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ASSESSING THE IMPACTS OF MACROALGAL COMPETITION AND PARROTFISH GRAZING ON CORAL COVER IN THE MIDDLE FLORIDA KEYS

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ASSESSING THE IMPACTS OF MACROALGAL COMPETITION AND
PARROTFISH GRAZING ON CORAL COVER IN THE MIDDLE FLORIDA KEYS

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
Biological Sciences

by
Kylie Smith
August 2015

Accepted by:
Dr. Michael Childress, Committee Chair
Dr. Saara DeWalt
Dr. William Bridges

ABSTRACT

The coral reefs of the Florida Keys National Marine Sanctuary (FKNMS) are diverse ecosystems that support thousands of marine organisms. Unfortunately, the live coral cover on these reefs has dramatically decreased over the last 30 years even in the most protected areas of the sanctuary. Environmental changes have contributed to this decline in coral cover by creating optimal conditions for macroalgal growth. These macroalgae species are fast growing and out-compete slow growing corals for space and nutrients. Herbivores known to forage on macroalgae, including long-spined sea urchins and parrotfishes, have decreased in abundance. A synthesis of data from across the Caribbean has suggested that this decline in coral is due to a top-down cascade where a decrease in herbivores has led to increase in macroalgae which out-competes corals. For my thesis research, I tested this Herbivore Cascade model by conducting surveys across 34 reef sites in the FKNMS and by an herbivore-exclusion coral transplant experiment. At each reef, macroalgae and coral cover was estimated by analysis of photo quadrants and parrotfish density estimated by a diver survey. Reefs were then classified into four reef types based on their depth, structural complexity and substrate composition. Analysis of all reefs together did not find negative correlations of macroalgae vs. corals nor parrotfish vs. macroalgae. However, these relationships varied within each of the four reef types. For example, within Hawk's channel patch reefs, I found strong evidence of macroalgae - coral competition, where percent coral cover was significantly lower on reefs where macroalgae cover was high. I also found a significant positive relationship between macroalgal cover and total parrotfish biomass on offshore shelf reefs. These patterns

were also corroborated by the results of my herbivore-exclusion coral transplant experiment. Eighty-four corals of two different species were transplanted to seven different reefs and placed within either open or closed topped cages with and without macroalgae addition. Pictures of each transplanted coral were taken immediately after transplanting and then quarterly for one year. Net coral growth for both species was essentially zero and not influenced by macroalgal abundance, parrotfish herbivory, or reef type. The results of these two studies do not support the predictions of the Herbivory Cascade Model and suggest that coral survival may be influenced by different factors on different reef types depending on their community structure. By identifying the factors that limit coral growth at each reef type, I can make better conservation decisions about strategies for transplanting corals or the benefits of increased protection for herbivorous fishes.

DEDICATION

I want to dedicate this thesis to my father who never failed to support me. You are the reason I fell in love with the ocean and its many wonders. You have always encouraged me to chase my dreams and I believe you have enjoyed this experience as much as I have. I also want to recognize and remember Dr. Kate McFadden. Her guidance challenged me to expect more of myself and her example of a woman in science is one I will strive for my entire career. Finally, I want to express my appreciation to the students I have taught during my time at Clemson. Each of them has taught me a valuable lesson and their passion to change the world will always inspire me.

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CHAPTER ONE

THE IMPORTANCE OF CORAL REEF ECOSYSTEMS AND THEIR DECLINE

Coral reefs are diverse ecosystems that support thousands of marine organisms, many of which are endemic to these ecosystems (Bell and Galzin 1984). The biodiversity these “hotspots” support match those of tropical rainforests (Sale 1999). The corals themselves serve as important food resources for fish and invertebrate species (Jones et al. 2004) and their structural complexity provides habitat, spawning sites, nurseries and protection from predators for many marine organisms during their lifecycle (Bejarano et al. 2011).

Coral reef communities also have large impacts on human populations. These ecosystems support global economies by providing habitat for commercial fishery organisms including crustaceans and game fish (Bhat 2003). Tourism is also a large contributor to global economies in tropical regions. The vibrant colors and large amount of biodiversity of these reefs draw snorkelers, scuba divers, boaters, fishermen and beach goers that add millions of dollars to economies annually (Jaap 2000). Recent studies have also found uses for corals and other organisms found in these ecosystems for advancement in medical technology including inflammatory diseases, bone repair and cancer (Cooper et al. 2014). The structure of the reef also protects coastal populations and property by absorbing energy from storms and decreasing shore erosion (Lugo et al. 2000, Sheppard et al. 2005). The services these ecosystems provide are numerous and impact global communities and ecosystems.

Corals are cnidarians of the class Anthozoa (Sumich and Collard 1999). Individual coral polyps secrete calcium carbonate that forms a skeleton and these polyps reproduce asexually to form large colonies. However, corals are also capable of reproducing sexually through spawning events (Barnes and Hughes 1999, Sumich and Collard 1999). Planulae larvae will drift with ocean currents and settle on suitable habitat where it will begin to grow into its own colony.

Corals have a mutualistic relationship with algal cells, known as zooxanthellae, which live within the coral polyp (Brown 1997, Barnes and Hughes 1999). When performing cellular respiration, a coral polyp produces carbon dioxide and water as byproducts. The zooxanthellae cells use these byproducts during photosynthesis. The sugars, lipids and oxygen that are produced during photosynthesis are used by the coral polyp to grow and increase cellular respiration. The presence of these algal cells increases the growth rate of corals drastically, which leads to greater productivity of reef ecosystems (Sumich and Collard 1999). These algal cells provide the corals with their coloration while the skeletal structure of the corals provides the algal cells with protection.

The growth rates of corals are impacted by many different factors including light intensity, water temperature, nutrient availability and pH levels (Sumich and Collard 1999). Corals and the zooxanthellae that inhabit them, require light in order to photosynthesize and grow. Increased sedimentation in the water column will block out the light and reduce coral growth (Dodge and Vaisnys 1977). Corals reach their optimal

growth rate in water ranging from 21°C to 29°C. When water temperatures move outside this preferred range, the growth rate of corals will decrease and corals may even die (Jokiel and Coles 1977). Corals thrive in low nutrient, or oligotrophic, waters (Orcutt 2012). Important nutrients including nitrate and phosphate are used by zooxanthellae during photosynthesis and aid in coral growth. The concentration of Hydrogen ions, or pH, in sea water can also impact coral growth rates or calcification rates. Corals have higher calcification rates in water ranging from 8.0-8.4 (Dubinsky and Stambler 2010). When pH decreases, calcification rates decrease and can even begin to dissolve in acidic water.

Coral cover is declining worldwide and this decline is a growing concern among marine conservation biologists (Pandolfi et al. 2003, Bellwood et al. 2004). Major environmental changes due to climate change are impacting water quality and causing a shift away from optimal conditions for coral growth. In the Indo-Pacific, average coral cover decreased from 42.5% in the 1980s to 22.1% in the early 2000s (Bruno and Selig 2007).

Throughout the Caribbean, this decline has been more severe than in the Indo-Pacific, with average coral cover declining approximately 80% since the 1970s (Figure 1.1) (Jackson et al. 2014). When coral reefs are degraded, there is a loss in food resources, structural complexity for habitat and nurseries, and overall biodiversity in

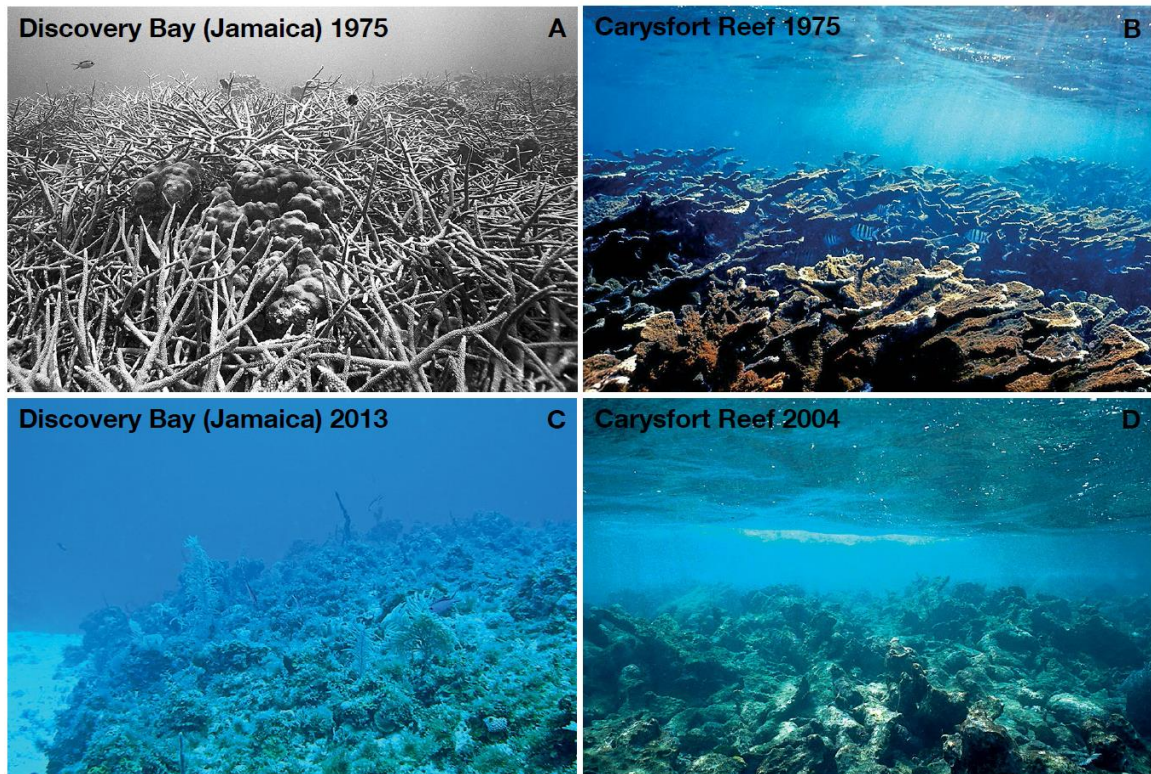


Figure 1.1 Coral cover has declined throughout the Caribbean over the past several decades. Discovery Bay in Jamaica in 1975 (A) compared to 2013 (C) after a decline in coral cover. Carysfort Reef, located in the Florida Keys National Marine Sanctuary off Key Largo, in 1975 (B) and in 2004 (D) after a decline in coral cover (modified from Jackson et al. 2014).

marine organisms. Stressful abiotic conditions, pollution and overfishing are only a few of the factors contributing to the decline in coral cover.

Stressful abiotic conditions can lead to massive bleaching events (Jaap 1979). A bleaching event occurs when the zooxanthellae cells inhabiting the coral polyps experience unfavorable abiotic conditions. These cells expel themselves from the coral polyp, leaving the coral white (Brown 1997). Unfavorable conditions include increased water temperatures, ocean acidification and sedimentation. The corals then become less productive, decrease in size and lose their ability to support the vast amount of biodiversity that relies on them. The shallow waters of the Caribbean experience greater changes in sea surface temperatures than the Indo-Pacific, contributing to the major loss in coral cover throughout the Caribbean (McWilliams et al. 2005). When damaged, corals are unable to absorb energy from storms and provide protection to coastal regions (Hughes and Connell 1999). These already weakened corals become more broken after storms and their recovery rates drastically decline.

The increase in coastal development and agricultural runoff has increased the amount of nutrients in marine ecosystems (Boyer et al. 2004, Dubinsky and Stambler 2010). The increase in nutrients lead to an increase in the abundance of microalgal species and cause algal blooms that block out sunlight from corals causing a decrease in their productivity. This increase in nutrients also leads to an increase in the abundance of macroalgal species that compete with corals (McCook et al. 2001).

Macroalgae is known to compete with corals for essential items such as nutrients, light and settlement space (LaPointe 1989, Miller 1998, McCook 1999). Macroalgae species have a high growth rate compared to corals. The increase in nutrient concentrations due to agricultural runoff increases the photosynthetic rate, and therefore growth rate, of these macroalgal species. This increases the abundance of macroalgal species that inhabit space where coral polyps would settle and covers existing corals shading them from light. Therefore, the negative effects of macroalgae on coral cover are increased in eutrophic environments where Nitrogen and Phosphorous are in excess.

Some macroalgae species compete with corals using allelopathic chemicals (Rasher and Hay 2014) . These species release chemicals that suppress the growth of surrounding substrate species. Coral species are capable of defending themselves using stinging cells called nematocysts (Nugues et al. 2004). Corals will expend long, string-like tissue called mesenterial filaments from inside their polyps. The nematocysts reside in this tissue and can sting competitors, including macroalgae. However, despite the ability to defend themselves, the corals are outcompeted by macroalgae due to their overabundance on the reefs.

This increase in macroalgal abundance and decrease in coral cover, has caused a shift from a coral reef ecosystem to an algal dominated ecosystem (McManus et al. 2000). Macroalgae species have fewer benefits to an ecosystem than corals (Mumby and Steneck 2008). Macroalgae species are relatively small and usually lack structural

complexity, making them a poor substitute for nurseries and providing refuge for marine organisms.

Herbivores can play an important role in the competitive interaction taking place between macroalgae and coral species. Herbivores control the abundance of macroalgae on reefs through their grazing activities (Lewis 1986, Burkepile and Hay 2011). In the Caribbean, overfishing since the 1960s has decreased the populations of herbivorous fishes that reduce macroalgal abundances (Hughes 1994). Without these fish grazing on macroalgae, the last major macroalgal grazers left in the Caribbean were the long-spined sea urchin, *Diadema antillarum*. These urchins experienced a massive die off due to a species-specific disease. After this decline in urchin abundance, macroalgal abundance significantly increased while coral cover plummeted (Hughes et al. 1987).

Since the die off of sea urchins, parrotfishes are the most abundant herbivores left on Caribbean reefs (Jackson et al. 2014). These parrotfish species are herbivorous and graze on macroalgae that compete with corals (Mumby et al. 2006, Mumby 2009, Rasher and Hay 2010b). Not only have parrotfish been found to regulate macroalgae abundance, but they also play a key role in facilitating coral recruitment (Hughes et al. 2007, Mumby et al. 2007, Jouffray et al. 2015). Certain parrotfish species will clear the substrate while grazing on macroalgae, providing clear surfaces for coral larvae to settle and develop into their own colonies. Parrotfish have been shown to play a key role in mediating the balance between corals and macroalgae through their grazing activity (Mumby et al. 2006, Mumby 2009, Dromard et al. 2015).

Throughout the Caribbean, parrotfish herbivory has been found to display top-down control on macroalgae and therefore regulate their population densities (Mumby 2009). Since macroalgae is in direct competition with corals for settlement space and nutrients, this regulation is crucial for aiding coral growth (Mumby et al. 2007). By grazing on macroalgae, parrotfish display an indirect positive effect on corals (Lewis 1986). When parrotfish herbivory was eliminated, macroalgae abundance rapidly increased and coral cover decreased (Lewis 1986, Lirman 2001, Kopp et al. 2010, Hoey and Bellwood 2011). These interactions taking place between parrotfish, macroalgae and coral are collectively termed the Herbivore Cascade model (Figure 1.2) (Bellwood et al. 2004, Jackson et al. 2014).

This model stresses the importance of herbivores as the major factor driving variation in coral cover and is comprised of three predicted interactions taking place between macroalgae, parrotfish and coral. These include that a competitive interaction exists between macroalgae and coral, parrotfish regulate macroalgal abundance through their grazing and that by reducing the competition from macroalgae, parrotfish display indirect positive effects on coral cover. The Herbivore Cascade model has been supported on reefs throughout the Caribbean and in the Pacific. Rasher and Hay (2010a) found that when corals were protected from herbivores, competitive macroalgae species increased in abundance. Coral fragments showed an increase in bleaching and tissue mortality. Treatments where herbivores grazed on macroalgae showed significantly less mortality in coral fragments.

M₁ Herbivory Cascade (Bellwood et al. 2004, Jackson et al. 2014)

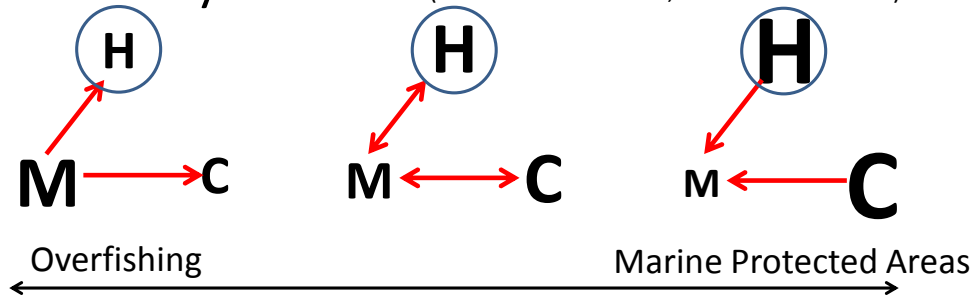


Figure 1.2 The Herbivory Cascade model suggests that herbivores are the main drivers in structuring coral communities. This model predicts that as herbivore abundance increases, macroalgae abundance will decrease and coral cover will increase. Herbivore and coral abundances will be higher on reefs that are protected than on reefs that are overfished.

The reefs in the middle Florida Keys have shown similar signs of decline in live coral cover (Donahue et al. 2008). As in the Caribbean, the reasons for coral decline are numerous and include increased bleaching (Porter et al. 1999), reduced growth (Dodge et al. 1974), recruitment failure (Rogers et al. 1984), increased competition with macroalgae (Tanner 1995), and physical disturbance (Hughes and Connell 1999). Each of these mechanisms has been linked to anthropogenic effects of either direct disturbance or rapidly changing water conditions such as increasing sea surface temperatures, ocean acidification, eutrophication, and tropical storm frequency (Hoegh-Guldberg et al. 2007).

The reefs in the middle Florida Keys stretch along the Atlantic Ocean from Islamorada to Marathon (Figure 1.3). These reefs have lower habitat complexity and substrate diversity than reefs in the upper and lower Florida Keys. They experience a greater influence of water from the Gulf of Mexico via Florida Bay which has highly variable water quality including wider fluctuations in temperature, pH and turbidity (Stumpf et al. 1999, Barnes et al. 2014). The increasing variation of these abiotic factors contribute to the degrading condition of these reefs, which are thought to be the model for the future reefs of the upper and lower Florida Keys.

Over the previous few decades, reefs in the Florida Keys have seen major increases in the abundance of macroalgae (Lirman and Biber 2000, Jackson et al. 2014). The three most abundant macroalgae species in the Florida Keys (Figure 1.4) are two species of fleshy, brown algae - *Dictyota menstrualis* and *Dictyota pulchella* - and a calcareous green algae, *Halimeda opuntia* (Herren et al. 2006). The *Dictyota* species are



Figure 1.3 The Florida Keys National Marine Sanctuary is located in south Florida. The reefs in the middle Florida Keys stretch from Islamorada to Marathon and commonly experience water from the Florida Bay.



Figure 1.4 Common reef building corals found on the reef tract in the Florida Keys and their macroalgal competitors (Humann and DeLoach 1993).

defended chemically by secreting toxic allelochemicals that suppress the growth of organisms around them (Rasher and Hay 2010a, Rasher et al. 2011). *Halimeda opuntia* secretes less toxic chemicals and also uses calcium bicarbonate to form a calcareous skeleton in its tissue, adding a degree of structural defense (Wray 1977). These differences in defense mechanisms may also contribute to differences in dietary preferences among herbivores that inhabit coral reefs (Ogden and Lobel 1978, Burkepile and Hay 2011).

Reefs in the middle Florida Keys also experienced a mass mortality of the long-spined sea urchin, *Diadema antillarum*. In the absence of these urchins, parrotfish are now the most abundant herbivores in the Florida Keys (Miller and Gerstner 2002, Jackson et al. 2014). There are nine species of parrotfish that inhabit the reefs of the Florida Keys and they account for a large majority of herbivorous biomass (Figure 1.5). These fishes are not targeted for fishing and are protected under spearfishing regulations, which contributes to their high abundance. However, even with higher parrotfish abundance, the reefs of the Florida Keys are still experiencing phase shifts from coral dominated to macroalgal dominated communities.

The Herbivore Cascade Model has explained the patterns in coral cover seen on reefs in the Upper Florida Keys. Lirman (2001) estimated the impact of grazers on the interaction between *Dictyota* spp. and three common species of corals (*Siderastrea siderea*, *Porites astreoides*, and *Montastraea faveolata* (Figure 1.4)) by conducting an herbivore exclusion study. In the absence of grazers, *Dictyota* spp. abundance increased

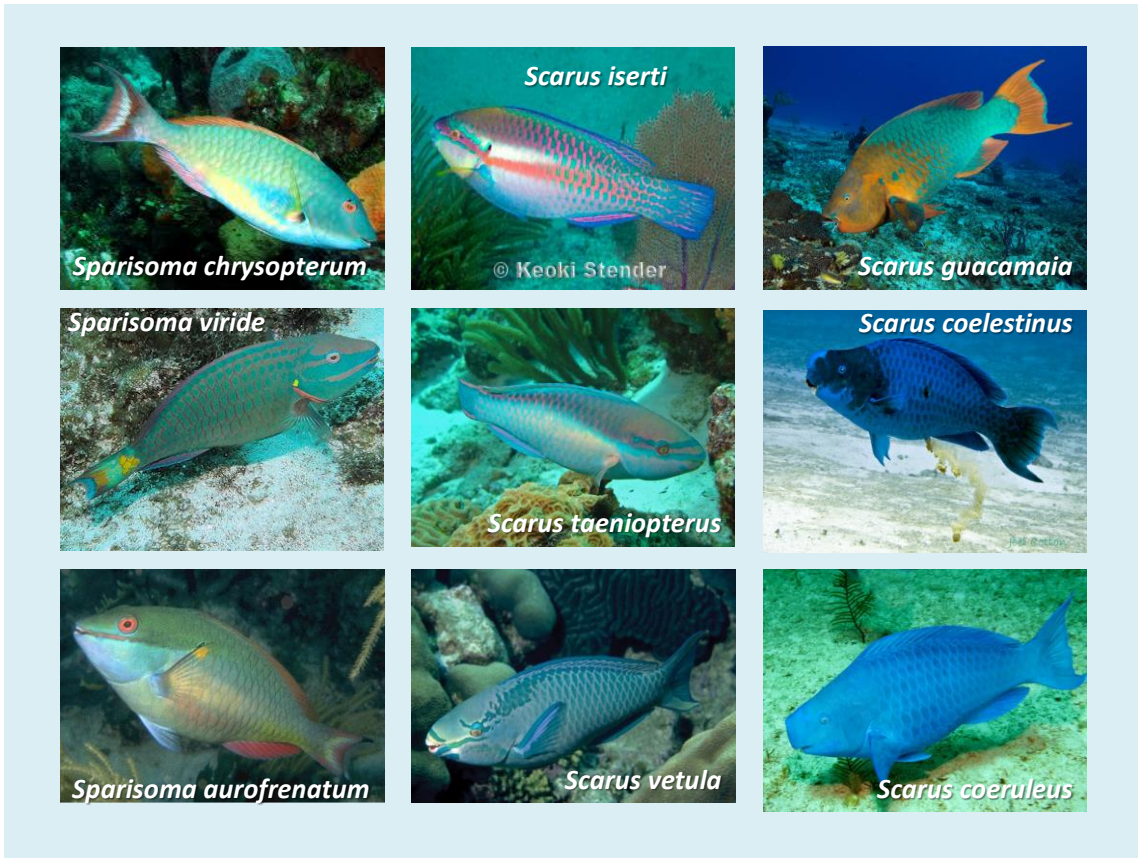


Figure 1.5 The nine parrotfish species that commonly inhabit the coral reefs of the Florida Keys.

and coral growth was reduced for *P. astreoides* but not for *S. siderea* corals. Furthermore, *M. faveolata* tissue mortality was greater when grazers were excluded (Lirman 2001). These results suggest that coral species can differ in their susceptibility to macroalgal competition.

The Herbivore Cascade Model has been supported on many reefs throughout the Caribbean (Lirman 2001, Bellwood et al. 2004, Jackson et al. 2014), but is unable to explain variation in coral cover on other reefs in the Florida Keys and in the Pacific (Kramer and Heck 2007, Burkepile et al. 2013, Dixon et al. 2014). Marine Protected Areas (MPAs) have been established to protect coral reefs by prohibiting fishing and direct contact with the substrate. The reduction in fishing pressure led to an increase in large piscine predators, including sharks, groupers and other large fish species (Kramer and Heck 2007). However, despite the abundance of top predators and increased predation attempts, herbivore abundance remained high inside these MPAs. Macroalgae abundance also remained high suggesting that herbivores were not able to regulate macroalgae through their grazing behavior (Kramer and Heck 2007). Coral cover inside these MPAs has continued to decline since their establishment, suggesting that the Herbivore Cascade Model may not offer the best explanation of the interactions that occur between herbivores and macroalgae to impact coral cover.

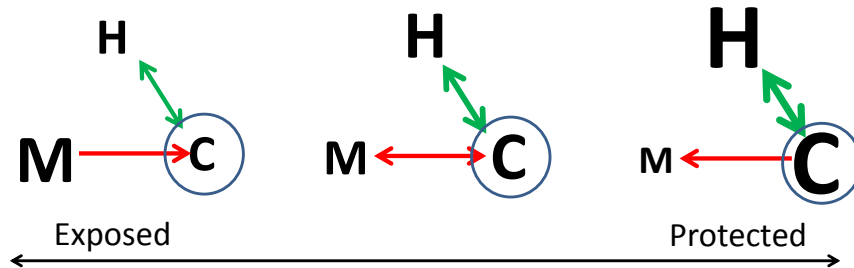
An alternative model to explain the variation in coral cover is the disturbance cascade model. This model suggests that coral cover and the structural complexity they provide are the driving factors that structure coral communities. Coral provide structural

complexity to reef communities that serve as nurseries for juvenile marine organisms and refuge from predators (McCormick 1994, Graham and Nash 2013). The corals themselves provide food and nutrients to many marine organisms as well (Jones et al. 2004). With the decline in coral cover, the complexity of the reef has also declined leading to a reduction in the number of parrotfish that reefs can support. The decrease in the parrotfish will lead to an increase in macroalgae due to a reduction in herbivory. This increase in macroalgae would lead to an increase in competition and a further decrease coral cover (Figure 1.6).

The Disturbance Cascade model has been supported in Marine Protected Areas in Fiji (Dixson et al. 2014). Dixson et al. (2014) showed that water from healthy coral reef communities attracted coral and reef fish larvae for settlement. Coral larvae were found to prefer waters taken from marine protected areas where coral cover was high and the reefs were considered healthy. Juvenile reef fish across six families also preferred the water from healthy reefs and avoided water collected from macroalgae dominated areas. The higher number of herbivores that a reef could support, the more macroalgae would be consumed and coral cover would benefit from the reduction in competition.

A major benefit of coral reefs to human populations as well as coastal ecosystems is the absorption of energy produced by storms (Lugo et al. 2000, Sheppard et al. 2005). As corals die, their skeletons remain, providing complexity for the community. However, these skeletons are fragile and break apart when exposed to disturbance such as storm and wave energy. Therefore, this Disturbance Cascade model predicts that as a reef becomes

M₂ Disturbance Cascade (Mumby & Steneck 2008, Dixon et al. 2014)



M₃ Nutrient Cascade (Burkepile et al. 2013)

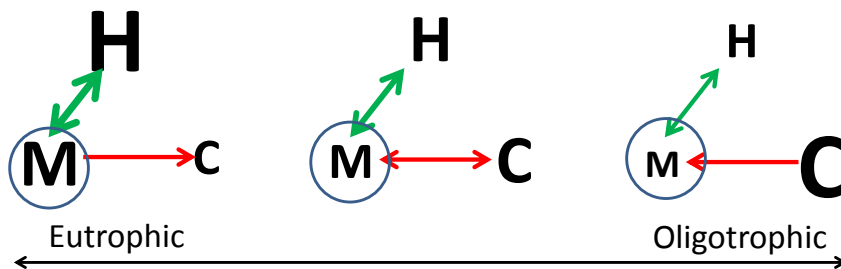


Figure 1.6 The Disturbance Cascade model (M₂) suggests that corals are the main drivers in structuring coral communities. As coral abundance increases, macroalgae abundance will decrease and herbivore abundance will increase. Coral cover and structural complexity will be higher on reefs that are protected than on reefs that are exposed. The Nutrient cascade model (M₃) suggests that macroalgae are the main drivers in structuring coral communities. As macroalgae abundance increases, herbivore abundance will increase, as will the nutrients they excrete. This increase in nutrients will lead to a further increase in macroalgae and corals will be outcompeted.

more exposed to storms, the more they will fragment. This loss of structure would decrease the number of herbivorous fishes it can support causing macroalgae abundance to increase (Figure 1.6).

Another alternative model to explain the variation in coral cover in reef communities is the Nutrient Cascade model (Figure 1.6) in which nutrients and macroalgae abundance may be the factors driving the coral community structure. In a study to determine the effects of nutrient loading on 54 reefs throughout the Caribbean, Burkepile and Hay (2006) found that as Nitrogen and Phosphorous, essential nutrients for primary production, increase, macroalgae abundance also increases. Eutrophic environments are over-enriched with these nutrients and are increasingly common in the Florida Keys due to an increase in agricultural runoff (Burkepile and Hay 2006). Fast growing macroalgae species thrive in these environments and outcompete corals for settlement space and light. Herbivores play an important role in regulating the abundance of macroalgae through their grazing behavior (Burkepile and Hay 2010, Ceccarelli et al. 2011). However, the nutrients that are excreted by herbivorous fishes increase the abundance of Nitrogen and Phosphorous, impacting the growth of macroalgae and coral (Burkepile et al. 2013). Depending on the concentration of nutrients in the environment, the excreted nutrients may benefit coral growth by providing essential nutrients or they may increase the already high concentration of nutrients and will be used by macroalgae to grow and out-compete corals (Koop et al. 2001). This Nutrient Cascade model suggests that in eutrophic environments, macroalgae abundance will be high and the abundance of herbivores will increase. The concentration of nutrients will also increase

due to the elevated excretion of waste from the herbivores. This will increase the abundance of macroalgae, as well as the competition of macroalgae on corals. When herbivore grazing is low, the macroalgae will be lacking essential nutrients to out compete corals and coral cover will be higher (Figure 1.6).

THESIS STRUCTURE

The goal of my thesis research was to determine what factors in coral reef communities influence coral cover. Specifically, I tested the Herbivore Cascade hypothesis / model by looking at the effects of macroalgal competition and parrotfish grazing on coral cover in the Florida Keys National Marine Sanctuary. In Chapter 2, I conducted an observational field survey to test the hypotheses that corals are most abundant where macroalgae is least abundant and where parrotfishes are most abundant. I conducted surveys of substrate composition and estimated parrotfish density across 34 reef sites in the FKNMS across a three-year period. In Chapter 3, I conducted a manipulative herbivore exclusion experiment to determine if the Herbivore Cascade model was supported under varying densities of macroalgae and presence of herbivores. In this experiment, I placed both open topped and closed topped cages around transplanted fragments of two common coral species on seven reefs in the Florida Keys National Marine Sanctuary. Cages were monitored for over a year and I measured changes in coral growth and macroalgal percent cover. I predicted that coral growth would be higher in cages with low macroalgae and in the presence of parrotfish grazers. In my final chapter, I explore the conservation implications of my work and discuss the

approach I will take in my dissertation research to test these other models that may explain coral decline and the variation in coral cover on the reefs of the middle Florida Keys.

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CHAPTER 2

FACTORS INFLUENCING CORAL COMMUNITIES IN THE MIDDLE FLORIDA

KEYS

INTRODUCTION

The coral reefs of the Florida Keys National Marine Sanctuary (FKNMS) are diverse ecosystems that support thousands of marine organisms (Bell and Galzin 1984). The reefs and their inhabitants attract millions of visitors each year and support much of the local economy (Bhat 2003). Unfortunately, live coral cover on these reefs has drastically decreased over the last 40 years, even in the most protected areas of the sanctuary (Downs et al. 2005, Alevizon and Porter 2015). The reasons for coral decline are numerous and include changing water temperatures, increasing disease outbreaks, increased competition, and overfishing (Jackson et al. 2014). The loss of coral cover has led to a decrease in biodiversity since these organisms are no longer able to provide the numerous resources they have in the past (Rogers 2013).

Macroalgae is known to compete with corals for essential items such as nutrients and space (LaPointe 1989, Miller 1998, Lirman et al. 2010). High macroalgae abundance can out-compete corals and cause a shift from a coral reef ecosystem to an algal-dominated ecosystem (Pandolfi et al. 2005). Previous research suggests this may be due to a reduction in reef herbivores, which lowers damage to coral tissue by controlling the abundance of harmful macroalgae (Mumby et al. 2006, Rasher and Hay 2010b, Jackson et al. 2014).

A recent review of the status of coral reefs in the Caribbean identified two important drivers of coral reef decline (Jackson et al. 2014). The first wave of coral decline was concomitant with a mass mortality of the herbivorous sea urchin *Diadema antillarum* in the mid-1980s (Carpenter 1988, Kissling et al. 2014). For some locations such as the Dry Tortugas, there was a sudden loss of live coral cover during this period and coral cover has remained low ever since (Jackson et al. 2014). However, other locations throughout the Caribbean, such as the upper Florida Keys, have experienced a more gradual loss of corals over the past 40 years (Precht and Miller 2007) suggesting some persistent driver such as a steady reduction in herbivorous fishes due to overfishing (Jackson et al. 2001). Both of these explanations suggest that there is a trophic cascade with coral abundance being affected indirectly through top-down effects of herbivores on macroalgal abundance and macroalgae on corals (Chapter 1 – Figure 1.2).

An indirect positive effect of this Herbivore Cascade model on coral abundance and growth is also suggested by herbivore exclusion studies. When herbivory was eliminated inside cages surrounding coral fragments in the upper Florida Keys, macroalgae abundance rapidly increased and coral growth declined (Lirman 2001). Parrotfish are abundant herbivores on the reefs in the Florida Keys and make up the majority of the herbivorous biomass on these reefs (Jackson et al. 2014). Their grazing on macroalgae regulates its abundance and its negative effects on coral cover (Lewis 1986, Burkepile and Hay 2011). Because macroalgae is in direct competition with corals for settlement space and nutrients, these top down effects of parrotfish grazing on

macroalgae decreases the shading effects on current coral fragments and clears space for new coral polyps to settle.

In this study, I test these predicted relationships between parrotfish, macroalgae, and coral for reefs in the middle Florida Keys by examining the strength and direction of correlation between the abundance of these three taxa. Specifically, I will determine if there is a positive trophic cascade between herbivorous fish and corals as hypothesized by Jackson et al. (2014). The reefs of the middle Florida Keys are degraded compared to the upper and lower Florida Keys. Some researchers believe that these reefs are providing a preview of the future of the healthy, more complex reefs in the other areas of the Florida Keys. By confirming the predictions of the Herbivore Cascade Model, I can form conservation management strategies that will prevent the future degradation of healthy reefs.

METHODS

Study area

To select my study sites in the Florida Keys National Marine Sanctuary, I conducted exploratory dives at 20 locations near Layton, FL recommended by research scientists at the Keys Marine Laboratory. I then selected 17 locations where there was sufficient contiguous hard bottom with live coral where I could establish a pair of 50 m transects separated by a minimum of 500 m (Figure 2.1). Each 50 m transect ($n = 34$) was considered an independent reef site for the purposes of this study (Table 2.1).

Reef site surveys were initiated in July 2012 with additional surveys added in July 2013, October 2013, March 2014, May 2014 and July 2014. All reef sites were surveyed at least once in July, while a subset of sites ($n = 14$) were surveyed quarterly (once per season). For the purposes of this study, data from reef sites with multiple surveys were averaged and analyzed only for differences among reefs.

In the middle Florida Keys, the primary reef herbivores are surgeonfish, parrotfish and the long-spined sea urchin (*Diadema antillarum*). *Diadema* urchins were plentiful prior to 1983 when they experienced a Caribbean-wide mass mortality (Carpenter 1988). Since 1983 *Diadema* urchins have remained at very low densities in the Florida Keys (Kissling et al. 2014). However, abundance of the ten species of parrotfish in the Florida Keys have remained relatively unchanged during that same time period (Alevizon and Porter 2015). Parrotfish are generalist feeders and are known to feed on several species of macroalgae including fleshy algae, calcareous algae and turf algae (Bruggemann et al. 1994, Cardoso et al. 2009).

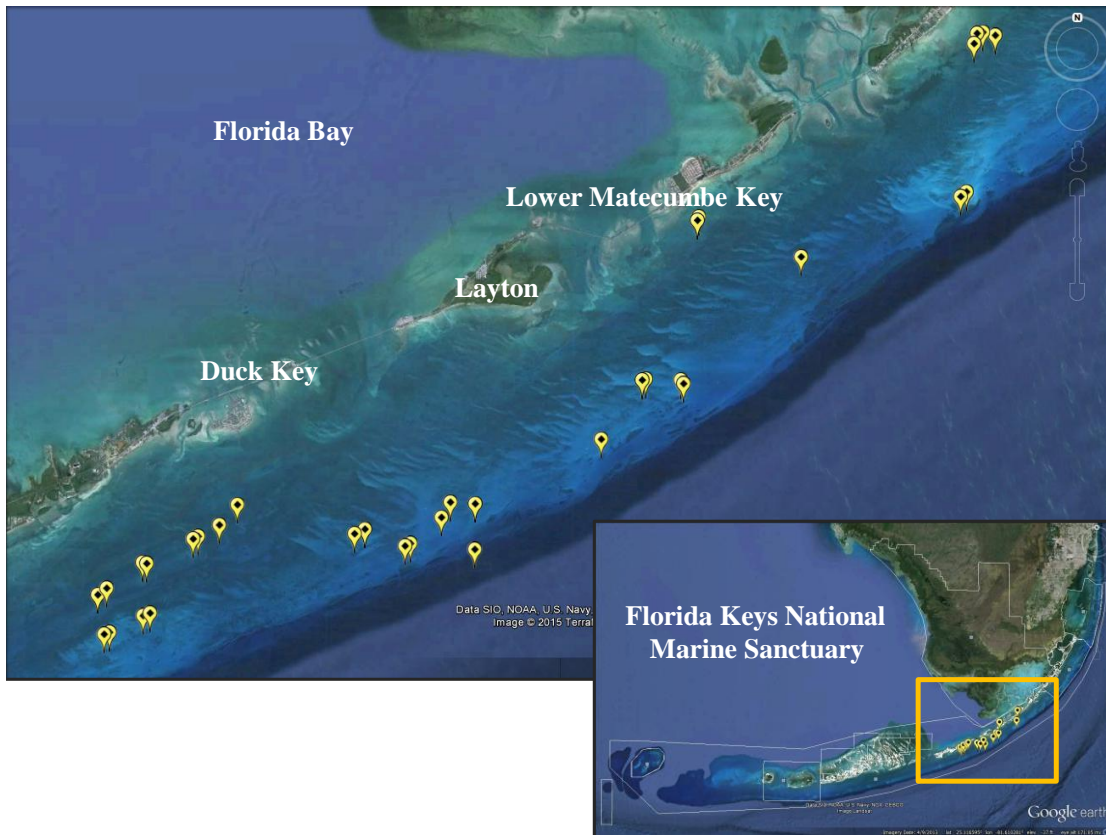


Figure 2.1 Map of reef sites (n = 34) located in the middle Keys region of the Florida Keys National Marine Sanctuary.

Table 2.1 Longitude, latitude and depth of the seventeen locations used in this study. Reef surveys were conducted at two sites at each of these locations.

Reef name	Longitude	Latitude	Depth (m)
11' Mound	24.72° N	80.86° W	6
Alligator	24.85° N	80.62° W	3
Cheeca Rocks	24.90° N	80.62° W	3
Cheeca Rocks SPA	24.90° N	80.61° W	4
Coffins Patch	24.96° N	80.96° W	6
Coral Gardens	24.84° N	80.73° W	4
East Tennessee	24.76° N	80.77° W	9
East Turtle Patch	24.73° N	80.91° W	6
Elbow	24.69° N	80.95° W	7
LK Bridge Rubble Pile	24.73° N	80.83° W	8
Long Key Ledge	24.72° N	80.84° W	7
Middle Turtle	24.71° N	80.95° W	4
Out Spa	24.78° N	80.75° W	6
Stag Party	24.78° N	80.74° W	5
Turtle Shoals	24.72° N	80.93° W	5
West Gator	24.82° N	80.69° W	6
West Turtle Shoals	24.70° N	80.97° W	4

Data collection

In order to examine the interactions taking place between macroalgae and corals, surveys of the substrate were conducted at the 34 reef sites described above using modified methods of Kramer and Heck (2007). At each of these sites, a 50 m transect reference line was established by permanent stakes marking the beginning and end of the transect (Figure 2.3). The starting position of each transect was chosen haphazardly and the transect was laid parallel to the main structure of the reef. Paired photographs (left and right side of the transect) were taken every 10 m along the tape using a PVC reference frame (0.25 m²). Pictures were taken from a fixed distance of 0.75 m with a canon PowerShot A710IS in a water-proof housing.

These pictures (n = 12 per site) were used to calculate the percent cover of live coral, macroalgae, octocoral, turf algae, and sponges on the substrate using Coral Point Count with Excel extensions (CPCe) software (Kohler and Gill 2006). This software estimates the percent cover by placing 25 random points on each photo (Figure 2.4). Each point was classified by species and used to calculate the percent cover of each substrate type. These percentages were averaged between the 12 pictures to estimate the average percent cover for each species for the site.



Figure 2.2 Each transect was marked with a permanent rebar stake and cap to ensure that the same 50 m of reef were monitored with each seasonal survey.

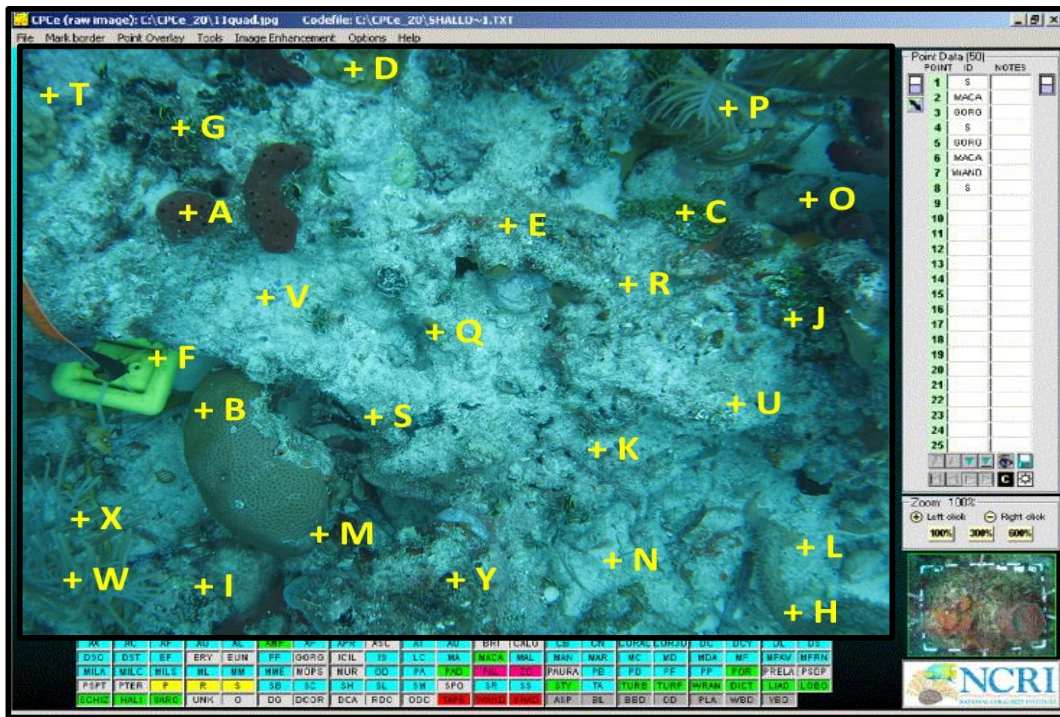


Figure 2.3 Twelve photographs from each reef were analyzed using Coral Point Count with Excel Extensions to estimate substrate cover. CPCe generated 25 random points for every 0.5 m X 0.5 m quadrat photograph and the proportion of random points for each category of cover (macroalgae, coral, octocoral, turf algae, calcareous algae, and sponge) were estimated from the total number of random points as a % cover.

Habitat complexity is a measure of the vertical relief and diversity of the substrate that is the product of both living and dead members of the reef community (McCormick 1994). This measurement has been shown to be an important predictor of the abundance, distribution and behavior of reef organisms (Raffaelli and Hughes 1978) especially reef fishes (Reese 1989). Habitat complexity, or rugosity, can be measured a number of different ways. McCormick compared different methods of measuring habitat complexity on coral reefs including using a profile gauge, calculating vector angles, and the chain-and-tape method (McCormick 1994). This study found that these methods all produced similar measures of reef complexity.

Therefore, I estimated reef complexity in the Florida Keys by collecting a video of the substrate beneath the transect tape using a Sony digital camcorder held perpendicular to the transect tape at a distance 0.5 m above the substrate. Complexity was classified into different rank categories (0-3 scale) depending on the relief of the reef by visual assessment at 2 m increments from the video footage. A score of 0 was considered low relief, such as sand and 3 was considered high relief with large coral heads and high octocoral abundance.

Parrotfish density was estimated using a visual survey belt transect (50 m X 10 m). Two divers swam along either side of the transect simultaneously while counting the number and species of parrotfish observed within 5 m of the transect tape (Figure 2.5) (Kramer and Heck 2007). Parrotfish species were further classified based on their developmental phase (juvenile, adult or supermale). At the end of each transect, divers

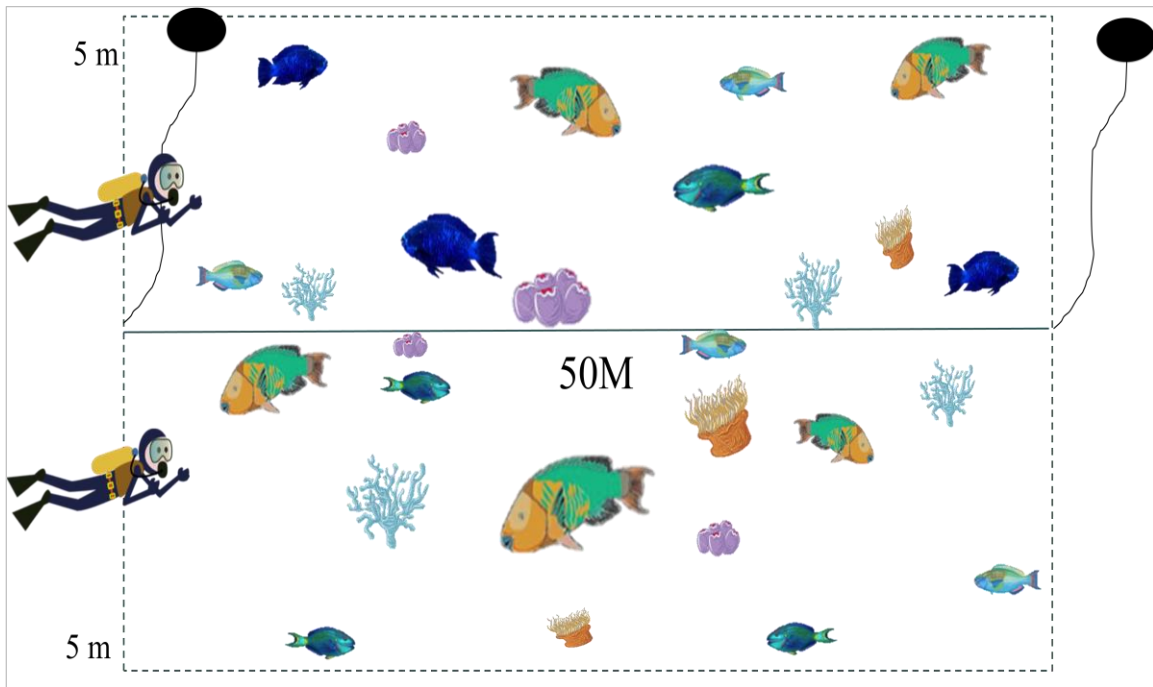


Figure 2.4 A visual representation of divers estimating parrotfish density on each site.

Parrotfish counts per 500 m^2 were converted to biomass (g/m^2) using previous published estimates of average length and mass for each species (Bohnsack et al. 1988).

switched sides and re-counted the parrotfish species that occurred along the transect by swimming back in the opposite direction. Parrotfish counts for each site were the average of the two divers' censuses. Parrotfish biomass was then estimated by multiplication of the species- and phase-specific counts by previously published length-weight relationships of the average-sized phase for each species (Bohnsack et al. 1988).

Depth and water quality measurements were taken at each site. Depth was estimated by the divers' depth gauge and by the depth sounder on the research vessel. Water quality measurements, including salinity, conductivity, pH, temperature and dissolved oxygen, were taken 1 m below the surface and 1 m above the substrate with a YSI MP556 multiprobe.

Regional Effects of Macroalgae and Parrotfish on Coral Cover

To test the hypothesis that parrotfish positively affect coral abundances through a reduction in macroalgae, I used linear regression analysis to determine if linear relationships existed between percent hard coral cover, percent macroalgal cover and total parrotfish biomass (g/m^2) for all sites ($n = 32$). Two sites (Alligator B and Cheeca Rocks B) were determined to be outliers with some values $> 2 \text{ SD}$ above the population means. These two sites were only sampled once and had extremely high measurements of total parrotfish biomass (g/m^2) and percent macroalgal cover respectively. These outlier sites were excluded from the final analyses. I first analyzed the data collected from each census separately (July 2012, July 2013, October 2013, March 2014, May 2014, July 2014). I found no significant and consistent relationships between any of the

community variables. This was likely the result of not visiting all 32 sites in any one census period resulting in low sample size and low statistical power. In order to have the largest possible sample size, replication and power, I analyzed the average values for coral cover, macroalgal cover, and total parrotfish biomass over all the sampling periods. This method minimizes within site differences due to season, observer or chance events. Using these average values produced qualitatively similar results as analyzing data from individual censuses with increased statistical power.

Local Effects of Macroalgae and Parrotfish on Coral Cover

Within these 32 reef sites, I observed large differences in coral cover, macroalgal abundance, parrotfish density, depth and habitat complexity. To evaluate these differences, I performed both K-means and hierarchical cluster analyses following the methods of Jouffray et al. (2015) using depth, habitat complexity and the percent cover of each substrate type including live coral, macroalgae, turf algae, calcareous algae, octocorals and sponge to distinguish the number of distinct reef communities present. The K-means cluster analysis identified 3 distinct reef types as having the lowest AICc score, but the hierarchical cluster analysis suggested that four reef types would allow me to capture important differences between mid-channel and offshore reefs that made up the majority of my reefs. To identify those factors that best describe the major differences between reef types, I conducted a principle component analysis on the correlations of depth, structural complexity and the percent cover of each substrate type including live coral, macroalgae, turf algae, calcareous algae, octocorals, and sponge following the

methods of Jouffray et al. (2015). I then regressed the first and second principle components against these community variables to determine which factors explain the majority of variation in community structure on these two orthogonal axes. I chose principle components analysis over discriminant function analysis so that these two composite variables were constructed independent of reef type. I then used generalized linear models to test the predicted species interactions between percent macroalgal cover, percent coral cover and total parrotfish biomass (g/m^2) while taking into account reef type differences. I also used linear regression analysis to determine if macroalgae cover, parrotfish abundance and coral cover were related within each reef types. This method has been used previously to determine if reefs are healthy or degraded and to explore how the role of herbivory changes with differences in reef type (Graham and Nash 2013). All statistical analyses were performed using JMP 11.0.0.

RESULTS

Analysis of Regional Effects of Parrotfish, Macroalgae on Coral Cover

For the 32 sites, there was no significant relationship between percent coral cover and percent macroalgal cover ($P = 0.7223$, $F_{1,30} = 0.1287$). There was a significant positive linear relationship between macroalgal percent cover and total parrotfish biomass (g/m^2) ($P = 0.0118$, $F_{1,30} = 7.1891$). There was no significant relationship between coral percent cover and total parrotfish biomass (g/m^2) ($P = 0.5615$, $F_{1,30} = 0.9633$).

Identification of Local Reef Types

Using hierarchical cluster analysis (Figure 2.5) and principle component analysis (Figure 2.6), I identified four distinct reef types based on the depth, structural complexity, and substrate composition. The factors that were most correlated with the first principle component were octocoral cover (negative), calcareous algae cover (positive), rugosity (positive) and depth (negative) (Table 2.2). The factors that were most correlated with the second principle component were negatively related for macroalgal cover (negative) and turf algae cover (negative) (Table 2.2). The variance in PC1 was 39.6% and 19.6% for PC2.

The four reef types were assigned names for their distinct differences in reef complexity and type of substrate (Figure 2.7). **Boulder** reefs (n = 6) have high complexity, shallow depth, high macroalgal cover, and are inshore, 1-2 km from the island chain. **Patch** reefs (n = 10) have medium complexity, medium depth, low macroalgal cover, and are mostly located in Hawks Channel 3-5 km offshore. **Shelf** reefs (n = 14) have low complexity, medium depth, high macroalgal cover, and are usually located along the shelf boundary 5-8 km offshore. **Artificial** reefs have low complexity, deep depth, low macroalgal cover, and are clustered 8-10 km offshore. Artificial reefs are human-made reefs that consist of concrete slabs and I-beams from the Long Key Viaduct Bridge that were dumped offshore in the 1970's (C. Lewis personal communication).

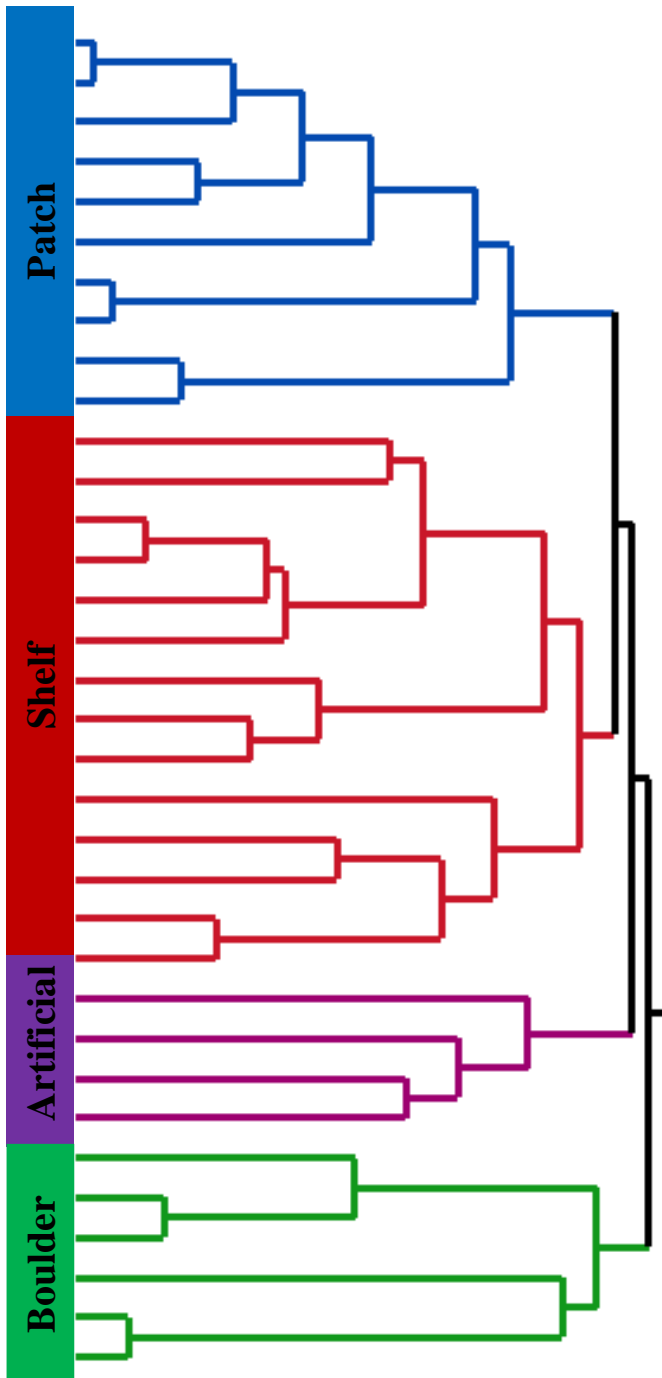


Figure 2.5 Cluster dendrogram of the four reef types including Shelf (red), Patch (blue), Boulder (green) and Artificial (purple).

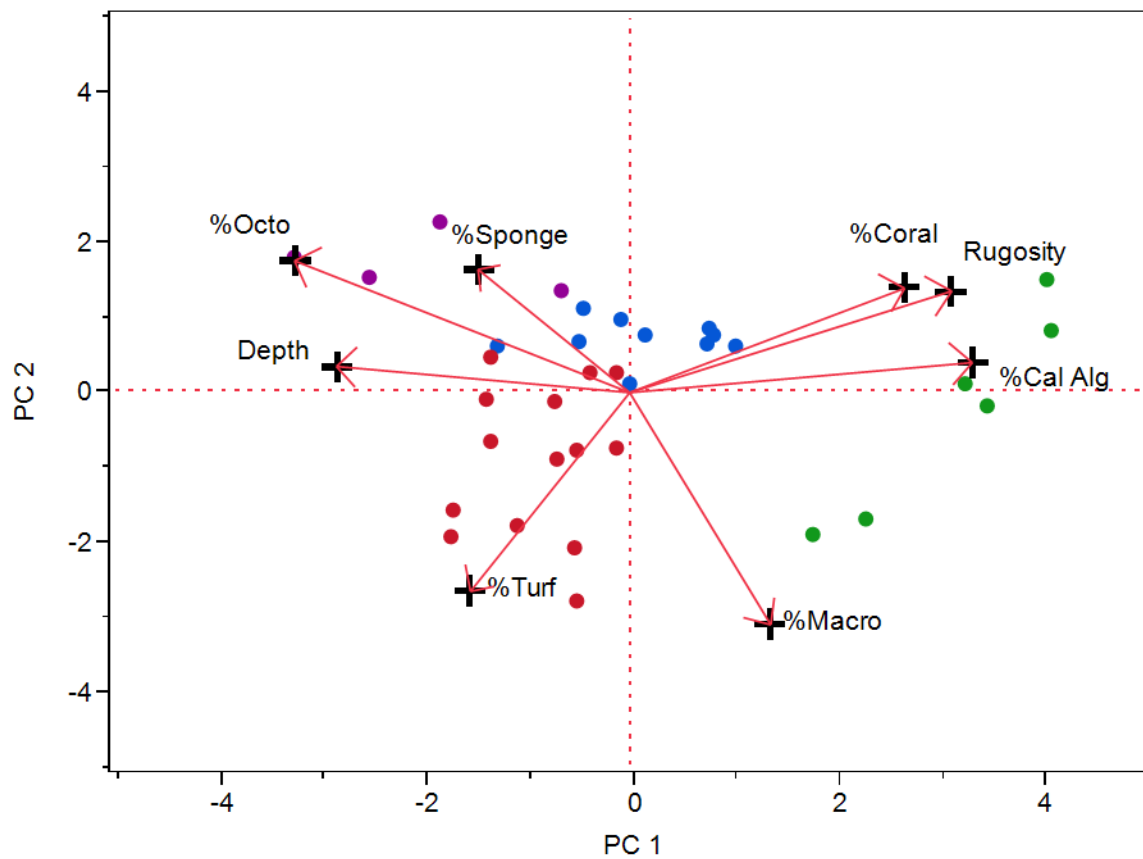


Figure 2.6 Principle component analysis showing the variation (PC1 = 39.6%, PC2 = 19.6%) in community structure of the reefs sites in the middle Florida Keys. Variables that load the principle components are shown as vectors and sites are categorized into reef types including Shelf (red), Patch (blue), Boulder (green) and Artificial (purple).

Table 2.2 Correlation coefficients and significance values for factors loading on the first and second principle components of reef structure and composition.

Principle component 1			Principle component 2		
Factor	Correlation	P	Factor	Correlation	P
% octocoral	-0.806	< 0.0001	% turf algae	-0.792	< 0.0001
% calcareous	0.805	< 0.0001	% macroalgae	-0.606	0.0001
rugosity	0.750	< 0.0001	rugosity	0.361	0.0355
depth	-0.705	< 0.0001	% octocoral	0.332	0.0548
% coral	0.656	< 0.0001	depth	0.198	0.2607
% macroalgae	0.358	0.0374	% calcareous	0.156	0.3774
% sponge	-0.352	0.0410	% coral	0.082	0.6425
% turf algae	-0.342	0.0479	% sponge	0.005	0.9759

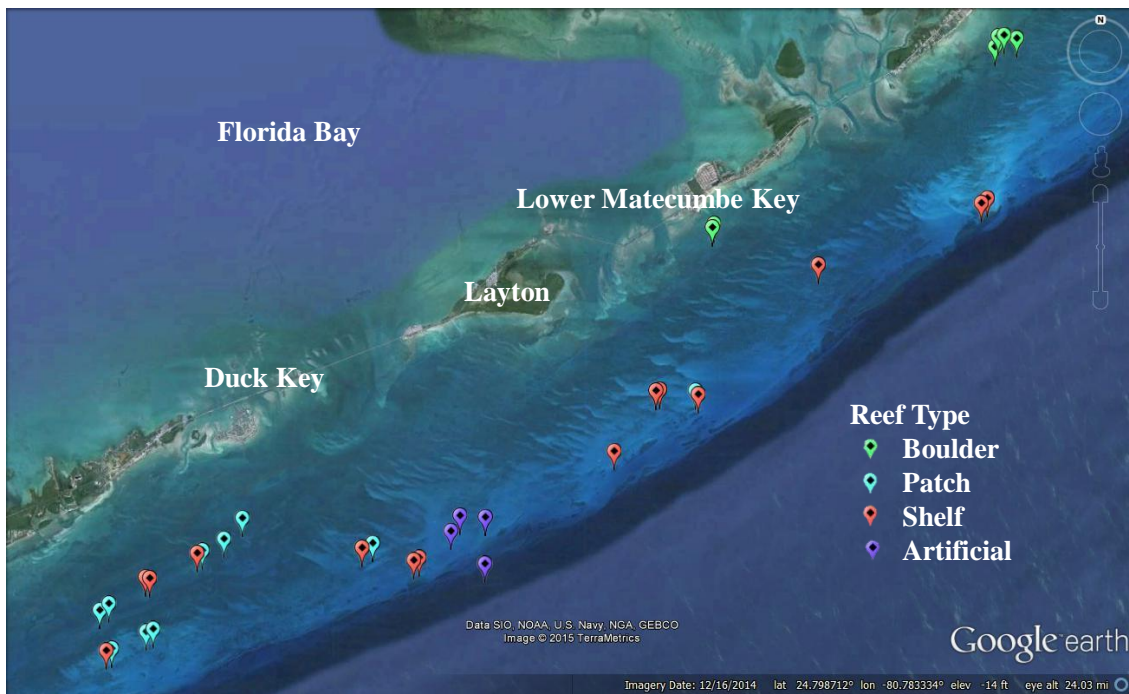


Figure 2.7 The four distinct reef types in the Florida Keys. Types include Boulder (green), Patch (blue), Shelf (red) and Artificial (purple) reefs.

Local reef types differ in both physical and community characteristics. Reefs closer to shore (Boulder and Patch) have shallower depths than reefs further from shore (Shelf and Artificial) ($P < 0.0001$, $F_{3,30} = 11.56$). There is also a cline in reef complexity as well with Boulder and Patch Reefs having higher habitat complexity, or rugosity, than Shelf and Artificial reefs ($P < 0.0001$, $F_{3,30} = 11.41$). Macroalgal cover is highest for Boulder, Patch and Shelf reefs and lowest for Artificial reefs ($P = 0.0033$, $F_{3,30} = 5.695$). Total parrotfish biomass also decreases from inshore to offshore with highest densities on Boulder reefs and lowest densities on Artificial reefs ($P = 0.0574$, $F_{3,30} = 2.792$).

Local Effects of Macroalgae and Parrotfish on Coral Cover

When looking for evidence of the predicted species interactions of the Herbivore Cascade model accounting for the differences in reef types, I found no significant effect of percent macroalgal cover on coral cover (Figure 2.8). However, there was a significant effect of reef type on percent coral cover and the interaction of reef type and percent macroalgal cover (Table 2.3). These effects suggest that the interaction between macroalgae and coral differ significantly between the four reef types as observed in Figure 2.8. There was a significant negative linear relationship between percent macroalgae cover and percent coral cover on Patch reefs ($P = 0.0257$, $F_{1,8} = 7.4752$). But there were no significant relationships between percent macroalgae cover and percent coral cover for Shelf ($P = 0.0584$, $F_{1,11} = 4.614$), Artificial ($P = 0.6892$, $F_{1,2} = 0.2138$) or Boulder ($P = 0.5480$, $F_{1,3} = 0.4557$) reefs. Boulder reefs are particularly interesting because they have both the highest coral cover and highest macroalgae cover and their relationship is more positive than negative.

Table 2.3 Generalized linear model of percent macroalgal cover on percent coral cover for 32 reef sites

Source	df	F Ratio	P-value	Adj r²
Macroalgal Cover	1	0.2180	0.6448	0.6372
Reef Type	3	10.6452	0.0001*	
Macroalgal Cover X Reef Type	3	4.0369	0.0186*	
Error	24			

* significant at $p < 0.05$

There was no significant effect of total parrotfish biomass (g/m^2) on percent macroalgal cover (Figure 2.9). There were no significant effects of reef type or the reef type by total parrotfish biomass (g/m^2) interaction on the percent macroalgal cover (Table 2.4). The positive linear relationship between parrotfish biomass and percent macroalgae cover found when analyzing all 32 sites is not found within the four reef types. There were no significant relationship between percent macroalgae cover and total parrotfish biomass (g/m^2) for Patch ($P = 0.5111$, $F_{1,8} = 0.4728$), Shelf ($P = 0.6015$, $F_{1,11} = 0.2891$), Artificial ($P = 0.4693$, $F_{1,2} = 0.7840$) or Boulder ($P = 0.9374$, $F_{1,3} = 0.0073$) reefs. The apparent positive relationship between macroalgae cover and parrotfish biomass is across reef types where parrotfish differ in species composition.

There was no significant effect of total parrotfish biomass (g/m^2) on percent coral cover (Figure 2.10). There was a significant effect of reef type suggesting that the interaction between parrotfish and coral cover differ between the four reef types (Table 2.5). There was no significant effect of the reef type and total parrotfish biomass (g/m^2) interaction on percent coral cover. There was a significant linear relationship between percent coral cover and total parrotfish biomass (g/m^2) for Artificial reefs ($P = 0.0338$, $F_{1,2} = 28.0900$). There were no significant relationships between percent coral cover and total parrotfish biomass (g/m^2) for Patch ($P = 0.9029$, $F_{1,8} = 0.0159$), Shelf ($P = 0.2414$, $F_{1,11} = 1.5330$) or Boulder ($P = 0.1491$, $F_{1,3} = 3.7276$) reefs.

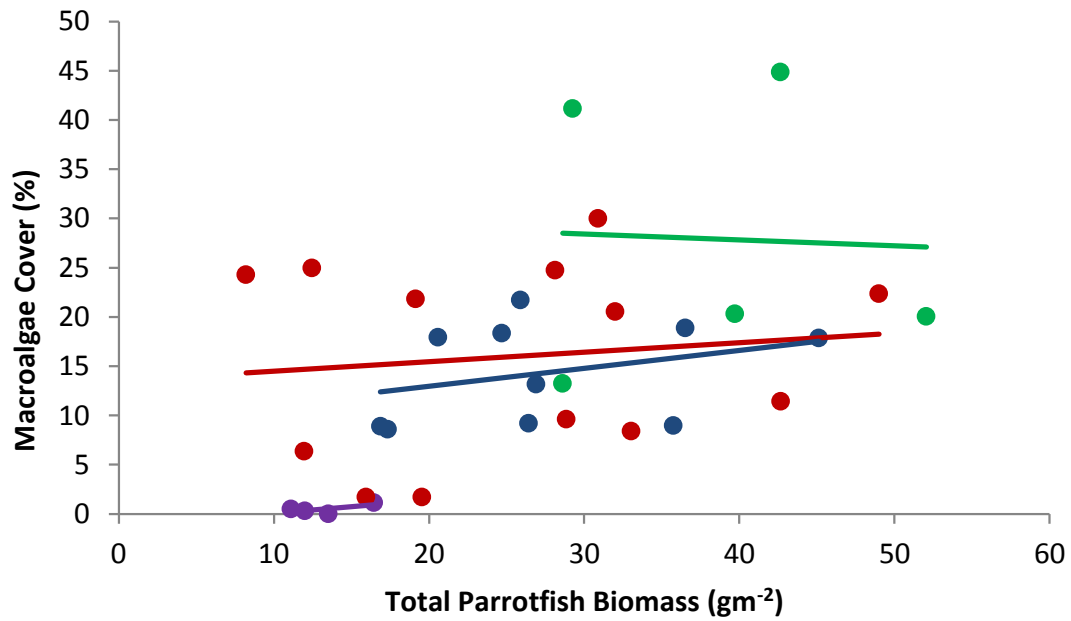


Figure 2.9 Macroalgal cover and corresponding parrotfish biomass for 32 sites. Sites are categorized by reef type (Boulder – green, Patch – blue, Shelf – red, Artificial – purple). Reference lines are included regardless of whether the relationship is statistically significant or not.

Table 2.4 Generalized linear model of total parrotfish biomass on percent macroalgae cover for 32 reef sites

Source	df	F Ratio	P-value	Adj r^2
Total Parrotfish Biomass (TPB)	1	0.0144	0.9056	0.2965
Reef Type	3	1.3399	0.2849	
TPB X Reef Type	3	0.0486	0.9855	
Error	24			

* significant at $p < 0.05$

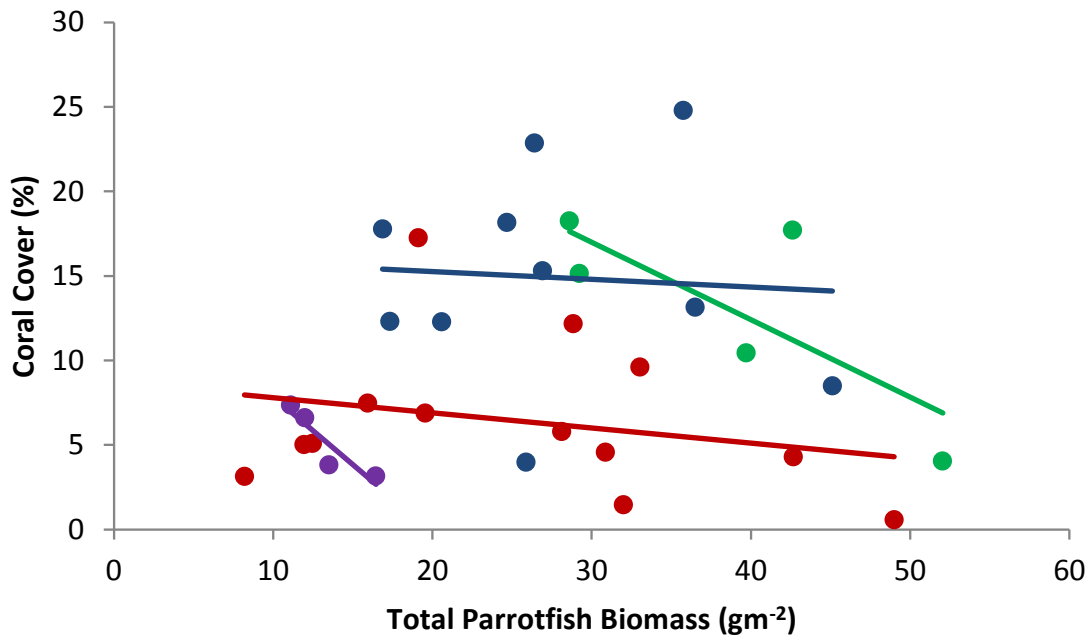


Figure 2.10 Coral cover and corresponding parrotfish biomass for 32 sites. Sites are categorized by reef type (Boulder – green, Patch – blue, Shelf – red, Artificial – purple). Reference lines are included regardless of whether the relationship is statistically significant or not.

Table 2.5 Generalized linear model of total parrotfish biomass on percent coral cover for 32 reef sites

Source	df	F Ratio	P-value	Adj r²
Total Parrotfish Biomass (TPB)	1	1.4306	0.2433	0.5259
Reef Type	3	12.6806	<.0001*	
TPB X Reef Type	3	1.0290	0.3985	
Error	24			

* significant at $p < 0.05$

DISCUSSION

The Herbivore Cascade model suggests that changes in herbivory explain patterns in coral cover and this model has been supported on coral reefs throughout the Caribbean (Lirman 2001, Bellwood et al. 2004, Jackson et al. 2014). This model predicts that a competitive interaction exists between macroalgae and corals for settlement space and nutrients (LaPointe 1989, McManus et al. 2000, Jackson et al. 2014). It also predicts that herbivory regulates the abundance of macroalgae (Lewis 1986, Burkepile and Hay 2011). The reduction in macroalgae reduces the competitive interaction of macroalgae on coral, resulting in a positive indirect effect of herbivory on coral cover (Lirman 2001). The goal of this study was to use survey data to test the predicted species interactions of the Herbivore Cascade model.

Previous studies have found strong negative relationships between macroalgal and coral cover, suggesting that these organisms are in direct competition with each other (Lirman 2001, Jackson et al. 2014). When looking at all 32 reefs sites, I did not find evidence of this relationship. After identifying the four distinct reef types, I tested again for evidence of this competitive relationship. The only evidence of a negative relationship between macroalgae and coral cover comes from Patch reefs. These reefs have moderate to high structural complexity and support moderate numbers of parrotfish. Located in Hawk Channel, these Patch reefs may have lower levels of physical disturbance from divers and storms allowing more time for competition between the corals and macroalgae to structure the reef community. An interesting observation is that all reefs with > 20%

live coral cover (1 Boulder and 2 Patch reefs) do have low macroalgal cover (< 20%). But reefs with < 20% live coral cover can have any level of macroalgae from 0% to 45%. This suggests that macroalgae may not be the only factor limiting coral cover. In the Florida Keys, periodic warm or cold water events cause significant loss of corals and may decouple the local relationship between coral cover and macroalgal cover (Colella et al. 2012).

Parrotfish preferentially feed on macroalgae (Cardoso et al. 2009) and may avoid reefs with insufficient macroalgae. This dietary preference might explain why overall parrotfish abundance is positively correlated with macroalgal cover. However, this relationship does not exist for all reef types. The strongest positive relationship between total parrotfish biomass and percent macroalgal cover is found on Shelf reefs which have a wide range of macroalgal cover. Parrotfish preferences for macroalgae might also explain why parrotfish are much less abundant on Artificial reefs which lack turf and macroalgae. An alternative explanation might be that parrotfish are most abundant on reefs with highest complexity (Boulder) and avoid reefs with low complexity (Artificial) and that this positive correlation with macroalgal abundance is unrelated to their dietary considerations.

If parrotfish have an indirect positive impact on coral cover, I would expect a positive relationship between these two variables. However, there is no significant relationship between parrotfish biomass and coral cover, which is not surprising given that the expected negative relationships between parrotfish--macroalgae, and macroalgae-

-corals are weak or absent. The only significant relationship was a negative one for Artificial reefs where both parrotfish biomass and coral cover are exceptionally low and there is little else for parrotfish to eat. Parrotfish biomass is associated more with reef type showing a decrease in biomass moving from inshore (Boulder) to offshore (Shelf) reefs. This difference in biomass is driven primarily by a shift in the relative frequency of the ubiquitous striped parrotfish (*Scarus iserti*) that are very common inshore and nearly absent offshore. Recent studies have found that substrate composition might also play a role in attracting parrotfishes (Dixson et al. 2014). They found that juvenile reef fish from six different families preferred waters taken from marine protected areas where coral cover was high and the reefs were considered healthy. They suggest that previous studies finding a positive relationship between coral cover and parrotfish biomass may not be due solely to an indirect trophic cascade (Mumby and Steneck 2008).

In conclusion, this study finds no support for the Herbivory Cascade model explaining the variation in coral cover on reefs in the middle Florida Keys. Reefs in the Florida Keys National Marine Sanctuary have lower than average coral percent cover relative to the greater Caribbean but higher than average parrotfish biomass (Jackson et al. 2014, this study). High parrotfish biomass may be due to relatively low fishing pressure on herbivorous fishes and the relatively high level of coral disturbance due to recreational boating and SCUBA diving (Medio et al. 1997, Hawkins et al. 1999). The establishment of marine protected areas throughout the FKNMS has increased the biomass of parrotfish but has had little effect on local grazing rates (Kramer and Heck 2007). These results, including the ones from this study, all suggest that the decline in

coral cover is not impacted by the loss of parrotfish herbivory and a corresponding increase in macroalgal competition.

There has been support for alternative models that may better explain the variation in coral cover found in the reef types in the middle Florida Keys. The Disturbance Cascade model predicts that changes in coral cover and habitat complexity might have stronger effects on reef community structure than changes in herbivore abundance (Chapter 1 – Figure 1.6). With the loss of complexity, predator and herbivore populations would decline due to the reduction in resources (Mumby and Steneck 2008). The variation in coral cover between the reef types might be better explained by determining the disturbance intensity and frequency on these reefs. The Nutrient Cascade model suggests that changes in macroalgae abundance are the primary factor driving the variation in coral cover (Chapter 1 – Figure 1.6). Certain reef types are located closer to shore where nutrient concentrations are increased due to agricultural runoff, and these eutrophic environments would have different interactions between macroalgae, herbivores and coral.

Coral reefs of the middle Florida Keys differ in their species composition and these differences may influence the interactions taking place between common organisms that inhabit these ecosystems. Several models have been proposed to explain the variation in coral cover on reefs throughout the Caribbean and the Florida Keys. The Herbivore Cascade model was not supported by my data and future work will examine if either the Disturbance Cascade model or Nutrient Cascade model provides a better

explanation for the variation in coral cover. These reefs of the middle Florida Keys include highly degraded reefs and they are believed to be the future of other reefs in the Florida Keys and Caribbean. By understanding which organisms are driving the patterns in coral cover, I can better form conservation strategies to preserve these ecosystems and the massive amount of biodiversity they support.

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CHAPTER 3

IMPACTS OF MACROALGAL COMPETITION AND HERBIVORY ON THE GROWTH OF TWO CORAL SPECIES – AN HERBIVORE EXCLUSION EXPERIMENT

INTRODUCTION

Over the past 40 years, live coral cover across the Caribbean has drastically declined (Jackson et al. 2014). In the Florida Keys, not only has the percent of live coral cover decreased (Donahue et al. 2008, Somerfield et al. 2008), but reef building corals that were once abundant on these reefs are now at risk of extinction (Carpenter et al. 2008). Changing environmental conditions, including increased water temperature, lower pH and increased nutrients have contributed to the decline in coral cover (Brown 1997). Because corals are sensitive to small changes in these factors, any increase in variation and/or duration of temperature, pH or nutrient deviations due to climate change place corals at even greater risk (Kleypas et al. 2005, Doney et al. 2012).

While corals are negatively influenced by higher temperatures, lower pH and increased nutrients, these changes may increase macroalgae growth (Graham et al. 2015). Macroalgae are fast growing primary producers that can out-compete corals for nutrients, settlement space, and light (Vermeij et al. 2010). Macroalgae may directly harm corals through the production of allelochemicals (Rasher and Hay 2010a) or through subtle changes in composition of the coral's microbial symbionts (Thurber et al. 2012). This

competition increases the stress on corals and leads to a further decline in live coral cover (Mumby and Steneck 2008) .

Coral species differ in their susceptibility to macroalgal competition (Lirman 2001). In a study in the upper Florida Keys, two common coral species, *Porites astreoides* and *Siderastrea siderea*, were caged with various species of *Halimeda* and *Dictyota* macroalgae. Macroalgae did affect the growth rate of *Siderastrea siderea* and they caused a four-fold reduction in growth of *Porites astreoides* corals. These effects differed among different reefs, however, suggesting that other factors might mitigate the coral-macroalgae interaction (Lirman 2001).

Corals may also be affected by herbivory. Reductions in herbivory can contribute to a phase shift from a coral dominated ecosystem to a macroalgae-dominated ecosystem (McCook et al. 2001, Hughes et al. 2010, Ferrari et al. 2012). Historically, herbivores such as parrotfishes, sea urchins and crustaceans played an important role in regulating macroalgae abundance (Jackson et al. 2014). However, disease (Carpenter 1988) and overfishing (Jackson et al. 2001) have reduced these populations and their impacts algal communities (Jackson et al. 2014).

The predicted effects of herbivores and macroalgae on coral cover have been summarized in the Herbivore Cascade model (Chapter 1 – Figure 1.2). This model suggests that herbivores can reduce the abundance of macroalgae and therefore its competitive effects on coral growth. These combined interactions would result in an indirect positive effect of herbivory on coral cover and growth.

In this study, I conducted a manipulative coral transplant experiment in the middle Florida Keys to test the predicted species interactions of the Herbivore Cascade model. Specifically, I tested the hypothesis that herbivory decreases macroalgae cover and greater macroalgae cover negatively affects coral cover. In this experiment, coral fragments were transplanted and caged to control for the amount of macroalgal competition and herbivory. I predicted that coral growth would be lowest in cages with high macroalgae and closed tops preventing herbivore access, and would be highest in cages with no macroalgae and open tops allowing herbivore access. As there is much interest in transplanting coral fragments as a method of reef restoration (Edwards and Clark 1999), it will be informative for conservation efforts to use these fragments to test if changes in herbivory influence the growth and survival of coral fragments.

METHODS

Study Sites

I transplanted fragments of two common species of corals, *Siderastrea siderea* and *Porites astreoides*, to seven locations in the Florida Keys National Marine Sanctuary. These locations were selected from 17 reefs surveyed that had sufficient contiguous hardbottom habitat with corals, macroalgae and parrotfishes present (see Chapter 2 for further analysis of reef site differences). These locations include 11' Mound (24.72° N, 80.86° W), Coral Gardens (24.84° N, 80.73° W), East Turtle Patch (24.73° N, 80.91° W), Elbow (24.69° N, 80.95° W), Out Spa (24.78° N, 80.75° W), Stag Party (24.78° N, 80.74° W) and Turtle Shoals (24.72° N, 80.93° W) (Figure 3.1).

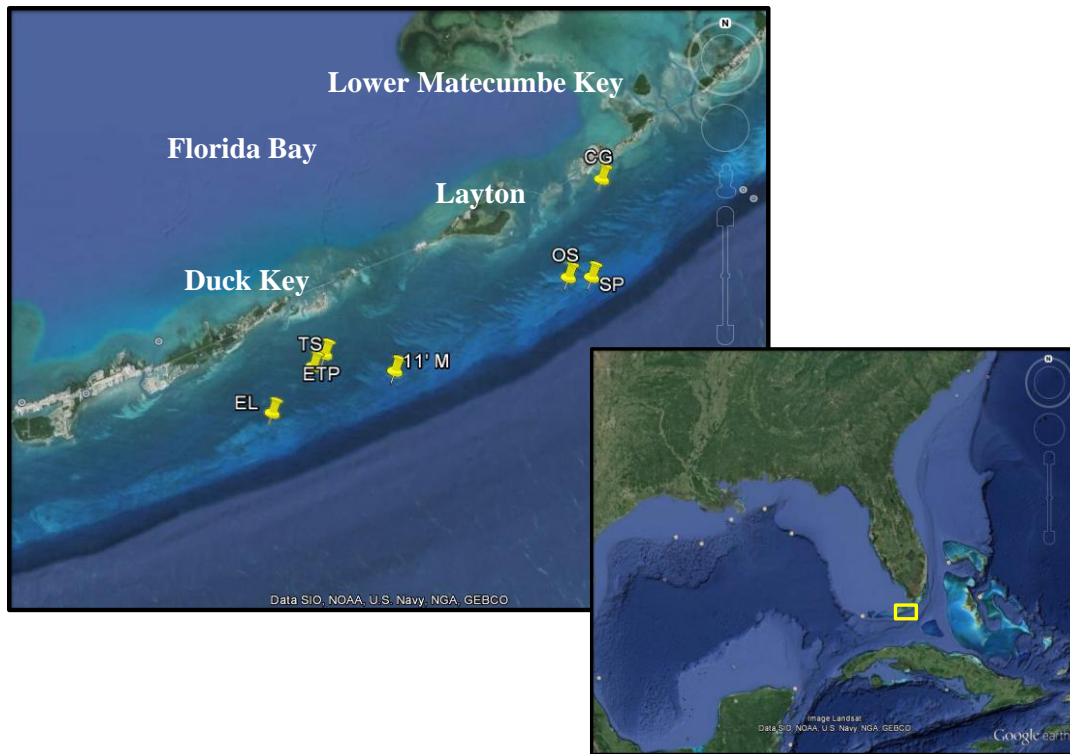


Figure 3.1 Locations of the seven coral transplant sites in the Florida Keys National Marine Sanctuary.

Coral Transplantation

Fragments of corals *Siderastrea siderea* (n = 42) and *Porites astreoides* (n = 42) from nurseries off-shore of Key West were donated by the Mote Tropical Marine Laboratory. These fragments were held in running seawater tanks at the Keys Marine Laboratory for 4 weeks (June-July 2013) during the transplantation process. Although the exact origin of each fragment is unknown, it is likely that the fragments are from 1-3 coral colonies recovered from ship groundings in the Florida Keys. Corals were transported from wet tables to the reef in coolers, and from boat to divers in mesh bags, following the methods of previous transplant studies (E. Bartels, pers. comm.).

At each transplant site, a 50 m permanent transect was established by selection of a random starting point run in a direction parallel to the primary axis of the reef. The beginning and end points of each transect were marked by a rebar stake capped with an orange cap to facilitate relocation. At regular intervals (approximately 4 m apart) along the transect, fragments of *S. siderea* and *P. astreoides* were transplanted within 1-2 m of the transect for a total of six fragments per species per site. The position of the corals alternated between the left and right side of the transect to assure that corals were at least 5 m apart and could be reliably relocated along the transect. Suitable transplant locations were identified as an area approximately 0.5 m X 0.5 m with a hard substrate and a minimal number of other corals, sponges or soft corals present. The substrate surface (approximately 10 cm diameter) was prepared by clearing all turf and macroalgae using a

hammer and chisel. Each coral fragment was then attached to the reef using a two-part, quick-setting epoxy mixed underwater.

Treatment Assignment and Cage Installation

The manipulative experiment was a fully-crossed three factor design with two species of transplanted corals, three levels of macroalgae addition, and two levels of herbivore access (Figure 3.2). Every transplanted coral was surrounded by a cage constructed of four rebar stakes, 2 cm diameter PVC square, and 2 cm Vexar mesh (Figure 3.3). The dimensions of the cage were 50 cm wide X 50 cm long X 50 cm deep. Cages were then secured to the rebar stakes using cable ties and hose clamps. A 10 cm flap of Vexar extended from the bottom edge of each side of the cage to conform to irregular surface of the substrate to assure that grazers could not enter the cage.

In order to vary macroalgae exposure, clumps of *Dictyota* spp. were added to the cages depending on the assigned treatment. The clumps of *Dictyota* spp. were collected from Bamboo Key (24.756222° N, -81.002823° W). Once collected, the algae was dried of excess water and measured. One cup of algae was added to a pouch constructed of 2 cm Vexar mesh. Macroalgae was added to the cages within two weeks of collection. The cages displayed a gradient of macroalgae abundance by the number of clumps attached to the inside of the cages. Cages with no clumps added were considered no algae. Cages with two clumps added were considered medium algae abundance, and cages with four clumps added were considered high algae abundance (Figure 3.2).

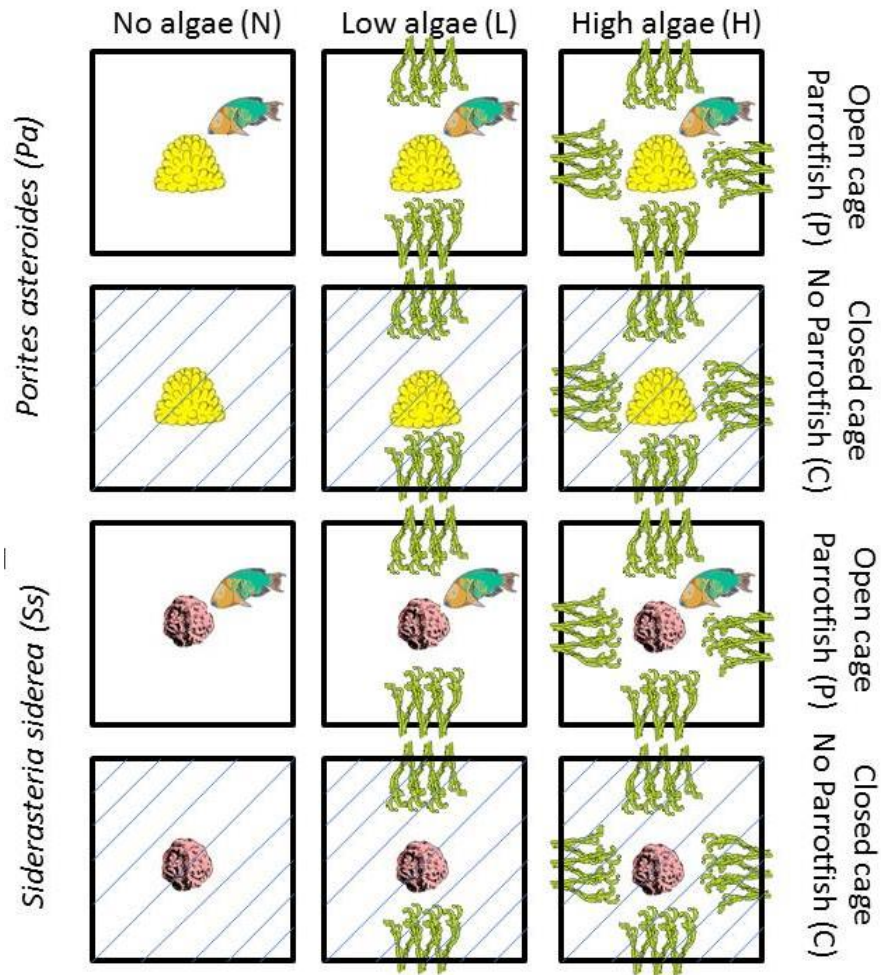


Figure 3.2 A visual representation of the experimental design. Cages of Vexar mesh were centered around transplanted corals of one of two species. Cages were either open-topped allowing parrotfish grazing (rows 1 & 3) or closed topped controls excluding parrotfish grazing (rows 2 & 4). Columns represent increasing volumes of attached macroalgae (left = no, middle = medium – 2 clumps, right = high – 4 clumps).



Figure 3.3 An installed open topped cage in the field.

Pouches of macroalgae were secured to the inside of the cages using cable ties. The Vexar pouches were small enough to keep the macroalgae in the cage but large enough to allow for grazing. To examine the influence of herbivory, cages were either open-topped (herbivore access) or closed-topped (herbivore exclusion) (Figure 3.2). Tops of the cages were constructed from 2 cm Vexar mesh and were 0.25 m² in area. Tops were attached to half of the cages using releasable cable ties.

Initial photographs were taken of the inside of all cages, and Image J software was used to estimate the area of the coral, perimeter of the coral and the amount of macroalgae in contact with the coral (Figure 3.4). Photographs were also used to determine the percent cover of coral, macroalgae, octocoral, sponge and turf algae using Coral Point Count with Excel Extensions (CPCe) software (Kohler and Gill 2006). I also took 12 photographs of the substrate outside of the cages on the left and right side of each transect to estimate the percent cover of coral, macroalgae, octocoral, sponge and turf algae across the reef. Photographs were analyzed using CPCe.

Surveying Methods

I monitored the transplanted corals three times during the 10 month period after transplantation in July 2013. I revisited the sites in October 2013, March 2014 and May 2014. In March 2014, I was unable to visit three of the sites due to poor weather conditions. I photographed the inside of every cage each census to determine changes in the area of the coral, perimeter of the coral and the amount of macroalgae in contact with the coral. I also estimated changes in the percent cover of the other substrate species inside and outside of the cages. During these surveys, I checked and repaired the cages

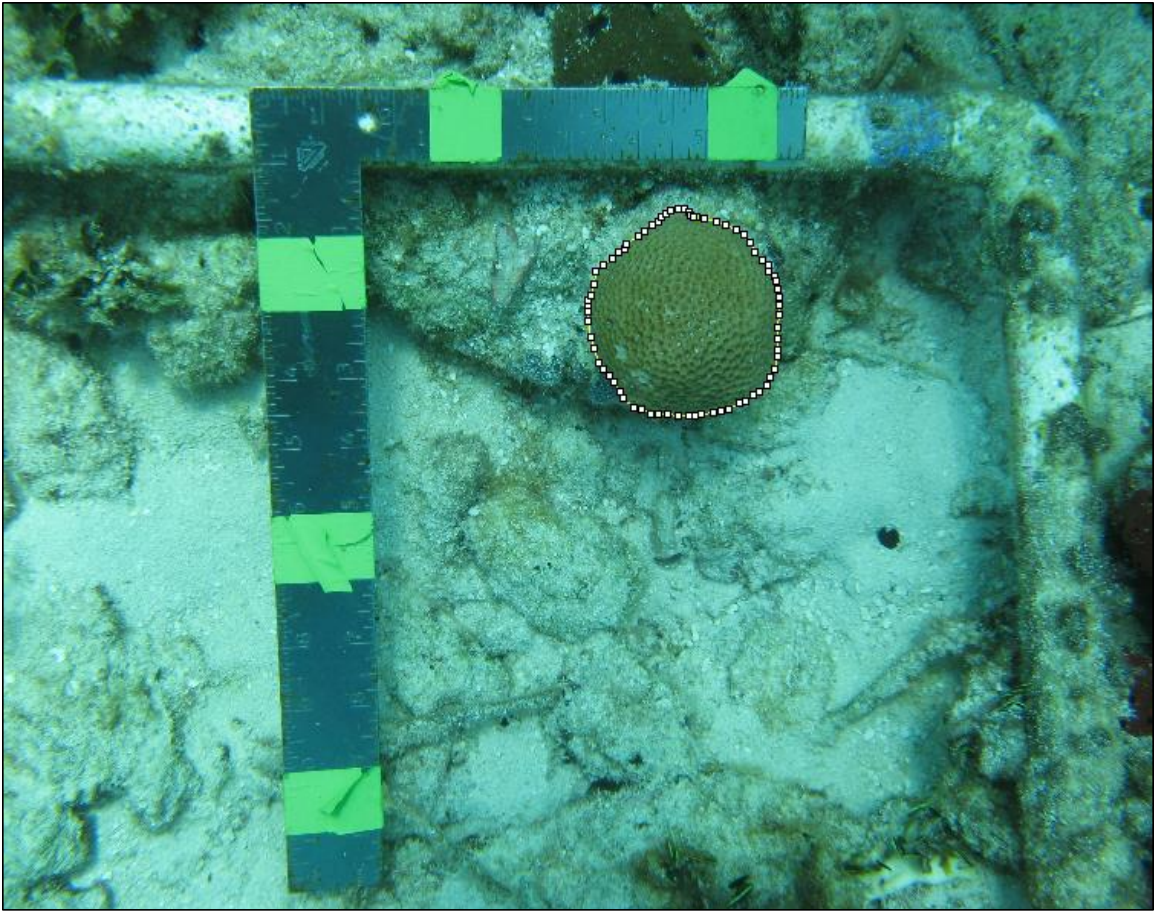


Figure 3.4 A transplanted *Siderastrea siderea* coral fragment was traced in Image J to calculate area. A ruler was laid next to each coral in order to set the scale in Image J.

to ensure the treatments were maintained and they were adequately secured to the reef. If a cage was missing and/or a coral could not be located during a census, I did not include the data on coral growth or macroalgae abundance for that cage. Over these sampling periods, I excluded 13 cages from the data analysis due to missing cages.

Maintaining the initial levels of macroalgae across the treatments proved very difficult as there was insufficient *Dictyota* spp. available to refill the macroalgae pouches. Instead, during the October and March monitoring trips, I cleaned off the attached macroalgae growing on the sides of the cages to maintain the differences among these treatments. The no macroalgae treatment had all four sides of the cage scrubbed; the low macroalgae treatment had two sides of the cage scrubbed; and the high macroalgae treatment had no sides of the cage scrubbed. The covers of all closed cages were scrubbed to avoid differences in overhead light levels.

Statistical Analyses

I calculated percent change in coral area (area of substrate with coral) and macroalgae perimeter (perimeter of coral in contact with macroalgae) as the difference between the final (May 2014) and initial (July 2013) measurements divided by the initial measurement. I tested whether the percent change in coral area or macroalgae perimeter were significantly affected by macroalgae treatment, herbivore exclusion, or a combination of those two effects using a fully-factorial randomized-block ANOVA with reef site as the block and coral species, macroalgal treatment, and herbivore exclusion as fully-crossed fixed factors. I also tested whether percent coral growth was directly related

to percent macroalgae perimeter using regression analysis. In addition, I ran alternative ANOVA models to test for the effects of reef type (boulder, patch, shelf), percent macroalgal cover, and total parrotfish biomass (g/m^2) on change in coral area and percent macroalgae in contact with the coral. However, these models also had no significant main effects or interactions as the randomized block ANOVA. I also conducted a repeated measures ANOVA (July 2013, October 2013, May 2014) to determine if the percent macroalgae cover inside vs. outside the cages was impacted by treatment (Open / Closed / Control), season or reef site.

RESULTS

Overall, the transplantation of the corals was successful. 13 corals were missing cages or could not be located during the final census in May 2014. However, the remaining 71 coral fragments remained secured on the substrate with a cage intact. These corals were used for analysis of changes in coral growth and percent macroalgae in contact with corals.

Coral transplants did not change significantly in percent area of live tissue after the 10 months following transplantation regardless of cage treatment (Figure 3.5). Percent change in coral area was unrelated to reef site, coral species, macroalgae treatment or herbivore exclusion cage treatment (Table 3.1). The amount of macroalgae in contact with the transplanted coral fragment, measured as a percent of the total coral perimeter, increased for some corals over the 10 month period after transplantation

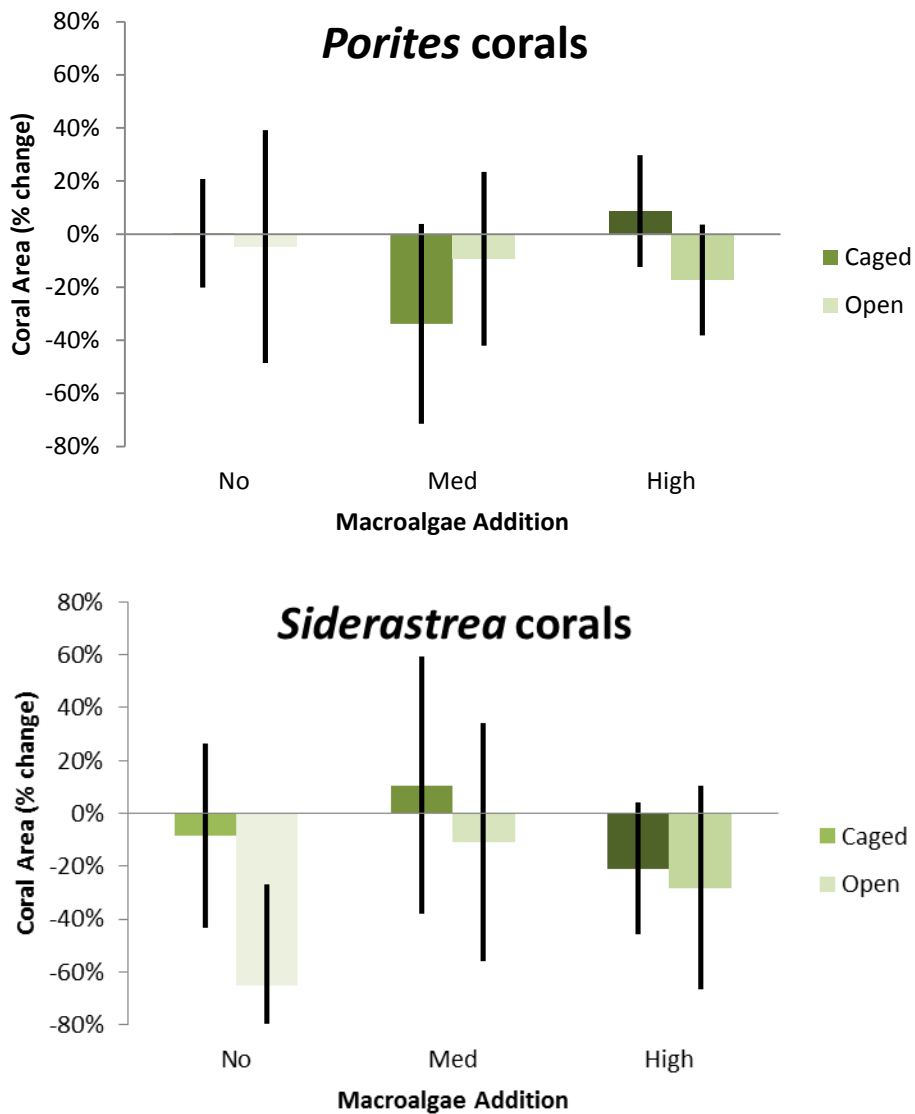


Figure 3.5 Net change in coral area (mean % \pm 95% CI) between July 2013 and May 2014 for two species of coral (*P. astreoides* and *S. siderea*) transplanted and caged with three levels of macroalgal addition (no, med, high) and two levels of herbivore access (caged vs. open).

Table 3.1 Analysis of change in coral area (%) between July 2013 and May 2014 for two species of coral (*P. astreoides* and *S. siderea*) using a fully-factorial randomized block ANOVA. Main effects of the model were two coral species, three levels of macroalgal addition (no, med, high), two levels of herbivore access (cage open, cage closed), and all main effect interactions. Reef site (n = 7) was the block variable.

Source	df	SS	F	p-value
Reef site (block)	6	2785	1.451	0.2129
Coral	1	840.3	2.627	0.1110
Macroalgal treatment	2	24.86	0.039	0.9619
Cage type	1	124.7	0.390	0.5351
Coral X Macroalgae	2	229.7	0.359	0.7000
Coral X Cage	1	51.32	0.160	0.6904
Macroalgae X Cage	2	10.30	0.016	0.9840
Coral X Macroalgae X Cage	2	994.9	1.555	0.2206
Error	53	16954		

(Figure 3.6) but it was unrelated to reef site, coral species, macroalgae treatment or herbivore exclusion cage treatment (Table 3.2). The change in coral area was unrelated to change in macroalgae perimeter ($F_{1,69} = 0.000$, $P = 0.997$). However, macroalgal cover did change with season and differed from inside to outside of the cages (Table 3.3). Macroalgal cover was higher inside cages (both open and closed) during the initial census, peaked in October and was similar to levels outside the cages (control) by the final census in May 2014 (Figure 3.7). Overall, some sites had more macroalgal cover than others (Coral Gardens = highest, Turtle Shoals = lowest) and some sites had more change in macroalgal cover from census to census than others (Stag Party = most change, Turtle Shoals = least change) leading to significant interactions of census with both site and cage treatment (Table 3.3).

DISCUSSION

In the upper Florida Keys, previous herbivore exclusion experiments have supported the Herbivore Cascade model, which predicts changes in herbivory regulate macroalgae abundance and indirectly positively effects coral growth (Lirman 2001). However, in this study, I did not find evidence that the Herbivore Cascade model explains the variation in coral cover of transplanted coral fragments in the middle Florida Keys. The growth rate of the two coral species, *Siderastrea siderea* and *Porites astreoides*, were not significantly influenced by the level of macroalgal addition or herbivore exposure. Neither species of corals showed significant positive or negative changes in the area of live tissue over the ten months post-transplantation. However, the

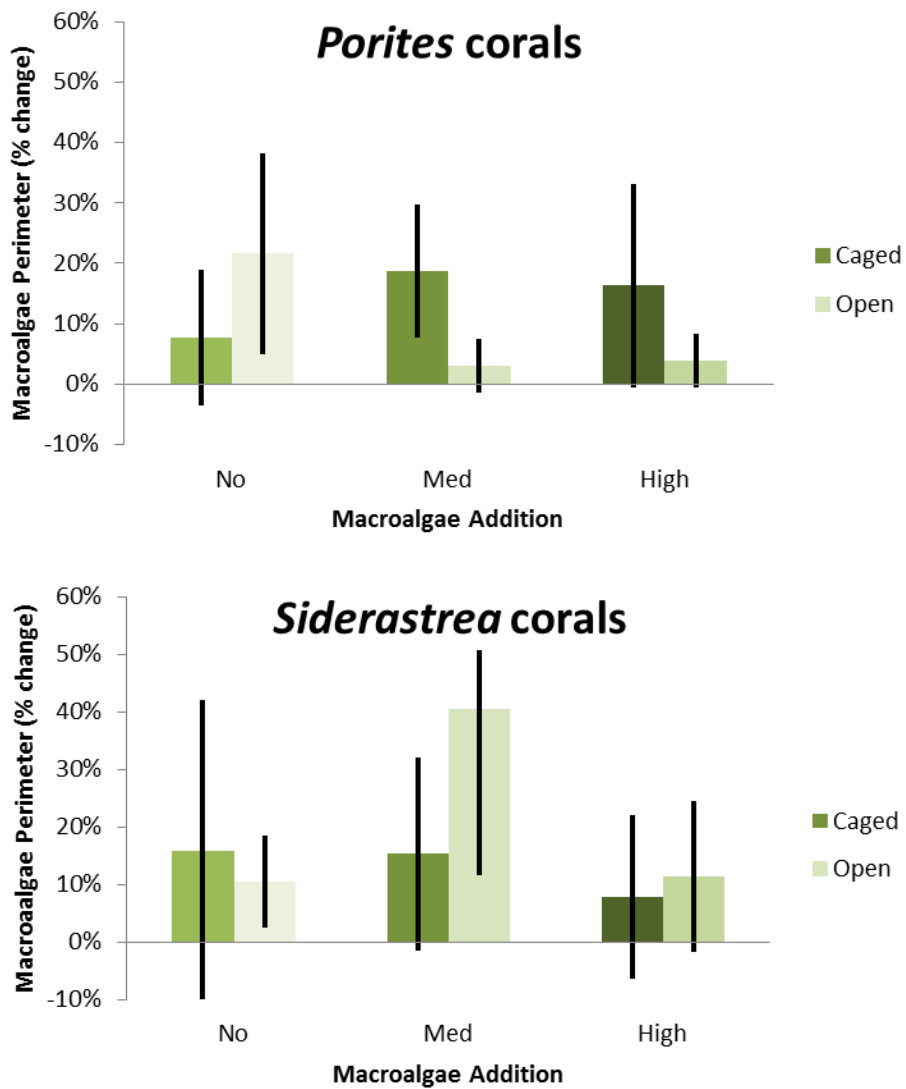


Figure 3.6 Net change in macroalgal-coral contact (mean % +/- 95% CI) between July 2013 and May 2014 for two species of coral (*P. astreoides* and *S. siderea*) transplanted and caged with three levels of macroalgal addition (no, med, high) and two levels of herbivore access (caged vs. open).

Table 3.2 Analysis of change in macroalgal-coral contact (% coral perimeter) between July 2013 and May 2014 for two species of coral (*P. astreoides* and *S. siderea*) using a fully-factorial randomized-block ANOVA. Main effects of the model were two species of coral, three levels of macroalgal addition (no, med, high), two levels of herbivore access (cage open, cage closed), and all main effect interactions. Reef site (n = 7) was the block variable.

Source	df	SS	F	p-value
Reef site (block)	6	103.8	0.615	0.7170
Coral	1	43.13	1.533	0.2210
Macroalgal treatment	2	45.60	0.811	0.4499
Cage type	1	9.984	0.355	0.5538
Coral X Macroalgae	2	37.84	0.672	0.5146
Coral X Cage	1	72.92	2.592	0.1133
Macroalgae X Cage	2	10.72	0.191	0.8269
Coral X Macroalgae X Cage	2	99.23	1.764	0.1812
Error	53	1490		

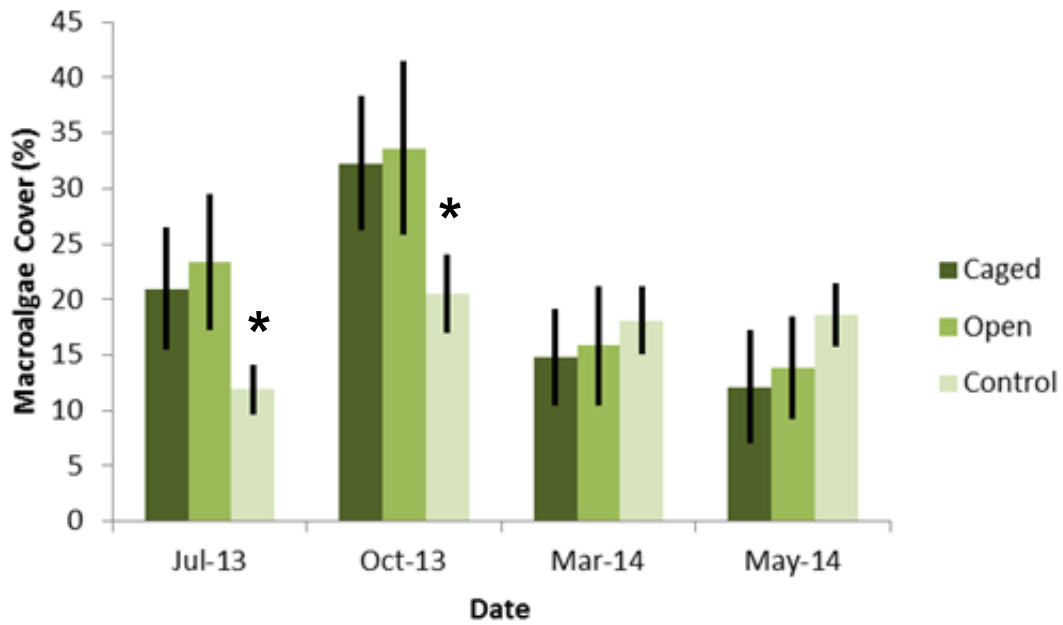


Figure 3.7 Macroalgal cover (%) by census date for each treatment of the herbivore exclusion experiment (closed cage, open cage, and uncaged control).

Table 3.3 Analysis of macroalgal percent cover for site and three conditions (closed cage, open cage, no cage control) using repeated measures ANOVA. Censuses were conducted at three time points July 2013, October 2013, and May 2014.

Comparison	Source	df	F	p-value
Between Subjects	Site	6, 157	23.59	<0.0001
	Cage type	2, 157	7.269	0.0010
Within Subjects	Census	2, 156	43.40	<0.0001
	Census X Site	12, 312	2.643	0.0022
	Census X Cage	4, 312	14.35	<0.0001

annual growth rates of these corals are extremely low (2.6 mm for *S. siderea* and 3.0 mm or *P. astreoides*) and future monitoring of these fragments over an additional year may allow us to detect these changes.

My attempt to influence the competitive interaction between macroalgae and corals by adding macroalgae at different densities had no influence on coral growth, percent macroalgae perimeter, or macroalgae cover. Likewise, my attempt to influence macroalgae by eliminating the effects of herbivores had no influence on coral growth, percent macroalgae perimeter, or macroalgal cover. However, macroalgal cover was significantly influenced by season, reef site, and their interaction. Some locations such as Coral Gardens had persistent high levels of macroalgal cover, while other sites like Turtle Shoals had persistent low levels of macroalgal cover. Other sites like Stag Party showed the greatest change in macroalgal cover with low levels in spring and summer and high levels in the fall.

Previous studies have found that coral species vary in their susceptibility to macroalgal competition (Lirman 2001). Lirman (2001) found that caged *P. astreoides* colonies had growth rates four times lower than uncaged colonies while the growth rate of caged *S. siderea* colonies were not affected. One difference in this previous study compared to my study is they introduced a much higher density of *Dictyota* spp. macroalgae to their cages. *Dictyota* spp. percent cover varies dramatically from reef to reef in the Florida Keys and was relatively low in this middle Florida Keys study compared to previous studies in the Upper Florida Keys (Herren et al. 2006).

Growth rates of each coral species vary seasonally, but *P. astreoides* has an average growth rate of 3.0 – 3.5 mm each year (Gladfelter et al. 1978) while *S. siderea* grows on average 2.6 mm each year but has high variation among sites (Kuffner et al. 2013). This translates to approximately a 4% annual increase in coral area for coral fragments the size I transplanted. My average increase in coral area for *S. siderea* was 8.6% +/- 7.5% and for *P. astreoides* was 1.9% +/- 3.9%. These estimates easily bracket the expected annual increase of 4% per year, but indicate large variation among individual transplants. While reef site did have a significant impact on percent of macroalgal cover, I did not find reef site to influence coral growth or macroalgae perimeter. This could be due to the strong effects of the cage on light levels critical to the growth of both corals and macroalgae. Future studies should compare the growth rates of uncaged corals on reef sites that differ in macroalgal cover to better tease apart the site-specific effects of macroalgal competition.

In addition to reef site effects on macroalgal cover, I also found a significant influence of season on macroalgal cover. In the fall, water temperatures are warmer than other times of the year. Previous studies have found that these warmer temperatures are beneficial for macroalgal growth (Lirman and Biber 2000). Ferrari et al. (2012) found that seasonal differences in light and temperature had a bigger effect on the abundance of *Dictyota* spp. than did the presence or absence of herbivorous parrotfishes.

Overfishing of large herbivorous parrotfishes has been suggested to have played a significant role in the shift of reefs from coral-dominated to algal-dominated throughout

the Caribbean (Jackson et al. 2001, Jackson et al. 2014). However, the loss of corals in the Florida Keys occurred even though parrotfish densities have remained relatively high (Bozec et al. 2015). Burkepile (2012) found that parrotfish grazers will feed directly on coral polyps and show dietary preferences towards specific coral species. On reefs in Key Largo in the upper Florida Keys, the abundance of the stoplight parrotfish, *Sparisoma viride*, was positively correlated with the frequency of coral predation on *Porites spp.* coral (Burkepile 2012). Rotjan and Lewis (2006) suggested that the differences in structure of the corals may explain these dietary preferences. *Porites spp.* corals tend to have higher structural complexity and their branches are more accessible to parrotfish than a rounded *Siderastrea spp.* (Rotjan and Lewis 2006). I looked for and recorded any scrapes to the surface of the transplanted corals to try and estimate if parrotfish grazing was contributing to the loss of coral area in this study. Only a few scrapes were ever observed and were more often the result of loose Vexar mesh than parrotfish corallivory. Thus, I can discount corallivory as a factor influencing coral growth in this study. However, future studies will specifically examine the diet of parrotfishes on these reefs to determine if these fishes show dietary preferences towards the coral species occurring on these reefs and if they differ between the species of parrotfish.

Given the sudden and pervasive loss of corals in the Florida Keys, much effort is being invested in the transplanting of coral recruits in order to accelerate reef recovery (Lirman et al. 2010). Much of the current research is focused on determining the best techniques of coral transplanting, the locations where these transplants are most successful, and the other abiotic and biotic factors contributing to the growth of

transplanted corals (Clark and Edwards 1995, Edwards and Clark 1999, Burkepile and Hay 2010). While the Herbivore Cascade model has explained the variation in the success of transplanted coral fragments in the Caribbean and other areas of the Florida Keys, I do not find support for this model in the middle Florida Keys. However, additional models might offer a better explanation. The Disturbance Cascade model suggests that corals that have higher structural complexity and that have higher protection from damage would be better able to support the herbivorous organisms around them and lead to lower macroalgae abundance (Chapter 1 – Figure 1.6). The Nutrient Cascade model suggests that changes in the nutrient concentration of the environment would alter abundances of macroalgae, which would drive the distribution of herbivores (Chapter 1 – Figure 1.6). In areas where nutrients were lower in concentration and more balanced, macroalgae not be over abundant and coral fragments would be more successful. Future research will be conducted to test these models to determine if they can better explain the reasons for the variation in the success of coral transplants. With the identification of the sites where these transplants are more successful, I can ensure that the conservation efforts being applied to these ecosystems are also successful.

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CHAPTER FOUR

CONCLUSIONS

Coral reefs are important marine ecosystems. They provide nurseries and protection for thousands of organisms including 4,000 species of fish and thousands of invertebrates (Reaka-Kudla et al. 1996). They support global economies through tourism and commercial fisheries (Costanza et al. 1998). They also provide structural protection to coastal regions around the world by absorbing energy from storms and decreasing shore erosion (Lugo et al. 2000).

Coral reefs have experienced a drastic reduction in coral cover worldwide since the 1970s (Bellwood et al. 2004, Jackson et al. 2014). Many studies have suggested that an increase in the abundance of competitive macroalgae species is a major contributing factor in the decline in coral cover (Tanner 1995, Lirman 2001, McCook et al. 2001, Jackson et al. 2014). Macroalgae compete with corals for nutrients, light, and settlement space and have a much faster growth rate (Tanner 1995, Lirman 2001, McCook et al. 2001). Macroalgae lack the structural complexity of coral reefs and are not capable of supporting the vast amount of biodiversity found in coral reef communities (Mumby and Steneck 2008).

A reduction in herbivores has been found to play a major role in the increase of macroalgae (Lewis 1986, Hughes et al. 1987, Lirman 2001, Mumby et al. 2006). Reefs throughout the Caribbean have seen declines in the populations of important herbivores such as urchins and parrotfishes due to disease and overfishing, respectively (Jackson et

al. 2014). In the absence of herbivores, macroalgae has grown unregulated and out-competed corals. These previous studies suggest that herbivores play a detrimental role in determining patterns in coral cover. This Herbivory Cascade (Chapter 1 – Figure 1.2) predicts that as herbivore abundance increases, macroalgae abundance will decrease and coral cover will increase (Hoey and Bellwood 2011, Jackson et al. 2014). Overfishing of parrotfish has been correlated with an increase in macroalgae due to a reduction in the grazing pressure on macroalgae (McManus et al. 2000). This has led to a call for an increase in Marine Protected Areas (MPAs) which have been shown to increase the biomass of herbivorous fishes (Bellwood et al. 2004, Mumby and Steneck 2008, Hughes et al. 2010) Therefore, the Herbivory Cascade model predicts that as sites move from being overfished to a protected status, parrotfish abundance and grazing would increase, macroalgae percent cover would decrease and coral percent cover would increase (Chapter 1 – Figure 1.2).

In my thesis research, I tested the predictions of the Herbivore Cascade model that parrotfish biomass drives a trade-off between macroalgae cover and coral cover. I did not find a significant negative relationship between percent macroalgae cover and total parrotfish biomass (g/m^2) across 32 reef sites in the middle Florida Keys (Chapter 2 – Figure 2.8). I did not find evidence that coral cover was negatively correlated with macroalgae cover (Chapter 2 – Figure 2.9) or positively correlated with parrotfish abundance across these reef sites (Chapter 2 – Figure 2.10). I also did not find evidence of a competitive interaction between coral and macroalgae when macroalgae density was

manipulated for one year in the presence and absence of parrotfish herbivory (Chapter 3 – Figure 3.5).

I did, however, find that reefs in the middle Florida Keys differ in their community structure, substrate composition, depth and habitat complexity and that these different reef types may have been differentially influenced by parrotfish herbivory. I found that reefs in the middle Florida Keys can be divided into four distinct types, Boulder, Patch, Shelf and Artificial (Chapter 2 – Figure 2.6). Boulder reefs have large reef structures with high structural complexity. These massive coral heads can reach up to 3 m high. Boulder reefs tend to have high coral cover and high macroalgal cover. Patch reefs are isolated by sand patches and have high coral cover with low macroalgal cover. Shelf reefs are continuous with low structural complexity. On these reefs, coral cover is low and macroalgal cover is high. The fourth reef types are the Artificial reefs where both coral and macroalgal cover is low (Chapter 2 – Figure 2.7).

Within these reef types, I did not find strong evidence of parrotfish and macroalgae impacting coral cover, as the Herbivore Cascade model predicted. My results show that percent coral cover is not affected by percent macroalgae cover but coral cover does differ between the four reef types. The relationship between coral and macroalgae also differs between these four reef types. In Patch reefs I found a negative relationship between macroalgae abundance and coral cover but this relationship was not consistent for all reef types. Generalized linear models revealed that parrotfish abundance did not affect macroalgae abundance when reef type was accounted for. The positive relationship

between these two variables for all sites was not found within any of the reef types. I did not find significant effects of parrotfish abundance on coral cover in Patch, Shelf, or Boulder reefs. In Artificial reefs I found a significant negative relationship between parrotfish abundance and coral cover. Although the predicted relationships between parrotfish, macroalgae and coral were found for specific reef types, they were not supported by all the reefs throughout the middle Florida Keys suggesting that top-down effects of parrotfish grazing do not always drive the abundance of macroalgae and coral as suggested by the Herbivory Cascade model.

The distinction of different reef types may play an important role in the future of coral reef research and conservation strategies (Adam et al. 2015, Jouffray et al. 2015). These reefs are classified by their species composition and complexity and show different levels of degradation. Some reefs have high coral cover and complexity with high macroalgae cover while others have extremely low coral cover and abundant macroalgae. The identification of these reef types suggests that there are major differences between these reefs and these organisms may respond differently to different biotic factors depending on their species composition and history (Jouffray et al. 2015).

Many researchers have put their efforts towards transplanting coral fragments in hope of restoring these degrading coral reef ecosystems (Edwards and Clark 1999). In attempts to determine if the Herbivore Cascade model best explains the variation in the success of transplanted coral fragments, I manipulated the density of macroalgae in the presence and absence of herbivores using an herbivore exclusion study. I transplanted 84

fragments of two coral species and exposed them to varying abundances of macroalgae. Half of the cages were closed to exclude herbivores, while the other half were left open. I did not find significant differences in coral growth or susceptibility to macroalgae between the two species of coral. Corals are slow growing species and I may detect changes in their growth over a longer monitoring period. I did, however, find a significant effect of month and site on the abundance of macroalgae on the substrate surrounding the coral fragment. This result suggests that changes in substrate community and how they differ between the reef types could help us understand if the Herbivore Cascade model or an alternative model best explain the variation in the success of coral transplantation projects.

FUTURE DIRECTIONS

Biodiversity in the Florida Keys has been declining over the previous four decades ((Precht and Miller 2007). Reefs have experienced a reduction in top predators and herbivores, such as urchins, due to overfishing and disease (Toth et al. 2014, Alevizon and Porter 2015); an increase in macroalgae abundance (Jackson et al. 2014); and a reduction in coral cover over the past four decades (Pandolfi et al. 2003, Jackson et al. 2014). However, unlike other regions throughout the Caribbean, parrotfish densities have remained at or above the Caribbean wide average during this period of rapid reef decline (Jackson et al. 2014, Alevizon and Porter 2015). Furthermore, there is no evidence of increased coral recruitment, increased coral growth, decreased macroalgae, or increased parrotfish herbivory in the Marine Protected Areas of the Florida Keys as

predicted by the Herbivore Cascade model (Kramer and Heck 2007, Toth et al. 2014). The results from this study also did not find support for the Herbivore Cascade model. Researchers are unsure of the factors driving the decline in coral cover and how various factors in coral reef communities interact to alter patterns in coral cover and community structure (Precht and Miller 2007).

While the Herbivore Cascade model and the strong impacts of herbivores on coral reef communities have been supported on reefs throughout the Caribbean, it may not explain the decline in coral cover in other regions. The Disturbance Cascade model (Chapter 1 – Figure 1.6) suggests that corals are the driving factor in structuring these communities. Corals provide structural complexity that serves as nurseries for juvenile marine organisms and refuge from predators (McCormick 1994, Graham and Nash 2013). With this support to their populations, these organisms would be better able to graze on macroalgae and other substrate competitors and contribute to the success of corals (Dixson et al. 2014). According to this model, coral cover would be higher in areas where disturbance from storms or direct contact from humans is reduced. The Nutrient Cascade model (Chapter 1 – Figure 1.6) predicts nutrients and macroalgae abundance may be the factors driving the coral community structure. In environments where essential nutrients used for primary production are in higher concentrations, macroalgae cover would be abundant (Burkepile and Hay 2006). This availability of food for herbivores would attract herbivores that would excrete more nutrients, contributing to the high nutrient concentrations and further increase macroalgae abundance (Burkepile et al.

2013). This increase in competition would cause coral cover to be extremely low due to its inability to compete with the extremely abundant macroalgae.

A recent review by Adam et al. (2015) suggests that the differences between reef types may determine which of these factors (coral, macroalgae or herbivores) has the strongest influence on structuring coral communities. They acknowledge that reef ecosystems may have declined due to specific factors but that different factors may be limiting the recovery of these reefs. They also discuss that these factors may be different based on the scale the reefs are compared (Adam et al. 2015). This idea suggests that macroalgae may be the main factors driving the community structure on that specific reef while on other reefs, coral structure or herbivore grazing may be the driving factor.

The results from my master's research seem to support this idea that the model that best explains the variation in coral cover on the reefs of the middle Florida Keys may differ based on the reef type. I identified four distinct reefs types based on the substrate composition, depth and habitat complexity. These reefs differed in the abundance and species composition of macroalgae, coral and parrotfish. If one of these factors was the driving force behind structuring the reef community, I could explain why I did not find strong significant relationships between parrotfish abundance, macroalgae abundance and coral cover that were consistent with the Herbivore Cascade model. In my future dissertation research, I will use the difference in reef types to test the different models that have been proposed to explain the variation in coral cover observed in the middle Florida Keys. These models include Herbivory Cascade (driven by parrotfish abundance),

Disturbance Cascade (driven by changes in coral cover and complexity), Nutrient Cascade (driven by changes in nutrients altering macroalgae growth) and the idea that the model depends on the community composition or reef type. In order to determine which of these models best explains the interactions between parrotfish, corals and macroalgae at each reef type, I will use Structural Equation Modeling (SEM). Structured Equation Modeling is a modeling technique that would allow me to use path analysis to better understand how the factors in these ecosystems interact to impact coral cover (Kline 2011). This modeling technique would allow me to estimate the impact of each of these factors on coral reef community structure and determine which model best fits the patterns I detect in each reef type in the middle Florida Keys.

In my future work I also will observe parrotfish grazing behavior to determine if they display dietary preferences and if these differ between parrotfish species. Previous studies have determined that parrotfish differ in their grazing behavior, as well as their impact on coral reef ecosystems. Parrotfish can be categorized into three functional groups based on their grazing activity (Cardoso et al. 2009, Jouffray et al. 2015). These groups include Browsers, Scrapers, and Grazers and each have positive effects on coral growth. Browsers feed primarily on fleshy algae species, reducing their abundance and competition with corals. Grazers consume mainly turf algae that occupy important settlement space on the reefs. Scrapers generally feed on turf algae as well but excavate the substrate in the process, providing new settlement space for coral polyps. By breaking the parrotfish biomass into these three groups, I may be able to determine if these groups differ in their impact on macroalgal abundance and coral cover. By determining the

impacts of specific species on reef communities and how their abundance changes over time might help us understand the impacts on future conservation.

There have also been studies that look at differences in the dietary preferences of individual species of parrotfish (Burkepile 2012). In a study in the upper Florida Keys, Burkepile used Strauss' Selectivity indices to determine if parrotfish species showed dietary preferences towards specific substrate types. He found that not only do parrotfish species differ in their preferences, but that they take noticeable bites out of coral. He also found that parrotfish species prefer specific species of coral over others.

This study sheds a new light on parrotfish as grazers. Burkepile's results suggest that parrotfish may have a direct negative impact on coral cover as corallivores, or coral eaters (2012). If these parrotfish are showing dietary preferences towards corals, their grazing could be contributing to the decline in coral cover. Differences in grazing behaviors between species suggest that the composition of parrotfish that inhabit each reef is important in order to understand the impacts these parrotfishes have on existing corals and transplanted coral fragments.

Although threats have devastated many reefs around the world, certain reefs are still healthy and fully functioning. The question scientists now ask is what characteristics allow these select reef ecosystems to remain more resilient to the world's drastic changes (Mumby and Steneck 2008). Studying the interactions taking place between the organisms inhabiting these reefs, including the coral themselves, competitors and predators would

provide information about their resilience and resistance. The knowledge gained from this could then be applied to conservation efforts on struggling reefs around the world.

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