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Cryptic Herbivorous Invertebrates Restructure the Composition of Degraded Coral Reef Communities in the Florida Keys, Florida, USA

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**CRYPTIC HERBIVOROUS INVERTEBRATES RESTRUCTURE THE COMPOSITION
OF DEGRADED CORAL REEF COMMUNITIES IN THE FLORIDA KEYS, FLORIDA,
USA**

by

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B.S. May 2010, Old Dominion University

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ABSTRACT

CRYPTIC HERBIVOROUS INVERTEBRATES RESTRUCTURE THE COMPOSITION OF DEGRADED CORAL REEF COMMUNITIES IN THE FLORIDA KEYS, FLORIDA, USA

Angelo Jason Spadaro
Old Dominion University, 2019
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Coral reefs have been on a trajectory of decline for nearly a century due to a variety of factors that have contributed to the shift in these communities away from dominance by reef-building corals, with commensurate changes on community composition and function. Florida's reefs are a compelling example of a degraded system that has undergone a phase shift, and thus offered an excellent model system for my study of the effects of grazing by cryptic herbivores on community composition and their potential restoration value. I had four major objectives: (1) determine the suitability of *Maguimithrax spinosissimus* for manipulating grazing intensity on reefs (Chapter 2); (2) test the effect of increasing *M. spinosissimus* density on the abundance and distribution of macroalgae (Chapters 2 & 3); (3) test the effect of enhanced grazing and reduced algae cover on composition of the reef fish community (Chapter 2 & 3); and (4) compare the grazing of multiple species of Mithracid crabs with that of *M. spinosissimus* (Chapter 4).

I found that *M. spinosissimus* are amenable to density manipulation and, at sufficient density, their effect on benthic macroalgae is deleterious. *M. spinosissimus* exhibited a high degree of philopatry on patch reefs, and that crabs >30mm carapace length reach a size refuge from predation and experience lower mortality. Reef fish abundance and species richness were also greater on reefs with high crab density than on controls. Manipulated reefs had higher densities of juvenile corals than did controls. This study is uncommon in that I replicated the experiment at another location and time. Those results (Chapter 3) confirmed those described in Chapter 2 and demonstrate the broader applicability of my findings.

In Chapter 4, I describe an experiment where I discovered that *M. spinosissimus* consumed more algae than any of the three other species of *Mithraculus* tested; but, when scaled for biomass, the relationship was reversed. There was no effect of multiple individuals on algae consumption except in treatment groups that included both Mithracid genera. These studies demonstrate the potentially transformative, and often overlooked, effect of cryptic invertebrates on patterns of reef community composition and function.

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This dissertation is dedicated to my amazing wife, Dr. Abigail Spadaro, and to my wonderful parents, Angelo and Lorrie Spadaro. Without your constant and unwavering support, this document and the endless hours of hard work that went into it would not have been possible.

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CHAPTER 1

INTRODUCTION

Recently, a previously unknown vast coral reef ecosystem in the alluvial plume of the Amazon river delta off the east coast of Brazil was discovered (Moura et al. 2016). The significance of such discoveries is troubling, considering the accelerating rate at which biological and ecological diversity are lost across the globe (Smith et al. 1993; Bradshaw et al. 2009). The decline of species, habitat, and communities to natural disasters, anthropogenic disturbance, global climate change, or any number of stresses threatens global biological and ecological diversity (Brooks et al. 2002; Cardinale et al. 2012). On one hand, there is an intrinsic value to the diversity of life on earth that need not carry with it a price tag; species have value because they are a living record of life on our planet (Ghilarov 2000; Justus et al. 2009). On the other hand, there is a very real and substantial economic value to biological and ecological diversity (Edwards and Abivardi 1998; Pearce and Moran 2013; Costanza et al. 2014). Many nations still rely heavily on foraging and hunting to feed their people (Svizzero and Tisdell 2015). For example, the economies of most tropical island nations are almost entirely reliant on thriving coral reef ecosystems (Spurgeon 1992). Coral reefs buffer the wave energy of storms and hurricanes (Moberg and Folke 1999; Kunkel et al. 2006), provide food to local communities, and are drivers of the tourism industry (Brander et al. 2007). In addition, chemical compounds found in or produced by marine plants and animals harbor untold value as pharmaceuticals for humans (Burton et al. 1992; Barbier and Aylward 1996; Erwin et al. 2010). The cost of lost biodiversity, such as that on coral reefs, to humanity is difficult to measure but would severely compromise

the security of human communities and the global economy will suffer greatly as these resources are lost to posterity (Díaz et al. 2006; Cardinale et al. 2012; Ceballos et al. 2015).

The value of maintaining and protecting biological diversity goes far beyond simply saving species from extirpation (Humphries et al. 1995). The loss of one species results in a reduction in the function it plays within a community that results in the competitive release of other species, in turn, increasing competitive interactions with other species and so on (Sanders et al. 2018). Further, the loss of species and their function in the community may have far-reaching effects in terms of energy transport, larval supply, nutrient cycling, and other biogeochemical processes (Loreau et al. 2001; Díaz et al. 2006; Hooper et al. 2012; Ceballos et al. 2015). Such disturbances can extend far afield and into the future, so the value of biodiversity is not restricted to its immediate spatio-temporal context (Edwards and Abivardi 1998). The loss of biological and ecological diversity on Earth is a global challenge and one that must ultimately be dealt with cooperatively on a global scale.

In tropical seas, there is perhaps no more important example of the need for cooperative international management than that for coral reef ecosystems. Most hermatypic (i.e., reef-building) corals are broadcast spawners with pelagic larval development of a few weeks. Although considerably shorter than that of other species such as fishes and spiny lobsters, larval residence time in the plankton can still result in sufficient larval dispersal to create coral reef systems that span multiple national coastlines (e.g., Great Barrier Reef, Mesoamerican Barrier Reef) (Van Woesik et al. 2006). However, after dispersal, coral larvae must ultimately encounter appropriate habitat in which to settle, survive, and eventually contribute to coral reef communities as spawning adults. Thus, in addition to understanding larval connectivity it is imperative that we ensure the quality of coral reef benthic habitats for their persistence.

Coral reefs, around the globe, have been in decline for over a century (Hodgson 1999; Gardner et al. 2003; Pandolfi et al. 2003; Carpenter et al. 2008). The synergistic effects of global climate change (e.g., rising sea surface temperature, ocean acidification, increasing frequency and severity of major storms), coastal development and eutrophication, gross overfishing, disease pandemics, and many more acute local and regional disturbances have all resulted in a ubiquitous decline in both the biological and architectural complexity of these ecosystems (Gardner et al. 2003; Hughes et al. 2003; Bellwood et al. 2004; Gardner et al. 2005; Meissner et al. 2012). Major coral bleaching and mortality events are becoming more frequent and more severe as we approach the second decade of the twenty-first century (Nyström et al. 2000; Pandolfi et al. 2003). The loss of living coral not only provides the conditions necessary for immediate shifts in the composition of these reef communities, it also strengthens this trend by increasing nearest-neighbor distances among coral colonies and increases the likelihood of recruitment failure due to strong Allee effects (Hughes 1994; Gardner et al. 2003; Hughes et al. 2007; Mumby et al. 2007; Williams et al. 2008; Van Woesik and Jordán-Garza 2011). Globally, but particularly in the Caribbean region and Florida Keys, there has been a major shift away from the typical reef community dominated by living scleractinian corals to one increasingly dominated by sponges, octocorals, rubble, and fleshy macrophytes – none of which contribute to the biogenic accretion of the carbonate reef matrix (Hughes and Tanner 2000; Bruno et al. 2009; Kennedy et al. 2013). The shift in these communities away from reef-building species can lead to major cascading effects on not just the composition of the ecological community, but also on the function of these systems – both ecological (e.g., nutrient cycling, carbon sequestration, sediment stabilization) and socio-economic (e.g., decreasing fisheries productivity, waning capacity for ameliorating wave energy, losses in tourism rates and revenues) (Kennedy et al. 2013).

A number of measures have been taken to protect, manage, and restore these imperiled ecosystems from continuing degradation and eventual collapse. For example, marine protected areas and national sanctuaries encompassing coral reefs have been established worldwide in an effort to limit destructive anthropogenic activities and to protect reproductive stocks to promote the “spill-over” of larvae into surrounding areas (Gubbay 1995; Edgar et al. 2007).

Unfortunately, with few exceptions, these marine protected areas are far too small, too few, and often are too remote to be effective as significant sources of larval spill-over (Selig and Bruno 2010).

A great deal of effort around the world has also been, and continues to be, invested in direct restoration of coral reef habitat by enhancing the abundance of living scleractinian coral colonies on reefs through transplantation (i.e., coral gardening; *sensu* Rinkevich 1995). Production of living corals for restoration is generally carried out with either sexually- or asexually-propagated corals that are then grown out *in-* or *ex situ* in coral nurseries. Asexual propagation of corals is by far the most common technique because it is logistically simple, can be done year-round, and has proven reasonably successful - especially for branching species (e.g., *Acropora* spp., *Porites* spp.) that naturally rely primarily on asexual reproduction (Rinkevich 1995; Oren and Benayahu 1997; Rinkevich 2005; Shafir et al. 2006). A disadvantage of this technique is that asexual recruits are, by definition, genetic clones rather than the recombinant genotypes produced by sexual propagation. For species that primarily reproduce sexually, laboratory-intensive larviculture methods have recently been developed in which coral gametes are collected in the field and then transferred to the laboratory where fertilization takes place and the resultant larvae then settle and are grown to an appropriate size before transplantation back into the field (Rinkevich 1995, 2005; Young et al. 2012; Guest et al. 2014; Barton et al. 2015). A major bottleneck to this method is not only a relative paucity of spawning

stock on many reefs but also the infrequency – often only annually – of natural spawning events (Ritson-Williams et al. 2009).

Most coral restoration efforts thus far have also concentrated on fast-growing “weedy” coral species (e.g., *Acropora* spp.) that were once ubiquitous reef-builders in the Caribbean. Branching corals have been out-planted onto Caribbean reefs by the tens or hundreds of thousands over the last quarter century with mixed results (Lirman and Schopmeyer 2016). Persistent and pervasive stresses have kept their biomass low on Caribbean reefs despite such concerted efforts to increase their live cover and abundance (Miller et al. 2016). Recently, restoration programs in the Caribbean have begun turning to slower-growing, but hardier massive-form coral genera (*Montastraea*, *Orbicella*, *Colpophilia*, *Diploria*, and *Pseudodiploria*) via a process called microfragmentation (Page et al. 2018). For this method, coral fragments are cut from a parent colony into much smaller pieces than used in asexual restoration methods, down to the size of a single corallite (Page et al. 2018). These microfragments grow substantially faster than larger fragments, larvicultured sexual recruits, and natural coral recruits (Forsman et al. 2015; Page et al. 2018). Thus, replacing a large, dead coral head with living coral may take years using microfragment transplants rather than the decades or centuries required for larger fragments or naturally recruiting corals (Page et al. 2018). The long-term goal of coral restoration programs is to bolster spawning stocks and increase larval supply, but to be effective there must be appropriate settlement habitat for larval settlers and young coral recruits.

The provision of appropriate habitat for coral recruits (and mature corals) is imperative to the long-term success of coral restoration programs and to the persistence of coral reefs as a functioning biogenic structure. Prior to the industrial revolution, coastal seas supported abundant and diverse fish communities, but after the adoption of more efficient fishing technologies, humans substantially reduced the abundance and diversity of large predatory and herbivorous

fishes (Jackson 2001; Stallings 2009). As industrial fishing further reduced the numbers of large fishes in coastal seas, local and artisanal fishermen began targeting herbivorous fishes (Koslow et al. 1988). In the Caribbean, this removal of herbivorous and predatory fishes released the long spine sea urchin, *Diadema antillarum*, from predatory and competitive pressures (Jackson 2001). The resulting population boom in *Diadema* filled the functional void left by the removal of herbivorous fishes. However, a disease pandemic swept through the Caribbean in the early 1980s resulting in the near extinction of *D. antillarum* and, *ipso facto*, a dramatic decline in grazing intensity on Caribbean reefs (Lessios et al. 1984). Shortly after the mass mortality of urchins, macroalgae proliferated on Caribbean reefs highlighting the importance of top-down regulation (Liddell and Ohlhorst 1986; Carpenter 1988; Hughes 1994). The functional extinction of *D. antillarum* certainly contributed to the Caribbean phase shift from a system dominated by scleractinian corals to one typically dominated by fleshy macroalgae, but it was likely only one of multiple proximate and chronic causes.

Nutrification of coastal seas is ubiquitous in areas with dense coastal human populations or when adjacent to agricultural watersheds (Bell 1992; Lapointe and Clark 1992; Lapointe 1997; Small and Nicholls 2003; Lotze et al. 2006). Nitrogen and Phosphorous are often the limiting nutrients in algal growth and are often found in high concentrations in runoff from anthropogenic sources (Lapointe and Clark 1992; Lapointe 1997). There is a large body of literature suggesting that nutrient enrichment of coastal waters is a driving factor in the proliferation of fleshy benthic macroalgae (see Littler and Littler 1984; Birkeland 1987; Steneck and Dethier 1994). However, there is discord in the literature about the relative importance of coastal nutrient enrichment as a causative agent in coral-algal phase shifts. There is a growing body of literature that suggests that anthropogenic nutrient enrichment is not the mechanism by which algae proliferate on coral reefs (see McCook 1999; Szmant 2002). Szmant and Forrester

(1996) suggest that the Florida reef tract, though close to land and coastal waters with higher than normal nutrient (N and P) concentrations, are largely influenced by upwelling as a nutrient source rather than anthropogenic nutrient enrichment. In fact, up to 30% of the nitrogen on Florida's coral reefs probably comes from nutrient-rich deep oceanic waters that are thrust upon reefs by internal waves (Leichter et al. 2003). Chiappone (1996) found the highest algal cover along the Florida reef tract to be on offshore reefs and very low algae cover and high coral cover on nearshore patch reefs suggesting that land-based nutrient enrichment was not driving the distribution and abundance of algae. In a recent study, Shantz et al. (2015) suggest that nutrient enrichment via dense fish aggregations leads, to higher grazing rates and lower algal abundance. Indeed, it has been suggested that nutrient enrichment actually makes algae more palatable to herbivorous reef fishes and thus, subject to higher grazing rates (Shantz et al. 2017). The notion that anthropogenic nutrification of coastal waters is a major driving factor in the proliferation of benthic macroalgae on coral reefs is predicated on the assumption that reef algae normally occur in nutrient depauperate waters, but this assumption applies only to very few reef systems and reef types – mostly isolated atolls – and thus, is a poor predictor of the distribution and abundance of benthic macroalgae and coral-algal phase shifts (McCook 1999; Szmant 2002).

Coral mortality is an obvious symptom of coral reef degradation and often is followed by an increase in macroalgae in the absence of high grazing intensity. Coral mortality is driven by a number of proximate mechanisms. Climate change has been implicated in the elevated extinction risk of more than 33% of reef-building coral species (Carpenter et al. 2008). Rising sea-surface temperatures and increasingly acidic waters due to climate change have resulted in increasingly frequent global mass-bleaching and mortality events which often lead to coral-algal phase shifts (Hoegh-Guldberg 1999; Hughes et al. 2003; Hoegh-Guldberg et al. 2007; Baker et al. 2008). Such chronic global climatic stresses are likely synergistic with local effects such as hurricanes

(Rogers 1993; Hughes 1994; Gardner et al. 2005), ship groundings (Riegl 2001; Negri et al. 2002; Jones 2007), anchor damage (Davis 1977; Dinsdale and Harriott 2004), destructive fishing practices (Saila et al. 1993; McManus et al. 1997; Edinger et al. 1998), and coral disease (Bruno et al. 2007; Weil et al. 2006; Harvell et al. 2007). Each of these stresses is capable of driving coral mortality events and precipitating phase shifts of coral reef communities, but it is likely that coral reef degradation and phase shifts are driven by multiple interacting stressors and their cumulative or synergistic effects (Hughes and Connell 1999; Porter et al. 1999; Burkepile and Hay 2006; Ban et al. 2014). The most parsimonious explanations of coral-algal phase shifts include a reduction in herbivory as a contributing catalyst of change in reef communities (Hughes et al. 2007; Ledlie et al. 2007; Vergés et al. 2014).

Recent geological evidence suggests that the carbonate accretion rates (i.e., reef-scale growth of a coral reef community) of Caribbean reefs are directly related to and potentially driven by the abundance and richness of parrotfishes (Scaridae) (Cramer et al. 2017). However, using a series of spatially-explicit simulation models, Mumby (2006) suggested that while the exploitation of herbivorous fishes (primarily parrotfishes) on extant Caribbean coral reefs contributes directly to coral-algal phase shifts, an unfished parrotfish community cannot maintain a reef in a low algal condition on its own. He asserts that only when urchins (particularly *Diadema antillarum*) and parrotfishes are both abundant is their combined grazing sufficient to maintain a reef in a grazed, low-algal-cover condition. Burkepile and Hay (2011) also emphasized the importance of herbivore identity in grazing, presenting evidence that slight differences in morphology and behavior among species and ontogenetic phases of reef herbivores leads to differences in their functional role on coral reefs. There is also a context-dependent component of an herbivore's functional role on reefs – herbivores, particularly in high-diversity systems such as coral reefs, often play different functional roles depending on the

composition of the community and on habitat complexity (Bonaldo and Bellwood 2008). Because over-fishing has reduced the abundance and richness of large herbivorous fishes and disease has resulted in the functional extinction of *D. antillarum*, grazing on Caribbean reefs is now largely restricted to small-bodied herbivores. Indeed, on Panamanian reefs, the parrotfish, *Scarus iseri*, and the urchin, *Echinometra viridis*, both diminutive small-bodied herbivore species, have filled the functional void left by large parrotfishes and *D. antillarum* with abundances approaching historic biomass estimates of these larger herbivores (Kuempel and Altieri 2017). Each of these studies suggests the value of a diverse and abundant community of herbivores in mitigating the type of degradation and community shifts that have occurred on Caribbean coral reefs.

Over the last three decades, the necessity of protecting, managing, and restoring grazing function to Caribbean coral reefs has come into sharp relief (Adam et al. 2015; Suchley and Alvarez-Filip 2017). A number of studies have highlighted the importance of protecting herbivorous fishes from exploitation – either directly or as bycatch - to preserve their critical function on reefs (Lewis 1986; Mumby 2006; Hughes et al. 2007; McClanahan et al. 2011). Indeed, legislative protection of parrotfishes in the Caribbean has increased their biomass in some areas primarily through a shift in size structure toward larger individuals, but their abundance has not significantly changed and neither has their effect on benthic algae (O’Farrell et al. 2015). Mirroring the conservation of corals, many scientists and managers have embraced active measures to restore grazing on Caribbean reefs, nearly all focused on rebuilding *D. antillarum* populations. Several small-scale studies have demonstrated that transplanted urchins rapidly reduce the cover of benthic macroalgae on degraded reefs resulting in increased coral recruitment (Macía et al. 2007; Myhre and Acevedo-Gutiérrez 2007; Burdick 2008). But scaling up those results has been hampered by difficulties in the development of reliable culture

protocols for producing aquacultured urchins and high post-transplant mortality (Nedimeyer and Moe 2006). In addition, high urchin densities such as those present on Caribbean reefs prior to the regional disease pandemic can also negatively affect coral recruitment (Sammarco 1980). When urchins are dense, their heavy grazing removes not only benthic algae but also newly settled coral recruits (Sammarco 1980). The same has been suggested of large-bodied parrotfishes when they are unusually dense (Mumby 2009a).

Yet another candidate for coral reef restoration aimed at mitigating algal dominance of degraded Caribbean coral reefs was identified in 2012 (Butler and Mojica 2012): a large herbivorous crab, *Maguimithrax spinosissimus* (formerly *Mithrax/Damithrax spinosissimus*). *Maguimithrax* is the largest brachyuran crab in the Western Atlantic (Rathbun 1925) and consumes a variety of types of macroalgae at rates that equal or exceed those of parrotfish (Butler and Mojica 2012). Although the crabs typically occur on reefs at low abundance (<0.01 crabs/m²), Butler and Mojica (2012) suggested that the species life history characteristics (e.g., short larval duration, rapid growth, site fidelity) make it a good candidate for aquaculture and stock-enhancement on reefs to help reduce algae on reefs.

The basis of my dissertation expands upon the work of Butler and Mojica (2012) and tests the hypothesis that increasing the density of this cryptic invertebrate grazer on degraded reefs will significantly reduce the cover and abundance of benthic macroalgae with positive effects on the recruitment of corals and coral-reef associated fishes, hence the maintenance of biodiversity. In Chapters 2 and 3 I tested this hypothesis in two independent year-long field experiments where I manipulated *M. spinosissimus* abundance on some patch reefs but not others, and then quantified algal cover, coral recruitment, and fish community structure. I quantified size-specific mortality of *M. spinosissimus* in the field with a tethering study and also estimated site fidelity of crabs with a tagging study to determine whether *M. spinosissimus* is

amenable to stock enhancement and transplantation; that study is described in Chapter 2. In Chapter 3, I tested with a series of *in situ* observational studies and *ex situ* mesocosm experiments the mechanisms by which enhanced crab density produces cascading effects on reef community composition. Finally, the laboratory experiments presented in Chapter 4 are an investigation of whether functional redundancy or complementarity exist among several species of Mithracid crabs that are common herbivores on Caribbean reefs.

CHAPTER 2

A CRYPTIC, HERBIVOROUS CRAB RESTRUCTURES DEGRADED CARIBBEAN CORAL PATCH REEF COMMUNITIES

2.1 Introduction

Anthropogenic activities have altered coral reefs since at least the industrial revolution. The degradation of coastal water quality, climate change, and over-exploitation of predatory and herbivorous taxa are all symptomatic of the Anthropocene (Jackson 2001; Jackson et al. 2001). The incidence and prevalence of disease has also increased on coral reefs due, at least in part, to the effects of anthropogenic stresses and have wreaked havoc on the biodiversity and trophic structure of reefs, particularly in the Caribbean (Harvell et al. 2004; Bruno et al. 2007; Lesser et al. 2007; Precht et al. 2016). Perhaps best known is the rise in macroalgal cover and associated decline in live coral on Caribbean reefs following the catastrophic mortality of a major herbivore, the long-spine sea urchin, *Diadema antillarum*, to disease (Mumby et al. 2006b, 2007; Lessios 2016). Today, the functional herbivory within many Caribbean coral reefs is significantly degraded (Mumby 2006; Mumby et al. 2006a; Arnold and Steneck 2011) and although once dominated by a diverse assemblage of scleractinian corals, those reefs are now largely barren of live coral (Done 1992; Hughes 1994; Hughes et al. 2007). Many scientists believe that coral reefs exist in one of two stable non-equilibrium states: one dominated by live coral or, alternatively, by fleshy macroalgae (McCook 1999; McManus and Polsenberg 2004; Bellwood et al. 2006). Others contend that the alternate stable states of coral reefs simply reflect a spectrum of coral cover phases, from coral-dominant to coral-depauperate (Mumby 2009b). In either case, there is consensus that the “health” of coral reefs is largely a reflection of the

relationship between live coral cover and the intensity of grazing by reef herbivores, and this is particularly the case in the Caribbean (Hughes et al. 2007; Mumby et al. 2007).

The conspicuous lack of herbivores has left grazing intensity on Caribbean reefs far below historical values (Jackson 2001; Jackson et al. 2001; Mumby et al. 2006a, b). The majority of studies on Caribbean coral reef herbivory have focused on the effects of *D. antillarum* and grazing fishes (e.g., parrotfishes) (Mumby et al. 2006a, b), but Caribbean reefs also harbor a guild of cryptic herbivorous crustaceans whose role in structuring benthic algal communities is poorly understood. In Belize, for example, diminutive spider crabs of the genus *Mithraculus* are responsible for the near exclusion of fleshy macrophytes in back-reef coral communities (Coen 1988a, b). Along the Caribbean coast of Panama, small-bodied herbivores such as the grazing sea urchin, *Echinometra viridis*, and the striped parrotfish, *Scarus iseri*, have become more abundant and account for a large proportion of the herbivore biomass, and thus grazing intensity (Kuempel and Altieri 2017). The conspicuous absence of fleshy macroalgae in shallow nearshore habitats on the opposite coast (i.e., Pacific) of Panama is due to the grazing effects of small-bodied grazing crabs (Menge and Lubchenco 1981; Menge et al. 1986). These and other examples suggest that cryptic species and sleeping functional groups (*sensu* Bellwood et al. 2006) may play a larger functional role than previously imagined in driving patterns of coral reef community assembly, particularly when abundant. The herbivorous Caribbean King Crab, *Maguimithrax spinosissimus*, (Crustacea; Decapoda; Mithracidae; Windsor and Felder 2009, 2014; Klompmaker et al. 2015) may be just such a species.

Maguimithrax spinosissimus is the largest crab in the Western Atlantic with carapace lengths (CL) of up to 180 mm and weighing more than 3 kg (Rathbun 1925; Creswell et al. 1989; Winfree and Weinstein 1989). These large, cryptic spider crabs are broadly-distributed throughout the Caribbean and Gulf of Mexico, dwelling at depths of just a few meters to more

than 200 m (Rathbun 1925; Williams 1965; Provenzano and Brownell 1977). Although common, *M. spinosissimus* is rarely abundant and is the target of only a few, small artisanal and bycatch fisheries in the Caribbean (Hartnoll 1963; Provenzano and Brownell 1977; Guzman and Tewfik 2004). However, the species is considered a promising candidate for commercial mariculture due to its short pelagic larval duration, large adult size, rapid growth, and palatability (Bohnsack 1976; Brownell et al. 1977; Creswell et al. 1989). Although its growth is maximized on an omnivorous diet, *M. spinosissimus* is largely herbivorous (Wilber and Wilber 1989; Winfree and Weinstein 1989; Guzman and Tewfik 2004) and is an effective herbivore with grazing rates exceeding most species of Caribbean parrotfish (Butler and Mojica 2012). Butler and Mojica (2012) suggested that *M. spinosissimus* grazing rates are high enough to substantially influence the abundance and distribution of benthic macroalgae on coral reefs in the Florida Keys (Florida, USA), but their generally low density (~ 0.007 crabs / m^2) precluded strong effects on the community.

My goal in this study was to test experimentally the effect of grazing by these cryptic, herbivorous crabs on the cover of benthic macroalgae on degraded patch reefs in the Florida Keys. I did so by manipulating both the initial amount of macroalgal cover and crab density on discrete patch reefs, then measured changes in benthic macroalgal cover, juvenile coral density, and the composition of the reef fish community for 1-2 years. I also measured the size-specific predation and site fidelity of translocated *M. spinosissimus* on patch reefs; both important metrics for assessing the feasibility of stocking crabs as a potential new tool in the restoration of degraded coral reefs.

2.2 Methods

Study area and general methodology

I conducted this study in the Florida Keys, Florida (USA), a 212 km-long island archipelago offshore of which lies the world's third longest barrier reef system (Fig. 1). In the back-reef lagoon of the Florida reef tract lie thousands of coral patch reefs with coral formations and community assemblages similar to those found throughout the Caribbean (Porter and Meier 1992; Jaap et al. 2003). These patch reefs historically have harbored a diverse community of scleractinian reef-building corals dominated by *Montastraea annularis*, *Colpophyllia natans*, and *Siderastrea siderea* and were reminiscent of the community found on the main off-shore barrier reef tract (Colella et al. 2012). However, following a catastrophic series of cold-stress events in 2010, many of these patch reefs became coral-depauperate and largely dominated by benthic macroalgae, predominantly *Halimeda* spp. (Colella et al. 2012). My field studies were conducted between May 2013 and August 2015 on 12 shallow (Fig. 1; 1.5-7 m depth) patch reefs (mean surface area: 10 m²) situated ~1.5 km offshore of Lower Matecumbe Key (24°50' N; 80°43' W) in the middle Florida Keys near the center of this coral reef ecosystem. I collected *M. spinosissimus* for my experiments from various habitats throughout the Middle and Lower Florida Keys and recorded the collection location as well as the sex and size: carapace width (CW; maximum distance between lateral margins of the carapace) of each crab.

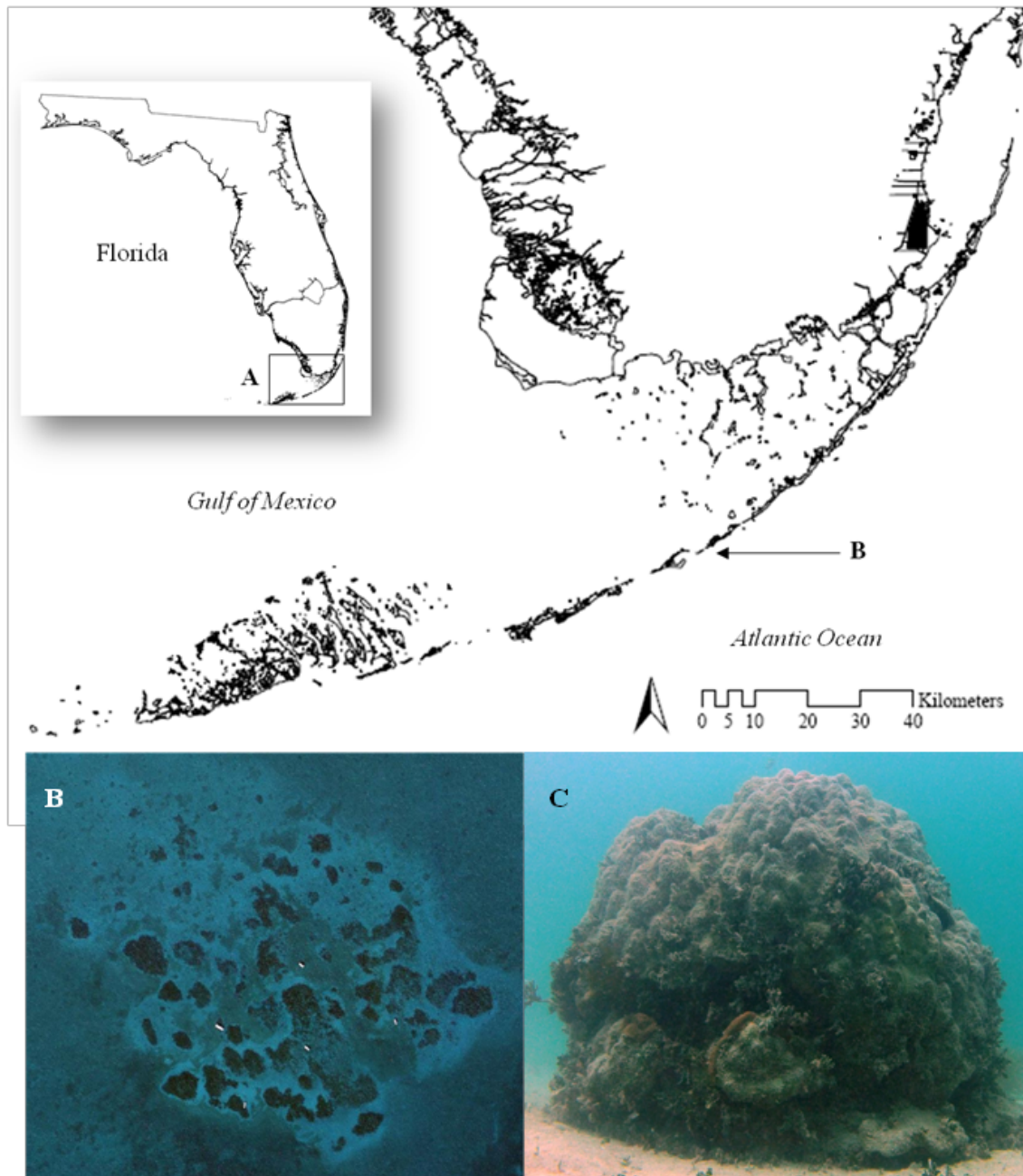


Figure 1. Study site location and photos of patch reefs. Map of Florida, USA (inset top) and the Florida Keys (A in top inset) with location of study area (B; marked by arrow). Satellite photograph (B; bottom left) of study area showing cluster of shallow patch reefs. Underwater photo of experimental patch reef (C; bottom right)

Predation and retention of *M. spinosissimus* on patch reefs in the field

I designed two field experiments to test the suitability of *M. spinosissimus* for *in situ* density manipulation. The first allowed me to estimate size- and sex-specific predation rates in the patch reef environment, whereas the second experiment was designed to test the site fidelity of crabs over 12 mos after being translocated into a coral patch reef habitat.

Predation mortality

Size- and sex-specific predation of crabs was tested in a tethering study. Crabs were sorted by sex and into four size classes (0-29.9, 30-59.9, 60-89.9, 90+ mm CW) and fitted with a monofilament harness (9.1 kg-test for crabs <50 mm CW; 22.7 kg-test for crabs >50 mm CW) with a snap swivel (18.1 kg-test) affixed dorsally to the carapace by a knot and cyanoacrylate gel adhesive. Divers deployed tethered crabs on patch reefs where the crabs were attached by a 1-m long 22.7 kg-test monofilament line to a concrete block shelter, around which the nocturnal crabs could forage. Replicate crabs were deployed a minimum of 5 m apart on each patch reef to ensure independence. The status of tethered crabs was assessed *in situ* by divers after 24 h. Crabs were considered victims of predation based on the condition of the tether and on evidence of the event (i.e., pieces of carapace and/or limbs remaining; Fig. 2). These data were analyzed in a three-way log-linear contingency analysis to determine the effects of size class and sex on crab mortality; subdivision of the data matrix prior to re-analysis (heterogeneity test; Zar 2010) allowed me to determine the effects of specific size classes and sex on mortality.

Crab Retention

To examine site fidelity and retention of crabs on patch reefs following translocation, and to ensure that crab density treatments were maintained through the study's duration (see below), I stocked tagged crabs on 8 coral patches within the study area at a density of 1 crab / m² of surface area and recorded their presence on those patch reefs and on nearby patch reefs periodically for 12 months. Only crabs > 30 mm CW were stocked due to high mortality of smaller crabs (see predation mortality results). Each crab was fitted with a unique color-coded external tag on the last walking leg, and with a colored Visible Implant Elastomer cohort tag (VIE; Northwest Marine Technology, Inc., Shaw Island, WA, USA) in the soft tissue at the insertion of the right cheliped. The VIE tags were best viewed with ultraviolet light under which the VIE tags fluoresce. External tags allowed me to track individual crabs in experiments until the crab molted and the tag lost, whereas VIE tags allowed me to track crabs through successive molts, and thus for the duration of the 12-month crab density manipulation study.

Due to the nocturnal and cryptic nature of the species, surveys of crab abundance were conducted at night by divers at 1 week, 3 weeks, 3 months, 8 months, and 12 months after the release of crabs onto experimental patch reefs. Crabs were not collected or manipulated during these surveys. When possible, the tag ID, sex, and size of crabs observed on the night dives were recorded. Divers searched not only the patch reefs onto which the crabs were stocked, but also nearby patch reefs. Crab density was calculated as the number of crabs observed m⁻² of reef surface area. The effect of experimental treatment through time was analyzed as a model I repeated measures general linear model (GLM). These data did not satisfy parametric assumptions and so were rank transformed prior to analysis. A post hoc Tukey test was used to evaluate homogenous subsets of the treatment factor.

Effect of increased *M. spinosissimus* density on macroalgal cover

I selected 12 coral patch reefs of similar size (range 6 - 18 m² surface area, mean 10 m²) and benthic community structure for use in an experiment testing the effect of crab density and initial macroalgal cover on macroalgal cover through time. Three treatment groups were assigned randomly to these 12 patch reefs by manipulating crab density via stocking and initial algal cover by manual removal of algae from the reefs. Those treatments were: (1) control (natural algal cover and no crabs added), (2) crabs added – no algae removed, and (3) crabs added – algae removed. This non-orthogonal design prevented a statistical assessment of the interaction between crab addition and manual algal reduction (i.e., reef scrubbing) or an independent assessment of the effectiveness of algal reduction alone. However, neither of those was of central interest to this study, and others have already shown the effect of the removal of algae on the abundance of corals on reefs over time (see McClanahan et al. 1994; Burdick 2008). My primary questions in this experiment were: (a) can crabs reduce and maintain macroalgae at low levels if stocked at sufficiently high densities, or (b) must the over-abundance of macroalgae first be reduced before the stocking of crabs is effective at maintaining low macroalgal cover.

Just prior to the stocking of crabs and removal of algae to establish the experimental treatments, ten 1 m² (1 m X 1 m) photo quadrats were taken at locations selected haphazardly on each experimental reef. Each reef was resampled in the same manner approximately monthly for one year. All digital photographs were processed using the Coral Point Count with Excel extensions (CPCe) software package to monitor changes in percent cover of macroalgae (Kohler and Gill 2006) estimated from an overlay of 25 randomly-placed points on each digital photograph. Data from all of the photographs from a single reef during a single sampling event were combined to calculate a mean percent cover of macroalgae for that reef during that sampling period and those data were used to calculate the mean algae cover for each treatment

group. The data violated parametric assumptions of homogeneity of variance and normality, so all data were rank transformed and analyzed in a 2-factor repeated measures general linear mixed effects model (fixed factor = treatment group; repeated measures factor = sampling event; random factor = experimental reef); a post hoc Tukey's test was used to identify homogenous subsets within the results.

Effect of increased *M. spinosissimus* density on juvenile coral density and reef fish community composition

Juvenile Coral Density

Two years after the initiation of my manipulations of crab density and algae cover, I censused each of the 12 experimental patch reefs to quantify patterns in the density of juvenile corals. I defined juvenile coral as any living coral colony visible with < 25 distinct coralites or < 25 mm in its longest dimension. A pair of divers counted and identified (to the lowest possible taxonomic level) all juvenile coral colonies on each experimental reef. I analyzed the relationship between treatment group and coral recruit density (# juvenile corals / m² of reef surface area) using a negative binomial regression with a log-link function within a generalized linear model. Homogenous subsets between and among the treatment groups were analyzed with *a priori* pairwise contrasts.

Reef Fish Community Composition

Shortly after the manipulation of crab density and algae, I observed a qualitative difference in the abundance of fish around reefs of the different treatment groups. I quantified this difference with a census of reef fishes on each experimental reef in August 2013, shortly after treatments were applied, then again in May and July of 2014. For each fish census, a diver

entered the water ~10 m away from the experimental reef and slowly approached each reef along the bottom to a distance of 2 m from the base of the experimental reef. The diver remained as still as possible for a 5 min acclimation period, after which the diver slowly orbited the experimental patch reef, carefully recording each fish observed to species, when possible. I analyzed the effect of treatment group and time on the composition of the reef fish community in a non-parametric (permutation-based) repeated measures MANOVA and visualized that complex set of data using a non-metric multidimensional scaling (nMDS) analysis (Fathom toolbox, Matlab).

2.3 Results

Predation and retention of *M. spinosissimus* on patch reefs in the field

Predation

Between May 2013 and August 2015, a total of 285 (160 male, 125 female) crabs were tethered and 51 of those were confirmed mortalities due to predation (17.9%). The sex of the crab had no effect on mortality ($X^2 = 0.039$, $df = 1$, $p = 0.843$). Size class, however, had a highly significant effect on crab mortality ($X^2 = 28.828$, $df = 3$, $p < 0.0001$),

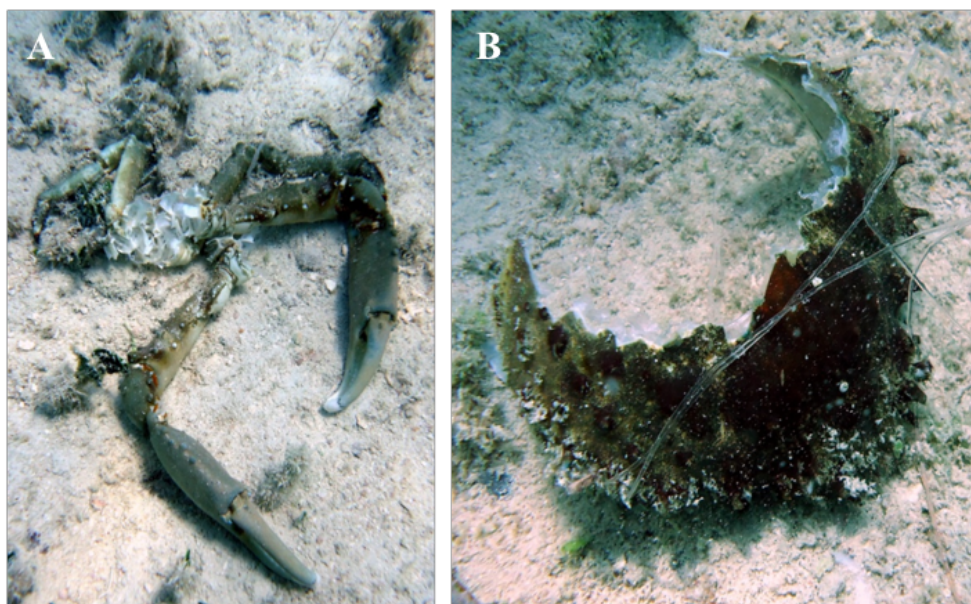
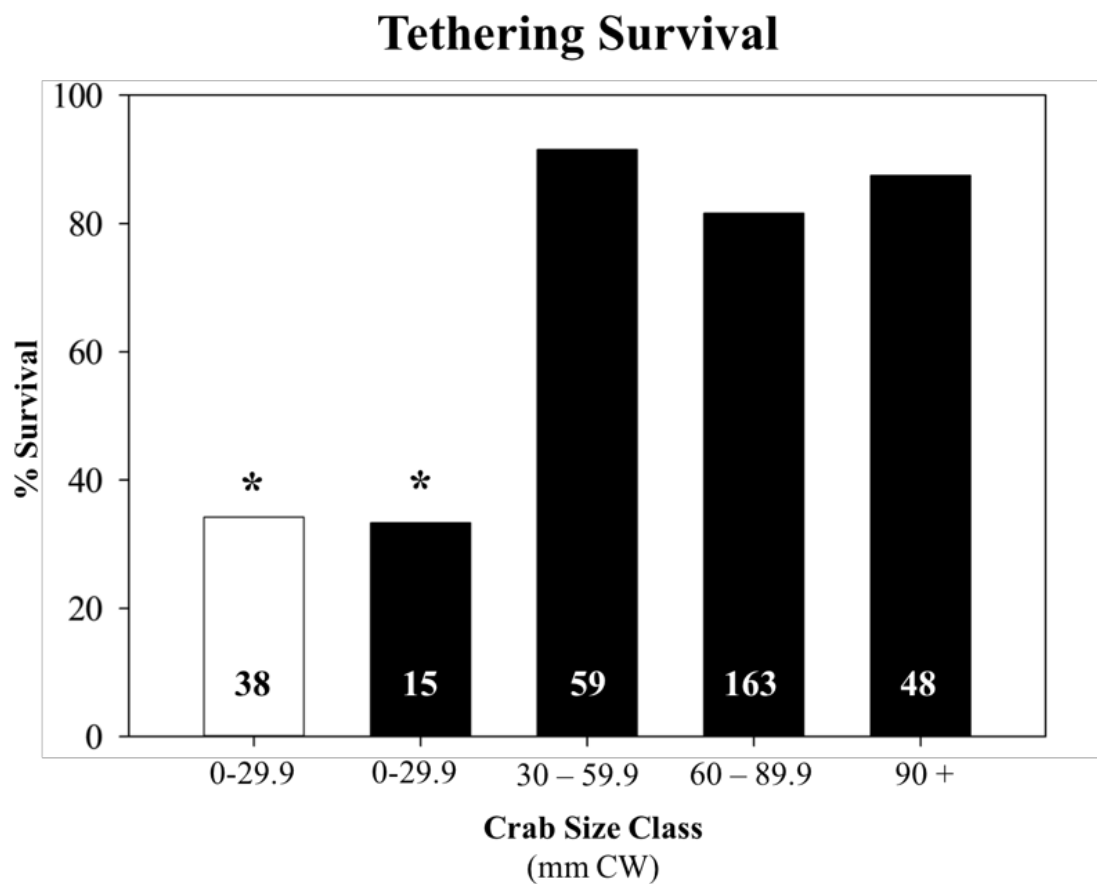


Figure 1. Results of tethering experiment comparing the relative survival of four size classes of *M. spinosissimus* (black bars) and one size class of *M. sculptus* (white bar). Size groups that differed significantly in survival are marked with an asterisk. Typical evidence of predation mortality (photos A and B bottom).

with the smallest size class (<29.9 mm CW) experiencing significantly higher (67%) mortality compared to that of all larger size classes (Fig. 2).

Out of concern that this size-specific difference in crab mortality could be an artifact of sample size (small *M. spinosissimus* < 30 mm CW are difficult to find in nature), in summer 2015 I collected and tethered another 38 (24 male, 14 female) crabs < 30 mm CW of another species of Mithracidae (*Mithraculus sculptus*) that is similar in morphology and behavior to *M. spinosissimus* to serve as a surrogate for very small *Maguimithrax* in assessing size-specific crab mortality. I compared the mortality of *M. sculptus* to that of similarly-sized *M. spinosissimus* but found no significant effect of species on mortality of individuals < 30 mm CW ($X^2 = 0.015$, $df = 1$, $p = 0.903$). Thus, these data were pooled with those of the smallest size class of *M. spinosissimus* and re-analyzed with the other size classes of *Maguimithrax*. Increasing the sample size of the smallest size class of crabs in this manner had no effect on the original results. The mortality of the smallest size class of crabs was still significantly higher than that of larger crabs ($X^2 = 66.281$, $df = 3$, $p = <0.0001$).

Crab retention

A total of 84 tagged crabs were released on eight patch reefs and tended to remain where they were released. Throughout the experiment, crab density remained significantly higher on patches on which crabs were stocked than on those on which no crabs were added (Table 1, Fig. 3). Crab density dropped by 40 – 50% one week after stocking (i.e., a decline from 1 crab / m² to ~ 0.6 crabs / m²), stabilized at ~ 0.4 crabs / m² for 10 months after stocking (until May 2014), then fell again.

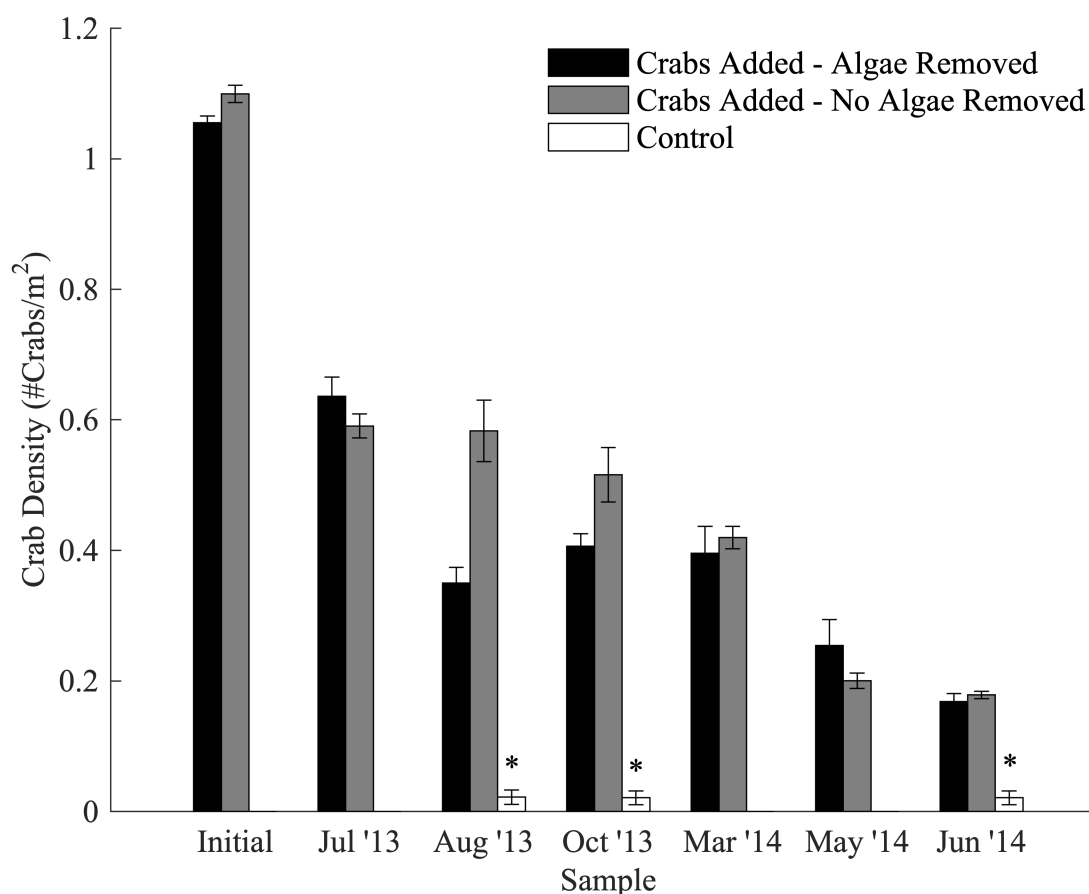


Figure 2. Summary of crab retention study results showing mean crab density (# crabs / m²) in each treatment group when stocked and during six subsequent surveys of crab abundance. Significantly different bars are marked with an asterisk

Effect of increased *M. spinosissimus* density on macroalgal cover

During every sampling event over the year-long study, reefs on which we stocked tagged crabs had significantly greater crab densities than reefs on which no crabs were added (Fig. 3). As planned in the treatment design, reefs in the 3-treatment groups fell into two homogenous subsets (i.e., reefs to which crabs were added and reefs to which no crabs were added), which differed significantly with respect to crab density (Table 1; Fig. 3). These data suggest that I was

successful in maintaining high and low crab density treatments throughout the duration of the experiment.

Table 1. Results of model I repeated measures ANOVA testing the effect of time (sampling event) and experimental treatment on the density of *M. spinosissimus* on patch reefs in the Florida Keys as measured during nocturnal diver surveys.

Source	<i>df</i>	MS	F	<i>p</i>
Treatment	2	2.07	111.586	<0.0005
Reef (random)	9	0.019	0.598	0.794
Sampling Event	6	0.464	14.94	<0.0005
Error	66	0.031		
Total	17			

Prior to the application of treatments, the cover of fleshy macroalgae on all twelve experimental reefs was 80% - 90%. The calcified and chemically-defended groups *Halimeda* spp. and *Dictyota* spp. (respectively) comprised the majority of the algal community on each of these experimental (and the surrounding) patch reefs. There was a significant interactive effect of treatment group and sampling event (time) on the cover of macroalgae on experimental reefs ($df = 16$, $F = 6.963$, $p < 0.0005$). Both treatment group ($df = 2$, $F = 129.076$, $p < 0.0005$) and sampling event ($df = 8$, $F = 20.249$, $p < 0.0005$) had significant independent effects on macroalgal cover through time (Table 2, Fig. 4). Each treatment group differed significantly from another (*post hoc* Tukey's test). Macroalgae cover was significantly lower on reefs to which crabs were added compared to those to which no crabs were added. Reefs where crabs were added, and algae removed had significantly lower algae cover than reefs to which crabs were added and no algae were removed; There was also a significant effect of variance in algae cover between individual reefs ($df = 9$, $F = 2.421$, $p = 0.018$).

Table 2. Results of model I repeated measures ANOVA testing effect of experimental treatment (i.e., manipulation of initial algae cover and crab density) and time (sampling event) on the percent cover of macroalgae on patch reefs in the Florida Keys

Source	<i>df</i>	MS	F	<i>p</i>
Treatment	2	33056.521	129.076	<0.0005
Reef (random)	9	256.1	2.421	0.018
Sampling Event	8	2142.417	20.249	<0.0005
Treatment *Sampling Event	16	736.68	6.963	<0.0005
Error	72	105.803		
total	91			

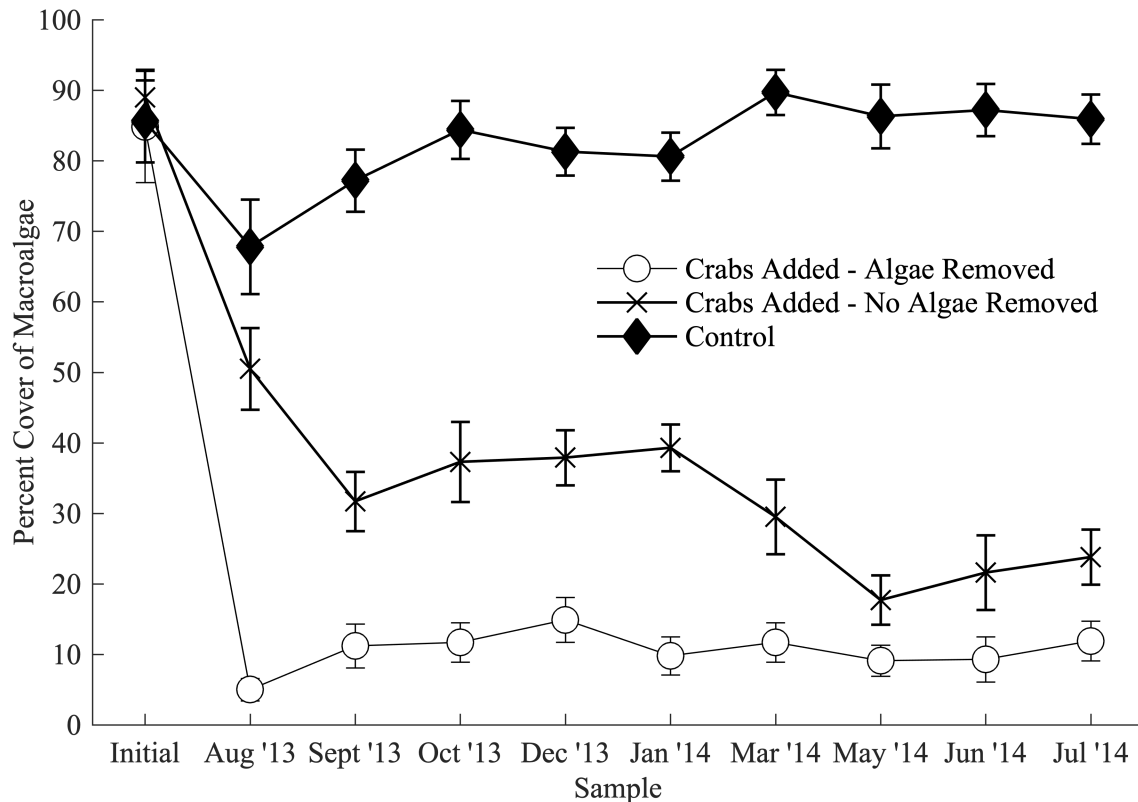


Figure 3. Mean percent cover of macroalgae on experimental patch reefs in each of the three treatment groups prior to treatment application and on each of nine subsequent photographic surveys. Each treatment group was significantly different from the other during every sampling event except during the pre-treatment photographic survey. No surveys were carried out in November, February, or April due to inclement weather.

Effect of increased *M. spinosissimus* density on juvenile coral density and reef fish community composition

Juvenile Coral Density

Treatment group significantly affected juvenile coral density on experimental patch reefs (Wald: 489.458; $df = 3$; $p < 0.0005$; Fig. 5). Pairwise comparisons revealed two homogenous subsets among the treatment groups. Reefs in the control treatment group had significantly lower juvenile coral density than reefs onto which the crabs were added but no algae removed ($p = 0.001$) and crabs added – algae removed ($p < 0.0005$) treatments were applied. Reefs on which the crabs were stocked and algae removed had, on average, more than a three-fold increase in the density of juvenile corals (mean $15.75 \pm 0.59 SE$) over reefs in the control treatment group (mean $3.75 \pm 0.37 SE$). Similarly, reefs onto which the crabs were stocked but algal cover maintained had on average a 3.5-fold increase in the density of juvenile corals ($16.5 \pm 0.75 SE$) over control reefs. However, coral recruit density ($p = 0.87$) was similar on both types of reefs where crabs were stocked (i.e., those with or without algal removal).

I observed a total of 131 recruits from seven scleractinian species (*Porites astreoides*, *Dichocoenia stokesii*, *Orbicella faveolata*, *Montastraea cavernosa*, *Siderastrea siderea*, *Stephanocoenia* spp., and *Agaricia agaricites*) and one hydrocoral (*Millepora alcicornis*). The most common species observed was *Dichocoenia stokesii* (57.25%) followed by *Porites astreoides* and *Siderastrea siderea* (19.08% and 13.74% respectively). None of the remaining species comprised more than 4% of the total observed. There was no apparent effect of treatment on the density of juveniles of the hydrocoral, *Millepora alcicornis*, as only three recruits were observed for this species and

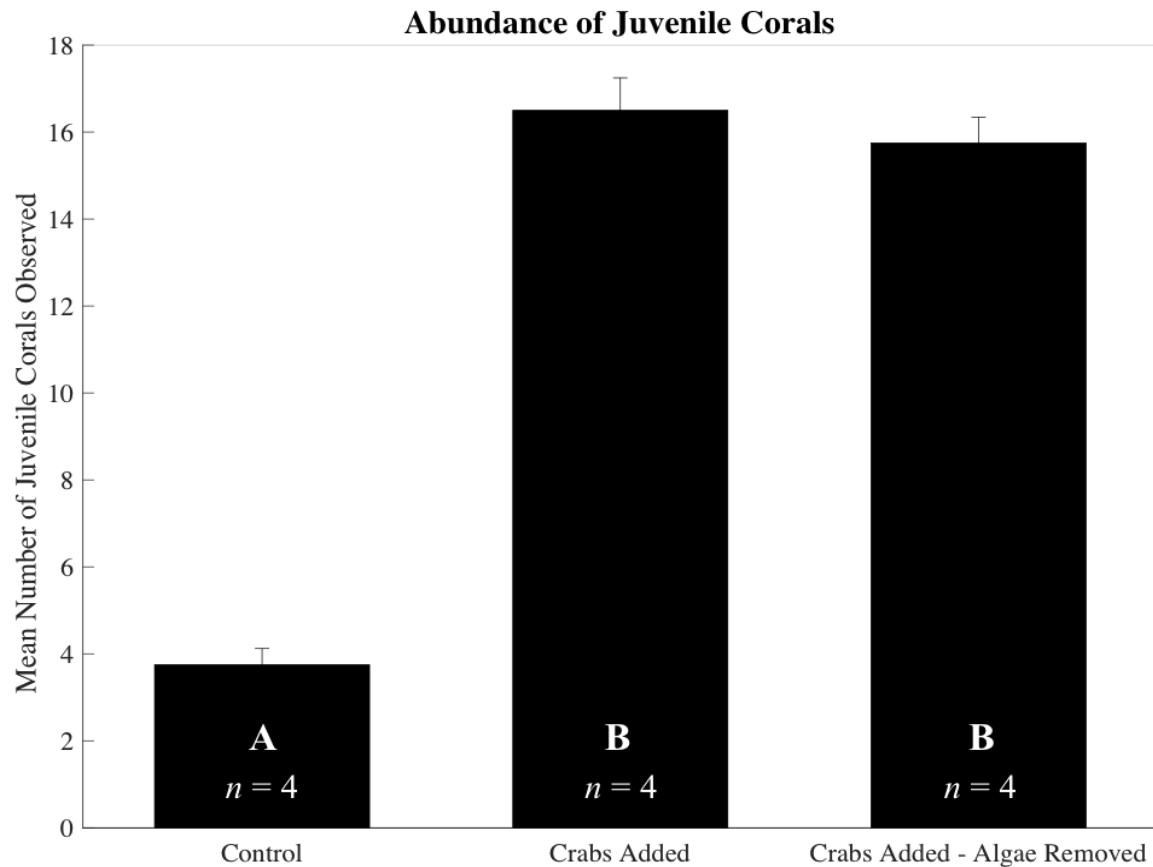


Figure 4. Mean coral recruitment per reef on experimental patch reefs in each of the three treatment groups two years after treatment application. Error bars are standard error of the mean. Bold letters denote homogenous subsets.

each occurred on a reef in a different treatment. Similarly, only a single individual of both *Agaricia agaricites* and *Stephanocoenia* spp. were observed and each occurred on different reefs within the crabs added – no algae removed treatment group. Three recruits of *Montastraea cavernosa* were observed and all occurred on reefs where crabs were stocked. Only one of the five recruits of *Orbicella faveolata* that I found was on a reef where crabs were stocked. But of the three coral species that comprised the bulk of the juvenile corals observed, a clear majority of all three occurred on reefs to which crabs were added (*Dichocoenia stokesii* 80%, *Porites astreoides* 92%, and *Siderastraea siderea* 89%).

Reef Fish Community Composition

Diver surveys indicated that reef fish community composition differed significantly among treatments ($F = 1.3914$; $df = 2$; $p = 0.0170$; Table 3) as well as among sample periods ($F = 2.2091$; $df = 2$; $p = 0.0010$). There was no significant interaction between treatment group and sample period ($F = 1.6351$; $df = 4$; $p = 0.9900$) (Table 3). Visualization of those data shows that the mean abundance of fish increased in both treatments where crabs were added as compared to the control treatment (Fig. 6). Interestingly, there appears to be no clear pattern in the richness of fish species with respect to treatment group and time (Fig. 7). Visual inspection of the data set indicates that the variance between and among treatment groups and time was driven primarily by strong responses in seven species of fish: two surgeon fish (*Acanthurus coeruleus* - 10.1% (of fish observed) and *A. bahianus* 7.83%), two grunts (*Haemulon flavolineatum* - 8.0% and *H. plumierii* - 7.41%), a snapper (*Ocyurus chrysurus* - 5.19%), and a parrotfish (*Scarus iseri* - 13.0%) (Fig. 9). There was no difference in the abundance of three species that are commonly fished (i.e., *H. flavolineatum*, *H. plumierii*, and *O. chrysurus*) between treatment groups in the first sampling event, but all increased substantially during later sampling events in 2014 in both treatment groups to which crabs were added. Those species remained at relatively low abundances on control reefs, similar to the initial sampling event. Both surgeon fish species were more variable in their abundance with respect to treatment group through time, although each was consistently more abundant on reefs to which crabs were added and reefs to which crabs were added and algae removed than on control reefs. The abundance of *S. iseri* was similar in all treatments during the first sampling event and then increased through time on all treatments. However, the magnitude of the increase was much greater on reefs in both crabs added treatments than it was on control reefs.

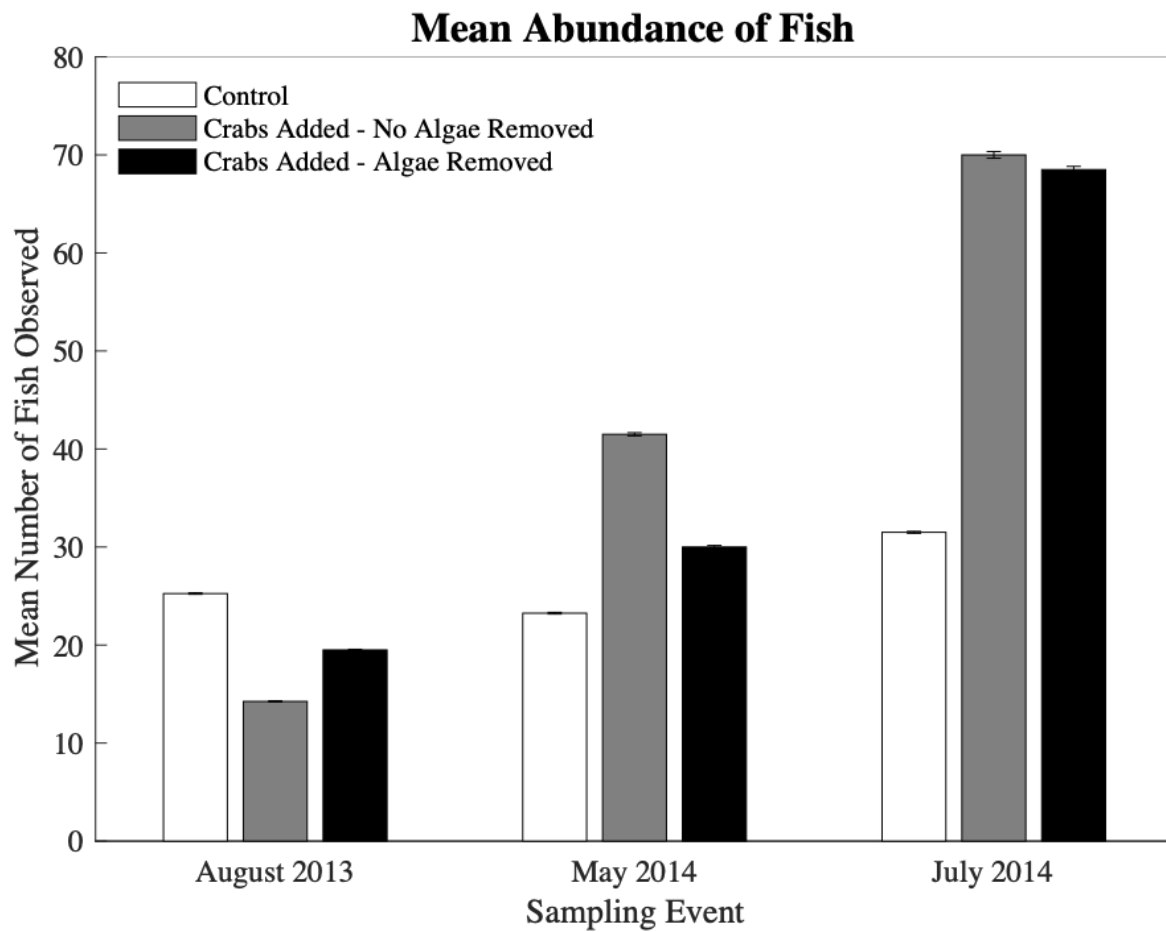


Figure 5. Mean abundance of fish on experimental patch reefs in each treatment group during three sampling events. Error bars are standard error of the mean.

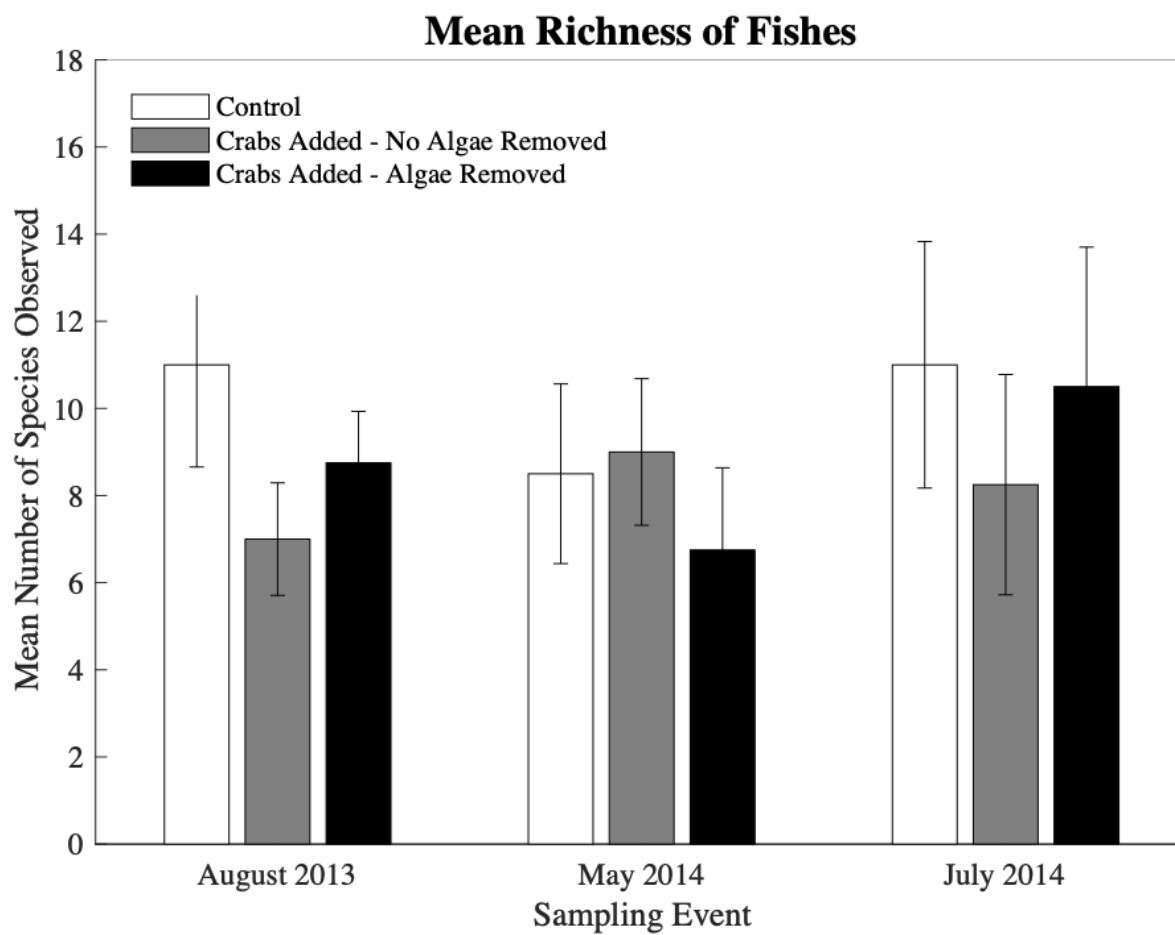


Figure 6. Mean species richness of fishes on experimental patch reefs in each treatment group during three sampling events. Error bars are standard error of the mean.

Table 3. Results of nonparametric (permutation-based) MANOVA testing the effect of experimental treatment (i.e., manipulation of initial algae cover and crab density) and time (i.e., sampling event) on the structure of the fish community around experimental patch reefs in the Florida Keys measured by roving diver visual census.

Source	<i>df</i>	SS	MS	F	<i>p</i>
Treatment	2	1.3914	0.6957	1.7019	0.0170
Sample Period	2	2.2091	1.1046	2.7021	0.0010
Treatment x Sampling Event	4	1.6351	0.4088	0.6853	0.9900
Residuals	27	16.1066	0.5965		
Total	35	21.3423			

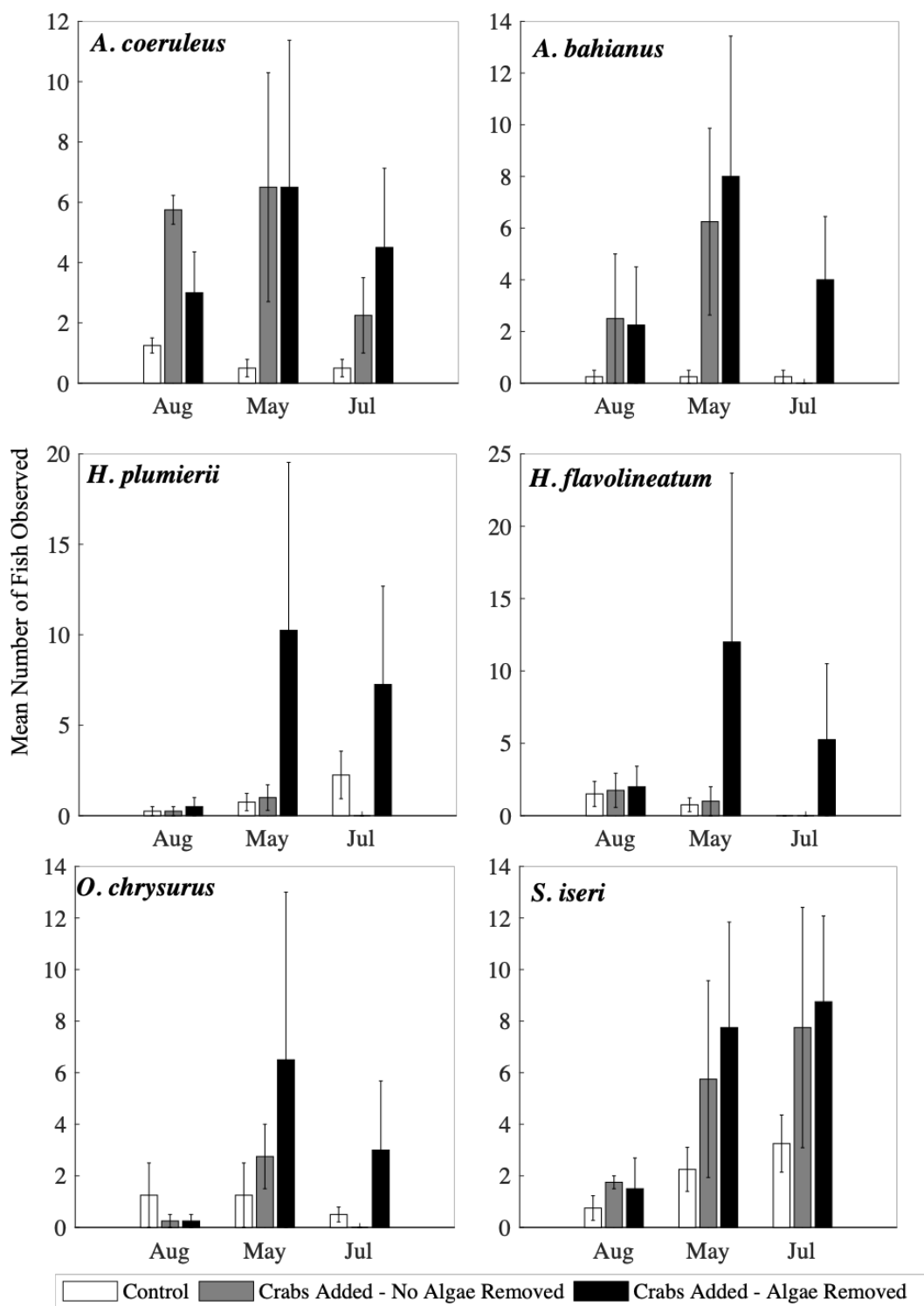


Figure 8. Mean abundance of each of the six fish species whose mean abundance showed the greatest response to treatments through time. Error bars are standard error of the mean.

2.4 Discussion

Mithracid crabs, and *M. spinosissimus* in particular, represent an under-studied cryptic guild of herbivores in Caribbean coral reef communities whose consumption of macroalgae and life history characteristics make them appealing candidates for use in coral reef restoration. My findings indicate that *M. spinosissimus* is philopatric and that its naturally low abundance is due, at least in part, to a type III survivorship curve (see Demetrius 1978) with high mortality of juvenile crabs (< 30mm CW). At typical natural densities, the effects of these cryptic herbivores on coral reef macroalgae communities is diffuse and weak relative to larger, more mobile herbivores such as parrotfishes and Acanthurids (Paddock et al. 2006; Butler and Mojica 2012). Yet, when I artificially increased crab abundance to densities similar to those prescribed for *Diadema* reintroduction (~ 1 individual / m²), the density-dependence of their functional effects became apparent. Crab grazing significantly reduced the cover of macroalgae by > 60% and maintained that low algae cover condition for 12 months following a single manipulation of crab density. Even more pronounced effects on macroalgal cover were measured when crab density enhancement was combined with the manual removal of algae suggesting that the effects of crabs can be more immediate and profound in other areas along the Florida reef tract or the wider Caribbean if initial algae cover is low. Perhaps even more noteworthy were the strong indirect effects of the reduction of algae on patch reefs by crabs; namely, a 3-fold increase in the density of juvenile corals and the development of a more abundant fish community.

Populations of *M. spinosissimus* occur throughout the Caribbean region, but their densities are low in most locations, similar to the natural densities reported for Florida (Butler and Mojica 2012). There is little information available regarding the life history and demographics of most species of Mithracid crabs, especially *M. spinosissimus*, so the factors that limit their abundance and the growth of their populations (e.g., resource availability, predation

pressure, fecundity, environmental conditions) are unresolved. Female *M. spinosissimus* reproduce continuously throughout the year (Spadaro, unpub. data) producing clutches of several thousand to several hundred thousand eggs from a single mating (Brownell et al. 1977; Tunberg and Creswell 1988, 1991; Creswell 2011). In the laboratory, survival of *M. spinosissimus* larvae to the first juvenile stage on the order of 90% is common (Tunberg and Creswell 1988, 1991). Thus, it is unlikely that *M. spinosissimus* populations are limited by fecundity, although rates of larval settlement in any habitat or location are unknown. The high algae cover (~70 – 90%) we observed on unmanipulated reefs suggests that food availability is also not likely to limit *M. spinosissimus* populations in Florida. However, our tethering experiment indicates that *M. spinosissimus* are extremely vulnerable to predation until they attain a body size of ~30 mm CW. Small Mithracid crabs are a primary component of the diet of the reef-obligate spotted spiny lobster (*Panulirus guttatus*) whose predation is believed to exert strong top-down control over several important invertebrate grazers on Caribbean reefs (Butler and Kintzing 2016). Crustacean predators are abundant and diverse in the Caribbean, so it is likely that *P. guttatus* is not alone in contributing to the recruitment bottleneck for *M. spinosissimus* and other invertebrate grazers in Caribbean reef communities.

Although the high mortality of small *M. spinosissimus* may be a likely explanation for the species' low natural abundance, there are a number of Mithracid crabs, especially those of the *Mithraculus* genus, that rarely exceed 30 mm CW as adults (Coen 1988a, b). To the best of my knowledge, my study is the first to examine natural predation rates of *Mithraculus* spp. in the field and my results suggest that predation in reef habitats is similar for all life history stages of *Mithraculus* spp. and for small *Maguimithrax*. However, all Mithracids are cryptic, nocturnal, and dwell in structurally complex habitats, characteristics that should serve to minimize predation.

The results of my crab retention study suggest that *M. spinosissimus* exhibit a high degree

of philopatry once translocated onto patch reefs. When one considers the fact that this species has a very short larval duration of just a few days and is only a swimming larva for a matter of hours (Brownell et al. 1977), it stands to reason that *M. spinosissimus* larvae likely do not disperse far. If so, then recruitment is likely to be localized perhaps explaining the patchy, low abundance of these crabs.

However, where *M. spinosissimus* is locally abundant and dense, their effect on the composition of the reef community is transformative. Herbivory is critical to the preservation and maintenance of coral reef benthic communities (see Hughes et al. 1987, 2007; Szmant 2002; Mumby et al. 2006a; McClanahan et al. 2011), and my results show that *M. spinosissimus*, when sufficiently dense, are capable of providing this critical function even in severely degraded systems subject to persistent and chronic stress – a condition that is becoming more and more ubiquitous on Caribbean reefs. As reef communities continue to face mounting environmental stresses, water quality degradation, and increasingly efficient fishing effort, cryptic grazers and sleeping functional groups may well shift from a subordinate functional role to one of primacy in coral reef systems (Kuempel and Altieri 2017). As water quality as well as grazing intensity and the redundancy in this critical function wanes in coastal seas, benthic macroalgae will continue to proliferate. This increasing abundance of algae in coral reef ecosystems will result in a continued loss of natural corals as well as a severe impediment to direct restoration efforts through acute and chronic coral mortality (van Woesik et al. 2018).

The results of this study confirm that the distribution and abundance of benthic macroalgae are drivers of community assembly patterns on Caribbean reefs, but algae can be effectively controlled with a modest effort. In addition to the direct effects of grazing by *M. spinosissimus* on the cover of benthic macroalgae, the presence of crabs also enhanced the local abundance of seven fish species, three of which (*A. coeruleus*, *A. bahianus*, and *S. iseri*) are

themselves important herbivores. These results reveal a previously undocumented facilitation cascade wherein crabs remove algae from the reef (including chemically and physically defended species) and promote the arrival of grazing fishes. These increases in grazing intensity should eventually, absent catastrophic disturbance, facilitate an increase in the cover of living reef-building corals by facilitating their increased survival, growth, and recruitment.

The effects of crab grazing also led to increases in the abundance of three predatory reef fishes (*H. flavolineatum*, *H. plumierii*, and *O. chrysurus*). While both grunt species likely contribute to the recruitment bottleneck for *M. spinosissimus* by consuming larval, post-larval, and early juvenile crabs, there is also evidence that abundant shoals of grunts create nutrient hot spots around coral formations which lead to significant increases in coral growth and grazing rates of herbivorous fishes (Shantz et al. 2015). Thus, by facilitating an increase in the number of grunts on experimental patch reefs, *M. spinosissimus* likely further facilitates the recovery of corals on degraded reef structures. Although the dramatic facilitative cascade I observed on small, experimental patch reefs is unlikely to occur on a wide spatial scale without direct intervention, the effects were profound and are relevant to coral reef restoration.

Implications for the Restoration of Degraded Caribbean Reefs

The fate of coral reefs, particularly those in the Caribbean region, is uncertain, though the prognosis is increasingly grim and uncontrolled algae growth is a major factor contributing to this dismal outlook. A great deal of popular and financial support is being invested globally in the conservation, management, and restoration of coral reefs to protect and preserve these unique ecosystems not only for posterity, but also for their vast socio-economic importance. In the Caribbean, much of this support is manifested in restoration of live coral and, to a lesser extent, the management of echinoid and piscine grazer populations (Mumby 2006). The latter are

focused almost exclusively on either the protection of parrotfishes (Mumby 2006; Kennedy et al. 2013) or the stock enhancement/assisted recovery of *Diadema antillarum* (Nedimyer and Moe 2006; Maciá et al. 2007; Burdick 2008; Sharp et al. 2018). However, parrotfishes are still heavily fished in many areas throughout the Caribbean region despite widespread legislative protection (Hawkins and Roberts 2003; Mumby 2006). The mobility and complex life history of parrotfishes preclude localized stocking of aquacultured fishes on reefs, and no programs exist for large-scale stock enhancement of herbivorous fishes. So, management of herbivorous finfish stocks on Caribbean reefs is based entirely on fisheries management. Direct enhancement of *D. antillarum* densities on targeted reefs shows some promise in reducing macroalgae abundance and increasing coral recruitment (Maciá et al. 2007; Burdick 2008), but as with finfish, their complex life history and high post-transplant mortality are bottlenecks to their use in reef restoration efforts. Unfortunately, due to strong Allee effects and high post-settlement mortality, in most areas of the Caribbean *D. antillarum* populations remain far below target densities now more than 30 years after the regional pandemic that decimated them Caribbean-wide (Lessios 1995; Miller et al. 2003; Lessios 2005, 2016).

My study demonstrates that local enhancement of other cryptic grazers may offer an alternative for Caribbean reef restoration, one that recognizes the ecological value that functional redundancy and complementarity plays in bolstering the resilience of complex ecological communities (Burkepile and Hay 2008, 2011) - an ecological lesson often overlooked in restoration studies. Although their low natural abundance probably renders *M. spinosissimus* less apparent as major grazers on coral reefs than herbivorous fishes or echinoid grazers, their per capita consumption of algae equals or exceeds that of other grazers (Butler and Mojica 2012). Moreover, *M. spinosissimus* are good candidates for reef restoration programs because they are native to the system, have high per capita grazing rates, exhibit a high degree of philopatry, do

not suffer high mortality associated with transplantation, and are relatively simple and inexpensive to culture in large numbers because of their short larval duration, rapid growth, and omnivorous, but largely algae-based diet (Creswell et al. 1989; Wilber and Wilber 1989, 1991). Production of crabs on a scale commensurate with large-scale reef restoration is possible and was demonstrated in commercial-scale mariculture studies conducted in late 1970s - 1990s (see Creswell 2011). However, commercial mariculture of *M. spinosissimus* was never realized because of high labor costs for laboratory-rearing to a marketable size (~120 mm CL; Brownell et al. 1977) and the lack of a developed market for the crab. That could change if the species became a commodity for reef restoration as well as food.

A potential alternative to high cost laboratory rearing of *M. spinosissimus* is its semi-wild mariculture in saltwater quarries, an approach that my collaborators and I have proposed based on my work in the Florida Keys. In the course of my dissertation, I have collected hundreds of *M. spinosissimus* from abandoned saltwater quarries: seawater-flooded rock quarries common throughout the Florida Keys, many left over from the construction of Henry Flagler's Overseas Railroad during the early 1900's. Somehow *M. spinosissimus* were introduced into some of those quarries, perhaps by hurricane overwash, and given the species' short larval duration, the crabs can complete their lifecycle within the protected semi-natural environments (Spadaro, pers. Obs.). In such quarries, the density of *M. spinosissimus* is often orders of magnitude higher than in natural populations, suggesting that such environments could be re-purposed for the large-scale production of crabs for coral reef restoration. This is an area of research that I am now exploring.

The results of my study suggest that with a reliable mode of crab production and distribution to the field, the resulting reduction of macroalgae on reefs by crab grazing may also result in strong cascading effects on coral recruitment success and the composition of the reef

fish community. Two years after I began my manipulation of crab density on patch reefs, I observed nearly a three-fold increase in juvenile coral density on reefs to which crabs were added as compared to control reefs. Alternatively, it is possible that the reduced algae cover on manipulated reefs allowed for more accurate detection of living juvenile coral colonies – an alternative hypothesis I plan to test in the future. On reefs to which crabs were added as well as reefs to which crabs were added and algae were removed, the reef fish community was substantially more abundant than that of unmanipulated reefs; herbivorous fishes from two families (*Acanthuridae* and *Scaridae*) were among those exhibiting the greatest response. Two species of schooling fish (*H. flavolineatum* and *H. plumierii*) reportedly capable of facilitating coral growth through bioavailable nutrient-enrichment (Shantz et al. 2015) and another species of fish (*O. chrysurus*) targeted by fishermen (da Silva et al. 2015) also showed strong positive responses to crab grazing. These experimental results are consistent with findings by others (see McCook 1999; Szmant 2002) that the abundance and distribution of benthic macroalgae are strong drivers of coral reef community assembly and perhaps function. Indeed, several recent studies have demonstrated the degradative effects of abundant and dense macroalgae on reefs. Nugues et al. (2004) report that dense benthic macroalgae may act as agents and vectors of coral disease. Algae also directly increase the mortality and decrease growth of transplanted and natural coral colonies (Box and Mumby 2007). With the continued global degradation of coral reefs, the identification of cryptic or "sleeping" functional groups is imperative as these groups should be targets for conservation and management in the interest of preserving what remains of the ecological resilience of coral reef ecosystems and as potential tools for algal management and the restoration of coral reef communities.

The results of my tethering study also demonstrate that crabs >30 mm CW have reached a critical size threshold at which risk of predation is sharply reduced, thus representing the

minimum size at which they should be transplanted. Reportedly, growout of crabs to this size takes ~5 - 6 months in aquaculture (Brownell et al. 1977; Wilber and Wilber 1989). Some attempts to develop commercial mariculture of the species for human consumption were economic failures because of the labor costs associated with raising the crabs to a large target size of 90 - 140 mm *CW* (Brownell et al. 1977) or ~1.8 kg (Rubino and Stoffle 1990) deemed most suitable for the seafood market. However, production of smaller (30 - 50 mm *CW*) crabs in large numbers for stock enhancement and coral reef restoration is more cost-effective (Adey, pers. Comm.; Creswell, pers. Comm.; Wilber, pers. Comm.; Brownell et al. 1977; Creswell et al. 1989; Wilber and Wilber 1989).

The philopatry that I observed in *M. spinosissimus* was based on crabs released in discrete coral patch reefs isolated from other reefs by several meters of open sand, but other studies indicate that patch size can affect site fidelity of motile species (Bach 1988; McIntyre and Wiens 1999; Saumure et al. 2010). Should *M. spinosissimus* be used for reef reclamation, the setting for its application will almost certainly include areas of contiguous reef habitat. I have not yet tested the effect of either habitat patch structure or crab density on their patterns of movement, though I suspect that stocking crabs in a more contiguous habitat and/or at higher densities may result in a diffusive movement away from their initial point of release. However, a previous study suggests that *M. spinosissimus* exhibits a degree of site fidelity even in contiguous, rugose habitat (Hazlett and Rittschof 1975). It is also likely that sex ratio and ontogenetic phase play an important role in the site fidelity of *M. spinosissimus* – an aspect of their life history that merits further examination.

Whether the stocking of *M. spinosissimus* ever sees practical application as a tool for reef reclamation and the management of macroalgae is yet unknown. Regardless, my research highlights the role of these cryptic herbivores in shaping the composition of the benthic

community on coral reefs via their herbivory. These, and other grazing invertebrates appear to play an underappreciated role in shaping coral reef community assembly and, when at sufficient densities, can be important players in the conservation and management of these fragile habitats.

CHAPTER 3

CASCADING EFFECTS OF THE CARIBBEAN KING CRAB, *MAGUIMITHRAX SPINOSISSIMUS*, ON THE COMMUNITY STRUCTURE OF CORAL PATCH REEFS IN THE FLORIDA KEYS

3.1 Introduction

The diversity of ecological communities, in both form and function, is influenced and driven by a number of factors (Hairston et al. 1960). Latitude, resource availability, local and regional climate patterns and environmental conditions, topography, bathymetry, disturbance regimes, the abundance and distribution of foundation species, as well as interactions between and among these and myriad other factors play a role in determining or limiting the composition of an ecological community. A ubiquitous driver of local biological and ecological diversity is habitat, particularly its architectural complexity (MacArthur and MacArthur 1961; Southwood et al. 1979; Brown and Southwood 1987; Redford et al. 1990; Brown 1991). Typically, more physically complex habitats support a greater number of individuals and species because these habitats offer greater structural diversity, hence refugia, and a greater capacity for ameliorating physical environmental stresses (e.g., thermal, desiccation, irradiance, wave/surge energy, scour; Murdoch et al. 1972; Lawton 1983; Bruno and Bertness 2001; Gratwicke and Speight 2005; Angelini and Silliman 2014).

Some habitats and their associated communities are biogenic, literally constructed by a single or few conspicuous "foundation species" whose physical structure maintains the community. Foundation species facilitate the establishment of a more diverse community than would be possible in their absence (Schöb et al. 2012), and frequently involve multiple levels of facilitation in a phenomenon known as a "facilitation cascade" (Angelini et al. 2011). An

excellent example occurs in forest and prairie habitats of the Southeastern United States where Live Oak (*Quercus virginiana*) trees are a common and conspicuous foundation species. These large trees facilitate the existence of a vast community of insects and small mammals by ameliorating environmental stresses (e.g., thermal, desiccation), providing refuge from predators, and (somewhat counter intuitively) simultaneously aggregating prey species (Angelini and Silliman 2014). In turn, Live Oaks promote establishment of another facilitator - Spanish Moss (*Tillandsia usneoides*) - by providing the moss with structure, moderating its thermal stress, and reducing its risk of desiccation (Angelini and Silliman 2014). Without the complex architecture, further reduction in thermal stress, and stabilizing effect on local humidity provided by Spanish Moss, a number of additional species that thrive in Live Oak habitat could not (Angelini and Silliman 2014). Thus, a cascade of ecological benefits accrues after the establishment of a primary foundation species whose presence promotes the subsequent arrival of secondary foundation species that, combined, materialize into a richer community than would be possible without each level of facilitation.

When the structure and refuge provided by foundation species is reduced or lost, however, a concomitant and potentially greater cascade of negative effects on biological and ecological diversity is often observed (see Ellison et al. 2005; Sackett et al. 2011; Peters and Yao 2012). This is particularly important in high diversity systems (e.g., tropical rainforests, coral reefs) where cascading facilitation generates interactions among a great many species (e.g., Alvarez-Filip et al. 2009, 2011).

On coral reefs, the complexity of biogenic habitat is an important driver of community composition. More architecturally complex habitats support a significantly greater abundance and richness of reef fishes than flatter, less complex habitats (Gratwicke and Speight 2005). But habitat complexity has declined on coral reefs around the globe - particularly in the Caribbean - a

trend that has continued for more than half a century and shows no signs of abating (Alvarez-Filip et al. 2009, 2011). A similar, concomitant trend in the richness and abundance of reef fish communities throughout the region (Paddack et al. 2009) may well be both a symptom of and a factor contributing to the flattening of Caribbean reefs (Alvarez-Filip et al. 2009, 2011).

Beginning in the 19th century, industrialized fishing began in earnest on Caribbean coral reefs and rapidly decimated the region's large-bodied predatory and herbivorous fish populations (Jackson 2001; Jackson et al. 2001; McClenachan 2009). This massive shift in the size structure and abundance of the predatory fish guilds largely released the long-spine sea urchin, *Diadema antillarum*, from predation pressure. At the same time, declines in herbivorous fishes released *D. antillarum* from competitive pressure. Thus, this reduction in fishes removed two important ecological controls on urchins throughout the region and facilitated a massive population explosion with *Diadema* reaching densities greater than 50 - 70 urchins / m² in some areas (Sammarco 1982; Hughes et al. 1987). These high urchin densities filled the functional void (i.e., grazing) created by the decline in herbivorous fish populations and facilitated the persistence of corals otherwise threatened by increased algal growth. But as has been documented elsewhere (Lafferty 2004), the high densities of urchins increased their susceptibility to disease and likely facilitated the rapidity with which a pandemic swept through the region in the early 1980s (Lessios et al. 1984; Hughes et al. 1987), ultimately resulting in the functional extirpation of *D. antillarum* in the Caribbean (Mumby et al. 2006b). Following the regional demise of *D. antillarum* in the region, much of the grazing function on Caribbean reefs was restricted to the remaining herbivorous fishes (Hughes et al. 1987). The resulting systemic decline in grazing function was, in many areas, followed by massive increases in the abundance and cover of benthic macroalgae as well as a significant decline in live coral cover – a phase shift from a

system dominated by corals to one largely depauperate thereof (Hughes et al. 1985; Hughes et al. 1987; Hughes 1994; Mumby 2009b).

On reefs with moderate to high coral cover (e.g., > 30-35% live coral cover), fish grazing may be sufficient to restrict algal over-growth (Mumby et al. 2007; Cramer et al. 2017). However, several major disease epidemics have caused significant declines in live coral cover (~80 – 90%) leaving coral reefs in the region largely devoid of live coral (Aronson and Precht 2001; Bruno et al. 2003; Aronson and Precht 2006). This phase shift has resulted in a community that is largely incapable of modulating the proliferation of benthic macroalgae and the near extinction of reef-building corals (Mumby 2009b). There remain instances of high coral recruitment on some Caribbean reefs, but Allee effects, persistent diseases, competition with macroalgae, and predation all keep the rate of successful coral recruitment low (Edmunds and Carpenter 2001; Carpenter and Edmunds 2006). These patterns of habitat degradation and collapsing architectural complexity are having, and will continue to have, strong negative effects on fish stocks, fisheries production, ecosystem services, and the multifunctionality of Caribbean coral reefs (Alvarez-Filip et al. 2009, 2011).

Although it is generally accepted that the “health” of Caribbean reef communities (e.g., resilience, fitness, function) is intrinsically tied to the recovery of *Diadema* and/or to the recovery and protection of large-bodied herbivorous fishes (e.g., Scaridae and Acanthuridae) as “keystone” herbivores, the role of other, small-bodied and cryptic herbivores in driving the dynamic composition of Caribbean coral reef communities has recently become more apparent (Kuempel and Altieri 2017). Kuempel and Altieri (2017) report that on degraded reefs in Panama, small-bodied herbivores (e.g. *Scarus iseri*, *Echinometra viridis*) make up >90% of the herbivore biomass and account for a large proportion of the grazing intensity in those systems. This strong effect of small-bodied herbivores may be an emergent phenomenon due, in part, to

over-fishing of large-bodied fishes including herbivores (Hughes 1994; Jackson 2001; Jackson et al. 2001). The results of an analysis of the geology of the same reef system studied by Kuempel and Altieri (2017) suggest that reef health – measured in terms of accretion rate – is intrinsically tied to the dynamics of parrotfish populations on a geologic time scale (Cramer et al. 2017); when large-bodied parrotfishes are abundant, reef accretion rates are high and when these parrotfish populations decline, so too does the accretion rate of Caribbean reefs. While many studies echo the view espoused by Cramer et al. (2017) that large-bodied parrotfishes and echinoid grazers exhibit a keystone effect on Caribbean reefs, others (Klumpp and Pulfritch 1989; Stachowicz and Hay 1996; Butler and Mojica 2012; Kuempel and Altieri 2017; this study) suggest that sleeping functional groups (*sensu* Bellwood et al. 2006) – guilds of species whose functional role is diffuse or cryptic and only becomes conspicuous following major phase shifts – may be important in driving the community dynamics of coral reefs, especially given the degraded state of reef communities around the globe.

In a previous study (Chapter 2) I demonstrated the significant effect that a cryptic herbivorous crab had, when sufficiently dense, on the composition of coral patch reef communities in the Florida Keys. Here, I repeat that study in a different location and two years later to verify those results. Further, I follow up on a particular set of results from my previous study by testing the effect of crab density and algae removal on the abundance and richness of the reef fish community. In the field, I also tested the effect of crab grazing and algae cover on the rugosity of the reef matrix.

3.2 Methods

Study area and general methodology

Each of the experiments in this study was conducted in the Florida Keys, Florida (USA), a 212 km-long island archipelago offshore of which lies the world's third longest barrier reef system. In the back-reef lagoon of the Florida Keys reef tract lie thousands of coral patch reefs with coral formations and community assemblages similar to those found throughout the Caribbean (Porter and Meier 1992; Jaap et al. 2003). These patch reefs once harbored a rich diversity of scleractinian corals dominated by *Montastraea annularis*, *Colpophyllia natans*, and *Siderastrea siderea* (Butler and Mojica 2012, Ruzicka et al. 2013). Following a series of successive major cold-water events in 2010, many of these nearshore patch reef communities suffered heavy coral mortality, which drove a substantial shift in the composition of the benthic community such that many of these patch reefs are now coral-depauperate and largely dominated by benthic macroalgae, predominantly *Halimeda* spp. (Kemp et al. 2011; Colella et al. 2012).

My field experiments for this study were conducted between August 2015 and August 2017 on 12 shallow (5-7 m) patch reefs (mean surface area: 21.35 m²; range 4.83 m² – 46.56 m²) situated ~2.25 km offshore of Upper Matecumbe Key on a series of coral patch reefs adjacent to the Cheeca Rocks Sanctuary Preservation Area (24°53' N; 80°37' W) in the middle Florida Keys near the center of the Florida Keys National Marine Sanctuary (FKNMS) and approximately 13 km away from the study site used for the experiments presented in Chapter 2.

Crabs (*M. spinosissimus*) for this experiment were collected from various habitats throughout the Middle Florida Keys by divers who recorded the collection location as well as crab sex and size (mm CW). Fishes for my mesocosm experiments were collected from shallow (~1-3 m) nearshore hardbottom habitats 0.5 – 2 km south of Long Key State Park, Long Key, FL, USA (24°21' N; 80°49' W).

Cascading effects of crab density on coral reef community composition

I replicated the primary field experiment described in Chapter 2 at a different location to verify those results. I tested the effect of crab grazing and algae cover on coral reef community composition but this time in a two-factor crossed (orthogonal) design: crab density (two levels: Crabs Added (1 crab / m²) or No Crabs Added) x initial algae cover (two levels: Algae Removed (algae manually removed from reef as in Chapter 2) or No Algae Removed (unmanipulated)). The twelve independent patch reefs were assigned to one of four treatment groups ($n = 3$): Control, No Crabs Added – Algae Removed, Crabs Added – No Algae Removed, and Crabs Added – Algae Removed. Based upon the results of Chapter 2, I hypothesized that increased crab grazing would significantly reduce the distribution and abundance (cover) of benthic macroalgae on reefs, thereby facilitating a more speciose and abundant fish community and more dense assemblage of juvenile corals.

Algae cover

Prior to and immediately following the application of treatments and quarterly thereafter for 12 months, I took a series of ten haphazardly placed 1 m x 1 m photographic quadrats on each of the 12 experimental reefs. These photographs were used to track changes in the composition and distribution of algae on each experimental reef through the duration of the experiment. All photo quadrats were taken using a Nikon D7200 24.1 MP digital SLR camera (Nikon USA, Melville, New York, USA). Each digital image was processed using the point intercept method in the Coral Point Count with excel extensions (CPCe) software package (Kohler and Gill 2006). A series of 25 random points were generated and overlaid on each image and each point was manually identified to the lowest taxonomic level possible. These data were then used to calculate mean percent cover for each benthic taxon for each site in each sampling

period. These site means were then reciprocally transformed to improve their fit to a gamma distribution and analyzed in a generalized linear mixed effects model in MatLab (using the *fitglme()* function with a gamma distribution and a log likelihood link function) to model the change in percent cover of macroalgae (response variable) on experimental reefs (individual reef set as a random effect) with respect to manipulations of crab density and initial algae cover treatments (predictor variables) through time (repeated measure; five levels: initial/pre-treatment application (July 2015), initial/post-treatment application (July 2015), October 2015, May 2016, and August 2016). Experimental reef or subject was included as a random effect.

Patterns in the density of juvenile corals

In July 2017, two years after crab and algae manipulations treatments were applied, I revisited each of the 12 experimental reefs and conducted a detailed visual census of Scleractinian coral recruitment. I defined “coral recruit” as any living Scleractinian coral that was less than 40 mm in its longest dimension, similar to the method described by Carpenter and Edmunds (2006). The larger of these corals are certainly not recent recruits, but I decided to include them because any patterns in their density relative to treatment group may indicate that not only does the improvement in habitat condition resulting from crab grazing likely attract a greater number of coral larvae, it also likely increases the fitness and survival of previously settled juvenile corals in the absence of any differences in larval supply. Each reef was systematically searched visually and all living coral recruits were identified to the lowest taxonomic level possible and its longest dimension measured to the nearest 1 mm. These data, along with an estimate of the surface area and rugosity of the patch reefs were used to calculate the mean number of coral recruits per m² (surface area) in each treatment group. I tested the effect of treatment group on coral recruit density (recruits / m²) with a general linear mixed-

effects model (*fitglm* function in Matlab with a gamma distribution and a log likelihood link function) where both crab factor (2 levels as above) and algae factor (2 levels as above) were orthogonally crossed fixed effects with reef size (surface area: m²) included as a random effect and potential co-variate.

Reef fish abundance and richness surveys

Immediately after treatments (described above) were applied and quarterly thereafter, each experimental reef was surveyed for reef fish abundance and species richness. I employed two different methods for measuring both the abundance and richness of reef fishes: visual census by divers and remote time-lapse photographic surveys.

Diver census

A single diver was used for each visual census of reef fishes. For each visual census, divers entered the water from an anchored vessel >10 m away from the experimental reef, dropped to the sea floor and slowly approached the experimental reef stopping at a distance of ~2 m. The diver then remained as still as possible for a 5 min. acclimation period. At the end of the acclimation period, the diver slowly orbited the experimental reef carefully recording the species and ontogenetic phase (e.g., adult, juvenile) of each individual fish observed. Statistical analyses are described below.

Time lapse photographic surveys

At the end of the visual census, the diver would mount a small submersible digital camera (GoPro Hero 2) to a concrete block situated 2 m from the base of the experimental reef. Camera position was haphazard with respect to compass bearing from the experimental reef. The camera was set to record a single 11-megapixel image every 30 s. The diver then vacated the area and

cameras were left to record during the day for no less than 1 hour. At the end of the time-lapse survey, divers returned to recover the cameras. For each survey, the first and last 30 frames (15 min.) were discarded to minimize bias in the sample from the presence of a diver leaving the area or returning to collect the camera. A random subsample of 25 frames was pulled from the remaining frames and were used for analysis. Each of these 25 frames was then post-processed for white balance, contrast, and brightness as necessary using the Picasa photo-editing software package. Each individual fish visible in the images was counted and identified to the lowest possible taxonomic level and ontogenetic phase. The sample size of 25 frames was determined using a Scree plot of Menhinick's richness index calculated for each frame in the first complete survey (e.g., first sample period) of each of the control reefs. I opted to use the Menhinick's richness index in calculating an appropriate sample size due to its relative simplicity among diversity indices. Menhinick's index is calculated as $D_{mn} = \frac{S}{\sqrt{N}}$ where S is the number of species and N is the total number of individuals in the sample, thus the Menhinick index is a simple, yet robust, measure of α diversity appropriate to this investigation of changes in the species richness and general abundance of the reef fish community associated with experimental reefs (Whittaker 1977; Magurran 2004).

I used non-metric multidimensional scaling (nMDS) to visualize the separation of fish community composition with respect to treatment group and time prior to analysis. The data matrices were then both analyzed in a non-parametric (permutation-based) MANOVA using the Fathom toolbox (Jones 2015) for Matlab as described in chapter 2.

Effect of algae on reef structural complexity

To test the effect that dense, late-successional stands of benthic macroalgae, particularly *Halimeda* spp., have on the structural complexity of the reef matrix, I measured the topography of 1.0 m line transects ($n = 14$) on algae-covered patch reefs before and after the removal of macroalgae. I haphazardly selected seven patch reefs near the study area whose physical characteristics were similar to that of the patch reefs used in the field experiment described above. On each patch reef I measured reef rugosity before and after algal removal at 2 haphazardly selected locations. I used a standard method for determining rugosity index value (Wilson et al. 2007; Alvarez-Filip et al. 2009, 2011) wherein a rugosity index of 1.0 represents a completely flat surface and values greater than 1.0 represent increasingly complex structure. To calculate the index, I measured a 1.0 m horizontal transect above the reef and marked each end by laying a 1.3 kg lead weight on the substratum. A length of negatively buoyant #6 aluminum ball chain was attached to one of the lead weights and was then carefully laid on the bottom along the 1.0 m transect. The length of chain needed to reach the second weight was carefully measured to the nearest 0.1 mm. The difference between the horizontal (1.0 m) and the contour (chain) distances was then used to calculate the rugosity index. I measured the rugosity along this 1.0 m transect twice, once with all algae present (D_i) and a second measurement was taken after divers had manually removed all benthic macroalgae along the 1.0 m transect (D_f). The difference between pre- and post-algae removal rugosity indices ($\Delta D = D_f - D_i$) was then calculated to determine the effect that algae removal had on fine-scale reef surface rugosity. I used a paired-samples t-test to compare rugosity index measurements prior to and after algae were removed.

3.3 Results

Cascading effects of crab density on coral reef community composition

Algae cover

I processed a total of 600 photo quadrats (10 photos per site x 12 sites x 5 sampling events) to monitor the effect of crab addition and algae removal treatments on the composition and distribution of the benthic algal community over the course of the 13-month experiment. Mean initial algae cover (i.e., prior to any treatment application or manipulations) across all sites was high at 63% (range 48% - 73%) and remained high on control reefs throughout the duration of the study ranging from 50% to 65%. The composition of the benthic algal community on all reefs throughout the entire study was relatively simple with *Halimeda* spp. and turf algae comprising the overwhelming majority of observations, though *Dictyota* spp., *Wrangelia* spp., and mixed or unidentifiable algal amalgams were infrequently observed. Immediately following the application of treatments in July 2015, reefs from which algae were manually removed by divers but no crabs were added (Scrubbed treatment) experienced an immediate reduction in mean algae cover from 69% (± 36 sd) to 7% (± 11 sd). Reefs from which algae were removed manually and crabs were subsequently added (Scrubbed + Crabs treatment) experienced a similar immediate reduction in mean algae cover from 59% (± 30 sd) to 9% (± 12 sd). Thus, reefs from which algae were manually removed by divers experienced an immediate mean reduction of algae cover of 87% (range: 79% - 91%) in July 2015, immediately following the scrubbing treatment application.

Over the course of the one year study, there was a significant effect of both crab addition ($t = 3.0063$, $df = 56$, $p = 0.0039$) and algae scrubbing ($t = 2.3904$, $df = 56$, $p = 0.0202$) treatments as well as their interaction ($t = -2.2358$, $df = 56$, $p = 0.0294$) on the cover of macroalgae on the experimental patch reefs; however, sampling event had no effect ($t = 0.9751$, $df = 56$, $p =$

0.1658) (Table 4; Fig. 11). Reefs from which algae were removed and crabs were added remained in a significantly lower algae-cover condition than control reefs throughout the duration of the study with cover remaining low between 9% and 16% (Fig. 11). Reefs to which crabs were added but algae were left unmanipulated experienced a steady and significant decline in macroalgae cover of 58% over the course of the study. Algae grew somewhat faster on all reefs, particularly turf algae, between the last two sampling events as reflected in the data for both the crab addition reefs and the Crabs Added – Algae Removed treatment reefs (Fig. 11 & 12). The cover of macroalgae, again primarily turf algae, fluctuated seasonally during the experiment on reefs in the No Crabs Added – Algae Removed treatment group. Following the significant reduction in the cover of both *Halimeda* spp. and turf algae, both groups increased between July 2015 and October 2015, then declined until May 2016 when they again increased through August 2016.

Juvenile coral density surveys

I recorded a total of 830 juvenile corals from 15 different species on the patch reefs. All three manipulative treatments (No Crabs Added – Algae Removed, Crabs Added – No Algae Removed, and Crabs Added – Algae Removed) had significantly higher recruit densities (coral recruits / m² of reef surface area) than did unmanipulated (i.e., negative control) reefs (Fig. 13; Table 5). There was a significant effect of crab addition ($t = 2.4911$, $df = 9$, $p = 0.0344$), removal of algae by scrubbing ($t = 2.3220$, $df = 9$, $p = 0.0453$), and their interaction ($t = -2.3446$, $df = 9$, $p = 0.0437$) on the density of coral recruits on patch reefs. Reef size, measured as surface area (m²), was included in the model as a random effect to control for potential covariance due to this parameter, but had no effect on coral recruitment patterns ($t = 1.2E-6$, $df = 11$, $p > 0.5$) (Fig. 13; Table 5).

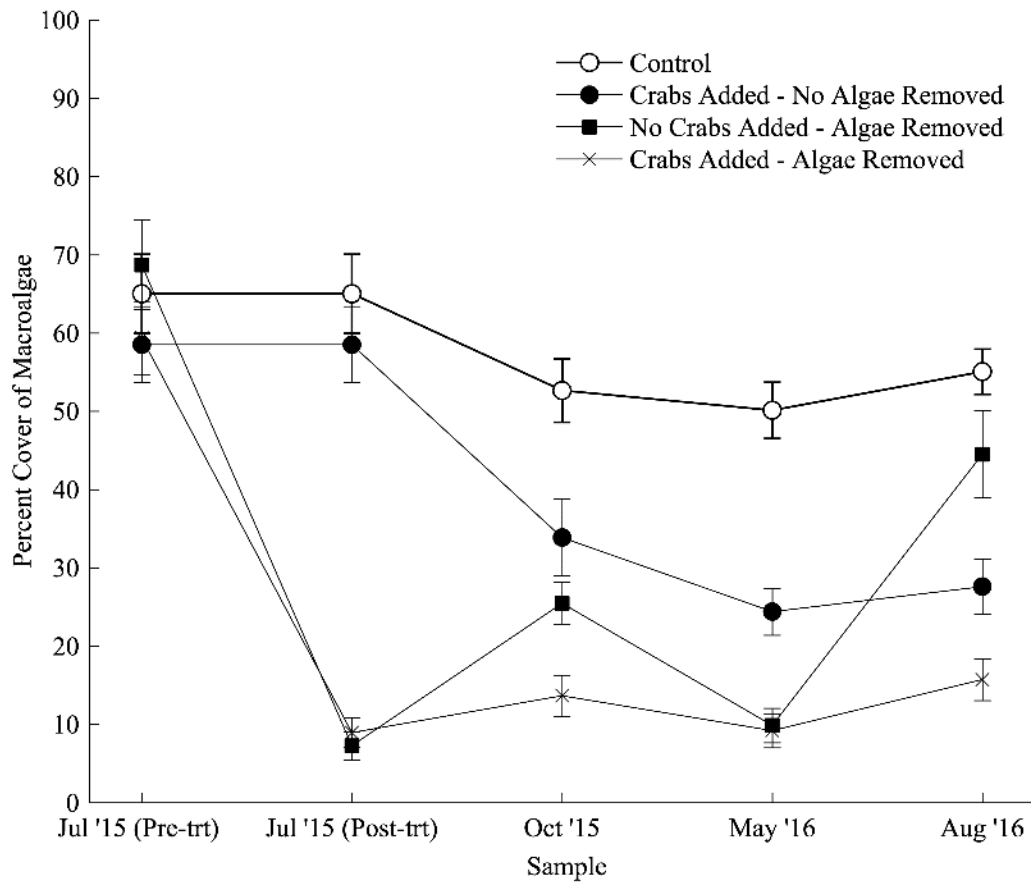


Figure 9. Mean percent cover of macroalgae in each treatment group through time. Error bars are standard error of the mean.

Table 4. Results of the generalized linear mixed effects analysis to model the effect of crab and algae treatments on the percent cover of macroalgae through time.

Fixed Effects	Estimate	Standard Error	<i>df</i>	<i>t</i> value	<i>p</i>
Crab Treatment	29.1840	9.7077	56	3.0063	0.0039
Algae Treatment	25.0850	10.4940	56	2.3904	0.0202
Sampling Event	-1.3691	0.9751	56	-1.4041	0.1658
Crab Treatment X Algae Treatment	-25.2630	11.2990	56	-2.2358	0.0294

Random Effects	Estimate
Reef	14.4720
Error	0.6451

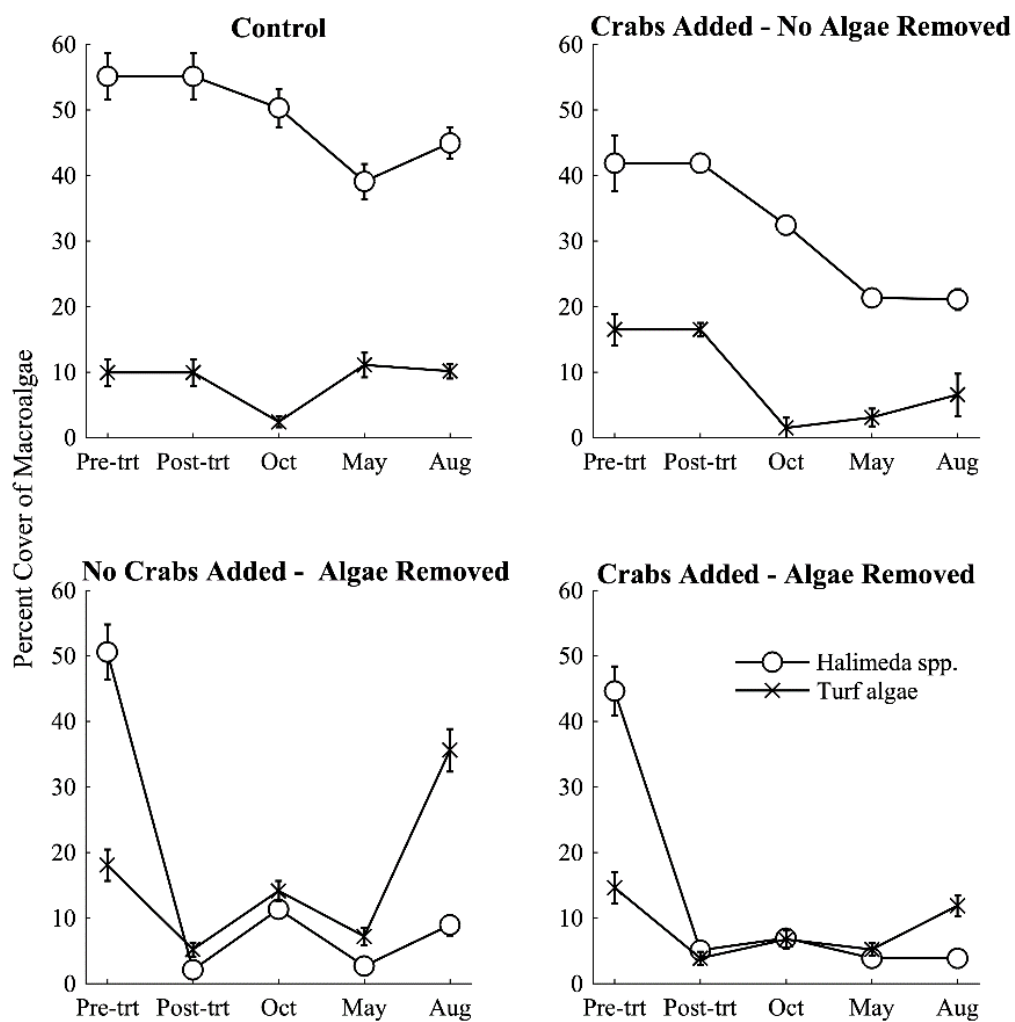


Figure 10. Mean percent cover of *Halimeda* spp. and turf algae in each treatment group through time. Error bars are standard error of the mean.

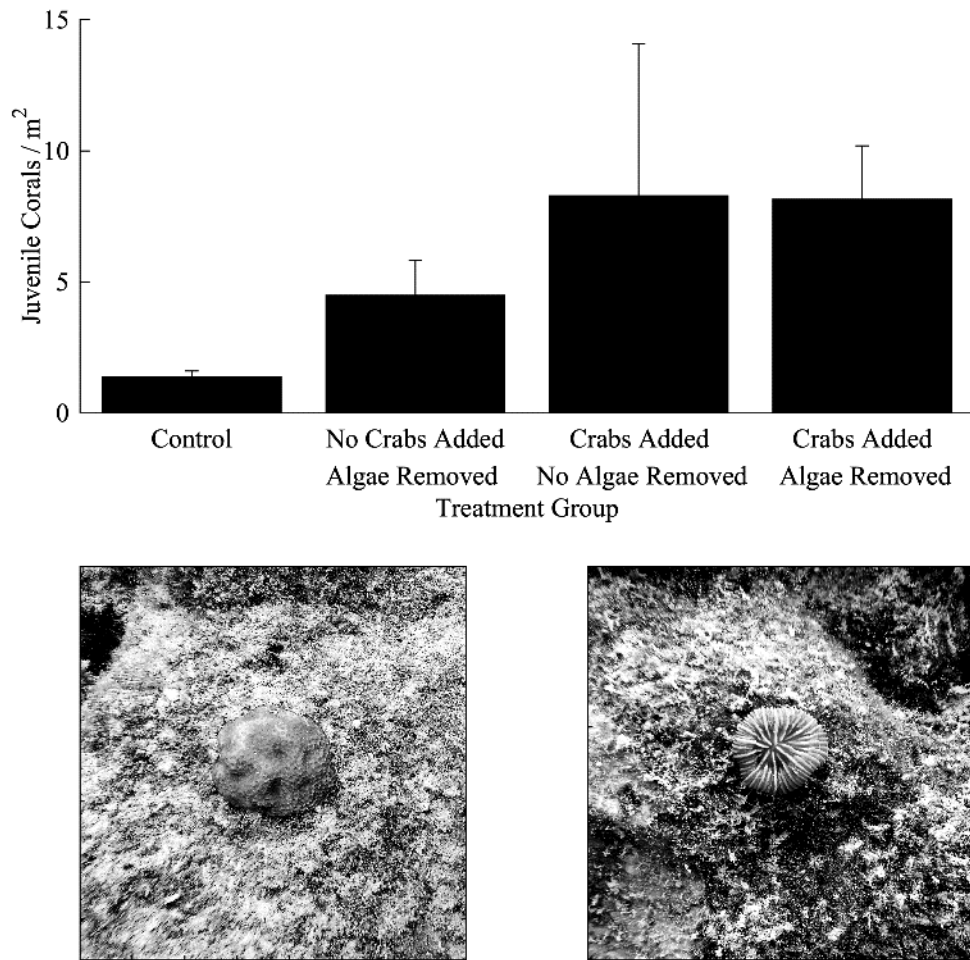


Figure 7. Mean density of juvenile corals in each treatment group. Error bars are standard error of the mean. Representative photos of coral recruits observed are also presented – *Porites astreoides* (bottom left) and *Meandrina meandrites* (bottom right).

Table 5. Results of the generalized linear mixed effects analysis to model the effect of crab and algae treatments on the number of coral recruits observed two years after treatments were applied.

Fixed Effects	Estimate	Standard Error	<i>df</i>	<i>t</i> value	<i>p</i>
Crab Treatment	0.0113	0.0046	9	2.4911	0.0344
Algae Treatment	0.0101	0.0043	9	2.3220	0.0453
Crab Treatment X Algae Treatment	-0.0078	0.0033	9	-2.3446	0.0437

Random Effects	Estimate
Reef Size	5.95E-07
Error	0.50391

Reef fish abundance and richness surveys

Diver census

The composition of the reef fish community was significantly affected by both crab addition ($df = 1$, $F = 4.4605$, $p = 0.0030$) and time ($df = 3$, $F = 3.8758$, $p = 0.0370$) whereas the removal of algae had a marginal effect on the composition of the fish community ($df = 1$, $F = 2.0583$, $p = 0.0630$). The two-way interaction between crab addition and algae removal was the only two-way interaction with a significant effect on fish community composition ($df = 1$, $F = 2.7993$, $p = 0.0250$). The three-way interaction among crab addition, algae removal, and time factors was not significant ($df = 3$, $F = 1.0137$, $p = 0.4050$; Table 6). A visual inspection of the data (Fig. 14) shows that both mean richness and mean abundance of reef fish remained relatively constant on Control reefs through the duration of the experiment. Mean richness likewise remained relatively consistent through time, but greater on the reefs where crabs and algae were manipulated in comparison to Control reefs. The abundance of fish on reefs in all three manipulative treatments generally increased through time with a dip in abundance in the May sample.

Table 6. Results of the three-way repeated-measures non-parametric (permutation-based) MANOVA investigating the effect of crab density manipulation, algae cover manipulation and sampling event (time) on the composition of the fish community as measured with visual census.

Source	<i>df</i>	SS	MS	F	<i>p</i>
Crab	1	0.9905	0.9905	4.4605	0.0030
Algae	1	0.4471	0.4471	2.0583	0.0630
Time	3	2.3714	0.7905	3.8758	0.0370
Crab x Algae	1	0.6588	0.6588	2.7993	0.0250
Crab x Time	3	0.6662	0.2221	0.9436	0.5580
Algae x Time	3	0.6517	0.2172	0.9230	0.5810
Crab x Algae x Time	3	0.7060	0.2353	1.0137	0.4050
Residual	32	7.4291	0.2322		
Total	47	13.2907			

Time lapse photographic surveys

The time lapse photo data indicated that fish community structure was significantly altered by the combined effects of crab addition, algal removal, and time of year as indicated by the significant three-way interaction among those factors ($df = 3$, $F = 41.8611$, $p = 0.001$; Table 7). Of the three possible two-way interactions, only the interaction between crab addition and algae removal factors was of marginal significance ($df = 1$, $F = 2.5523$, $p = 0.051$). When the three factors were considered individually, algae removal had a strong effect on reef fish community composition ($df = 1$, $F = 6.1481$, $p = 0.004$), crab addition had only a marginally significant effect ($df = 1$, $F = 2.4451$, $p = 0.055$), and sampling date was not significant ($df = 3$, $F = 2.4696$, $p = 0.980$). The data from photo surveys showed similar trends to those observed in the diver census (Fig. 15). Mean richness and abundance were both consistent on control reefs through the duration of the experiment. Mean richness generally increased on all manipulative treatments through time, but declined slightly in August in all but the control treatment group. Fish were more abundant on all manipulative treatments than on control reefs during every sampling period, although fish abundance on all reefs changed through time: fish abundance

increased during the first three quarterly samplings (Aug, Oct, May) then leveled off after one year's duration.

Table 7. Results of the three-way repeated-measures non-parametric (permutation-based) MANOVA investigating the effect of crab density manipulation, algae cover manipulation and sampling event (time) on the composition of the fish community as measured with remote time lapse photography.

Source	<i>df</i>	SS	MS	F	<i>p</i>
Crab Factor	1	8.3113	8.3113	2.4451	0.055
Algae Factor	1	22.9452	22.9452	6.1481	0.004
Time (Random)	3	32.9783	10.9928	-2.4696	0.98
Crab x Algae	1	29.5623	29.5623	2.5523	0.051
Crab x Time	3	10.1976	3.3992	0.2935	0.996
Algae x Time	3	11.1961	3.732	0.3222	0.995
Crab x Algae x Time	3	34.7476	11.5825	41.8611	0.001
Residual	1184	327.5999	0.2767		
Total	1199	477.5382			

Effect of algae on reef structural complexity

There was a significant difference in the rugosity index values measured prior to the start of experimental manipulations ($\bar{X} = 1.4$, st. dev. = 0.2) and those measured after benthic macroalgae were removed ($\bar{X} = 2.069$, st. dev. = 0.610) ($t = -3.702$, $df = 13$, $p = 0.003$, Fig. 16). Following the removal of macroalgae, the mean reef rugosity index value increased by 43%. Similarly, there was a nearly seven-fold increase in the variance of rugosity measurements after algal removal, likely due to the exposure of voids and complex three-dimensional structure following the removal of macroalgae.

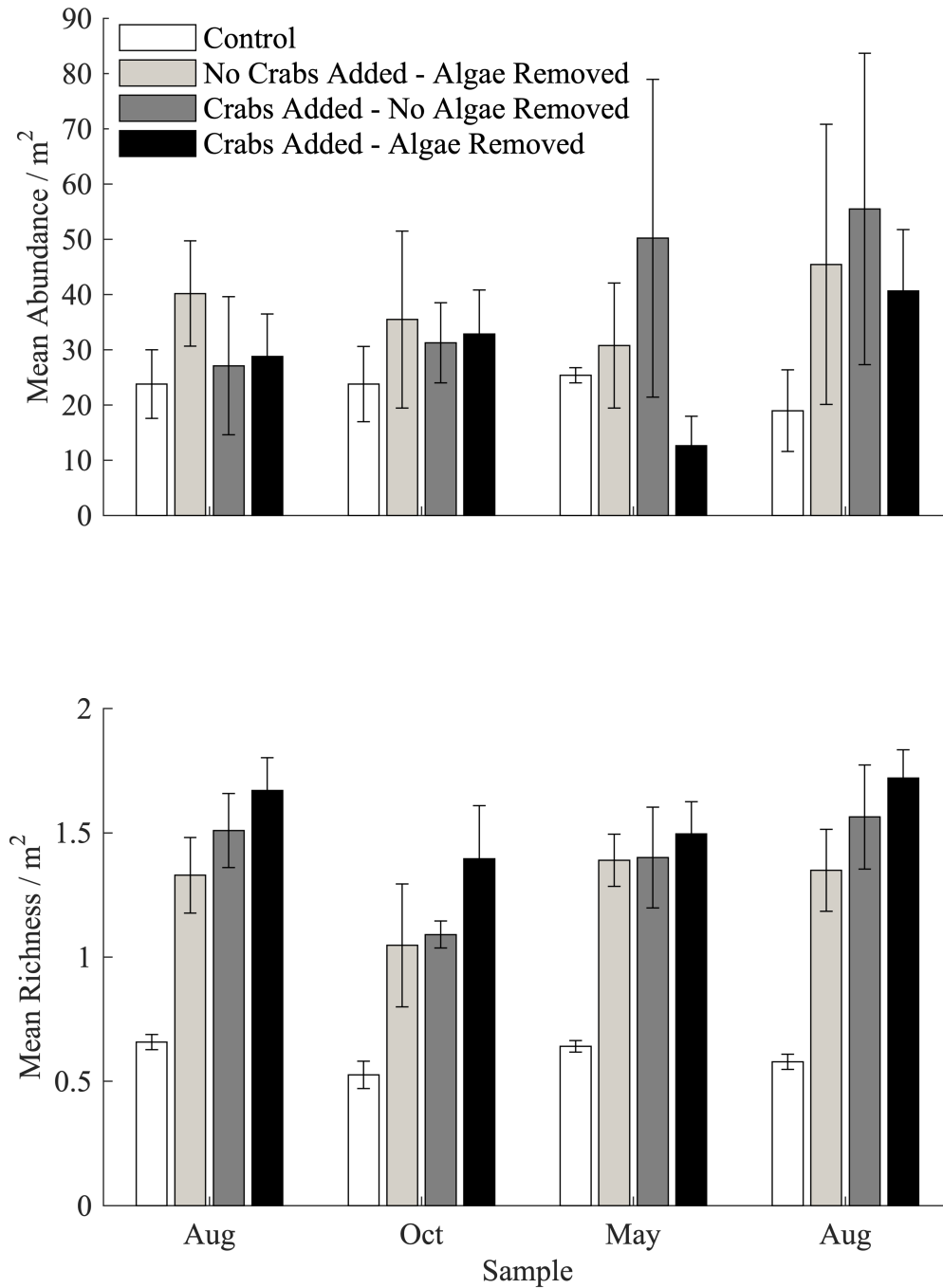


Figure 8. Mean abundance (top) and species richness(bottom) of reef fishes from diver visual census.

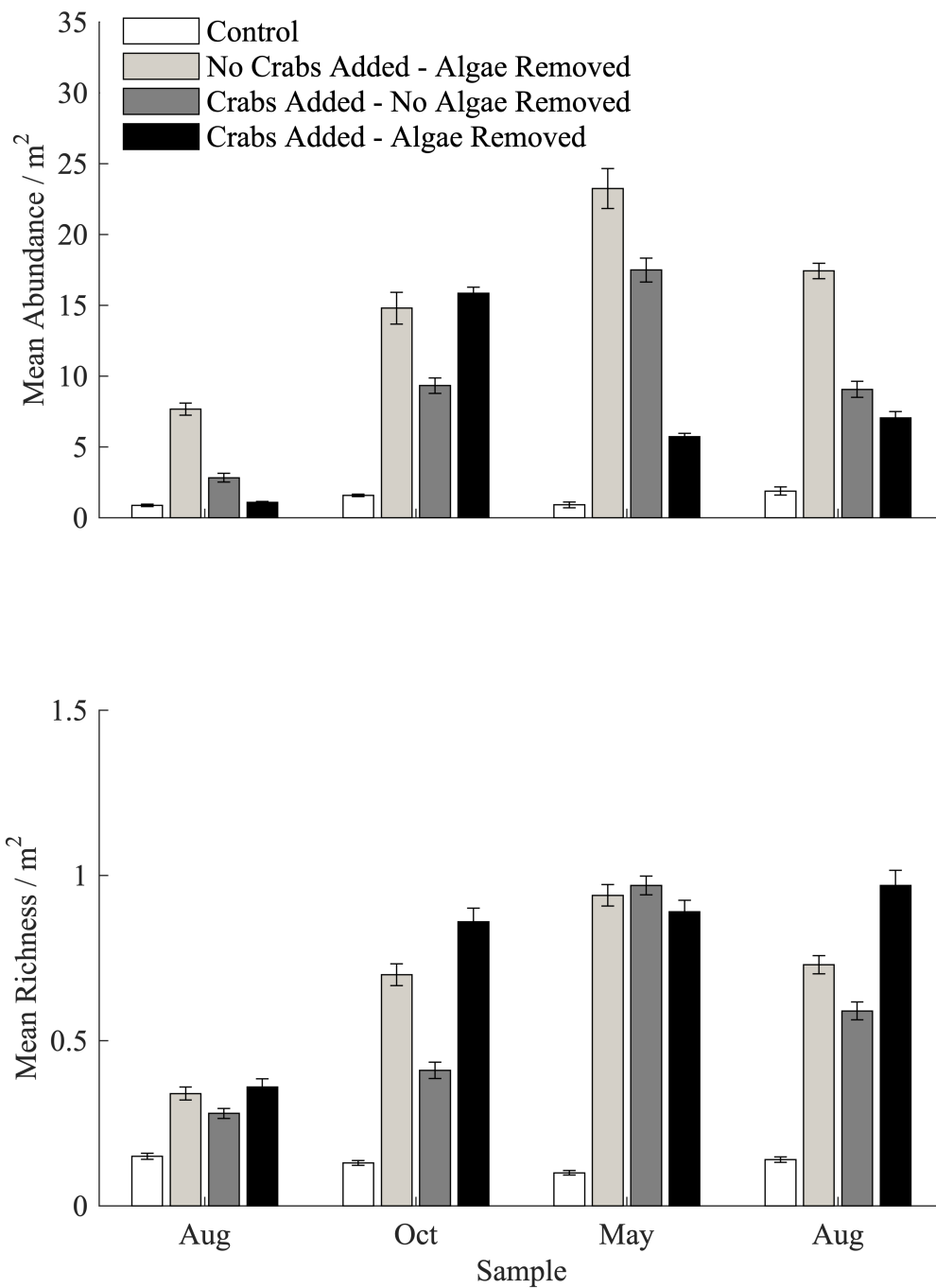


Figure 93. Mean abundance (top) and species richness (bottom) of reef fishes from time lapse photographic survey.

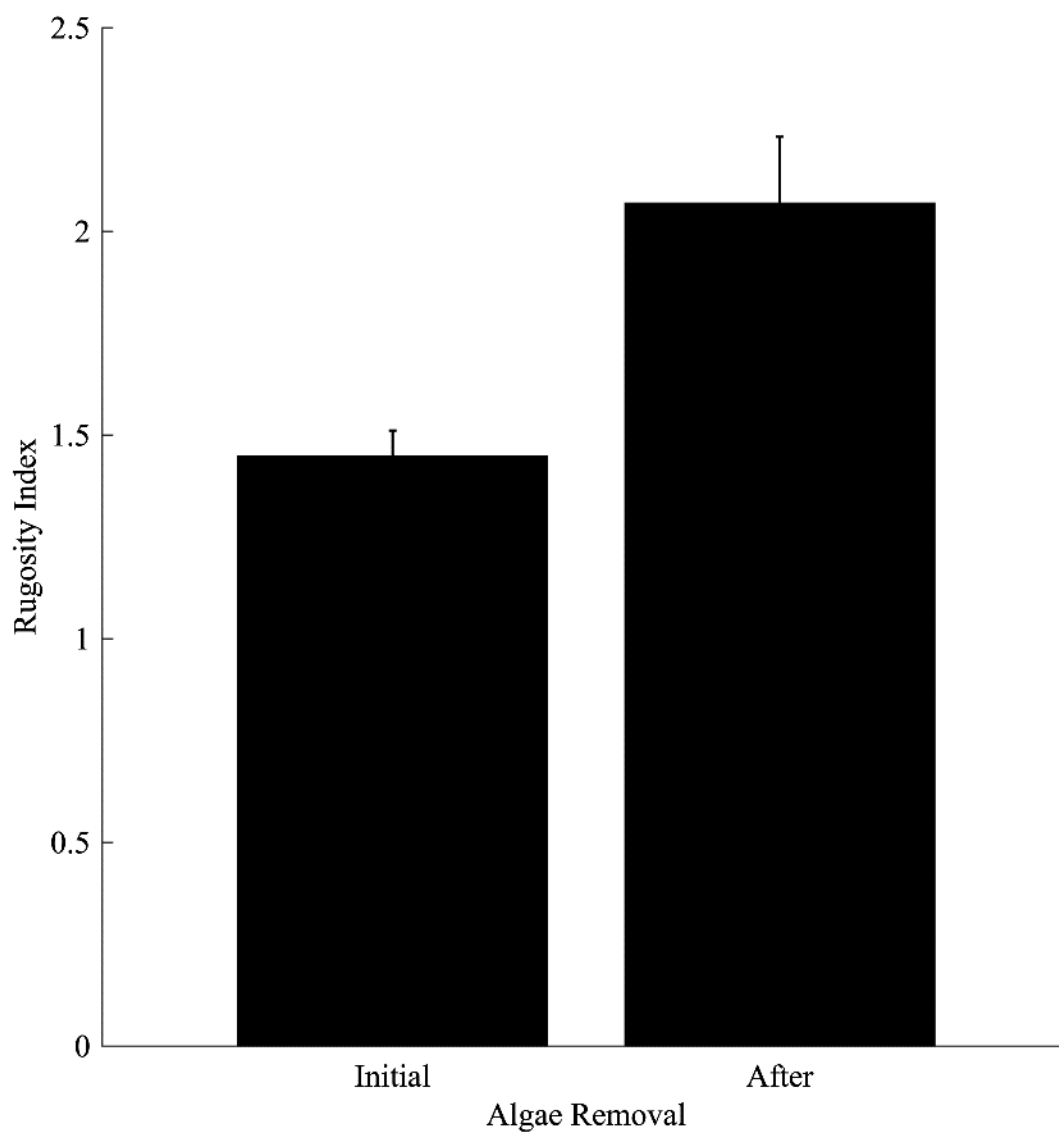


Figure 104. Mean rugosity indices prior to and following the removal of benthic macroalgae. Error bars are standard error about the mean.

3.4 Discussion

In their current degraded state, Caribbean coral reef ecosystems are fragile and have likely become reliant upon a diverse community of small-bodied invertebrate and finfish grazers to provide the critical grazing function necessary to moderate the proliferation of benthic macroalgae that compete with scleractinian corals already stressed by adverse environmental conditions and disease. As I have demonstrated in this study, cryptic grazers such as *M. spinosissimus* represent sleeping functional groups whose effects on reef communities are complex and density-dependent. *Maguimithrax spinosissimus* occur naturally in the Caribbean and my study area, but their density is typically so low that their grazing effects are diffuse and often imperceptible on a wider spatial scale (Butler and Mojica 2012) – in essence, these grazers are cryptic in both form and function. When aggregated, however, their effect on the benthic and demersal reef communities is rapid and intense. Crab grazing reduced macroalgae cover on experimental reefs by 60%, revealing 43% more rugose reef structure, which resulted in nearly a 5-fold increase in the density of juvenile corals, a two-fold increase in the abundance of fish, and 2.5-fold increase in the richness of fish species compared to control reefs.

Beyond the direct effects of *M. spinosissimus* grazing in reducing the abundance of benthic macroalgae, the cascading indirect effects of the crab's increased density on the structure and composition of the coral patch reef community was substantial. A modest increase in the density of *M. spinosissimus* resulted in a massive reduction in benthic macroalgae, a significant increase in live juvenile coral density (i.e., coral recruitment success), and significant increases in both the richness and abundance of coral reef fishes. These cascading effects of enhanced density of *M. spinosissimus* shed a new light on the intricacies of coral reef ecosystem function, especially in highly disturbed systems such as those I investigated in the Florida Keys.

This study is also novel in that the year-long, manipulative field experiment was repeated in a separate location and at a different time than the original study (see Chapter 2). The remarkably similar results of both experiments confirms the study's reproducibility and generality. Confirmation that the results of ecological studies are reproducible and generalizable under other conditions is rare (Cassey and Blackburn 2006; Schnitzer and Carson 2016).

Not only do my results indicate a reversal in the direction of the phase trajectory of reefs supplemented with *M. spinosissimus*, but contrary to prevailing dogma, they suggest that grazing function in coral reef systems is not restricted to large-bodied herbivorous finfishes and echinoderms. Crustacean grazers too can have a strong density-dependent effect on the benthic community. My results also confirm that algae, particularly when well-established and in a late successional stage, play a major role in driving not only patterns in coral recruitment and survival, but also in the composition of the benthic and demersal fish communities of shallow nearshore coral reef systems. In deterring coral recruitment, juvenile coral survival, and fish aggregation, dense algae strengthen the stability of the coral depauperate phase in which many Caribbean reefs now exist (Gardner et al. 2003; Ruzicka et al. 2013).

This study highlights the role herbivory plays in driving reef community assembly, suggesting strong top-down control in these systems at the coral-depauperate end of the phase continuum (e.g., Mumby et al. 2007, Steneck et al. 2017). My results, along with those reported for other herbivores (Burdick 2008; ; Cheal et al. 2010; Kuempel and Altieri 2017), strongly suggest that the resilience and function of coral reefs is dependent upon a rich and abundant community of herbivores, rather than on the abundance of a single or small group of species (e.g., *Diadema* and large-bodied parrotfishes). The strong, community-level response I observed in this study suggests that grazing crabs may be an important component of this diverse group of herbivores. *Maguimithrax spinosissimus* is the largest Mithracid crab in the Western Atlantic, but

it is by no means, the only grazer within the family. In fact, *Mithraculus sculptus*, a close relative of *M. spinosissimus* has been a mainstay of the marine aquarium trade for decades due to its high grazing rate and ability to maintain low algae cover in closed aquarium systems. These diminutive grazers, along with a number of other closely-related crab species, occur naturally on Caribbean reefs and in back-reef lagoon habitats where they may play an unrealized role in moderating algal productivity. Algal management is becoming a very important aspect of coral reef management and restoration, therefore a better understanding of the role of cryptic and small-bodied herbivores in structuring the benthic algal community is not only important to the study of natural history and community ecology but is imperative to the success of coral restoration efforts.

The results of my study highlight another interesting and new aspect of coral reef ecology – the effect of algae on the structural complexity of degraded reef matrices. The role of architectural complexity in driving patterns of fish community composition is well-studied (Gratwicke and Speight 2005; Alvarez-Filip et al. 2011; Kovalenko et al. 2012; Shantz et al. 2015), as is the role algae play in driving fish community dynamics (McClanahan et al. 1994; Fabricius et al. 2005; Idjadi 2013; Brooker et al. 2016a, b; Shantz et al. 2017). Once benthic algae are well-established on a coral reef, they tend toward a stable dominance of the benthic community (Mumby 2009b). The stability of macroalgal communities is due, in part, to the phenomenon wherein the grazing rates of herbivorous fishes is more than 3-fold lower in areas of dense algae than in areas where algae have a more patchy or moderate distribution (Shantz et al. 2015). Reef fishes also consume less algae when presented with a homogenous backdrop of dense benthic algae cover (Idjadi 2013) and they avoid the chemical cue of dense algae on degraded coral reefs (Dixon et al. 2014). However, to the best of my knowledge, this is the first study to investigate the role that dense algae plays in reducing the rugosity of the reef matrix,

hence the availability of small crevice shelters so important for small reef fishes whose susceptibility to predation is high (Alvarez-Filip et al. 2011).

The dense cover of benthic macroalgae I observed in the field significantly reduced the rugosity of the reef matrix (Fig. 16) by filling in interstitial spaces, crevices, and holes, thereby denying small fish access to structural refuges and interior areas of the reef. Removing this dense algal growth significantly increased the rugosity of the reef structure, presumably increasing the availability and quality of habitat for small reef fish. The results of this simple study suggest that in addition to the visual and chemical cues of algae which reduce the grazing intensity of herbivorous fishes, dense algae also reduce the availability of reef fish habitat, which is particularly important for larval and juvenile reef-associated fishes (Alvarez-Filip et al. 2011; Dixon et al. 2014; Brooker et al. 2016b; Lecchini et al. 2017). It has also been reported that dense algae substantially reduce flow and O₂ concentrations within the reef matrix (Stocking et al. 2016), which likely results in avoidance of those areas by reef fishes as well.

It is possible that the removal of algae from the reef structure removes the chemical deterrents to fish produced by dense algae (see for example Dixon et al. 2014; Brooker et al. 2016b). However, it is unlikely that this would explain the results observed in the field where chemical cues from the numerous natural algae-dominated reefs that completely surrounded all of the experimental reefs may perhaps swamp olfactory cues available to fish. It is also possible that the reduction in algae cover by crab grazing resulted in a reduction of the visual deterrent associated with dense algae cover (Idjadi 2013; Brooker et al. 2016a). The most parsimonious explanation of the results from my field studies is that reef fish abundance is strongly affected by microhabitat availability and quality. However, the increase in large-bodied fishes I observed in the field is likely an indirect effect of an increased abundance of prey for piscivorous fishes (e.g., snappers, groupers) and suitable grazing substrates (e.g., exposed algal turf) for herbivorous

fishes (e.g., surgeonfishes, parrotfishes) rather than a direct response to habitat availability.

These results further support the hypothesis that algae cover has a strong effect on coral reef community assembly through a variety of mechanisms affecting corals and fishes. If true, then a top-down (herbivory) approach should be taken when considering the management, preservation, and restoration of Caribbean coral reef communities.

Here, I have laid the foundation for a potential new approach for bioremediation facilitating the restoration of Caribbean coral reefs. By manipulating the density of *M. spinosissimus*, I was able to effectively increase localized grazing intensity enough to have a significant and deleterious effect on the cover of benthic macroalgae that, in turn, elicited a strong response in the survival of juvenile corals as well as in the abundance and richness of reef fishes. Adding crabs to algae-dominated reefs reduced the cover of algae opening up the natural rugosity of the reef to shelter-seeking fishes. Thus, the manipulation of crab density in carefully selected areas of reef may well facilitate a manipulation of the phase trajectory at least of localized sections of the reef. Obviously, disturbance regimes will dictate the degree to which any such mechanism or restoration scheme might ultimately be successful in altering the structure and composition of the benthic community. However, predicting or manipulating those effects is beyond the scope of this study and of most practical efforts in restoration ecology. Ecological restoration, by definition, is an attempt to return some system to a previous ecological state (Suding et al. 2015). If the disturbance regime has been altered and is the proximate cause of degradation, without addressing the source of disturbance, restoration is unlikely to last at best and futile at worst.

It is likely that applying such a manipulative method on a landscape-scale would be logistically challenging with many herbivore species as has been realized with efforts to enhance herbivorous fishes and *D. antillarum* for restoration. However, the life history of *M.*

spinosissimus (and Mithracid crabs in general) offers some concession in this respect. *M. spinosissimus*, like other Majids, hatches as a swimming zoea, has two zoeal and a single megalopal larval stage before metamorphosing to first crab (i.e., juvenile) in 5 to 6 days (Brownell et al. 1977; Provenzano and Brownell 1977). The juvenile crabs then grow rapidly and are estimated to reach large (>125 mm CL) adult size between 1 and 4 years after hatching (Creswell et al. 1989; Wilber et al. 1992). In a previous study (See Chapter 2) I demonstrated that, at least on shallow nearshore patch reefs, *M. spinosissimus* essentially escape their high post-larval mortality rates after reaching only ~30mm *CW* which equates to roughly 2-5 months post-hatch (Wilber and Wilber 1989). Maricultural production of the species has previously been investigated and production of juvenile crabs is relatively simple both logistically and with respect to labor-intensity (Creswell et al. 1989; Tunberg and Creswell 1991). Thus, it is very likely that with minimal investment of time, effort, and money, producing crabs for the purpose of reef-scale stock enhancement-based restoration operations is possible and practical.

A great deal of effort and funding have been expended in support of a similar system involving *Diadema antillarum*, but urchin life history has proved to be less than ideally suited to mariculture and thus, production of urchins in numbers sufficient for restoration has been a major bottleneck to their use in reef restoration of any ecologically meaningful scale (Leber et al. 2008; Moe 2010). Although it would be unwise to abandon the efforts underway throughout the Caribbean to reintroduce and re-establish *Diadema*, it would likely be just as unwise to ignore the potential of alternative or complementary species such as *M. spinosissimus* in approaching restoration programs aimed at controlling the proliferation of benthic macroalgae on degraded Caribbean reefs. Finally, the continued existence of coral reefs, in the Caribbean and around the globe, depends on either rapid adaptation of coral reef communities to climate change, or a concerted effort to ameliorate anthropogenic effects on the climate and Earth as an ecocosm.

Unless the degradation of Earth's biomes is stopped or slowed, it is likely that coral reef ecology will be a course offered in the history department of universities for future generations.

CHAPTER 4

MULTIPLE CONSUMER EFFECTS OF THE *MITHRACIDAE* FAMILY OF GRAZING CRABS ON CORAL REEFS IN THE FLORIDA KEYS

4.1 Introduction

A current paradigm in theoretical community ecology holds that the resilience of a community to perturbation is, at least in part, determined by the complexity of its attendant ecological community (Loreau et al. 2001; Tilman et al. 2001). Generally, as species richness increases, so too does the richness of function in the community (Schwartz et al. 2000; Loreau et al. 2001; Duffy 2009). With a greater number of species performing the same or similar functions, redundancy in those functions increases (Naeem 1998; Rosenfeld 2002; Guillemot et al. 2011; Kang et al. 2015), and so too does the community's resilience to perturbations that in turn can result in the loss of species, their abundance, and their ecological function (McNaughton 1977; Tilman et al. 1997; Naeem 1998; Rosenfeld 2002; Guillemot et al. 2011). Thus, high-diversity systems with greater functional redundancy are predicted to function and recover more rapidly from perturbation than less species rich systems. When species richness and functional redundancy are low, perturbations can have strong effects on ecosystem functioning – in some cases resulting in phase shifts among alternative stable states. These concepts form the basis of the “insurance hypothesis” wherein increased biological diversity and, by extension, functional redundancy serve as ecological “insurance” against major shifts in the status of ecological communities and ecosystems (McNaughton 1977; Vitousek et al. 1997; Yachi and Loreau 1999; Loreau et al. 2001; Fetzer et al. 2015).

An excellent example of these ecological tenets comes from Caribbean coral reef ecosystems. Once diverse and stable, increasing anthropogenic effects from industrialized fishing, coastal development, and climate change have led to a reduction in the richness and abundance of the grazing community on Caribbean reefs (Jackson 2001). First came declines in predatory and large herbivorous fishes (Jackson et al. 2001; McClenachan 2009) that led to the emergence of the long spine sea urchin (*Diadema antillarum*) as the dominant grazer in the region and substantially reduced grazing redundancy (Jackson et al. 2001; Mumby 2006; Mumby et al. 2006a). In the early 1980s, a regional pandemic caused by an as yet unidentified pathogen almost completely extirpated *D. antillarum* and the species' functional extinction as a dominant grazer (Lessios 2016), which led to a massive and catastrophic phase shift from coral- to algal-dominated coral reef communities throughout much of the region (Mumby et al. 2006b; Mumby et al. 2007; Mumby 2009b). That condition persists today more than 30 years later despite concerted efforts to reintroduce and protect fish and urchin grazers on the region's reefs (Moe 2010; Lessios 2016). The regional demise of *D. antillarum* was not the only factor contributing to the Caribbean phase shift (e.g., coastal eutrophication, thermal stress, ocean acidification, increased fishing effort/efficiency), but it represented a tipping point that resulted from a paucity of functional diversity, hence a lack of ecological insurance against a changing environment.

Yet, biological diversity alone does not always provide the ecological insurance necessary to thwart change in coral reef ecosystems. Reef communities of the Indo-Pacific region are some of the most diverse on the planet (Paulay 1997; Barber 2009); indeed, the "coral triangle" (Indonesia, Malaysia, and the Philippine Islands) contains the global maximum in marine biological diversity (Barber 2009). Despite this rich diversity, the coral triangle harbors the highest proportion of vulnerable and near-threatened coral species on the planet (Carpenter et al. 2008). Even with the highest richness of species in the sea, the coral reef communities of the

Indo-Pacific region are proving vulnerable to a changing environment associated with global climate change (Carpenter et al. 2008).

Bellwood et al. (2003) report that within this nexus of marine diversity there is surprisingly low functional redundancy on Pacific coral reef communities, with such functional roles as bioerosion restricted to a single dominant species (i.e., the humphead parrotfish, *Bolbometopon muricatum*). On Australia's Great Barrier Reef (GBR), herbivory of an abundant macroalgae (*Sargassum* spp.) is likewise restricted to a single grazing fish (*Naso unicornis*; Hoey and Bellwood 2009). Even though grazers may be locally abundant, a lack of grazer diversity may limit functional redundancy as observed in a recent study on three coral reefs within the GBR system that had undergone a strong coral-algal phase shift despite an abundant parrotfish community, but one with limited species richness (Cheal et al. 2010).

These examples suggest that high-diversity per se may not necessarily equate with increased functional redundancy and thus resilience of communities (Hooper et al. 2012). Species within a functional guild are not equal in their ecological impact. Thus, "species identity", that is, the specific role and impact of species differ. In the ecological plant literature this effect is known as "transgressive overyielding": specifically, when a mixture of plant species surpasses the additive productivity of the same species in monoculture (Schmid et al. 2008).

The identity of species in a community is increasingly recognized as a strong factor in determining the strength and direction of species interactions and community functioning (Hooper et al. 2005). Traditionally, ecologists have placed a great deal of emphasis on negative interactions (e.g., predator-prey interactions, competition, parasitism, disease) as the ecological processes driving the composition and function of communities, but increasingly, ecologists are recognizing the importance of positive interactions (e.g., mutualism, facilitation) in driving the composition and function of community assemblages and the importance of species identity for

those positive interactions (Bertness and Callaway 1994; Bertness and Leonard 1997; Stachowicz 2001).

When multiple co-occurring species are simultaneously performing the same function they are said to be functionally redundant (Walker 1992). Functional redundancy is a basic component of the insurance hypothesis – multiple functionally redundant species provide resilience of a function to perturbation in that a modest loss in diversity does not remove a function or functional group from the community and thus the community continues to operate even in the face of disturbance (Walker 1992; Yachi and Loreau 1999; Valone and Barber 2008; Leary and Petchey 2009). However, few species are truly redundant in their functional roles (e.g., Rosenfeld 2002; Loreau 2004). More often, differences in species niches are subtle and they perform very similar functions such that one or more species' functional role(s) facilitate the function of other species in a series of subtle cascading facilitative interactions (e.g., Burkepile and Hay 2008, 2010). These often more subtle interactions are said to be complementary – the function of one (or multiple) species is complementary to the function of another (or multiple) species (Frost et al. 1995; Blüthgen and Klein 2011).

These types of redundant and complementary interactions are common in coral reef communities (see Coen 1988a, b; Bertness and Callaway 1994; Stachowicz and Hay 1996, 1999; Stachowicz 2001; Stachowicz and Whitlatch 2005). In a recent study, Burkepile and Hay (2011) demonstrated that within and among three common genera of herbivorous fishes there were both complementary and redundant ecological relationships. They posit that detecting these relationships is often context-dependent (i.e., dependent upon the initial benthic community composition), and that the nature of these interactions depends upon the identity of the species involved. In previous chapters (Chapters 2 & 3), I demonstrated the substantial density-

dependent effects of a large herbivorous crab, but *M. spinosissimus* is just one among many co-occurring species of grazing crabs on Caribbean coral reefs.

Mithracid crabs are a diverse group (Windsor and Felder 2009, 2014; Klompmaker et al. 2015; Assugeni et al. 2017; Magalhães et al. 2017; Ng et al. 2018). Many species in the Mithracidae are grazers on Caribbean reefs and backreef habitats (Coen 1988a, b; Stachowicz and Hay 1996, 1999; Windsor and Felder 2009, 2014; Klompmaker et al. 2015). Their morphology and life history patterns are similar, but still different enough that one may reasonably expect variation in their ecological roles as cryptic grazers in these habitats (Windsor and Felder 2009, 2014; Klompmaker et al. 2015). Many species of *Mithraculus* are abundant and commonly co-occur as mutualist associates of various cnidarian and algal hosts throughout the Caribbean region (Coen 1988a, b; Stachowicz and Hay 1996, 1999; Giraldes et al. 2017; Gonzáles-Gómez et al. 2018). Previous studies of such mutualistic interactions involving *Mithraculus* spp. have focused on the interaction of a single Mithracid species and its host (e.g., Coen 1988a, b; Stachowicz and Hay 1996, 1999). However, with the subtle differences in life history, morphology, and ecological function among Mithracid species that co-occur to the point of sharing a single Cnidarian host, it is likely that their functional (e.g., grazing) effects are synergistic in mediating the proliferation of benthic algae (Coen 1988a,b).

Here, I investigate the hypothesis that multiple Mithracid species are complementary in their effects on benthic algal communities using a series of laboratory experiments investigating dietary preference among an array of common benthic macroalgae. I then tested the effect of multiple individuals on the net consumption of algae in an assay designed to test for independent, synergistic, or antagonistic effects of multiple individuals and multiple species of Mithracid crabs on consumption of macroalgae.

4.2 Methods

Study areas and general methodology

I conducted this experimental laboratory study in three locations: The Smithsonian Institution's Caribbean Coral Reef Ecosystems (CCRE) field station on Carrie Bow Caye, Belize; The Smithsonian Institution's Smithsonian Marine Station (SMS) in Ft. Pierce, Florida, USA; and Goshen College's J.N. Roth Marine Biology Station (GC) on Long Key, Florida, USA. At two locations (Belize and Long Key), the algae required for the experiments were collected from nearby coral reef structures and transported to the laboratory in aerated seawater. These algae were either used immediately or maintained in flow-through seawater systems with natural lighting for no longer than 48 hours before being used in consumption trials. Aquacultured macroalgae of three genera (*Ulva*, *Gracilariaria*, and *Chaetomorpha*) were used in the trials conducted at Ft. Pierce, FL because natural coral reef associated algae were not locally available.

I collected crabs for the experiments at all three sites from nearshore backreef habitats in Belize and Florida. The location, species, sex, and size (carapace width; *CW*) was recorded for each crab collected. In Belize, I was able to collect a sufficient number of individuals of four Mithracid crab species (*Maguimithrax spinosissimus*, *Mithraculus sculptus*, *Mithraculus coryphe*, and *Mithraculus cinctimanus*; Fig. 17), so experiments there were conducted with all four crab species. I could not locate *Mithraculus cinctimanus* in the nearshore habitats in Florida Keys, so that species was not included in the experiments conducted in Florida. The size structure (*CW*) and sex ratio of the three Mithracid species collected and used in my investigation at all locations is presented in Figure 18. The disparity in sample sizes among species is a reflection of their relative abundance and the equipment (e.g., oven size) and logistical limitations (e.g., time constraints, weather conditions) I encountered.

Mithracid grazing

Biomass index

To measure the relationship between wet and dry weight for the four species of crabs of interest, I retained a subsample of the crabs used in feeding experiments. After blotting the animal dry with a dry paper towel, I measured the wet weight (M_W) of each crab to the nearest 0.1 g. The crabs were then humanely sacrificed by rapid freezing then dried in an oven at 60° C to a constant weight (24 – 36 h). Once the crabs were dried, I measured their dry weight (M_D) again to the nearest 0.1 g and used these data to build a regression model describing the relationship between wet weight and dry biomass for each crab species (Fig. 19). I also built a regression model describing the relationship between crab size (mm CW) and wet weight (Fig. 20). Crabs that were not used in dry weight measurements were returned to the location from which they were collected immediately after each algae consumption trial.

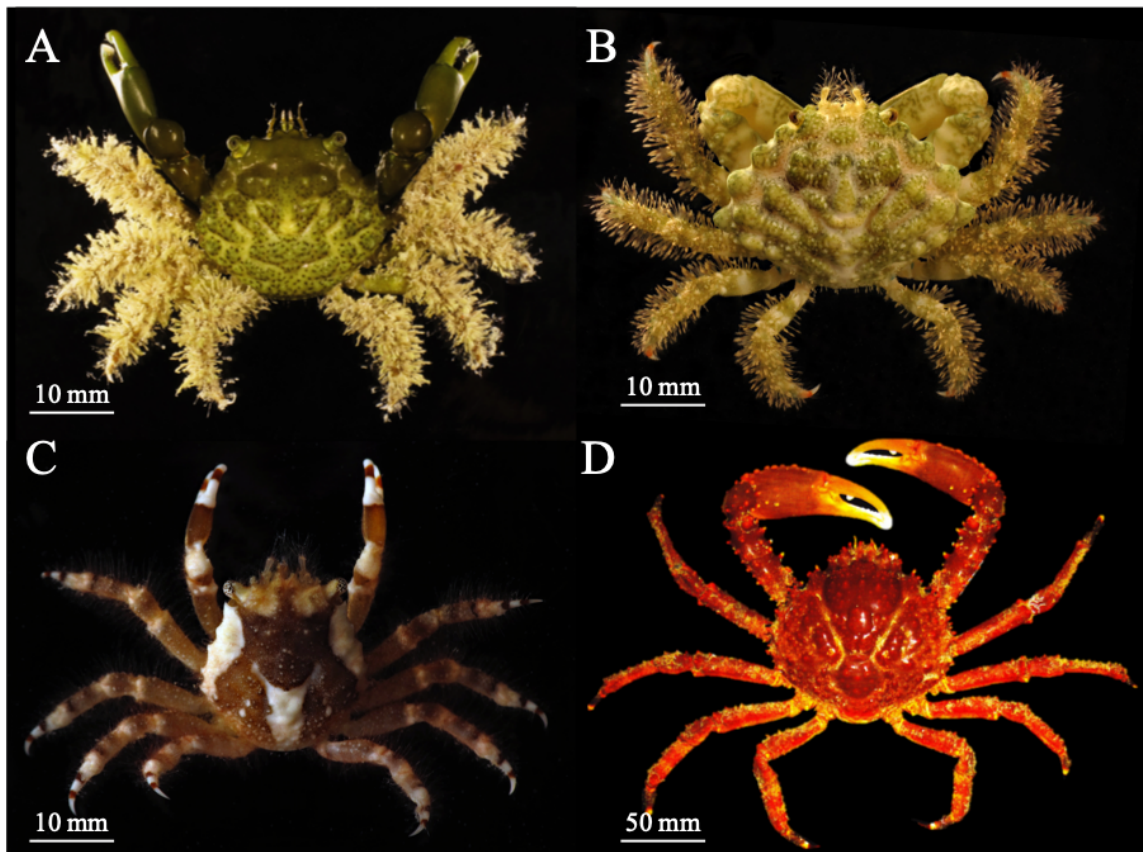


Figure 115. Photographs of the four species of mithracid crabs used in this study. A. *Mithraculus sculptus* B. *Mithraculus coryphe* C. *Mithraculus cinctimanus* D. *Maguimithrax spinosissimus*.

Note the difference in scale in figure D for the much larger *M. spinosissimus*. Photo credit: (A,B,C) A Spadaro (D) A Baeza.

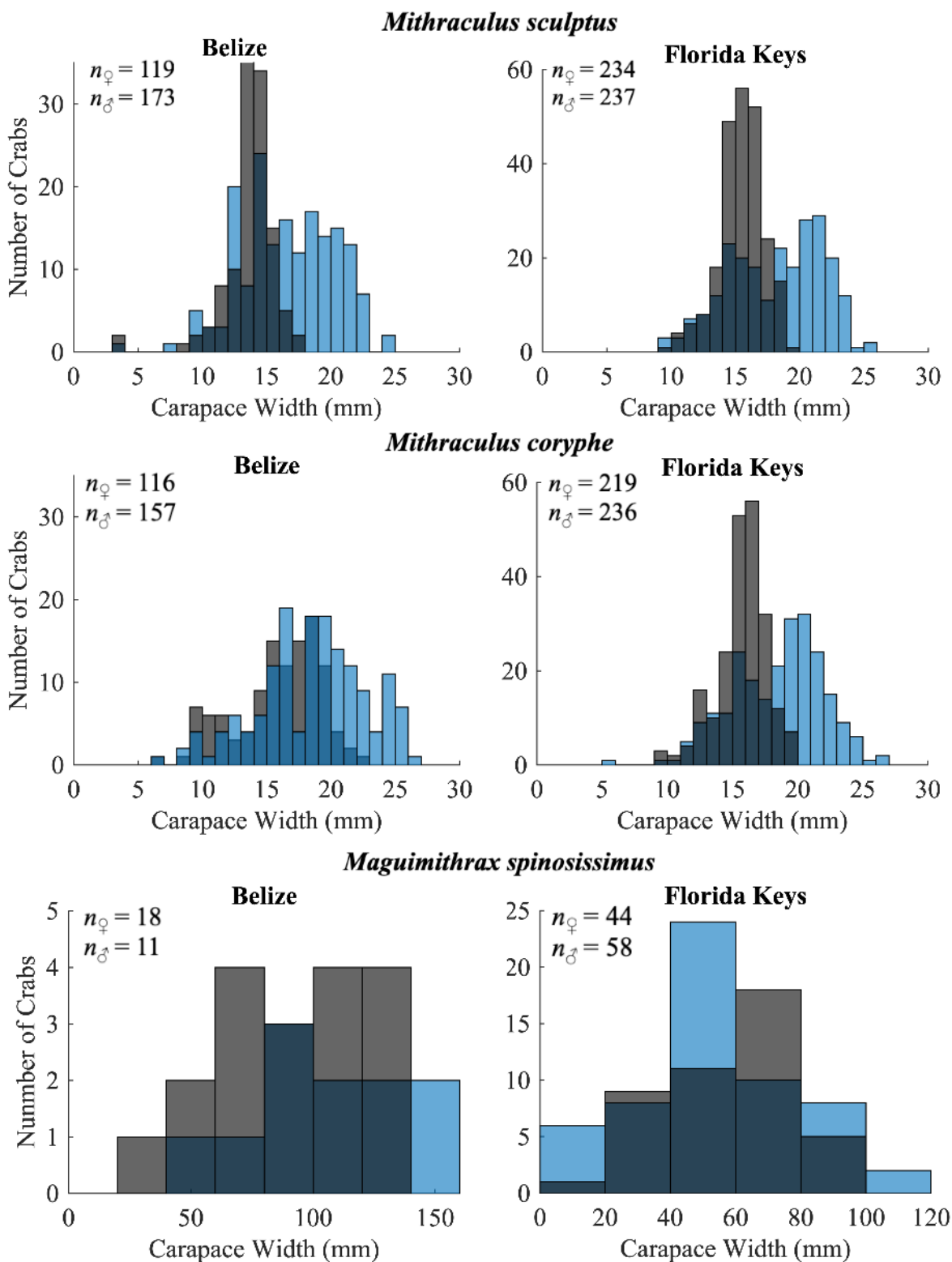


Figure 126. Histograms detailing the size structure of males (blue bars) and females (black bars) for the three Mithracid crab species that co-occurred in both study locations. The number of female ($n_{\text{♀}}$) and male ($n_{\text{♂}}$) crabs measured for each species are included.

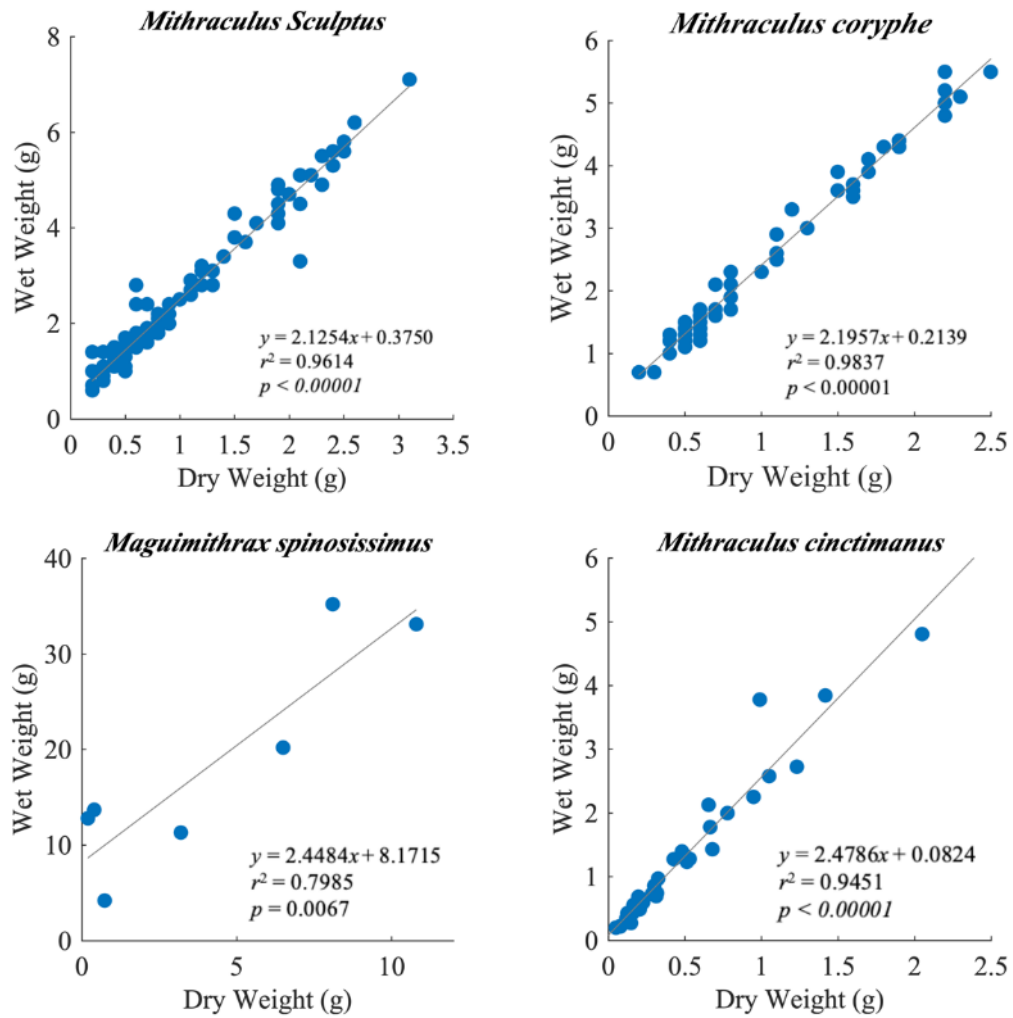


Figure 17. Regression plots of the relationship between wet weight (g) and dry weight (g) for the four Mithracid species used in the biomass index experiment: r^2 values, p values, and regression model are included in each plot.

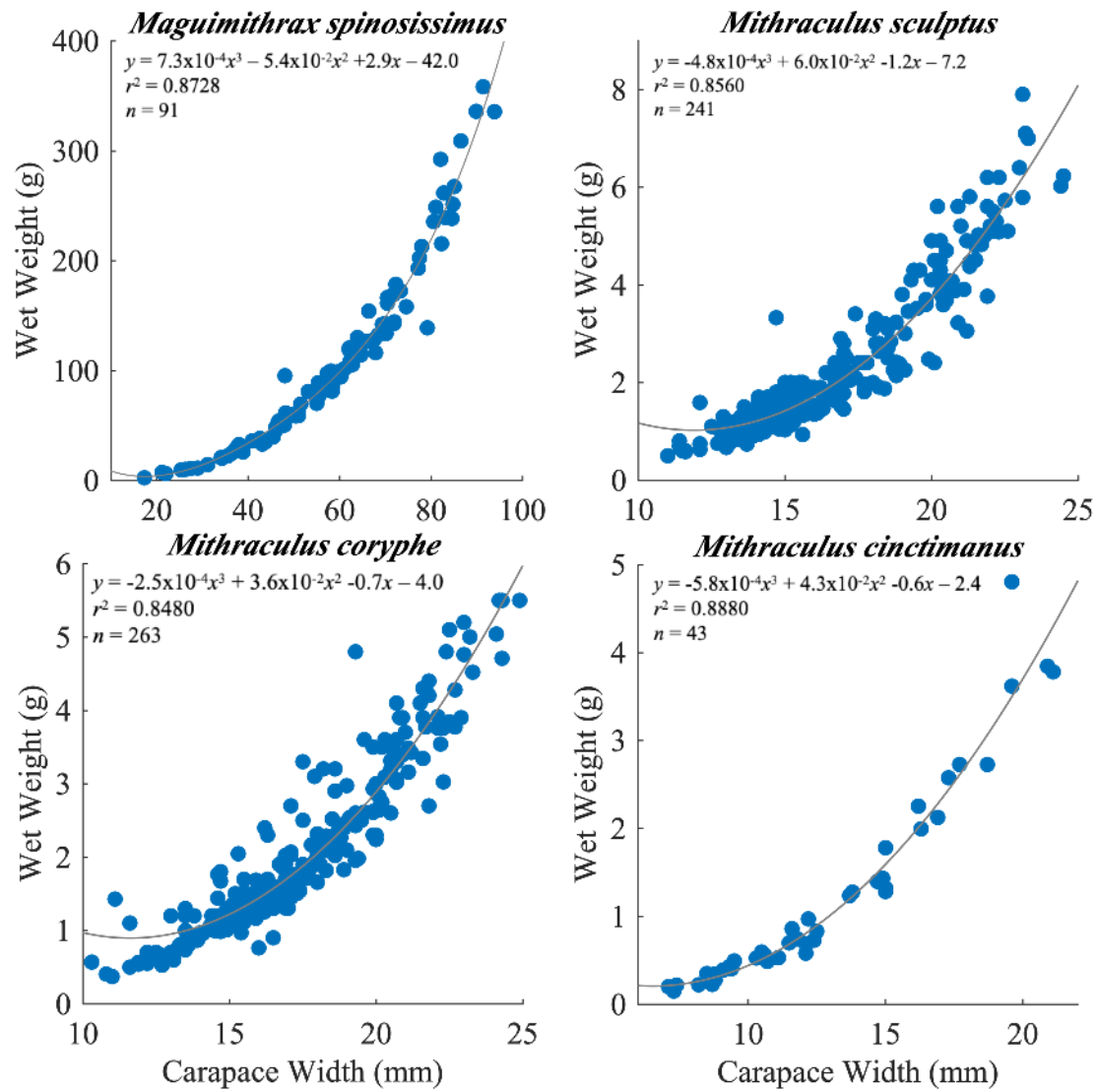


Figure 18. Regression plots of the relationship between carapace width (mm) and wet weight (g) of the four Mithracid crab species used in consumption experiments. Regression model equation, r^2 values, and sample size (n) is included for each species.

Algae consumption rates

To estimate multiple consumer effects of Mithracid crabs, I first measured the mean daily individual grazing rates of each species as a baseline. To do so, I collected crabs as described above, returned them to the laboratory in aerated seawater, and starved them for 24 h prior to starting each trial. A single crab was placed in an individual tank of aerated running seawater; 4.73 L plastic tanks for all *Mithraculus* spp. trials and 18.93 L plastic tanks were used for the larger *Maguimithrax* crabs. Into these tanks I added a pre-measured amount of macroalgae.

I used a plastic salad spinner to spin dry natural clumps of algae, and then measured the initial wet weight (A_i) of the algae to the nearest 0.1 g. The pre-weighed clumps of algae were then added to the tanks and crabs were allowed 24 h to consume algae. After 24 h, all remaining algae was collected, spun dry, and weighed to the nearest 0.1 g again (A_f). The following equation was used to calculate the mass of algae consumed (A_c) per 24 h: $A_c = A_i - A_f$. To account for any natural variation in the change in algal wet weight (A_Δ), I ran concurrent control trials wherein tanks (of both size) were set up and algae were added just as above but no crabs were added.

I regressed mean daily consumption (g / 24 h) for each species against crab size (CW) and wet weight (M_W) to evaluate the relationship between crab size/weight and algal consumption. The rationale behind these regression analyses was to develop a model for predicting algae consumption of crabs based on size or biomass. A previous study (Butler and Mojica 2012) reported no relationship between crab size and algae consumption for *M. spinosissimus*. In the event that this trend held true for other Mithracid species, I also calculated a simple mean

consumption rate for each species (\pm SE) to predict the consumption of algae / 24 h based on the number of crabs (Fig. 21 & 22).

Diet preference

To evaluate whether there are differences among crab species in their preference for algal taxa, I selected five genera of algae ubiquitous on Florida and Caribbean coral reefs: *Padina* spp., *Halimeda* spp., *Dictyosphaeria* spp., *Dictyota* spp., and *Amphiroa* spp. I tested for diet preference of all four Mithracid crab species described above and used two different tank sizes to account for differences in species-specific mean size of crabs. I added a single individual crab to each tank of aerated running seawater as described above for mean daily individual consumption rates. Algae, for this experiment, were collected, sorted, and used in experiments daily such that algae were not held *ex situ* for more than 24 h after collection. Algae were sorted into the categories described above. I spun the algae dry in a plastic salad spinner as described above before weighing clumps of each taxon to the nearest 0.1 g (W_i). I then added all five pre-weighed clumps to the experimental tank and allowed crabs to graze freely for 24 h. I ran concurrent no-crab control trials to account for any change in algal mass over the 24 h trial period not due to crab grazing.

After the 24 h trial concluded, I removed all remaining algae and re-sorted, dried, and weighed it to the nearest 0.1 g (W_f). I then calculated total algal consumption (T_c) as $T_c = W_i - W_f$. I used W_i and W_f to calculate the proportion of each algae taxon remaining at the end of each trial as $W_f / W_i = p_A$. Differences in consumption of algae among crab species was determined using Manly's α for variable prey populations. Manly's α is calculated as: $\alpha_i = \log p_i / \sum p_j$ where p_i and p_j are the proportions of prey i or j , respectively, remaining at the end of the trial (Manly 1974). I used Manly's α to measure preference for algae taxa by crabs because I did not

replenish any of the algae consumed after the initial offering in each trial and I provided enough algae to each crab to ensure that none was likely to be completely consumed over the course of the trial period. A Manly's α index value of 1 represents singular preference for one algae taxon and zero consumption of any other. Because I included five different algae taxa in the experiment, a Manly's α index value of 0.2 represents a lack of or equal preference. Manly's α index values below 0.2 represent avoidance whereas index values greater than 0.2 indicate preference. I tested for differences in diet preference among algae taxa and between crab species in a two-factor split-plot ANOVA (fixed whole plot factor = crab species; fixed subplot factor = algae taxon; block = individual/crab).

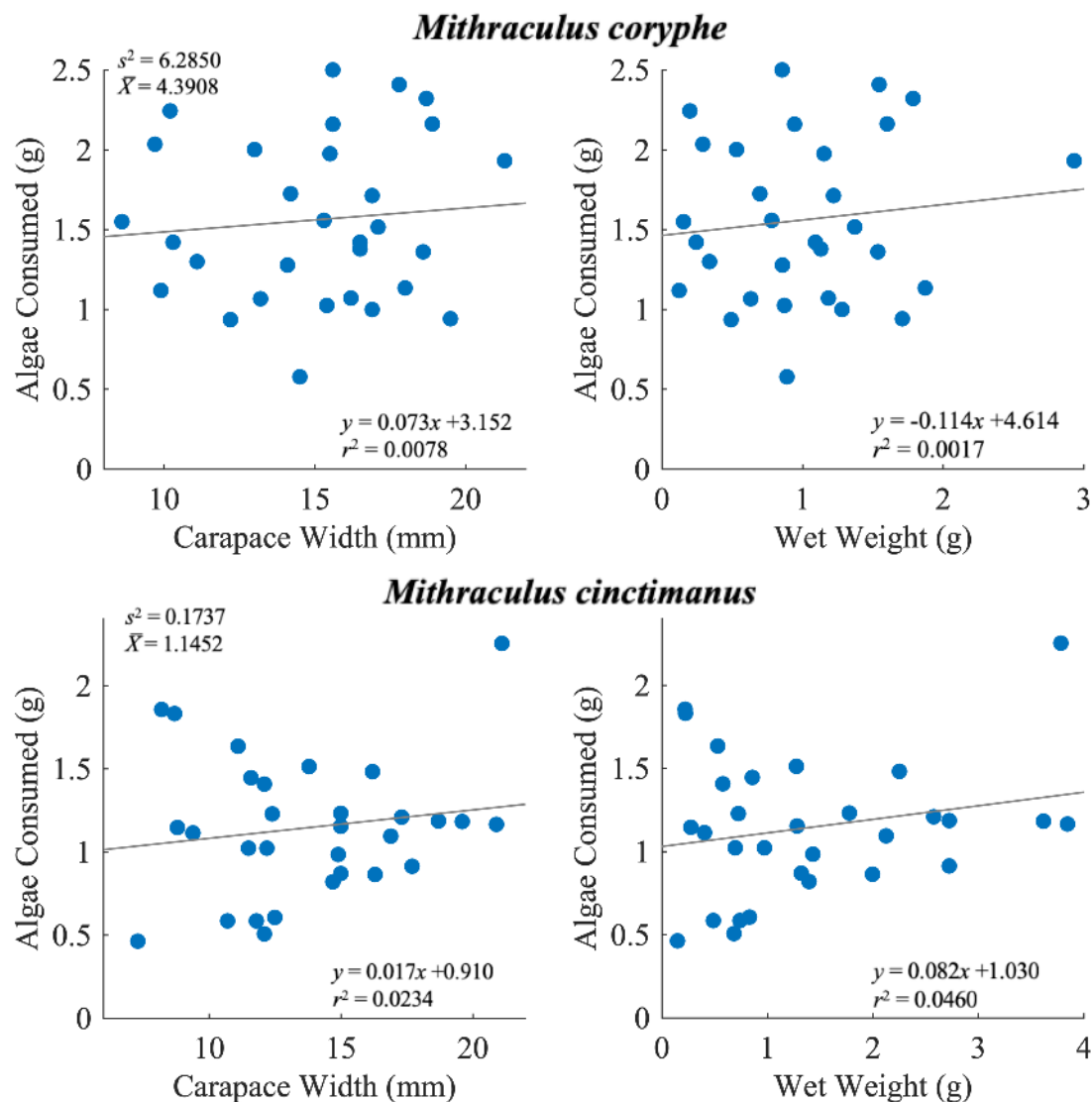


Figure 19. Regression plots displaying the lack of correlation between consumption of algae (g algae consumed / 24 h) with both crab size (mm CW, top and bottom left) and crab wet weight (g) for *Mithraculus coryphe* and *M. cinctimanus* in Belize. r^2 values and variance (s^2) are included to illustrate the poor relationships. Mean (\bar{X}) algae consumption values are included (top and bottom left) as a more reliable means of estimating algae consumption of crabs.

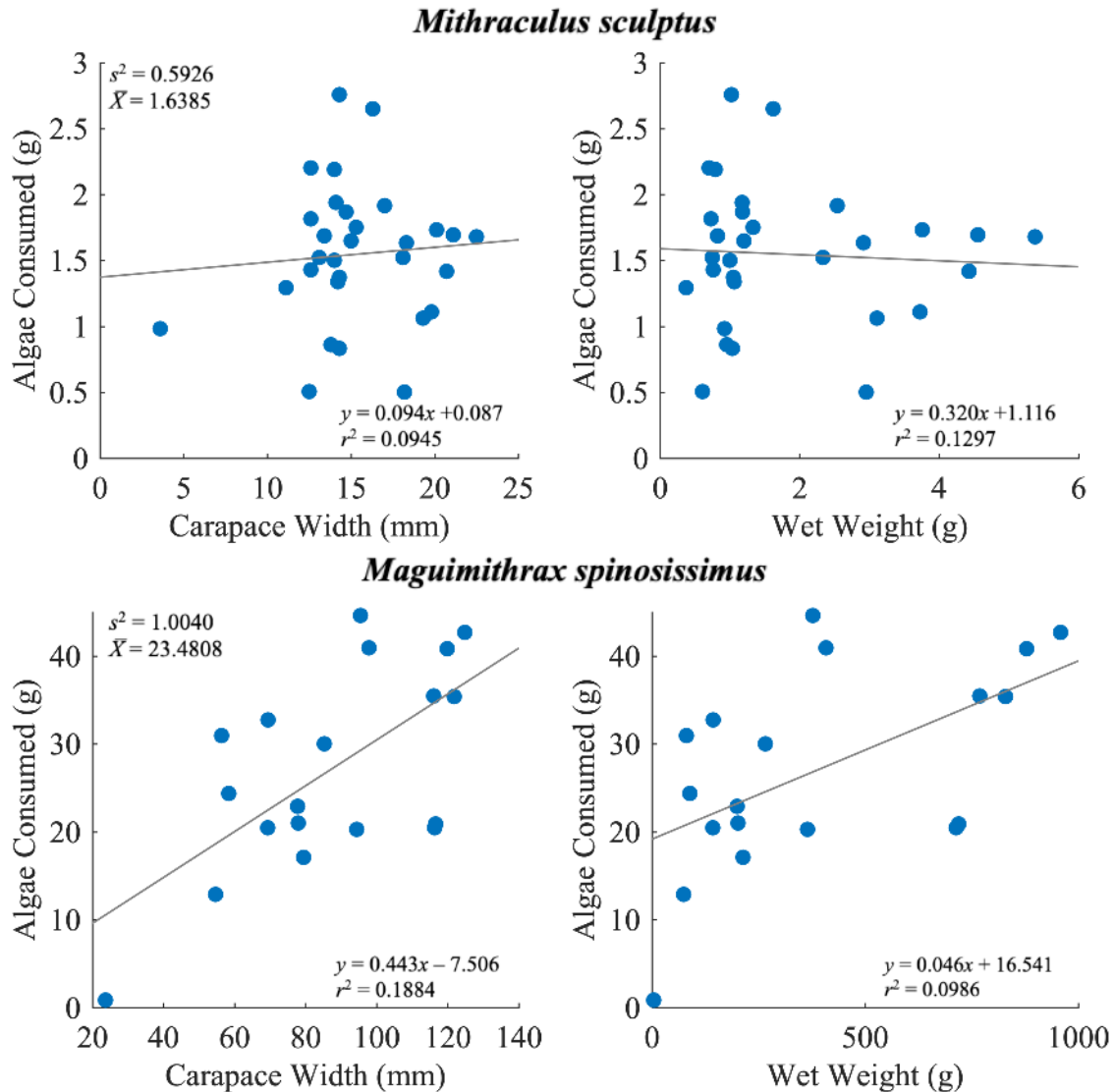


Figure 20. Regression plots displaying the lack of correlation between consumption of algae (g consumed / 24 h) with both crab size (mm CW, top and bottom left) and crab wet weight (g) for *Mithraculus sculptus* and *Maguimithrax spinosissimus* in Belize: r^2 values and variance (s^2) are included to illustrate the poor relationships. Mean (\bar{X}) algae consumption values are included (top and bottom left) as a more reliable means of estimating algae consumption of crabs.

Multiple consumer effects

To investigate the effects of multiple Mithracid consumers, I designed a pair of experiments identical to the consumption rate experiments above, but with multiple crabs added to the experimental tanks. I used a second series of individual consumption rate experiments identical to those described above to generate baseline individual consumption rates to which I compared the consumption rate of multiple individuals. Multiple consumer effects experiments were conducted at both SMS (Ft. Pierce, FL USA) and GC (Long Key, FL USA). A separate set of individual consumption rate experiments were conducted in each location to produce separate baseline consumption rate values for each algae type in each location. *M. spinosissimus*, *M. sculptus*, and *M. coryphe* were all relatively abundant in Florida, so were all used for multiple consumer effects experiments.

Individual consumption rates

To generate baseline daily consumption rates per crab species, I conducted an identical consumption experiment to those described above. I used the preliminary results of the consumption rate experiment as a guide in determining the mass of algae to offer crabs. To ensure that algae were not completely consumed, and thus consumption estimates biased, I added substantially more algae (~three times more) than my preliminary experimental results predicted would be consumed in one day. A single crab was added to the experimental tank and allowed to graze freely for 24 h. At the end of each trial, I carefully collected all remaining algae in an experimental tank, spun the algae dry again, and re-weighed the algae to the nearest 0.1 g. I ran concurrent control trials in which algae were added to experimental tanks as described above, but no crab was added to account for any natural variability in the mass of algae over the course of the 24 h trial period.

Consumption of algae was calculated as described above: $T_c = W_i - W_f$. These data were then regressed for each species against both crab size (CW). If the r^2 value was greater than 0.50, then the equation of the regression curve produced by each species was used to predict expected individual consumption of algae for multiple consumer experiments. In the event that there was no relationship between crab size (CW) and algae consumption ($r^2 < 0.50$), I calculated the mean daily consumption rate (\bar{X} g consumed per 24 h) for each species. This mean daily consumption rate, calculated separately for each study location, would serve as the expected individual daily consumption rate for each species in the following multiple consumer effects experiments.

Intraspecific multiple grazer consumption rates

To measure potential intraspecific multiple consumer effects of Mithracid crabs on grazing rates, I used the same experimental set up as described above. Using preliminary data from the individual consumption rate experiment above, I provided each experimental tank with ~50% more algae than would be expected to be consumed when individual consumption rates were multiplied by the number of crabs in a trial. Two individuals of the same species of crab were then added to the experimental tank and allowed to graze uninterrupted for 24 h. At the end of the 24 h trial, I carefully removed all remaining algae from the experimental tank, spun it dry in a salad spinner, and re-weighed the algae mass to the nearest 0.1 g. Algae consumption was again calculated as $T_c = W_i - W_f$.

Estimated individual consumption rates for each species in each location were used to calculate expected individual consumption values for each species in each location. In the intraspecific multiple grazer consumption rates assay, I obtained an expected consumption value for each trial by adding the expected individual consumption value for each individual crab in a

trial together. I then compared the observed consumption value for each trial to this estimated/expected consumption value as:

$$P_c = \frac{O_c}{E_c}$$

Where O_c is the observed consumption value (g algae consumed / 24 h) for a trial and E_c is the expected consumption value for the trial and P_c is the multiple consumer effects index value or the proportional relationship of observed consumption to expected consumption of algae. If $P_c = 1$, I determined that the effect of multiple individuals on algae consumption was neutral; consumption of multiple individuals can be estimated by taking the sum of their respective expected consumption values. If $P_c > 1.0$, I considered the relationship facilitative or synergistic; consumption rate of multiple individuals was greater than the sum of their individual expected consumption values. If $P_c < 1.0$, I considered the relationship antagonistic or competitive; consumption rate of multiple individuals is less than the sum of their individual expected consumption values.

Interspecific multiple grazer consumption rates

To evaluate any interspecific effects on multiple Mithracid consumer grazing rates, I designed an experiment identical to the intraspecific multiple grazer consumption rates experiment described above but with a different set of treatment groups. For interspecific multiple grazer consumption rates, I used a fully orthogonal experimental design with three Mithracid species: *M. sculptus* x *M. coryphe*, *M. sculptus* x *M. spinosissimus*, and *M. coryphe* x *M. spinosissimus*. Algae were collected, spun dry in a salad spinner, and weighed to the nearest 0.1 g. Pre-weighed clumps of algae (~50% greater than predicted to be consumed based on individual consumption rates experiments) were added to experimental tanks. Two crabs (treatment groups described above) were added to each experimental tank and left to graze

uninterrupted for 24 h. At the end of each 24 h trial, I carefully removed all remaining algae, spun it dry, and re-weighed it. Consumption was again calculated as: $T_c = W_i - W_f$.

I analyzed the multiple consumer effects data using a one-way ANOVA evaluating the effect of treatment group (6 levels: 3 intraspecific and 3 interspecific) on multiple consumer effect index values. If the ANOVA returned a statistically significant result, a post hoc Tukey test was run to identify any homogenous subsets among and between treatment groups.

4.3 Results

Mithracid grazing

Biomass measurement

There was a strong positive relationship ($r^2 > 0.9$) between wet and dry weight in all three species of *Mithraculus* I tested (Fig. 19). The relationship between crab size (mm CW) and wet weight (g) was also strong ($r^2 > 0.79$) for all four species of crab that I tested (Fig. 20).

Algae consumption rates

I measured daily consumption (g algae consumed / 24 h) for a total of 109 crabs in Belize ($n = 30$ for each species of *Mithraculus* and $n = 19$ for *Maguimithrax spinosissimus*) (Fig. 21 & 22). There was no relationship between crab size (mm CW) and consumption of algae (g consumed/24 h) for any species of *Mithraculus* tested ($r^2 < 0.03$). Similarly, there was no relationship between crab wet weight (g) and consumption of algae (g consumed/24 h) for any of the species of *Mithraculus* tested ($r^2 < 0.05$). In contrast, there was a strong correlation between both crab size (mm CW) and wet weight (g) and consumption of algae (g consumed / 24 h) for *M. spinosissimus* ($r^2 = .9917$ and $.9986$ respectively). Mean daily consumption rates (g consumed / 24 h) were similar for the three species of *Mithraculus* I tested. *Mithraculus coryphe*,

M. sculptus, and *M. cinctimanus* consumed a mean of 1.5603 g, 1.1452 g, and 1.5475 g of algae / 24 h (respectively). The mean daily consumption rate by *M. spinosissimus* was many times greater than those measured for all *Mithraculus* spp. (\bar{X} = 29.972 g consumed / 24 h) given the much greater size of this species.

Diet preference

I ran a total of 70 crabs (25 *M. sculptus*, 26 *M. coryphe*, 15 *M. cinctimanus*, and 4 *M. spinosissimus*) through the diet preference assay in Belize. *Maguimithrax spinosissimus*, as previously reported by Butler and Mojica (2012), preferred fleshy macroalgae over calcareous algae with the notable exception of *Padina* sp. whose alpha index value was on par with that of the two calcareous algae tested: *Amphiroa* sp. and *Halimeda* sp. As Butler and Mojica (2012) reported, *M. spinosissimus* consumed the chemically-defended calcareous algae *Amphiroa* sp. and *Halimeda* sp. even though portions of the preferred algae remained unconsumed in the tank. All four species of crab preferred *Dictyota* sp. over all other algae tested, again similar to the results reported for *M. spinosissimus* previously by Butler and Mojica (2012). *Mithraculus cinctimanus* and *M. sculptus* seemingly avoided *Dictyosphaeria* sp. algae but not *Amphiroa* sp. and *M. coryphe* exhibited the opposite: neutral preference for *Dictyosphaeria* sp. and moderate avoidance of *Amphiroa* sp. (Table 8).

Table 8. Manly's alpha index of preference for five common benthic macroalgae consumed by four species of Mithracid crabs in simultaneous-choice laboratory feeding assays. Alpha index values range from 0 to 1.0. For this experiment, values above and below 0.20 indicate preference or avoidance (respectively) of an alga in a crab's diet.

Crab Species	Manly's Alpha Index of Preference by Algae Genera				
	<i>Dictyosphaeria</i>	<i>Padina</i>	<i>Dictyota</i>	<i>Amphiroa</i>	<i>Halimeda</i>
<i>M. spinosissimus</i>	0.32	0.08	0.44	0.11	0.06
<i>M. cinctimanus</i>	0.13	0.22	0.34	0.19	0.11
<i>M. coryphe</i>	0.19	0.21	0.34	0.15	0.10
<i>M. sculptus</i>	0.16	0.19	0.36	0.19	0.10

Multiple consumer effects

Individual consumption rate

In the Florida Keys, I ran a total of 280 crabs through the individual consumption rate feeding assay. At the SMS in Ft. Pierce, FL (USA), I ran a total of 77 crabs through the individual consumption rate feeding assay.

There was no relationship between crab size and consumption of aquacultured algae in any of the crab species I tested at the SMS, or for either *Mithraculus* spp. I tested in the Florida Keys. However, the relationship between crab size and consumption of algae in the Florida Keys suggests that a weak linear relationship exists for *M. spinosissimus* ($r^2 = 0.4599$; Fig. 23). The relationship between crab size (CW) and consumption of natural macroalgae for *M. spinosissimus* in the Florida Keys was weaker than the trend I measured for *M. spinosissimus* in Belize (Fig. 22 & 23).

Mean consumption of algae for each species differed substantially between the two locations in Florida (Fig. 23 & 24); *M. sculptus* consumed more natural algae in the Florida Keys ($\bar{X} = 3.7550$ g / 24 h) than cultured algae at SMS ($\bar{X} = 1.6385$ g / 24 h). Both *M. coryphe* and *M. spinosissimus* exhibited the opposite trend. *Maguimithrax spinosissimus* consumed nearly twice

as much aquacultured macroalgae at SMS ($\bar{X} = 23.4808$ g / 24 h) than natural algae in the Florida Keys ($\bar{X} = 12.4314$ g / 24 h). Similarly, *M. coryphe* also consumed nearly twice as much of the aquacultured algae at SMS ($\bar{X} = 4.3908$ g / 24 h) than natural algae in the Florida Keys ($\bar{X} = 2.5260$ g / 24 h).

Intraspecific multiple grazer consumption rates

In all intraspecific multiple grazer treatment groups, multiple consumer effect index values fell below the 1.0 index value, a result indicative of antagonistic or competitive multiple consumer effects (Fig. 25 & 26).

Interspecific multiple grazer consumption rates

In all interspecific multiple grazer treatment groups, multiple consumer effect index values were either indicative of independent or synergistic effects of multiple interspecific grazers on algal consumption rate. It is noteworthy that while the interspecific treatment group composed of both *Mithraculus* species exhibited a neutral effect, both interspecific treatment groups including *M. spinosissimus* exhibited a synergistic or facilitative effect (Fig. 27 & 28). There were no significant differences in the multiple consumer effect index values for the *M. sculptus* x *M. coryphe* treatment group (Table 11, Fig. 29).

4.4 Discussion

In Chapters 2 and 3, I demonstrated the density-dependent effects of *M. spinosissimus* on the composition of the benthic algae communities of degraded coral reefs and the cascading effects of algae removal on coral and fish recruitment. Here I examined the effects of multiple Mithracid crab consumers on grazing of algae. I found no relationship between crab size or mass and algae

consumption in any of the *Mithraculus* spp. and a strong positive relationship between both crab size and mass and algae consumption for *M. spinosissimus*. The smaller *Mithraculus* spp. consumed less algae per individual per day than did *M. spinosissimus*. In the diet preference assay, *M. spinosissimus* exhibited a preference for fleshy brown algae, but still readily consumed chemically- and physically-defended macrophytes, consistent with the results of a previous study (Butler and Mojica 2012). There were some subtle differences in the diet preference of *Mithraculus* spp., however, suggesting niche differentiation. This was supported by the results of the multiple consumer effects assays: intraspecific pairs consumed less than the expected mass of algae whereas interspecific pairs tended to consume greater than the expected mass of algae per trial. These results suggest that *M. spinosissimus* and the *Mithraculus* spp. are not redundant, but complementary in their grazing function.

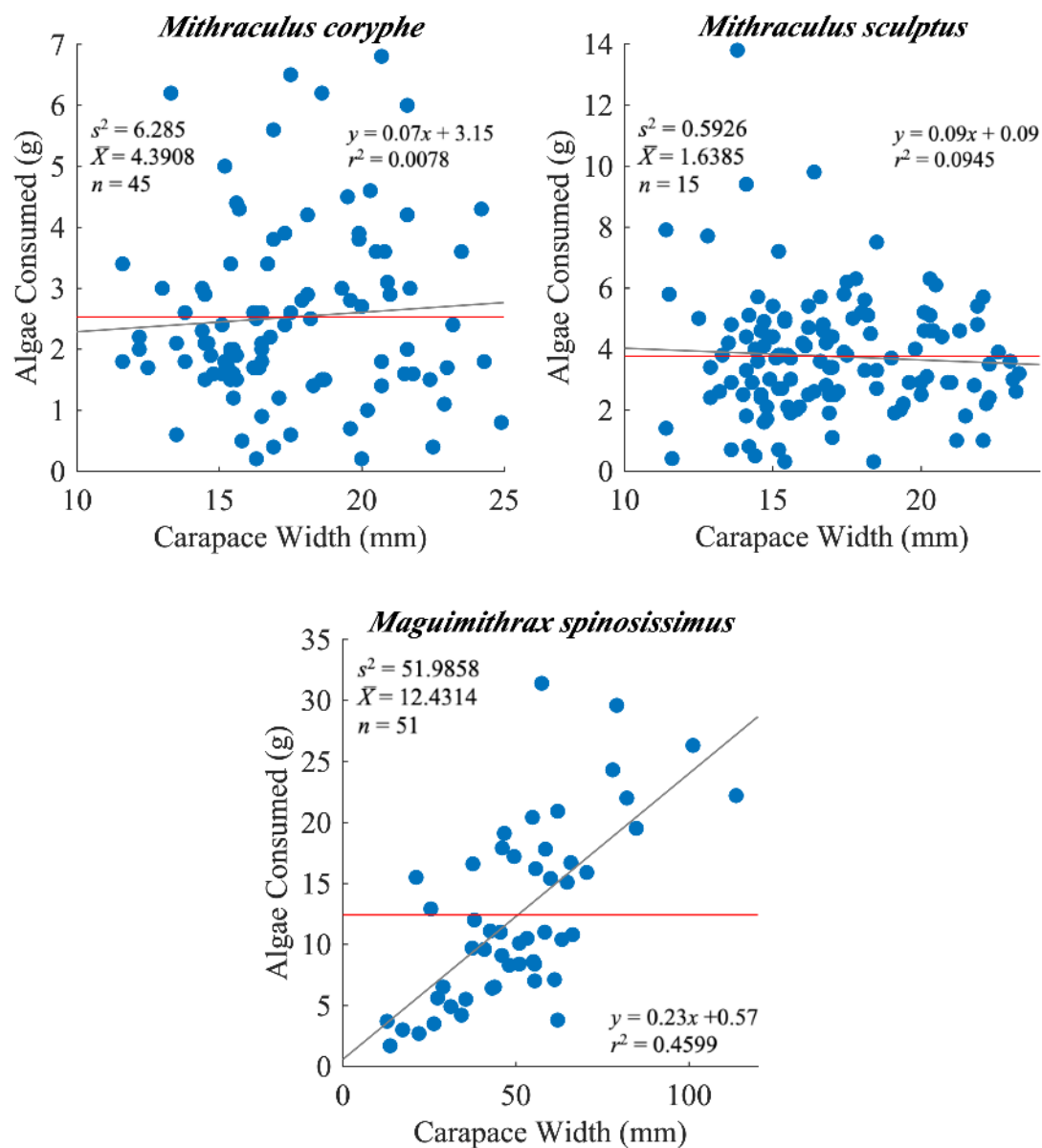


Figure 21. Regression plots of crab size (mm CW) by algae consumed (g consumed / 24 h) in individual consumption trials conducted with natural algae in the Florida Keys. Regression model and r^2 values are included for each species. Both the regression model (grey line) and the arithmetic mean of algae consumption (\bar{X} algae consumed; red line) are shown to illustrate the species-specific differences in their relative relationship.

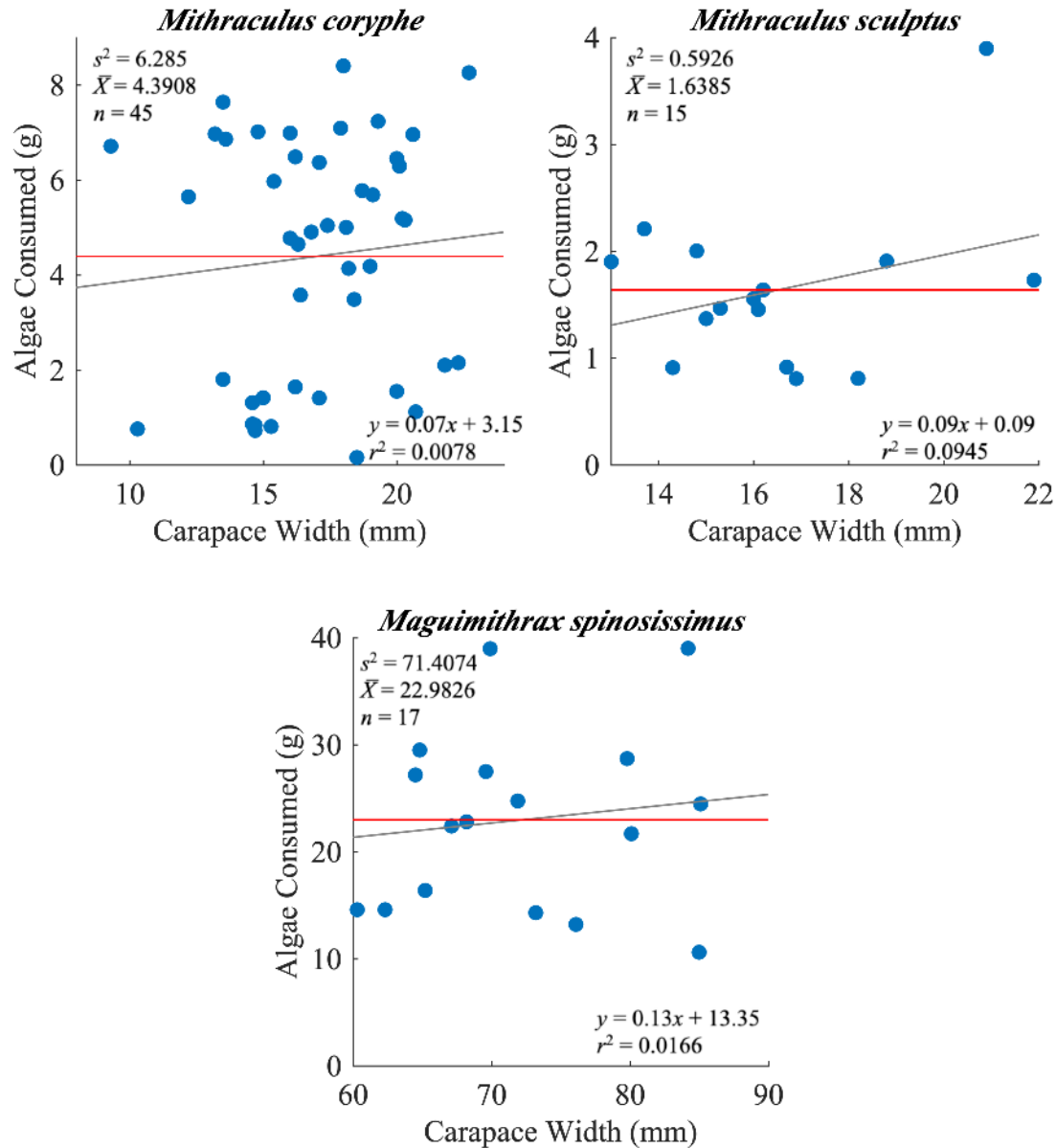


Figure 22. Regression plots of crab size (mm CW) by algae consumed (g consumed / 24 h) in individual consumption trials conducted with aquacultured algae at the Smithsonian Marine Station, Ft. Pierce, FL. Regression model and r^2 values are included for each species. Both the regression model (grey line) and the arithmetic mean of algae consumption (\bar{X} algae consumed; red line) are shown to illustrate the species-specific differences in their relative relationship.

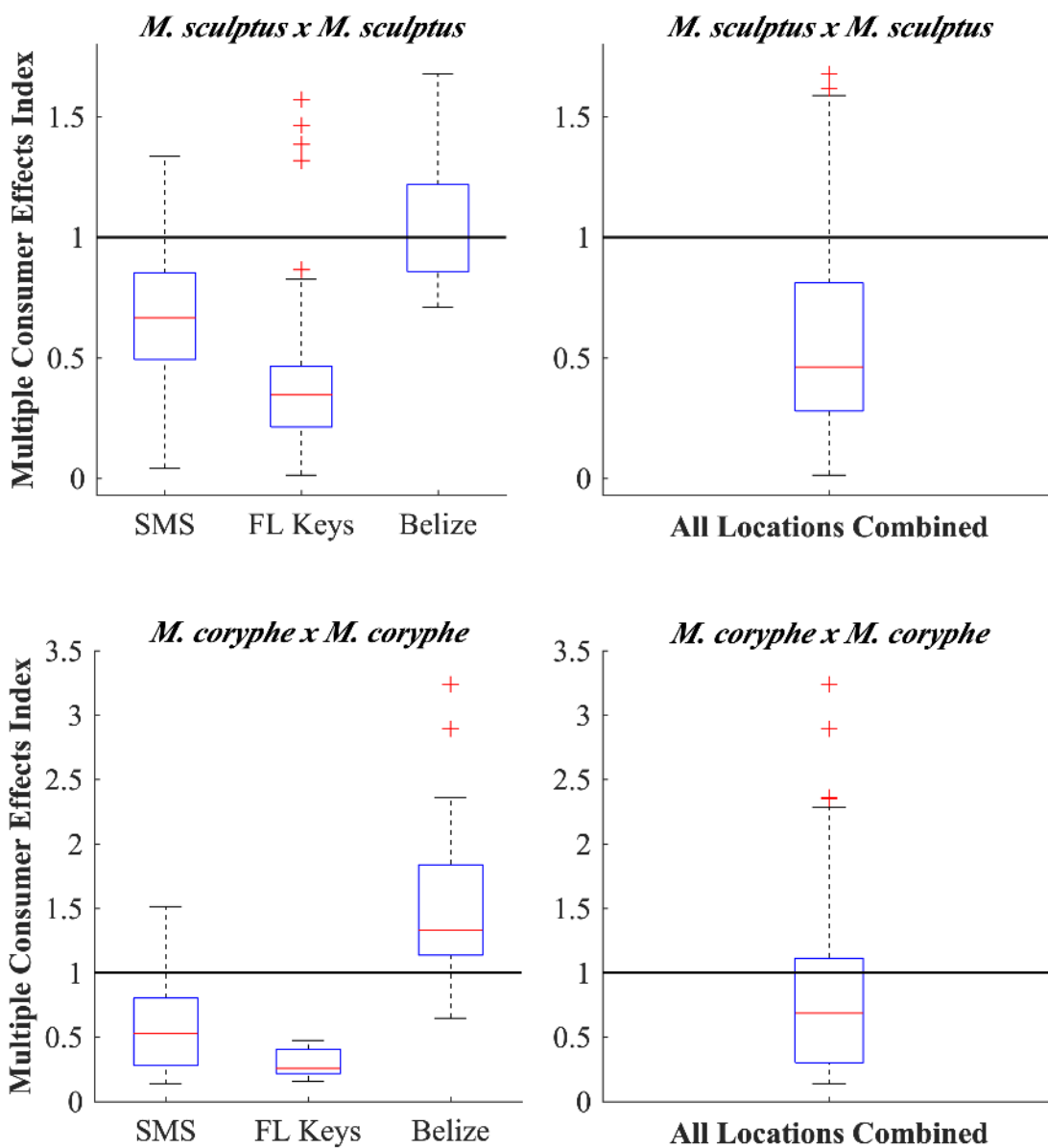


Figure 133. Box plot describing the combined effect of multiple individuals of *M. sculptus* (top) and *M. coryphe* (bottom) on algae consumption (g algae consumed / 24 h) relative to mean individual grazing rates by study location (left) and with all locations combined (right). Heavy black horizontal line represents independent or isometric multiple consumer effect (e.g., observed grazing rate = expected grazing rate). Red points (+) represent individual trial outlier values.

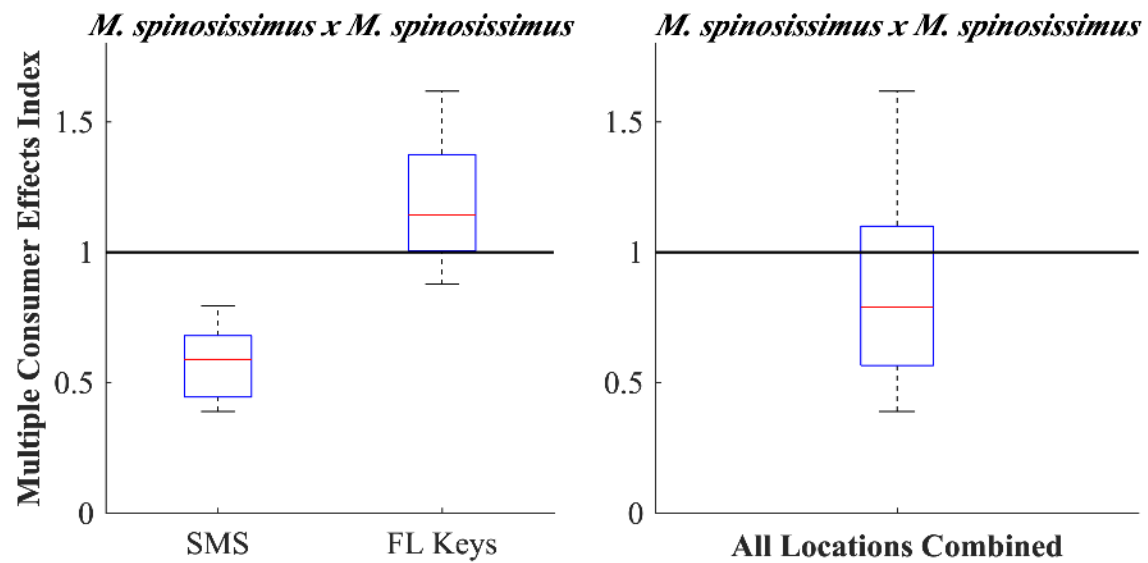


Figure 144. Box plot describing the combined effect of multiple individuals of *M. spinosissimus* on algae consumption relative (g algae consumed / 24 h) to mean individual grazing rates by study location (left) and with all locations combined (right). No trials in this treatment group were run in Belize, so results from only two study locations are presented. Heavy black horizontal line represents independent or isometric multiple consumer effect (e.g., observed grazing rate = expected grazing rate).

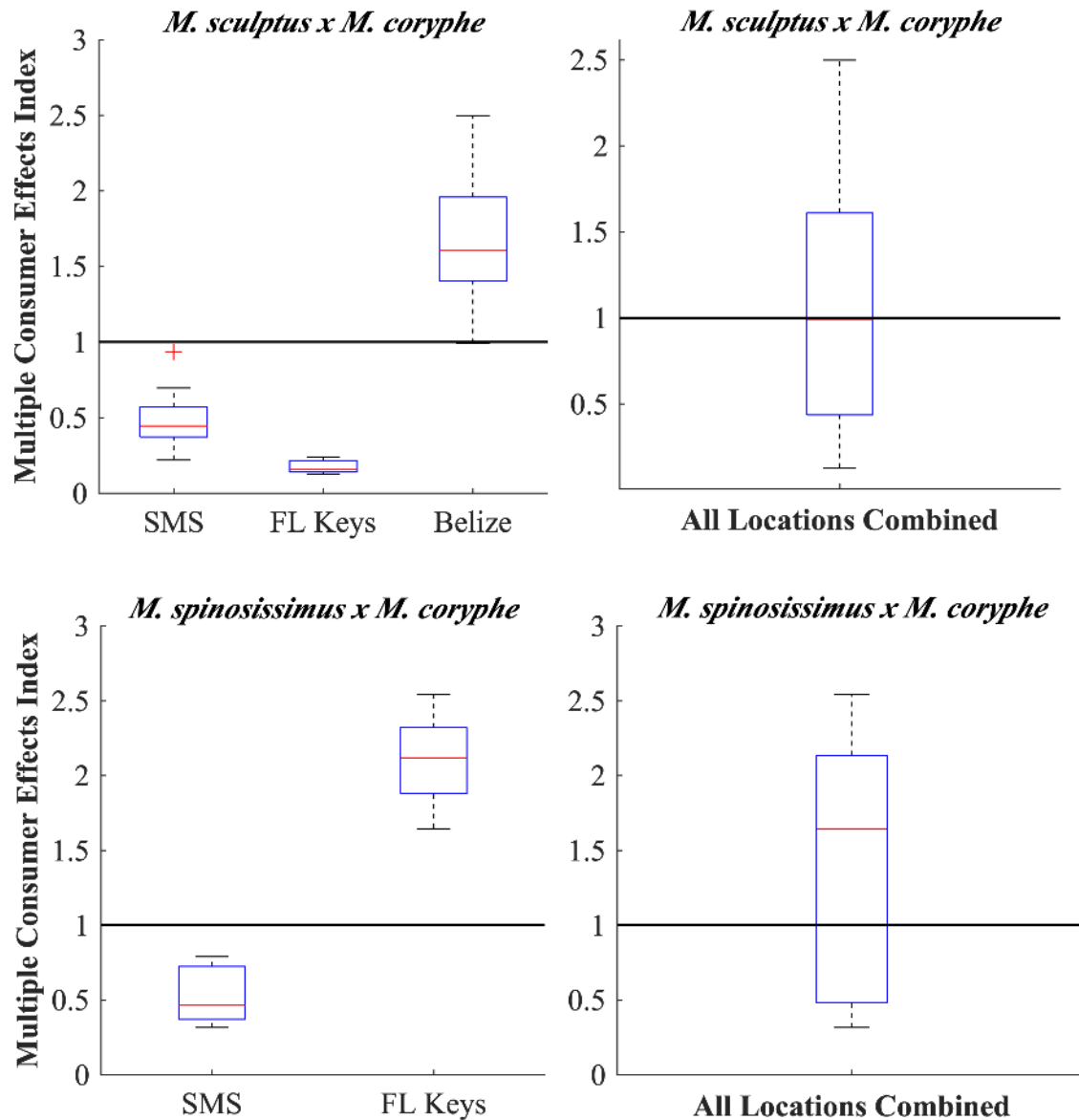


Figure 155. Box plots describing the effect of multiple consumers on algae consumption (g algae consumed / 24 h). The top two plots present the multiple consumer effect results by location (left) and with all locations combined (right) for the *M. sculptus* with *M. coryphe* treatment group. The bottom two plots present results from the same experiment for the *M. spinosissimus* with *M. coryphe* treatment group. No trials of the *M. spinosissimus* with *M. coryphe* treatment group were run in Belize, so results from only two locations are included for that treatment. Heavy black horizontal line represents independent or isometric multiple consumer effect (e.g., observed grazing rate = expected grazing rate).

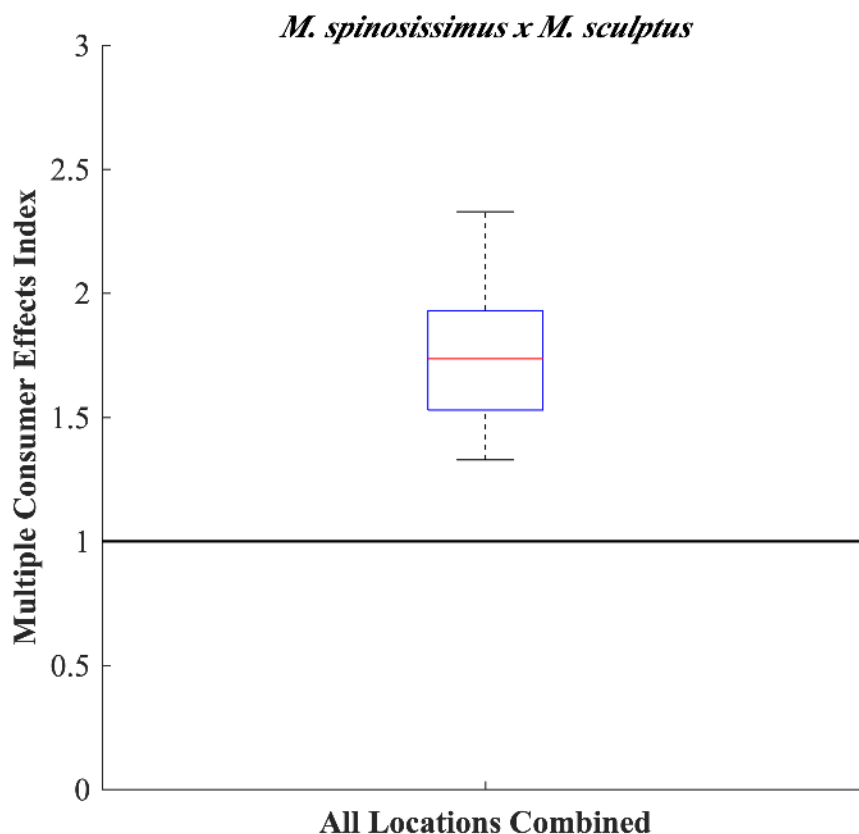


Figure 166. Box plot describing the effect of multiple consumers on algae consumption (g algae consumed / 24 h) in the *M. spinosissimus* with *M. sculptus* treatment group. Trials for this treatment group were only run in a single location (Florida Keys) so only a single box plot is displayed. Heavy black horizontal line represents independent or isometric multiple consumer effect (e.g., observed grazing rate = expected grazing rate).

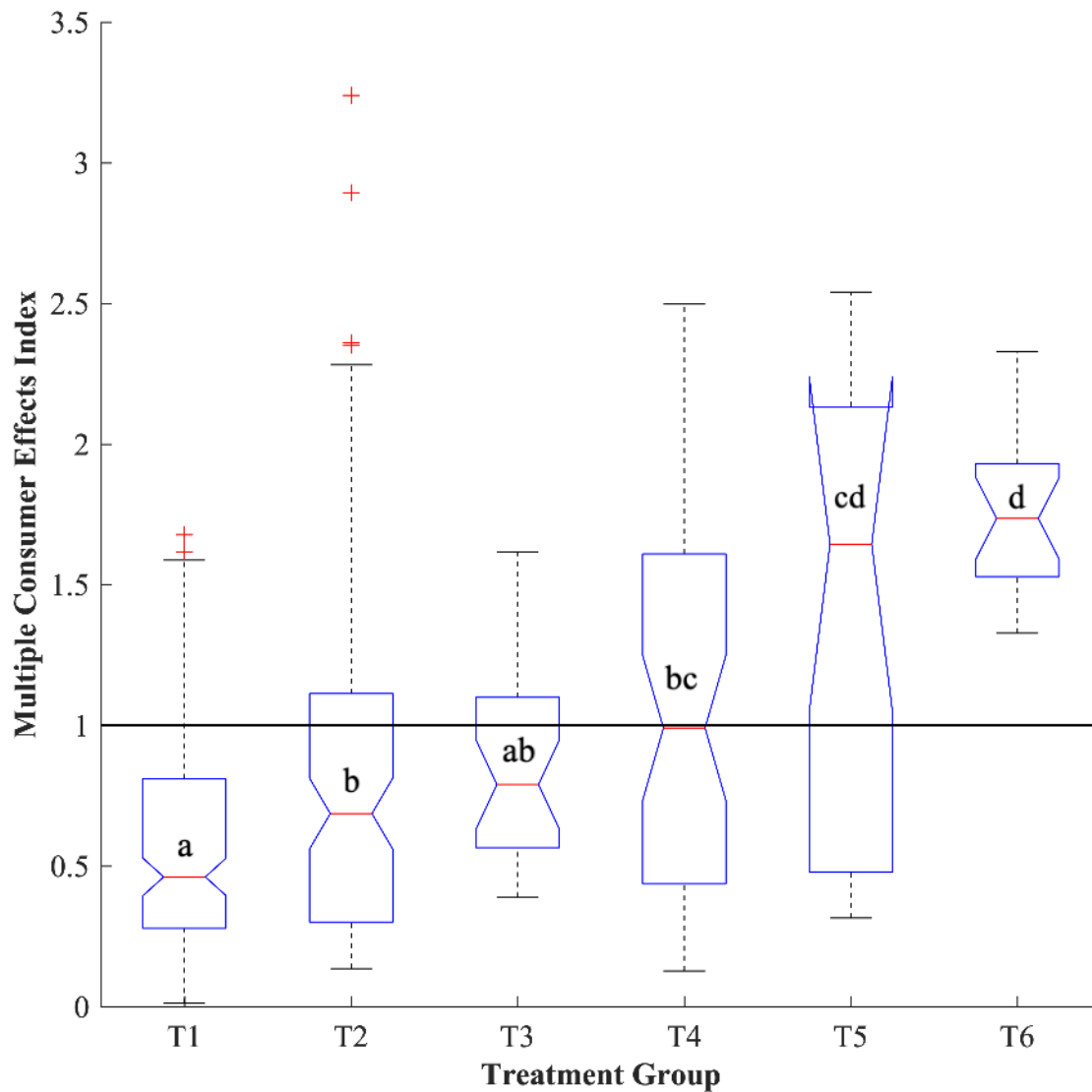


Figure 177. Box plot describing the results of an analysis of variance between all six multiple consumer effects treatment groups I tested. T1 = *M. sculptus* x *M. sculptus*; T2 = *M. coryphe* x *M. coryphe*; T3 = *M. spinosissimus* x *M. spinosissimus*; T4 = *M. sculptus* x *M. coryphe*; T5 = *M. spinosissimus* x *M. coryphe*; T6 = *M. spinosissimus* x *M. sculptus*. Letters in each box plot describe homogenous subsets. The thick black line represents the 1.0 multiple consumer effects index value indicative of independent effects. Values above 1.0 indicate synergy or facilitative effects whereas values below 1.0 indicate antagonism or competitive effects. Small red + symbols represent outlier values.

Recent studies suggest that the bulk of grazing on today's Caribbean reefs is carried out by small-bodied cryptic species such as the rock-boring urchin, *Echinometra viridis*, and the Striped Parrotfish, *Scarus iseri* (Kuempel and Altieri 2017). Although these species are diminutive, their high abundance and lack of fishing and competitive pressures have allowed their populations to boom in numbers and biomass across the region, filling - at least partially - a functional grazing void in the system left by the mass mortality of *D. antillarum* and declines in parrotfish abundance and size.

Table 9. Results of a one-way analysis of variance investigating the differences between the six multiple consumer effects treatment groups I tested. As not all treatment groups were tested in all locations, I did not test for a site effect among all treatments.

Source	SS	df	MS	F	p
Treatment Group	33.914	5	6.78281	23.73	1.09588E-20
Error	105.199	368	0.28587		
Total	139.113	373			

Here I have demonstrated the potential contribution of a sleeping functional group of diminutive, cryptic, but abundant herbivores. Given the grazing rates measured for each species in multiple locations and on multiple algal species assemblages, as well as their very high densities in certain reef habitats, Mithracid crabs almost certainly represent major components of the grazing guild on Caribbean reefs. In several locations around the Caribbean and Central America, grazing crabs drive the abundance and distribution of macroalgae (Coen 1988a, b; Stachowicz and Hay 1996, 1999; Altman-Kurosaki et al. 2018). On the Pacific coast of Panama, there is a paucity of benthic macroalgae in nearshore habitats largely due to grazing by crabs (Menge and Lubchenco 1981; Menge et al. 1986). Similarly, the persistence of shallow back-reef

thickets of *Porites divaricata* in Belize is the result of a mutualism between *Porites* and several species of *Mithraculus* (e.g., *M. coryphe*, *M. sculptus*, *M. cinctimanus*) the species whose grazing function I investigated here (Coen 1988 a, b). A similar relationship occurs in Florida between *M. sculptus* and *Porites divaricata* on shallow back-reef banks (Spadaro, pers. Obs.). Although *M. sculptus*, *M. coryphe*, *M. cinctimanus*, and *M. spinosissimus* all co-occur in coral reef and back-reef habitats in Belize, the distribution of the various Mithracid species I included in these studies tends to be patchy and more species-specific.

For example, in the Florida Keys, I did not observe *M. cinctimanus*, whereas numerous *M. sculptus* were collected from nearshore rubble and hardbottom habitats as well as from *Porites divaricata* thickets. I only found *M. coryphe* further offshore in discrete rubble zones just inside the barrier reef crest and among living corals on the reef slope. In contrast, *M. spinosissimus* was most abundant in shallow back-reef hardbottom habitats inhabiting sponges, natural rocky structures (e.g., solution holes, living and dead coral heads), anthropogenic structures (e.g., concrete blocks, bridge/construction rubble, rip-rap jetties), and coral patch reefs. I collected a number of larger *M. spinosissimus* from coral reefs throughout the Middle Florida Keys, but their densities in these habitats are substantially lower than in the other habitats listed above (Butler and Mojica 2012), presumably due to the substantially greater predation risk in reef habitats (see Chapter 2). Octopus are abundant and effective predators of crabs and crustaceans of all sizes (Butler and Lear 2009), and small crabs comprise the largest portion of the diet of the reef-obligate spotted spiny lobster (*Panulirus guttatus*; Butler and Kintzing 2016).

Because of the mutualistic association of Mithracid crabs and branching corals, especially for the more diminutive *Mithraculus* spp., it is likely that this is an evolutionary response to high predation pressure in coral reef communities. In high-risk habitats, the complex structure provided by branching corals likely ameliorates the risk of predation to small crabs. Historically,

coral reef environments in both locations supported vast thickets of the now-endangered branching *Acropora* spp. corals. These corals are still naturally abundant on the reefs in the Belize location I used, but not on the Florida reef tract except as transplanted colonies in restoration areas. In Belize, I observed several different *Mithraculus* spp. on nearly all of the natural *Acropora* spp. colonies surrounding the study location. *Maguimithrax spinosissimus* were also observed among larger colonies of *A. palmata* and in large and dense colonies of *A. cervicornis*. In every case where I observed Mithracid crabs inhabiting *Acropora* colonies, there was no fouling epilithic algae among coral branches or around the coral colonies' base (pers. obs.). It is likely that the ubiquitous distribution of crab species in nearshore environments in Belize and the contrasting species-specific distribution in Florida can be explained by the greater abundance and richness of branching coral species in Belize than in Florida.

The differences I observed in the distribution of crab species among study locations likely results in similarly subtle differences in the distribution of grazing function and intensity. In Belize, algae in the shallow backreef and reef crest habitats appear to be generally less abundant than in similar habitats in Florida and the benthic algal community in Belize appears to be dominated by *Dictyota* spp., a chemically-defended and early-successional species that all of the Mithracid crabs I tested preferred. In Florida, the nearshore and reef habitats exhibit a much greater cover of macroalgae than Belizean reefs and the algal community is more often dominated by chemically- and physically-defended calcareous species (e.g., *Halimeda* spp.) that are consumed by crabs, but not preferentially.

There is no evidence of niche differentiation among *Mithraculus* spp. with respect to diet preference. However, there are strong differences in diet preference between *M. spinosissimus* and the *Mithraculus* spp. The apparent lack of strong differentiation in diet preference among *Mithraculus* spp. is likely evolutionarily beneficial due to their high degree of philopatry and

nearly obligate association with Cnidarian and algal hosts (e.g., Coen 1988a, b; Stachowicz and Hay 1996, 1999). A clade of species such as these whose opportunities for foraging are strongly limited by their reliance on structure, presumably as refuge from diverse and abundant predators, would likely not persist with a specialized diet. Thus, it is likely that *Mithraculus* spp. have adapted a relatively generalist life history strategy in terms of diet as a result of strong top-down control on the distribution of the genus.

When one considers the difference in the relative density of these crabs, their grazing rates, and generalist diet, in terms of ecological function, many Mithracid crab species may be complementary with grazing finfishes and echinoderms on coral reefs and backreef habitats in the Caribbean. The fact that many of the algae, particularly *Dictyota* spp. and *Halimeda* spp., that they consume are generally avoided by herbivorous fishes suggests that the Mithracidae may also represent an important sleeping functional group in the region. The results of this study suggest that Mithracid crabs are an important cryptic guild of generalist herbivores with the capability of significantly altering the composition of the benthic community when and where they are locally abundant.

There is potential for the facilitation of ecological restoration efforts involving the direct enhancement of branching corals on Caribbean and Florida coral reefs by manipulating the density of Mithracid crabs in conjunction with transplanted corals. In a series of previous studies, I demonstrated that directly enhancing the density of *M. spinosissimus* on degraded coral patch reefs results in a trophic cascade facilitating recovery of reef fish abundance and species richness as well as a significant increase in the density of juvenile corals. Here, I have demonstrated that other species of Mithracid crabs are likely redundant in grazing function. The differences in their life history strategies and their ecology offer insights into the different possibilities in terms of their species-specific or multi-species roles facilitating coral restoration efforts. Whereas *M.*

spinosissimus is a fantastic candidate for removal of algal biomass and maintenance of low algae cover on restoration sites, *Mithraculus* spp. may represent excellent candidates for co-transplantation with the branching *Acropora* spp. corals most commonly used in reef restoration efforts. Indeed, the aquarium industry has advertised *Mithraculus sculptus*, the “emerald crab,” for many decades as a very effective herbivore in dealing with nuisance algae which compete with scleractinian corals in living coral reef aquarium systems (Calado et al. 2003; Rhyne et al. 2005). The results of this study suggest that *M. coryphe* may actually be a better choice for this purpose, but that all three species of *Mithraculus* that I tested likely perform a similar function in nature and have potential applications in coral restoration efforts on Caribbean reefs.

The differences in multiple consumer effects index values based on genus could, in part, be explained by the lack of strong niche differentiation between *Mithraculus* species as opposed to the much stronger differences in diet preference between *M. spinosissimus* and the *Mithraculus* spp. I tested. However, it is difficult to speculate on the mechanism by which different crab genera might facilitate each other’s grazing rates especially given the typical difference in body size between the genera I tested.

It is possible that a stronger signal of multiple consumer effects may have been detected if algal turfs had been included among the algae offered in diet preference assays. Turf algae are likely more important in areas where these crabs occur on rocky structures rather than in and among branching corals – on Florida reefs, for instance – but in coral thickets and among living branching corals, macroalgae, particularly *Dictyota* spp. and *Halimeda* spp. are often more common and abundant than turf algae (Spadaro, Pers. Obs.). This may help explain the consistent preference for *Dictyota* spp. algae among all of the species tested. *Dictyota* spp. are ubiquitous on Caribbean and Florida reefs, grow rapidly, and generally are present in all stages of algal community succession.

Another potential confounding factor in this study was the experimental set up. Each experimental unit was composed of a simple container filled with aerated seawater. The only structure offered to crabs within each experimental tank was algae. It is possible that the lack of any natural substratum or shelter altered the behavior of and, by extension, the consumption rates of one or more of the crab species I tested. Thus, in moving forward, it is worth investigating the effect of structure and refugia on the consumption rates of invertebrate grazers such as mithracid crabs. The results of such a study would offer insight into the effect of habitat complexity on such functional groups and would also offer insight into the potential effects one might expect when using these grazers in conjunction with coral restoration efforts, especially with structurally complex branching corals such as *Acropora cervicornis* and *A. palmata*.

Here, I have demonstrated that the Mithracidae are likely an important sleeping functional group of functionally complementary species in nearshore habitats of the Caribbean region and potentially offer resource managers and restoration programs an interesting and inexpensive natural tool for the management of algal overgrowth. There is much left to study with respect to the function and natural history of this family of crabs but, when one considers the results of this study along with my previous work with *M. spinosissimus*, the facilitative effect of these crabs in benthic communities where they are abundant and dense is potentially transformative.

CHAPTER 5

CONCLUSIONS

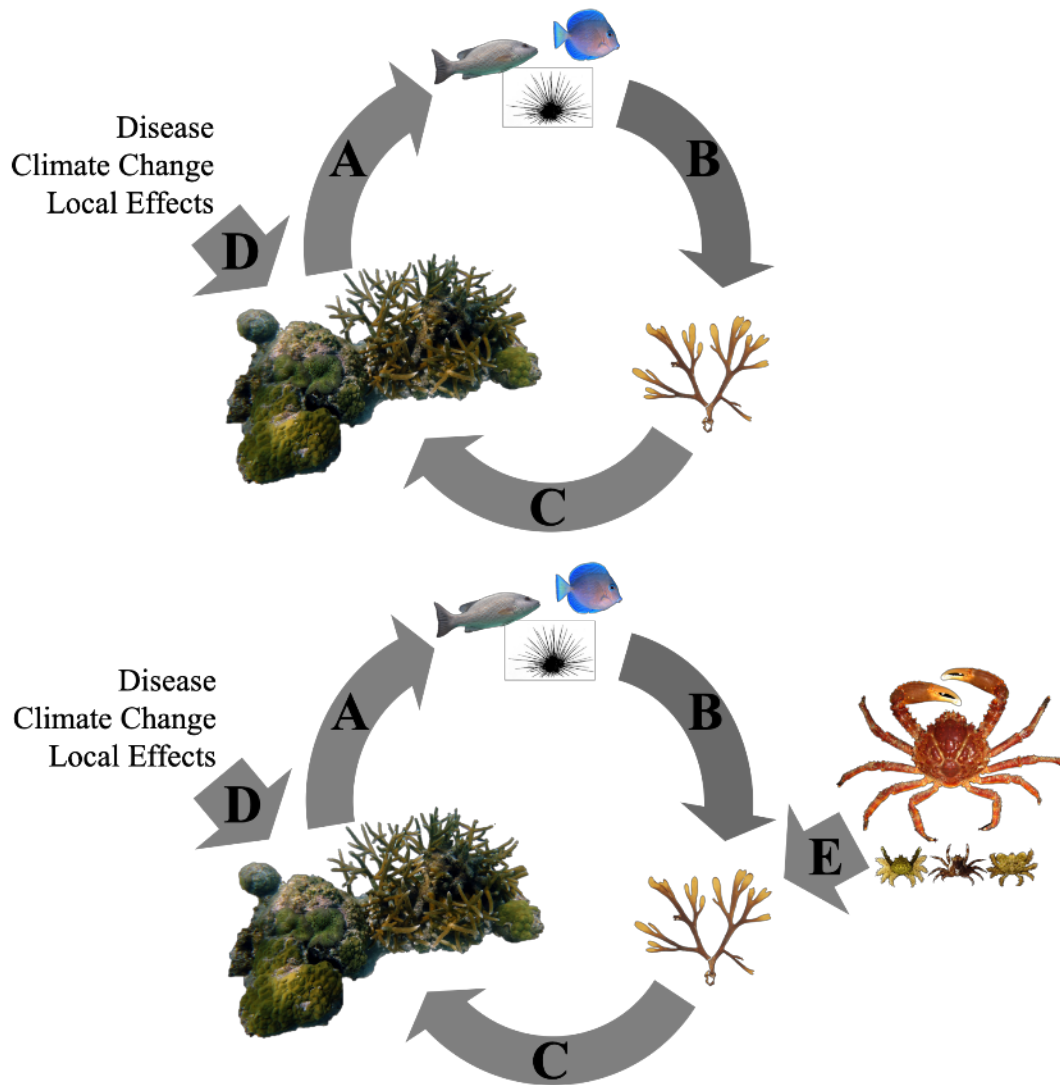


Figure 28. Graphical representation of general interactions on Caribbean coral reefs wherein live coral facilitates reef fishes and invertebrates (A) which, in turn, consume and mitigate the growth of macroalgae (B), which compete with live coral for resources and space (C). A number of stresses adversely affect live coral, fishes, and invertebrate communities (D). Enhanced Mithracid crab density, however, results in the removal of macroalgae (E) which, in turn, facilitates the recovery of live coral and reef fish communities.

Coral reefs cover less than 0.1% of the seafloor (McAllister 1995; Spalding and Grenfell 1997), but harbor more than 30% of Earth's marine species (Plaisance et al. 2011) and account for more than 10% of global fisheries production (Smith 1978; Moberg and Folke 1999). The rapid and chronic degradation of these ecosystems threatens the global economy, food security, and the ecological functioning of the biosphere (Bellwood et al. 2004).

In the Caribbean region, the degradation of coral reefs is particularly apparent with more than 80% of the region's living corals having disappeared in the last half century (Gardner et al. 2003, 2005). The loss of large-bodied fishes and the restriction of ecological function to fewer and fewer species has undermined the resilience of these communities to disturbances such as coastal eutrophication, hurricanes, climate change, acidifying oceans, and thermal stress (Jackson 2001; Jackson et al. 2001). A large body of scientific literature highlights the need for direct intervention to prevent the ultimate demise of coral reefs as functional ecosystems in the Caribbean and around the globe (see, for example Epstein et al. 2003; Rinkevich 2005; Shafir et al. 2006; Young et al. 2012). However, a majority of restoration efforts on Caribbean coral reefs have focused on the enhancement of coral biomass and density for a single genus – *Acropora* (Young et al. 2012). The necessity of taking a more holistic view of coral reef restoration is becoming more apparent with a growing body of literature emphasizing the importance of ecosystem services, ecological function, and - in particular - herbivory as essential components of any successful coral reef restoration plan (see Jackson et al. 2001; Bellwood et al. 2004, 2006; Hughes et al. 2010).

Numerous studies have investigated the effects of herbivores on coral reefs (e.g., Bellwood et al. 2006; Hughes et al. 2007; Burkepile and Hay 2008, 2010), and several have documented the role of grazing crabs as herbivores in coastal communities (e.g., Coen 1988a,b; Coen and Tanner 1989; Stachowicz and Hay 1996, 1999; Butler and Mojica 2012). However,

this is the first study to examine the density-dependent and cascading effects of grazing crabs in a coral habitat restoration context. In Chapter 2, I demonstrated the potential of *Maguimithrax spinosissimus* as a tool for ameliorating the overgrowth of coral habitat by chemically-defended benthic macroalgae. I demonstrated that *M. spinosissimus* is amenable to transplantation onto degraded reef structures and identified a critical point in crab size at which mortality drops off significantly – an appropriate size of crabs for transplantation. I also demonstrated that a large proportion of transplanted crabs exhibit site fidelity even after being translocated onto discrete coral reef structures. Finally, I demonstrated that increasing crab density on coral reefs significantly reduced the cover of benthic macroalgae on par with physical removal, resulting in increased coral and fish recruitment.

This study highlights the conspicuous absence of critical grazing function on degraded reefs in the Florida Keys. Recently, van Woesik et al. (2018) reported that transplanted corals exhibit much greater survival where algae are sparse or absent than in areas where algae, particularly *Dictyota* spp., are abundant. The results of this study suggest that increasing the density of crabs on a Caribbean reef can substantially improve conditions for the recruitment, growth, and survival of reef-building corals by directly and significantly reducing the cover of benthic macroalgae. Interestingly, this study also hinted at the potential of crab density enhancement in altering the composition of the benthic and demersal fish community around coral reefs.

In Chapter 3, I replicated the large field study from Chapter 2 in a new location. The demonstrable effects of crab grazing on the abundance of benthic macroalgae and the recruitment of corals and fish were replicated. Crab grazing again significantly reduced the cover of benthic macroalgae on reefs to which crabs were added, and increased coral recruitment as well as the richness and abundance of reef-associated fishes. Using a simple field study, I also

demonstrated that algae reduce the surface rugosity of coral patch reefs and that crab grazing increases the rugosity of the reef structure by opening up the interstices and holes in the carbonate matrix. This increased rugosity is likely the mechanism by which fish community composition is altered by crab density. As crabs remove algae, reef rugosity increases which, in turn, increases the availability of habitat to juvenile and small-bodied reef fishes, thus offering greater prey abundance to predatory fishes – a cascading response leading to a more abundant and speciose reef fish community. These results supported my hypothesis that increasing the density of crabs on degraded reefs can improve conditions for coral restoration and recovery. Indeed Shantz et al. (2015) report that fish grazing rates and coral growth are both significantly greater in areas where reef fishes (primarily *Haemulidae*) are abundant than in areas where they are less abundant and advise that coral restoration efforts should strive to increase structural complexity to drive increases in the abundance of fishes and facilitate increased grazing intensity and coral growth of transplanted corals.

This study also demonstrates the potential of grazing crabs as a management tool for improving conditions for coral restoration at the community-level. While *M. spinosissimus* represents an excellent candidate for such efforts, its low natural abundance along with a cryptic and nocturnal habit make large-scale use of the species for restoration logistically challenging. Production of crabs via mariculture is possible and the species' aquaculture potential has been well-documented (see Brownell et al. 1977; Provenzano and Brownell 1977; Tunberg and Creswell 1988, 1991; Creswell et al. 1989; Wilber and Wilber 1989, 1991; Wilber et al. 1992; Creswell 2011). Thus, with a modicum of investment, the commercial-scale production of crabs for restoration is practical and achievable.

Although *M. spinosissimus* represents a potential candidate for improving conditions for Caribbean coral reef restoration efforts, it is only one of many herbivores in the system.

Recently, a growing body of literature has demonstrated that small-bodied microherbivores are important grazers on coral reefs (see Kuempel and Altieri 2017; Altman-Kurosaki et al. 2018). Therefore, in Chapter 4 I evaluated the intra- and interspecific grazing interactions among several Mithracid species in combination with *M. spinosissimus*. *Mithraculus sculptus*, *M. coryphe*, and *M. cinctimanus* are all common and abundant on Caribbean coral reefs and backreef habitats, and are morphologically similar to *M. spinosissimus*, although much smaller as adults. Previous studies have demonstrated that these diminutive Mithracids are capable of effecting similar reductions in the distribution of benthic macroalgae and, in some cases, facilitating coral growth and survival (Coen 1988a, b; Stachowicz and Hay 1996, 1999). This is the first study, however, to compare the grazing capabilities and effects of multiple Mithracid species. I found that *Mithraculus* spp. consume less algae per individual than *Maguimithrax spinosissimus*, but when scaled to crab biomass *Mithraculus* spp. consume significantly more algae than does *M. spinosissimus*. When multiple individuals are present, intraspecific pairs exhibited a neutral or mildly antagonistic relationship in terms of net consumption. Whereas interspecific pairing that included *Mithraculus* and *Maguimithrax* resulted in grazing facilitation and higher-than-expected net consumption of macroalgae. These results suggest that while enhancing the density of *M. spinosissimus* on degraded reefs has rapid and significant effects on the benthic community, incorporating other Mithracid species into any biological remediation plan aimed at improving conditions for coral reef restoration will likely increase the net effect of grazing and may also increase redundancy in their ecological function (i.e., grazing).

In summary, these studies have demonstrated the potentially enormous density-dependent and cascading effect of certain cryptic species on community structure. Although sublime in their effect at natural densities, fostering the ecological emergence of such species in destabilized ecosystems may offer a means to radically redirect the declining trajectories of disturbed

ecosystems. My research with a suite of herbivorous crabs offers promise for coral reefs caught in the smothering grasp of macroalgal overgrowth. Modest increases crab abundance can have profound effects on the character of coral reef benthic habitats, with cascading effects on the composition of the greater reef community. It is imperative that resource managers and restoration activities harness these positive interactions and use facilitation to effect community-level restoration rather than focusing simply on the enhancement of a single or very few foundation species (*sensu* Shaver and Silliman 2017).

My studies also highlight the substantial knowledge gap that exists with respect to the functional significance of small-bodied and cryptic invertebrate species in coral reef communities. There remains a substantial gap in our knowledge of how such density-dependent and cryptic functional groups may (or may not) facilitate active coral reef restoration. Although *M. spinosissimus* represents a viable candidate for mediating the pervasive growth of algae on Caribbean reefs, it is possible that the natural history of *Mithraculus* spp. offers another opportunity for facilitating active coral restoration efforts. The diminutive *Mithraculus* spp. share a mutualistic relationship with structurally-complex Cnidarian hosts such as *Acropora* spp. and branching *Porites* spp. This aspect of *Mithraculus* natural history suggests that the insidious effects of coral-algal competition might ameliorated in coral nurseries and in colonies outplanted onto reefs if crabs were added to branching coral colonies. The mutualistic relationship between corals and crabs is yet to be studied in depth. The effect of multiple Mithracids as well as other mutualistic herbivore species on coral reef community ecology and restoration is an exciting and open avenue of study and should be investigated further. Fostering such positive interactions in a restoration framework should be the goal of restoration ecologists and resource managers.

It is likely that coral reef communities will continue along a trajectory of decline through the 21st century. Restoration ecology may offer avenues for staving off or reversing the loss of

critical ecosystem function as these complex communities are exposed to anthropogenic disturbances directly (e.g., fishing, anchor damage, ship groundings, pollution) and indirectly (e.g., changing climatic conditions, acidifying oceans, increasing sea-surface temperatures, increasing UV exposure). This new and burgeoning field also offers an excellent opportunity for the investigation of general ecological theory (e.g., founder effects, succession, competition, facilitation) in a changing environment.

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APPENDIX A

FIELD SITE GPS COORDINATES

Location	Site ID	Chapter	Latitude	Longitude
Coral Gardens	1291	2	24 50'.308N	080 43'.782W
Coral Gardens	1298	2	24 50'.309N	080 43'.792W
Coral Gardens	1294	2	24 50.721'N	080 43.786'W
Coral Gardens	1297	2	24 50'.310N	080 43'.803W
Coral Gardens	1296	2	24 50.310'N	080 43.807'W
Coral Gardens	1287	2	24 50.302'N	080 43.806'W
Coral Gardens	1300	2	24 50'.318N	080 43'.793W
Coral Gardens	1299	2	24 50.314'N	080 43.791'W
Coral Gardens	1267	2	24 50.320'N	080 43.797'W
Coral Gardens	1742	2	24 50.320'N	080 43.796'W
Coral Gardens	1289	2	24 50.322'N	080 43.806'W
Coral Gardens	1285	2	24 50.303'N	080 43.806'W
Cheeca Rocks	001	3	24 54.310'N	080 37.082'W
Cheeca Rocks	003	3	24 53.837'N	080 37.240'W
Cheeca Rocks	004	3	24 53.852'N	080 37.218'W
Cheeca Rocks	006	3	24 53.858'N	080 37.176'W
Cheeca Rocks	007	3	24 53.854'N	080 37.119'W
Cheeca Rocks	008	3	24 53.872'N	080 37.105'W
Cheeca Rocks	010	3	24 53.883'N	080 37.085'W
Cheeca Rocks	011	3	24 53.890'N	080 37.073'W
Cheeca Rocks	012	3	24 53.889'N	080 37.059'W
Cheeca Rocks	013	3	24 54.381'N	080 36.837'W
Cheeca Rocks	014	3	24 54.377'N	080 36.854'W
Cheeca Rocks	015	3	24 54.320'N	080 36.808'W

APPENDIX B

CO-AUTHORSHIP STATEMENT AND MANUSCRIPT PUBLICATION STATUS

The studies presented in this dissertation were designed by Angelo J. Spadaro, with guidance and input from Dr. Mark J. Butler, as well as from committee members Dr. Daniel Barshis, Dr. Seabird McKeon, Dr. Eric Walters, and Dr. John McConaugha. All data for the experiments detailed here were collected and analyzed by Angelo J. Spadaro. Chapter 4 (Multiple Consumer Effects) was carried out in close collaboration with Dr. Seabird McKeon. All manuscripts resulting from these works were written by Angelo J. Spadaro, with editing and creative assistance from co-authors.

Three manuscripts are the expected outcome of this dissertation. The manuscript resulting from work presented in Chapters 2 and 3 (Density manipulation) is in preparation for submission to the journal *Science*, co-authored by Dr. Mark J. Butler. The manuscript resulting from the remaining work presented in Chapter 2 (Mortality and site fidelity) is in preparation for submission to the *Journal of Crustacean Biology*, co-authored by Dr. Mark J. Butler. The manuscript resulting from the work presented in Chapter 4 is in preparation for submission to the journal *PeerJ*, co-authored by Dr. Seabird McKeon and Dr. Mark J. Butler. I have included a table below detailing how my dissertation will be parsed among the proposed manuscripts.

Chapter	Experiment Description	Manuscript
2	Crab Predation Mortality	3
	Crab Retention	3
	Crab Density Manipulation	1
	Fish Community Composition	1
	Juvenile Coral Density	1
3	Crab Density Manipulation	1
	Juvenile Coral Density	1
	Fish Community Composition	1
	Reef Rugosity	1
	Fish Shelter Selection	1
4	Biomass Index	2
	Algae Consumption Rates	2
	Diet Preference	2
	Multiple Consumer Effects	2

Manuscript	Target Journal
1	Science
2	Peer J
3	Journal of Crustacean Biology

VITA

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Education

- Current Ecological Sciences Ph.D. – Old Dominion University, Department of Biological Sciences, Norfolk, VA
- B.S. Biological Sciences, 2010 – Old Dominion University, Department of Biological Sciences, Norfolk, VA

Publications

- Anderson JR, **Spadaro AJ**, Baeza JA, Behringer DB. 2013. Ontogenetic shifts in resource allocation: colour change and allometric growth of defensive and reproductive structures in the Caribbean spiny lobster *Panulirus argus*. *Biological Journal of the Linnean Society*, 108: 87-98.
- Baeza JA, Anderson JR, **Spadaro AJ**, Behringer DB. 2012. Sexual dimorphism, allometry, and size at first maturity of the Caribbean king crab, *Mithrax spinosissimus*, in the Florida Keys. *Journal of Shellfish Research*, 31(4): 909-916.

Employment

- 2011 – 2019 Graduate Research Assistant, Department of Biological Sciences, Old Dominion University
- 2009 – 2011 Research Technician, Department of Biological Sciences, Old Dominion University

Honors and Awards

- Paul W. Kirk, Jr. Wetland Research Award, Department of Biological Sciences, Old Dominion University
- Student Achievement Award for Academic Excellence, Gulf and Caribbean Fisheries Institute, Grand Cayman, Cayman Islands
- Fellowship in Ecological Restoration, Garden Club of America
- First place, Poster Presentation, Benthic Ecology Meeting, Quebec, Canada
- Graduate Research Fellowship, Smithsonian Institution, Fort Pierce, FL
- Student Engagement and Enrollment Services, Old Dominion University, Travel Award