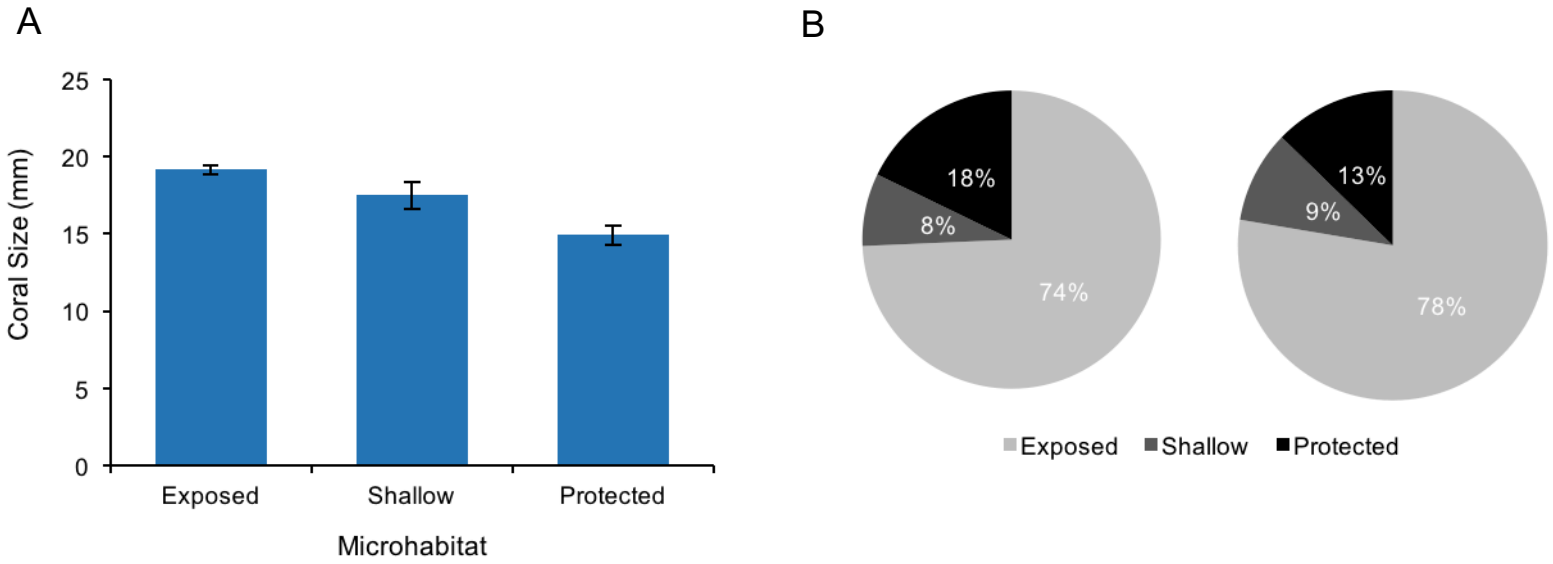


Figure 3.3 (A) Bar graph of the average coral diameter (± SEM) in each of the microhabitats with all sites and depths pooled. (B) Pie charts of the proportion of juveniles found in each microhabitat at 5-m depth (left) and 7–9-m depth (right).

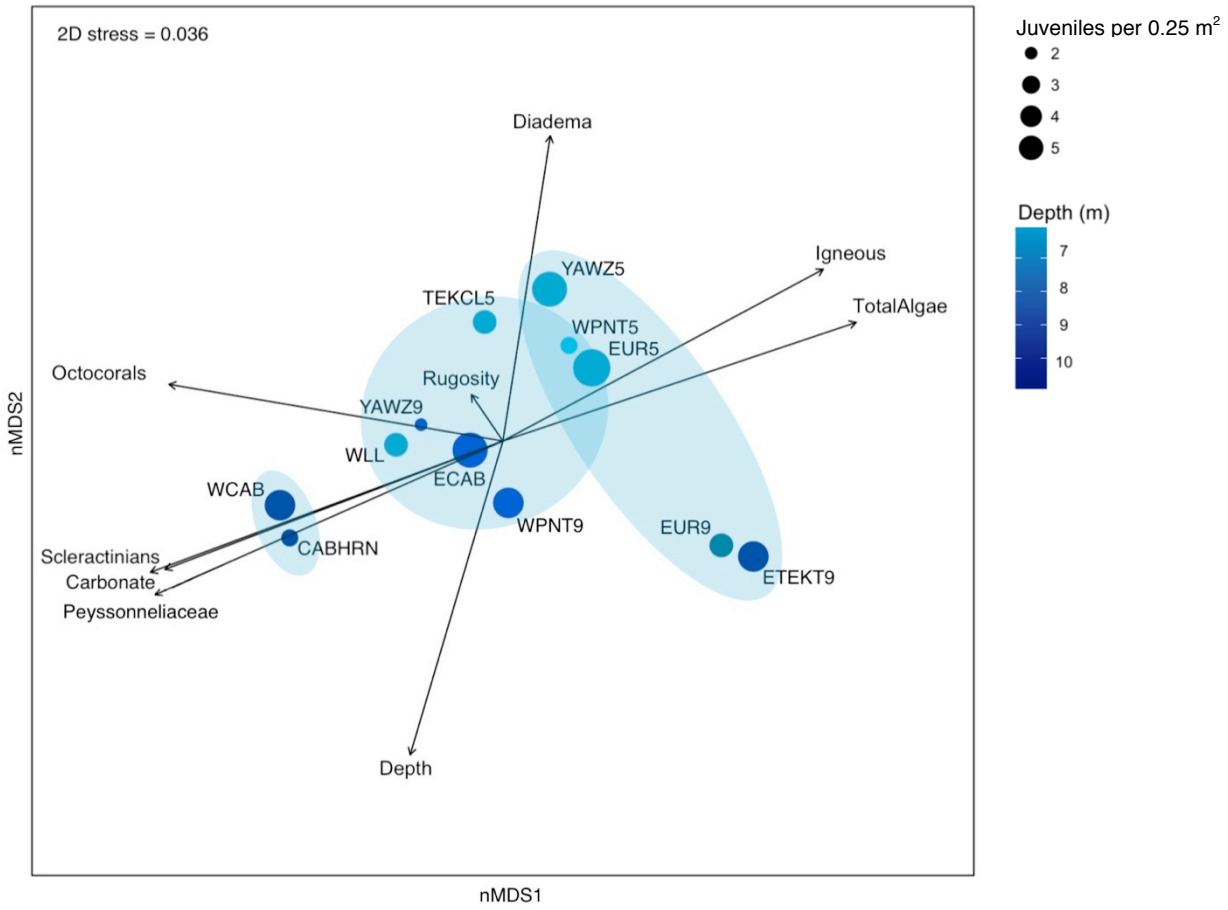


Figure 3.4 Non-metric multidimensional scaling analysis of the site characteristics. Each site is labeled with an abbreviated name and is color coded by depth. The size of the site bubble is proportional to the density of juveniles per 0.25 m^2. The ellipses indicate clusters of sites that are more similar to each other, determined by a cluster analysis ($\propto = 0.95$). The cluster of WCAB (West Cabritte) and CABHRN (Cabritte Horn) is significantly different from the rest of the sites, which are considered one cluster with two primary groups within it, although these are not significantly different from each other. In the overlapping zone, WPNT5 was more similar to the sites grouped with ECAB, and EUR5 was more similar to the grouping with EUR9. The vectors indicate the features measured to determine how similar or different sites were. The vectors are igneous rock percent cover, abundance of *Diadema*, rugosity or topographic complexity of the site, octocoral percent cover, scleractinian percent cover, carbonate rock percent cover, *Peyssonneliaceae* percent cover, depth of the site, and total algae which is the percent cover of macroalgae and turf algae.

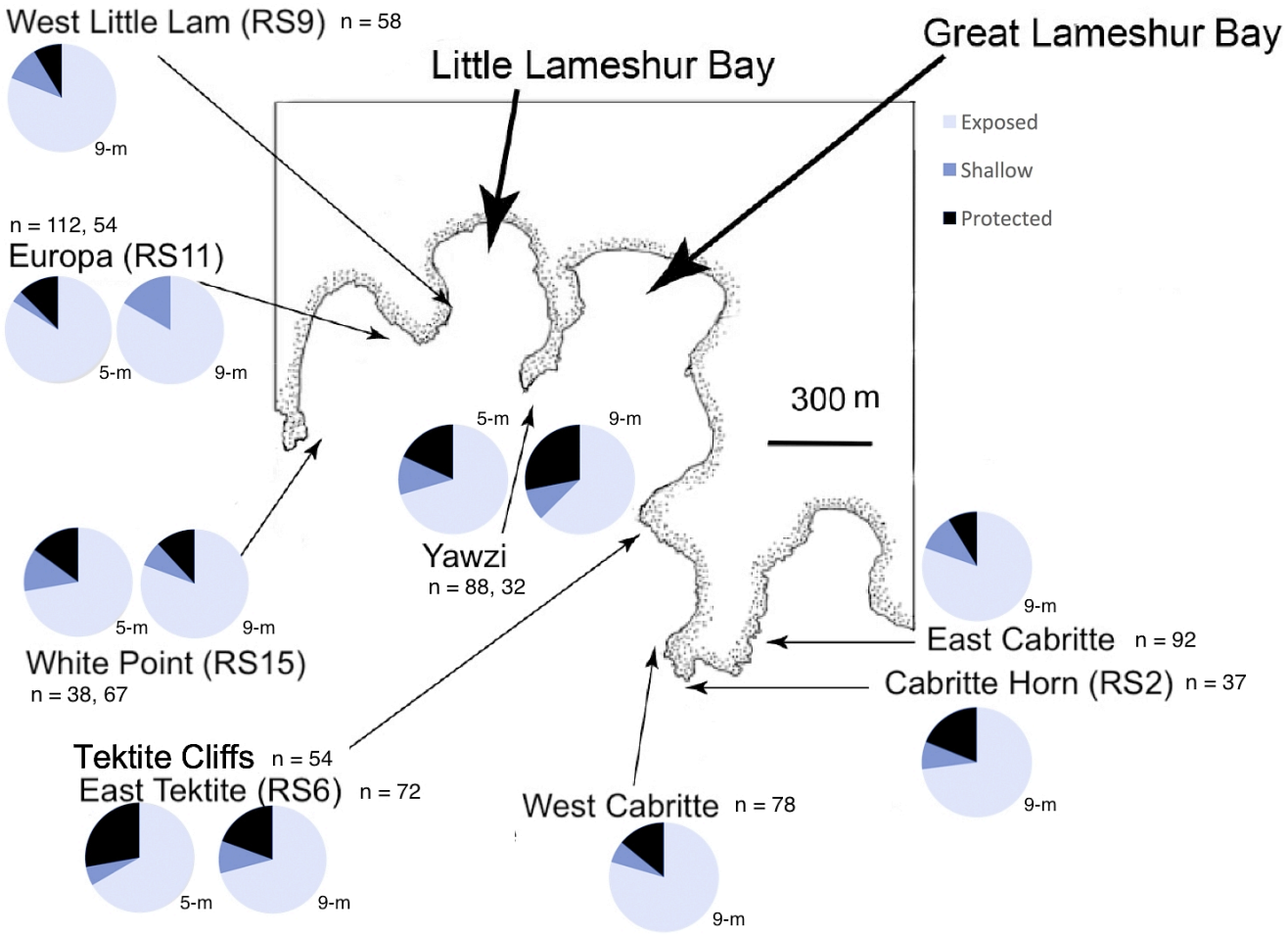
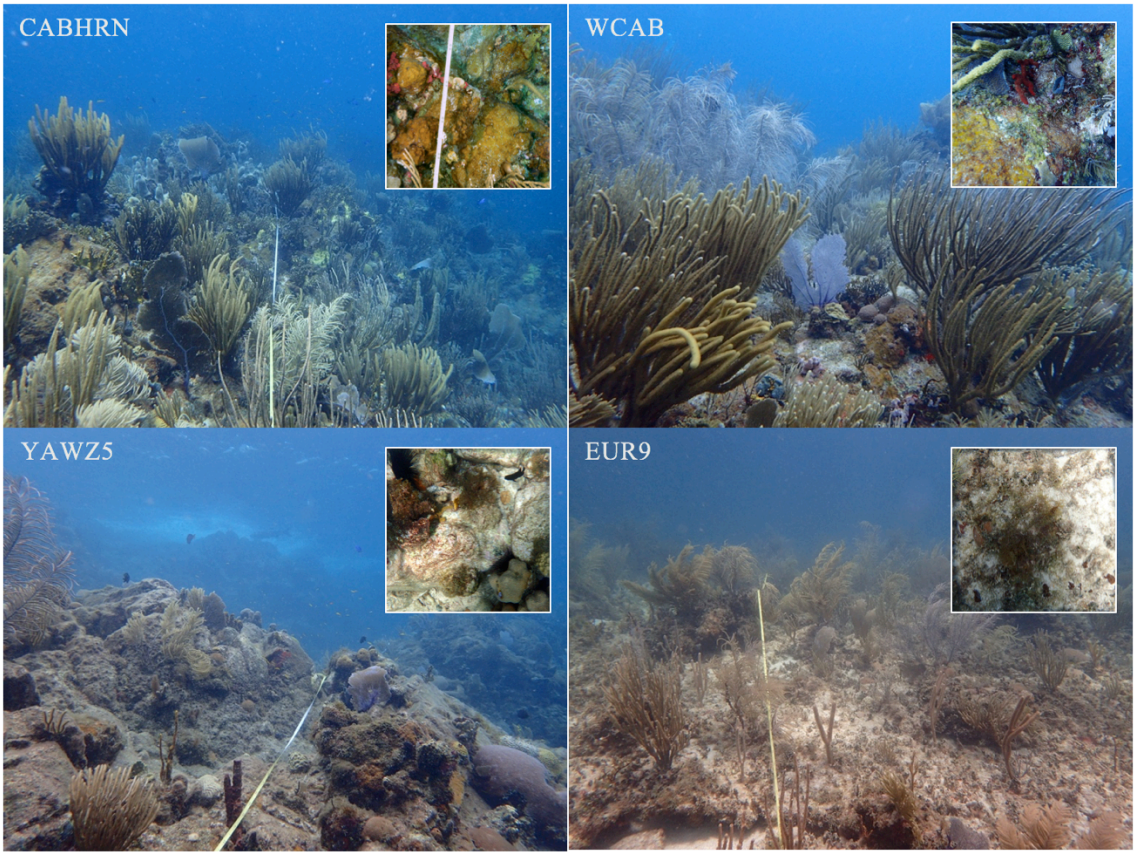


Figure 3.5 Map of the sites studied in St. John, with pie charts for each site depicting the percent of juveniles in each microhabitat; sample sizes are written next to the site names. Light blue portions indicate the percent of juveniles in exposed habitats, dark blue indicates the percent of corals in shallow microhabitats, and black is the percent of corals in protected microhabitats. Sites with two pie charts have one for the 5-m site (on the left) and one for the 9-m site (right) which are labeled with subtext. The rest of the sites were all at ~ 9-m depth and are represented by only one pie chart.

Supplemental Figures



Supplemental Figure 3.6 Photo-panel of four of the sites surveyed in St. John which correspond to the sites that were most different on the PCA biplot (Figure 3.4). Each site is labeled with the abbreviated name that matches the principle component analysis biplots (names in Table 3.1) and were at 9-m depth, except for Yawzi in the lower left which was taken at 5-m depth. The inset within each photo is an image of a quadrat along the transect.

Chapter 4:

Concluding Remarks

Many scleractinian-dominated reefs are undergoing shifts to macroalgal-dominated reefs (Edmunds and Carpenter, 2001; Smith et al., 2006; Stewart, 2008; Diaz-Pulido et al., 2009; Fabricius et al., 2011; Bulleri et al., 2013; Enochs et al., 2015; Vieira et al., 2016b). Theoretically, these changes are reversible, but cases of recovery to coral dominated states after phase shifts are rare and may require changes in the extrinsic environment first (i.e., cooling temperatures) (Edmunds and Carpenter, 2001; Idjadi et al., 2006; Dudgeon et al., 2010). Due to these phase shifts, interactions between corals and macroalgae have become much more common (Rasher and Hay, 2010; Rasher et al., 2011). Particularly vulnerable to competition with macroalgae are early life stages of corals (i.e., larvae, recruits, and juveniles), which are also integral to coral community recovery (Doropoulos et al., 2015). Juvenile coral colonies can be overgrown by macroalgae more rapidly due to their small size (Zilberberg and Edmunds, 2001; Box and Mumby, 2007), and are more vulnerable than larger corals to effects of shading and abrasion (Bak and Engel, 1979; Box and Mumby, 2007).

Despite the susceptibility of juvenile corals to damage or mortality by macroalgae, many studies of macroalgae-coral competition have been done on adult coral fragments (River and Edmunds, 2001; Smith et al., 2006). Juvenile corals that are small in size (i.e., $\leq$ 4-cm diameter) have high mortality rates (Bak and Engel, 1979; Edmunds, 2000), and coral recruitment and growth may be hindered by competition with macroalgae (Box and Mumby, 2007; Doropoulos et al., 2014). Poor post-settlement

success could be indicative of a “recruitment bottleneck” in which a decline in coral cover is related to poor recruitment (Arnold et al., 2010; Doropoulos et al., 2014; Edmunds et al., 2015). This could be caused by a decline in larval survival and settlement (Olsen et al., 2015), or factors affecting the recruit and juvenile life stage (Box and Mumby, 2007).

The goal of my research was to quantify how environmental features, predominantly macroalgal cover, affect the abundance, distribution, and growth of juvenile corals in two locations in the tropics: Moorea, French Polynesia, and St. John, U.S. Virgin Islands. The first study was designed to determine if macroalgae in the back reef of Moorea was reducing coral larvae survival and juvenile growth via chemical cues, and whether contact (i.e., abrasion) or algal cover was an important factor in affecting juvenile growth. The second study was designed to investigate if site characteristics (including macroalgal cover and abundance of herbivores) affected the abundance and distribution of juvenile corals among microhabitats.

In Moorea, macroalgae did not differentially affect the survival of larvae or growth of juvenile corals via chemical cues alone. A second study found that there was no effect of high, medium, and low macroalgal cover on coral growth, but there were differences in growth rates between the two taxa, and protection by a cage elevated growth rates (8–50% change in growth). The fish community seemed to be affected by the manipulation of algal cover, and the change in fish behavior affected each of the macroalgal cover study plots differently. The high cover algal plot (~90% cover) was not observed to be impacted by fishes, but abrasion by algae was detrimental to at least two colonies resulting in partial mortalities. Fish were observed frequenting the low cover

plot and damaged a few cages and corals. This study shows the importance of investigating how certain changes in a community (i.e., macroalgal cover) can affect an entire community and the way other species interact, in order to better understand how perturbations may affect coral survival and growth.

In St. John, the site characteristics accounted for 75.9% of variation in sites, but did not account for variation among juvenile coral abundance and distribution within microhabitats. Approximately 75% of the juveniles at each site were found on exposed surfaces, and this did not correspond to the hypothesized environment based on site characteristics and the ecological tradeoff model by Doropoulos et al. (2016). In the future, it would be interesting to test the hypothesis that site characteristics may link more to juvenile survival over time within each microhabitat, rather than be predictive of their distribution.

Overall, macroalgae did not significantly affect growth and survival of juvenile and larvae in the Pacific, although interactions between fish, macroalgae, and coral damage (grazing and predation) were observed. Future studies should address the interactions between corals, herbivores, and macroalgae in quantitative ways to determine how the change in abundance of one impacts the whole community. In the Caribbean, variation among sites was not a significant predictor of juvenile coral microhabitat distribution. Future studies should compare survival of juvenile corals over longer time frames (> 30 days) in different macroalgal cover plots and microhabitats in order to track survival rates. This thesis contributes to the growing field on coral to macroalgae phase shifts by finding that in Moorea and St. John chemical effects of macroalgae do not play a primary role in reducing growth and survival of early life stages of corals. Instead,

macroalgae may impact juvenile corals primarily through competition for space and decreased survival either due to direct (i.e., abrasion, shading) and indirect (i.e., fish community changes) effects. Growth and distribution of juvenile corals are valuable parameters in assessing community dynamics, but future studies should assess survival rates of juveniles to determine where corals survive and are able to contribute to population growth as adults.

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