ASSOCIATIONS BETWEEN HERBIVORE FUNCTIONAL GROUP DIVERSITY AND DENSITY AND ECOSYSTEM FUNCTIONING IN THE CARIBBEAN

by

Advait Mahesh Jukar
A Thesis
Submitted to the
Graduate Faculty
of
George Mason University
in Partial Fulfillment of
The Requirements for the Degree
of
Master of Science
Environmental Science and Policy

Committee:

Dr. Thomas E. Lovejoy, Thesis Director

Dr. Chris Kennedy, Committee Member

Dr. Nancy Knowlton, Committee Member

Dr. Jeremy Jackson, Committee Member

Dr. Albert P. Torzilli, Graduate Program Director

Dr. Robert B. Jonas, Department Chairperson

Dr. Donna Fox, Associate Dean, Student Affairs & Special Programs, College of Science

Dr. Peggy Agouris, Dean, College of Science

Date: 4/28/2014

Spring Semester 2014
George Mason University
Fairfax, VA

Associations Between Herbivore Functional Group Diversity and Density and Ecosystem Functioning in the Caribbean

A Thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at George Mason University

by

Advait Mahesh Jukar
Bachelor of Arts
Reed College, 2011

Director: Thomas E. Lovejoy, Professor
Department of Environmental Science and Policy

Spring Semester 2014
George Mason University
Fairfax, VA

This work is licensed under a creative commons attribution-noderivs 3.0 unported license.

ACKNOWLEDGEMENTS

To all those who helped me through this journey called Thesis, I am eternally grateful. First and foremost, Dr. Thomas Lovejoy, for being my mentor, for always encouraging me, for seeing my potential and always bringing it out in me. My committee members, Dr. Jeremy Jackson and Dr. Nancy Knowlton, for helping me understand the complexities of coral reef ecology and Dr. Chris Kennedy, for helping me understand the statistical techniques I needed to use. Mary Donovan for sharing the data without which this thesis would not have been possible. Dr. Gene Hunt and Dr. Arndt Laemmerzahl for their help with R and the modeling effort. Dr. Rebecca Forkner, for her help with the diversity metrics. Dr. Carole Baldwin for her help with the fish functional groups. And last, but not least, I want to thank my parents and family and friends for their constant encouragement.

TABLE OF CONTENTS

Page
List of Tables vi
List of Figures vii
List of Equations viii
Abstract ix
Introduction 11
Changing Face of the Caribbean 14
Historical Overfishing and Altered Food webs 14
Decline in Coral Cover 15
Mass Mortality of *Diadema antillarum* 15
Consequences of the Loss of *Diadema* and Coral Cover 16
Modern Day Heterogeneity in the Caribbean 17
Herbivorous fish and ecosystem functioning in the Caribbean 19
Herbivorous Fish and Functional Groups 19
Importance of functional diversity of herbivorous fish on coral reefs 22
Importance of herbivore density in the function of herbivory on coral reefs 23
Goals of this study 25
Methods 26
Database 26
Functional Classification 29
Data Analysis 30
Benthic cover 30
Explanatory Variables 31
Statistical Techniques 31
Results 34
Benthic Cover 34
Fish Assemblages 35

Model Selection 40
Relationship of the Functional Variables to Macroalgal Cover 42
Alternative hypotheses for Macroalgal Cover 45
Relationship of the Functional Variables to Coral Cover 45
Discussion 48
Herbivory on Caribbean Reefs: Size Matters 49
Diversity and the Function of Herbivory 53
Absence of the Browsers 55
Associations between Grazers/Detritivores and Benthic Cover 55
Habitat Preference of the Territorial Damselfish 58
Alternative Explanations for Benthic Cover 59
Conclusion 60
Appendices 62
Appendix A: Log-Likelihood Ratio Test Tables for Model Selection for Models with Macroalgal Cover as the Response Variable 62
Appendix B: Log-Likelihood Ratio Test Tables for Model Selection for Models with Coral Cover as the Response Variable 63
References 64

LIST OF TABLES

Table Page
Table 1: Site Summary 28
Table 2: Fish Functional Groups 29
Table 3: Description of models derived from the model selection procedure 41
Table 4: Comparison of terms from models for macroalgal cover 43
Table 5: Comparison of terms from models for coral cover 45
Table 6: Model Ranking 46

LIST OF FIGURES

Figure Page
Figure 1: Sites used in this study. 27
Figure 2: Average percent cover of coral and macroalgae. 34
Figure 3: Diversity of the herbivorous functional groups used in this study..... 36
Figure 4: Density of the herbivorous functional groups used in this study. 37
Figure 5: Relationship of the fixed effects to macroalgal cover..... 42
Figure 6: Relationship of the fixed effects to coral cover..... 44
Figure 7: Relationship of the densities of individual species within the LSE to total density and diversity. 50
Figure 8: Relationship of the densities of individual species within the SSE to total density and diversity. 51
Figure 9. Relationship of the densities of individual species within the GD to total density and diversity..... 56
Figure 10: Relationship of the densities of individual species within the TDF to total density and diversity. 58

LIST OF EQUATIONS

Equation Page
Equation 1: Shannon-Weiner Diversity Index 31

ABSTRACT

ASSOCIATIONS BETWEEN HERBIVORE FUNCTIONAL GROUP DIVERSITY AND DENSITY AND ECOSYSTEM FUNCTIONING IN THE CARIBBEAN

Advait Mahesh Jukar, M.S.

George Mason University, 2014

Thesis Director: Dr. Thomas E. Lovejoy

With an increase in the rate of biodiversity loss, much research has been focused on understanding the relationship between biodiversity and ecosystem functioning. Past research has shown that both the diversity and density of functional groups is positively related to ecosystem functions. This thesis explores the relationship between the variation in macroalgal and coral cover and five herbivorous fish functional groups on 51 reefs in the Caribbean. The main aims are to determine which functional groups significantly affect macroalgal cover and coral cover, both direct and indirect proxies for herbivory, and to understand the relative importance of functional group diversity and density in the function of herbivory. Linear mixed effect models are used to determine the relationships. The primary findings are 1) large parrotfish are negatively associated with macroalgal cover. These fish are known to consume large quantities of macroalgae, suggesting that this functional group is playing an important role in the function of herbivory, and 2) the density of territorial damselfish is negatively associated with macroalgal cover and positively with

coral cover. A more detailed analysis of the functional group revealed high densities of only two species-*Stegastes partitus* and *Stegastes adustus*. It is known that these species do not exclude macroalgae from their territories, but prefer habitats with high coral cover and low macroalgal cover, suggesting that the relationship between territorial damselfish density and benthic cover is a result of habitat preference rather than herbivory. In addition to these findings, diversity was not a robust predictor of benthic cover, suggesting that merely increasing the species richness of an assemblage will not result in increased functioning; a proportional increase in fish density is required.

INTRODUCTION

Research driven by the recent loss of biodiversity has shown that species influence the structure of habitats, biogeochemical cycles and the productivity of ecosystems (Cardinale et al. 2012). A corollary to such studies is that a loss of biodiversity can significantly change the functioning of ecosystems. A functional group perspective of biodiversity and ecosystem functioning has emerged (Naeem et al. 2012).

The functioning of an ecosystem is not determined by the phylogenetic make up of the biota, but by the distribution of functional traits (Naeem and Wright 2003). A functional trait is a phenotypic trait that is associated with a particular biogeochemical function or ecosystem property (Naeem and Wright 2003). In an ecosystem, multiple species that share functional traits are classified as functional groups (Naeem and Wright 2003). Complex functions like herbivory, which involve interactions among a great number of species at different trophic levels, can be governed by a number of functional groups, each performing a different role in the larger process (Steneck and Dethier 1994).

While much of what we know about the role of biodiversity in ecosystem functioning comes from experiments on plant functional diversity and functions such as primary productivity, nitrogen processing and biomass, some general trends have been documented (Naeem et al. 1995; Tilman et al. 1996; Tilman 1997; Loreau et al. 2001; Hooper et al. 2005; Cardinale et al. 2011). For instance, how well an ecosystem function is performed depends on the diversity within functional groups (and among functional groups if the

function is governed by more than one), and the abundance of individual functional groups (Hooper et al. 2002; Cardinale et al. 2012). Greater species diversity within functional groups can increase the efficiency of performing the function by complimentary resource use, also known as resource partitioning (Loreau and Hector 2001). For example, Bueno and colleagues found that tapirs and spider monkeys disperse seeds of different sizes in different locations in the rainforest, but both contribute to the function of seed dispersal (Bueno et al. 2013). A loss of either of these species would change the floral composition of the forest by preventing the recruitment of some tree species. Similar effects have also been seen in pollinator communities, in steppe sagebrush communities and in reef fish, thus highlighting the importance of species diversity within functional groups across a range of ecosystems (Anderson and Inouye 2001; Burkepile and Hay 2011; Fründ et al. 2013). Diversity also increases the probability of finding a more productive species in the functional group (Tilman 1997; Cardinale et al. 2006).

Functional groups can exhibit complementarity of resource use as well (Tilman 1997). Studies on insectivory by bird functional groups showed that an increase in insectivorous bird functional groups resulted in an increase in the number of arthropods consumed (Philpott et al. 2009). They also showed that certain functional groups were responsible for a disproportionate amount of arthropod removal suggesting that particular functional groups play a larger role in the overall function (Philpott et al. 2009). Similar effects have been seen on temperate grasslands where certain plant functional groups are more efficient at performing a particular function (Tilman 1997).

The numerical abundance of a functional group also results in greater functioning. On coral reefs, the density of certain herbivorous functional groups is positively related to

the amount of algae grazed (Lewis and Wainwright 1985; Steneck and Dethier 1994; Cheal et al. 2010).

While both diversity and density are important factors that influence functioning, we still lack a clear understanding of the relative contribution of diversity and density in ecosystem functioning in many ecosystems, i.e. is a function mediated by one very abundant species or is the function performed better when multiple, equally abundant species contribute to it. Knowledge of how functional groups influence ecosystem processes will improve our understanding of how biodiversity loss affects these processes.

Coral reefs provide an excellent model to study these relationships. These are highly diverse ecosystems with a number of different functional groups, each including many species. The herbivore guild, which consists of a number of smaller functional groups, is important in maintaining resistance and resilience against macroalgal phase shifts (Hughes et al. 2007; Green and Bellwood 2009; Hughes et al. 2010). Most studies in the past have looked at reef herbivores as a singular functional group or have divided them on a phylogenetic basis (Lewis 1985; Lewis and Wainwright 1985; Lewis 1986), but recent studies have shown the importance of dividing herbivorous fish into groups based on their mode of feeding, diet or morphology (Bellwood and Choat 1990; Bellwood et al. 2003; Bellwood et al. 2004; Green and Bellwood 2009; Heenan and Williams 2013; Johansson et al. 2013). This functional approach has been largely studied on reefs in the Pacific and only a few studies have looked at herbivorous functional groups in the Caribbean (Cardoso et al. 2009). Previous studies have related metrics such as biomass and abundance of the functional groups to the function of herbivory, but have seldom considered diversity as a metric even though it is now clear that herbivorous fish within the same functional group feed

preferentially on different algal species, at different levels of succession, and at different times of the year (Mantyka and Bellwood 2007; Burkepile and Hay 2008; Burkepile and Hay 2010; Lefevre and Bellwood 2011). These fish also indirectly increase coral cover by reducing macroalgae on the reefs, thus allowing for the settlement of more coral recruits (Burkepile and Hay 2008; Burkepile and Hay 2011).

The primary objective of this thesis is to determine which herbivorous fish functional groups facilitate the process of macroalgal herbivory on Caribbean coral reefs and whether the function is controlled by one or by a number of highly abundant species, i.e. diversity. Caribbean reefs are a good model system to study the relative importance of diversity and density of different functional groups on the process of herbivory because of the considerable variation in both fish and benthic communities across the region.

Changing Face of the Caribbean

The Caribbean has undergone many changes since prehistoric times (Pandolfi et al. 2003). The following sections illustrate how multiple natural and anthropogenic factors have resulted in the heterogeneity that we see in both fish and benthic communities across the region today.

Historical Overfishing and Altered Food webs

The Caribbean has changed since the first European explorers came to the region (Jackson 1997). Overharvesting of key species, disease and hurricanes have degraded the entire region (Pandolfi et al. 2003). The food web was once complex with many large vertebrates dominating higher trophic levels (Jackson et al. 2001). However, by the early 1900s, populations of the once abundant green turtles, hawksbill turtles, west Indian manatees and the now extinct Caribbean monk seal were in heavy decline (Jackson 1997).

Artisanal fishing further reduced the populations of large predatory fish and herbivorous fish by the 1950s (Jackson 1997). The remaining populations of fish have been declining since (Paddack et al. 2009).

Decline in Coral Cover

Since the 1970s, coral cover in the Caribbean has fallen on average by about 50%-80% (Gardner et al. 2003; Jackson et al. 2013). Much of this decline is a result of the decimation of *Acropora cervicornis* and *Acropora palmata*, the two ecologically dominant and abundant species of reef building corals (Aronson and Precht 2006; Pandolfi and Jackson 2006). The causes for this decline are varied. A cold water upwelling was responsible for the decline of acroporids in the Florida Keys in the 1970s (Davis 1982). Jamaican arcoporids were mostly wiped out when Hurricane Allen passed over the region in 1980 (Woodley et al. 1981). The region-wide spread of white band disease is also responsible for the decline from the late 1970s to the 1990s (Aronson and Precht 2001; Aronson and Precht 2006; Schutte et al. 2010; Weil and Rogers 2011). These declines led to the opening up of space on the reefs (Aronson and Precht 2006). But, the consequences of this loss were not apparent till the early 1980s.

Mass Mortality of *Diadema antillarum*

In 1983, soon after the decline of the acroporids, *Diadema antillarum*, one of the most abundant herbivorous urchins on Caribbean reefs suffered a mass mortality caused by an unidentified pathogen (Lessios 1988). The pathogen spread in two waves, one from the mouth of the Panama Canal to Bermuda and the other from the Panama Canal to Tobago (Lessios 1988). Before 1983, the density of *Diadema* ranged from about $5/m^2$ to about $25/m^2$ (Hughes et al. 2010). After the pathogen hit in 1983 and spread, the densities dropped to

almost zero within a year (Lessios 1988; Jackson et al. 2013). Recovery has been scarce, though some locations show densities of around 3-5/m^2 (Edmunds and Carpenter 2001; Carpenter and Edmunds 2006; Idjadi et al. 2006).

Consequences of the Loss of *Diadema* and Coral Cover

After the sudden loss of *Diadema antillarum,* many Caribbean reefs showed dramatic increases in macroalgae in the benthos (Hughes et al. 1987; Steneck 1993; Shulman and Robertson 1996; McClanahan and Muthiga 1998). Macroalgae became more dominant while the cover of crustose corraline algae decreased (Lessios 1988). The effect of the *Diadema* die-off was however not felt equally across the region (Lessios 1988). For example, at Jamaica, algal cover increased from 1% to almost 95% in the first two years after the mass mortality while Curacao experienced only a 30% increase (Lessios 1988).

A plausible hypothesis to explain this heretogeneity is the variation in herbivory on the reefs. Algae and coral compete for space on reefs and macroalgae are held in check by the process of herbivory (Mumby and Steneck 2008). The process of herbivory depends on the proportion of the area grazed per unit time (Mumby and Steneck 2008). Therefore, the probability that an algal bloom will occur depends on the area available for colonization and the intensity of grazing (Mumby and Steneck 2008). These dynamics are governed by complex feedback mechanisms that result from interactions between algae, coral and herbivores (Mumby and Steneck 2008). When grazing pressure is low because of low densities of herbivores or the extirpation of a dominant herbivore and space for colonization is high due to coral mortality, macroalgae are released from grazing pressure, initiating a negative feedback loop. As algal succession proceeds, the community will change from turf algae to macroalgae (Ceccarelli et al. 2011), both of which indirectly suppress coral growth

by decreasing recruitment (Kuffner et al. 2006; Arnold et al. 2010). This further suppresses coral cover and promotes more algal growth if the resident herbivores cannot compensate by increasing their populations. If coral recruitment drops below replacement, the structural complexity of the reef decreases, which reduces fish habitat, further reducing herbivory, and increasing macroalgae (Wilson et al. 2008; Vergés et al. 2011). The reverse happens on reefs with a healthy herbivore community and high cover of corals (Mumby and Steneck 2008), examples of which have been seen in reefs in the Pacific and Indian Oceans (Arthur et al. 2005; Gilmour et al. 2013).

The freeing up of substratum because of the loss of the acroporids and the mortality of the dominant herbivore *Diadema* coupled with historical overfishing primed the region for these negative feedbacks. Yet, the strength of the feedbacks varied from location to location. Studies in the mid 1980s on the competition between *Diadema* and fish on grazing revealed an inverse relationship such that overfished reefs had a higher density of urchins and lower abundances of herbivorous fish (Hay 1984; Hay and Taylor 1985; Lewis and Wainwright 1985). Therefore, reefs that had a fish community large enough to functionally compensate for the loss of *Diadema*, such as ones in the San Blas Archipelago, showed lower increases in macroalgae; whereas reefs that have been historically overfished and had *Diadema antillarum* filling the role of the dominant herbivore, such as the ones in Jamaica and the US Virgin Islands, showed greater macroalgal proliferation (Lessios 1988; Hughes 1994; Aronson and Precht 2006; Mumby et al. 2007).

Modern Day Heterogeneity in the Caribbean

There is considerable variation in both the benthic and fish communities in the Caribbean today. A number of factors such as bleaching and hurricanes have kept coral

cover low in many locations (Gardner et al. 2005; Eakin et al. 2010). Live coral cover ranges from 2.8 % for southeast Florida to 53.1% for the Flower Garden Banks (Jackson et al. 2013). There is also a great deal of variation in macroalgal cover since 2005 with cover averaging 19.6% on less fished reefs and 31.5% on heavily fished reefs (Jackson et al. 2013).

Since the early 1980s, a number of marine protected areas have been established in the Caribbean and different management practices for fishing have been implemented, which has significantly affected fish populations (Mora et al. 2006; Newman et al. 2006; Edwards et al. 2014). Greater protection results in a higher biomass of herbivorous fish, which then results in more grazing (Mumby et al. 2006; Edwards et al. 2014). Human populations have also increased in the region, resulting in overharvesting of non-protected reefs (Hughes et al. 2003; Mora et al. 2011). These factors, coupled with historical overfishing have resulted in a great deal of variation in the fish communities in the Caribbean (Williams and Polunin 2001; Newman et al. 2006). For example, Williams and Polunin surveyed 7 reefs between 1997 and 1998 and found herbivorous fish biomasses ranging from 2-5g/m^2 in Jamaica to 17.1g/m^2 in Barbados while surveys conducted by Newman and colleagues (2006) in 2004-2005 showed a gradient of fish biomass, which ranged from 14 g/m^2 to 593g/m^2.

These trends in fish, coral and algal populations suggest a shifted baseline in the Caribbean (Knowlton and Jackson 2008). A feature of this new baseline is that grazing pressure on reefs is low and has been insufficient to return macroalgae to pre-1983 levels (Paddack et al. 2006). It has even been suggested that a grazing threshold exists for herbivorous fish (Williams and Polunin 2001; Williams et al. 2001). Other studies have shown that present herbivore populations are able to prevent the further growth of

macroalgae, but are unable to reduce the overall cover to historical levels (Paddack et al. 2006). However, it is clear that a negative association exists between macroalgae and herbivorous fish (Williams and Polunin 2001; Newman et al. 2006).

Herbivorous fish and ecosystem functioning in the Caribbean

It is clear now that the fish communities on reefs can be viewed as indicators of the strength of the process of herbivory. It has also been seen that some of the variation in macroalgal cover on reefs is driven by differences in the density and composition of the herbivore guild (Lewis and Wainwright 1985; Paddack et al. 2006). But the effect of herbivore diversity on macroalgal cover has rarely been studied or fully explored despite significant variation in the composition of herbivores across reefs (Paddack et al. 2006). This section highlights the importance of dividing herbivorous fish into functional groups and discusses the importance of diversity and density of herbivorous fish in ecosystem functioning on coral reefs.

Herbivorous Fish and Functional Groups

Herbivorous fish on reefs comprise of a variety of families including the *Acanthuridae* (surgeonfish), the *Scaridae* (parrotfish), and *Pomacentridae* (damselfish) (Green and Bellwood 2009). Other families such as the *Blenniidae* (blennies) and *Gobiidae* (gobies) have some herbivorous members as well (Green and Bellwood 2009). These fish feed on a variety of algae (macroalgae, turf algae, corraline algae), detritus and the coral itself (Choat 1991; Steneck and Dethier 1994; Green and Bellwood 2009). Observational and experimental studies on Caribbean reefs show differences in diet and feeding behavior among different taxa which can allow us to classify these fish into functional groups (Ogden and Lobel 1978; Lobel 1980; Lobel and Ogden 1981; Lewis 1985, 1986; Bruggemann et al. 1994; Bruggemann

et al. 1996; McAfee and Morgan 1996; Paddack et al. 2006; Cardoso et al. 2009; Burkepile and Hay 2010, 2011).

One can first start classifying herbivorous fish into functional groups based on whether they are territorial or mobile. Fish from the family *Pomacentridae* are territorial (Green and Bellwood 2009). The damselfish farm algae within their territories and guard them against other roving herbivores (Lobel 1980). The role these fish play in controlling macroalgae and turf algae on the reefs in still unclear. Some studies have shown that macroalgae tends to grow within their territories (Ceccarelli et al. 2005), while others have shown farmers exclude macroalgae (Ceccarelli et al. 2011). It is likely that these effects are species specific as shown in a study by Hoey and Bellwood (2009). They showed that 4 out of 6 species of damselfish on the Great Barrier Reef excluded macroalgae while the territories of 2 species were characterized by brown macroalgae (Hoey and Bellwood 2009a). Few studies have looked at the effect of damselfish on the benthic community in the Caribbean. Lobel (1980) showed that *Stegastes nigricans* feeds primarily on epiphytic blue green algae but does not feed on the red macroalgae, *Gelidium pulchellum* (Lobel 1980). Similarly, Hinds and Ballantine found that *S. nigricans* allows the growth of macroalgae such as *Dictyota* and *Halimeda* (Hinds and Ballantine 1987). While these fish might result in more macroalgae on the reefs, their role is still unclear since the literature mostly comprises of studies of one species out of a family that includes 9 species in the Caribbean (Choat 1991).

Acanthurids and Scarids are not territorial and can be classified as mobile herbivores. These mobile fish can be further classified into other functional groups based on the impact they have on the substratum. Grazers like the surgeonfish feed on epilithic turf algae and smaller macroalgae, but do not scrape off or remove parts of the substratum (Burkepile and

Hay 2010; Marshell and Mumby 2012). Other families such as the blennies also play a role in grazing (Wilson 2009). Like the grazers, detritivores also remove turf algae in their search for food, thus preventing the recruitment of macroalgae and removing smaller macroalgae from the substratum (Lewis 1986). Collectively, this group is called the grazers and detritivores (Green and Bellwood 2009). The other functional group that does not have an impact on the substrate is the browser group. These fish, for example, *Sparisoma radians*, preferentially feed on macroalgae without scaring the substrate (Lobel and Ogden 1981).

Parrotfish from the family *Scaridae* that scrape the surface of the substratum to feed on epilithic turf algae can be classified as scrapers and excavators (Bellwood and Choat 1990; Green and Bellwood 2009). Scrapers remove small amounts of the matrix while excavators take deeper bites (Green and Bellwood 2009). They have specialized beaks and teeth that allow them to do so (Bellwood and Choat 1990). These fish prevent the settlement and overgrowth of macroalgae and provide a clean surface for coral recruitment (Paddack et al. 2006; Hughes et al. 2007; Hoey and Bellwood 2008).

Scrapers and excavators can be further separated by size since studies have found different size classes have significantly different impacts on the benthic community (Green and Bellwood 2009). Bonaldo and Bellwood (2009) showed that per kilogram of biomass, small individuals from the species *Scarus rivulatus* grazed a greater area while large individuals removed a larger volume of algae and matrix. This suggests that smaller individuals might control the height of algal turfs but are unable to remove large amounts of it and free up substratum for coral colonization (Bonaldo and Bellwood 2008). In the Caribbean, *Scarus vetula* and *Sparisoma viride* are the largest excavators. They feed on epilithic algal turfs by taking large bites of the substratum. A study on the foraging behavior of different size

classes of these two fish showed that larger individuals were responsible for more epilithic algal turf removal and more bioerosion, a key process for the recruitment of crustose corraline algae and corals (Bruggemann et al. 1996). Other studies in the Caribbean have shown that when the density of large bodied parrotfish increases in unfished areas, the grazing intensity almost doubles and macroalgal cover is significantly reduced (Mumby et al. 2006). Experimental studies have also shown similarities in the feeding behavior of large bodied species like *Scarus guacamaia* and *Sparisoma viridae* (Burkepile and Hay 2011).

Importance of functional diversity of herbivorous fish on coral reefs

Theory would suggest that greater herbivore diversity would benefit the function of herbivory because different herbivores have different feeding strategies, dietary preferences and tolerances towards algal defenses (Lubchenco and Gaines 1981; Paul and Hay 1986; Duffy and Hay 1990; Duffy 2002). Diversity provides redundancy and complementarity of function as well has a high probability that a high functioning species or group is present in an assemblage, all of which have been studied on reef herbivores (Bellwood et al. 2003; Bellwood et al. 2006; Burkepile and Hay 2008; Hoey and Bellwood 2009b; Burkepile and Hay 2011).

Observational studies in the Caribbean have shown that herbivorous fish within the same functional group show shared resource use, but the proportion of resources consumed by each species is different, showing some amount of complementarity with the group (Bruggemann et al. 1994; McAfee and Morgan 1996; Cardoso et al. 2009). These effects apply to functional groups as well. Caged exclosure studies that test the effect of herbivore species richness on macroalgae on coral reefs have shown that mixed species treatments (species richness=2) decreased the abundance of macroalgae by 54-76% as compared to

single species treatments (Burkepile and Hay 2008). The species that were used were *Acanthurus bahianus, Sparisoma aurofrenatum and Scarus taeniopterus. Acanthurus bahianus* belongs to the grazer/detritivore functional group while the other two species are small scrapers and excavators. *Acanthurus bahianus* and *Sparisoma aurofranatum* and *Scarus taeniopterus* fed on different species of macroalgae, showing complementarity within a functional groups and between functional groups. Similar experiments have shown that *Acanthurus bahianus* and *Scarus taeniopterus* reduced the cover of upright macroalgae and turf algae in early successional stages but did not have an effect on late successional macroalgae, whereas *Sparisoma aurofrenatum* did not have any effect on early stage macroalgae, but significantly reduced late stage species (Burkepile and Hay 2010). This study further highlights the importance of feeding complementarity both within and between functional groups. Other studies have also shown some redundancy in function within functional groups. For example, caged experiments in the Florida Keys showed that *Sparisoma aurofrenatum* and *Sparisoma chrysopterum*, both small scrapers and excavators are functionally redundant and *Acanthurus coerulus* and *Acanthurus bahianus*, both grazers/detritivores are functionally similar (Burkepile and Hay 2011). However, limited functional redundancy is becoming increasingly apparent, implying either the importance of one high functioning species (Bellwood et al. 2003; Mantyka and Bellwood 2007; Hoey and Bellwood 2008; Hoey and Bellwood 2009b).

Importance of herbivore density in the function of herbivory on coral reefs

Studies suggest that the population density of herbivores is related to grazing intensity (Mumby and Steneck 2008). Experiments on reefs have shown that grazing intensity is highly correlated with herbivore abundance (Lewis and Wainwright 1985; Lewis 1986). Studies on the Great Barrier Reef have also shown that the abundance of different

functional groups along is an important factor in controlling macroalgal proliferation after a disturbance. For example, Cheal et al. (2010) conducted a long-term study on the role of functional diversity on phase shifts on three reefs in the Great Barrier Reef system between the years 1997 and 2007. In 1998, a mass-bleaching event caused significant coral mortality and subsequent cyclones and crown of thorn starfish outbreaks further reduced coral cover. However, only one out of the three reefs surveyed showed increases in macroalgae (Cheal et al. 2010). They found that the reef that showed the increase in algae had low abundance of grazers and browsers (Cheal et al. 2010). Similarly, studies on the Scott Reef system in Western Australia have shown that algal turfs and macroalgae were controlled after corals suffered mass mortality due to the 1998 bleaching event because of the high densities of herbivorous fish (Gilmour et al. 2013). High herbivore abundance has also been linked to reef resilience against macroalgal growth post the 1998 bleaching event in the Lakshadweep Islands off the south western coast of India (Arthur et al. 2005). In the Caribbean, spatial variation in algal consumption rates has been attributed in part to the density of herbivorous fish (Paddack et al. 2006). Mumby et al. (2006) studied the process of grazing by parrotfish inside and outside the Exuma Cays Land and Sea Park. Within the park where fishing is banned, the density of large bodied parrotfish like *Sparisoma viridae* and *Scarus vetula* was nearly double of that on reefs where fishing was allowed whereas the density of small parrotfish did not differ between fished reefs and the park (Mumby et al. 2006). The high density of large parrotfish inside the park resulted in an increase in grazing intensity such that macroalgal cover was four times as low in the park as opposed to outside the park (Mumby et al. 2006).

Goals of this study

The aim of this study was to investigate the association between the diversity and density of five herbivorous functional groups-grazers/detritivores, browsers, large scrapers and excavators, small scrapers and excavators and territorial damselfish, on macroalgal cover and coral cover (surrogates for the process of herbivory) on Caribbean coral reefs. This study uses data from a number of different reefs, collected for the Global Coral Reef Monitoring Network's Report on the Status and Trends of Caribbean Coral Reefs from 1970 to 2011, to explore these relationships. Specifically, this thesis tests the hypothesis that functional diversity and density is negatively associated with macroalgal cover and positively with coral cover in an effort to determine the relative importance of these characteristics to the function of herbivory. Using such an approach, this thesis hopes to provide an understanding of how herbivorous fish affect the process of herbivory on profoundly disturbed reefs and assess the relative importance of different functional groups in this new Caribbean baseline.

METHODS

Database

The data for this study was a subset of the data collected for the Global Coral Reef Monitoring Network's (GCRMN) report on the status and trend of Caribbean reefs for the years 1970-2011. The report used data that consisted of records for percent cover of macroalgae, percent coral cover and fish density from 90 reef locations distributed among 34 countries, states and territories. These records were obtained from published literature, scientific reports and raw data from principal investigators (Jackson et al. 2013). Data were nested and organized as follows: every country had one or many geographic locations determined by oceanographic conditions and political boundaries. Each location had reef sites clustered within that were sampled to gather the data. Each site is characterized as an individual geographic location with unique spatial coordinates. The basic sampling unit was a survey, which is a set of replicate data points collected at that site, at a particular depth on a particular date. The majority of surveys were conducted by belt transects and by stationary point count.

For the purposes of this study, only sites where the entire fish assemblage was surveyed were chosen. This limited the dataset to 23 locations. Out of these locations, only locations where data for coral cover, macroalgal cover and fish density were present were selected. This brought the number of locations down to 21. Data for fish, macroalgae and coral cover were paired up within locations and only sites with paired data were retained. While some sites were sampled over multiple years, the majority of sites were sampled in the

years 2005, 2010 and 2011. This study only used sites sampled in the latter three years. When sites were sampled in more than one of these years, the earliest sampling year was used in the analysis. To reduce any errors caused by differences in sampling technique, only surveys conducted by the belt transect sampling technique were considered. The final dataset consisted of 51 sites from 14 locations in 7 countries and territories (Table 1, Figure 1).

Figure 1: Sites used in this study.

Data points in the analyses represent individual sites. Percent cover of coral and macroalgae and fish densities were averaged across surveys at a particular site. When multiple depths were surveyed, these results were averaged such that each site consisted of only one data point. In order to maintain comparability between sites, only sites sampled at depths of

5-15m were used since this range contains the herbivorous fish assemblage in question (Fox and Bellwood 2007; Froese and Pauly 2011).

Table 1: Site Summary

Country	Location	Site	Latitude (N)	Longitude (E)	Year
Bahamas	Bahamas other	Rocky Point	25.996612	-77.400922	2011
		Little Harbor	26.323901	-76.991601	
		Pelican Cay	26.397833	-76.988495	
		Man o War	26.621217	-77.0055	
		Fowls Cay	26.637166	-77.038481	
		Guana Cay	26.709667	-77.154083	
Belize	Belize Atoll Windward	South Middle Cay	16.72875	-87.82867	2010
		Middle Cay	16.73703	-87.80536	
		Half Moon	17.2056	-87.54679	
	Belize Central Barrier	Calabash	17.26147	-87.8197	2010
		South Water	16.81346	-88.07756	
		Tobacco	16.91911	-88.04757	
		Alligator	17.1966	-88.05115	
	Belize Northern Barrier	Hol Chan	17.86343	-87.97238	2010
		Tackle Box	17.91056	-87.95083	
	Belize Southern Barrier	Southwest	16.1123	-88.25586	2010
		Nicholas	16.11247	-88.27107	
		Ranguana	16.28501	-88.15031	
		Pampion	16.3731	-88.08913	
Cuba	Cuba Southwest	Ebano	22.079144	-81.075994	2005
		Punta Perdiz	22.110027	-81.116257	
		Cueva Peces	22.166266	-81.138273	
	Jardines de la Reina	Paradaiso	20.713095	-78.813317	2005
		Pulpo	20.949168	-79.180373	
		Cana	21.031985	-79.318677	
French Antilles	Martinique	PB	14.44716667	-60.90505	2005
		FB	14.6579	-61.15755	
	St. Barthelemy	IC	17.88815	-62.81255	2005
		PS	17.8993	-62.87713333	
Jamaica	Jamaica North Central	Dairy Bull	18.470777	-77.39473	2005
		Braco	18.486326	-77.505606	
		Rio Bueno	18.49458	-77.636601	
	Montego Bay	MBMP hani	18.454019	-77.973051	2005
		MBMP W	18.468007	-78.018775	
		MBMP C	18.462512	-77.950237	
		MBMP N	18.495691	-77.931944	

USA	Dry Tortugas	Loggerhead E	24.628755	-82.920176	2005
		Long Key	24.621159	-82.862619	
		Marker K	24.625486	-82.814166	
		Loggerhead W	24.634734	-82.927347	
	Lower Keys	Easy Key	24.6525583	-82.801914	2005
		Loggerhead NW	24.667616	-82.913323	
		Sambos	24.468372	-81.69593	
		Rock Key	24.481884	-81.996363	
		Sand Key	24.492668	-82.037831	
		Nice Foot	24.521693	-81.538687	
		American Shoals	24.531217	-81.485918	
		Looe Key	24.5521	-81.397816	
USVI	St. Croix	Great Pond	17.71097	-64.65221	2005
		Eagle Ray	17.7615	-64.6988	
		Buck Island	17.785	-64.60917	

Functional Classification

This study classifies herbivorous fish into five functional groups-grazers/detritivores (GD), browsers (B), large scrapers/excavators (LSE) and small scrapers/excavators (SSE) and territorial damselfish (TDF). Species were sorted into these five categories (Table 2)

Table 2: Fish Functional Groups

Species Name	Family	Functional Group
Archosargus rhomboidalis	*Sparidae*	B
Sparisoma radians	*Scaridae*	B
Acanthurus bahianus	*Acanthuridae*	GD
Acanthurus chirurgus	*Acanthuridae*	GD
Acanthurus coeruleus	*Acanthuridae*	GD
Acanthurus UNK	*Acanthuridae*	GD
Centropyge argi	*Pomacanthidae*	GD
Coryphopterus eidolon	*Gobiidae*	GD
Cryptotomus roseus	*Scaridae*	GD
Gnatholepis thompsoni	*Gobiidae*	GD
Melichthys niger	*Balistidae*	GD
Ophioblennius macclurei	*Blenniidae*	GD
Scartella cristata	*Blenniidae*	GD

Scarus coelestinus	*Scaridae*	LSE
Scarus coeruleus	*Scaridae*	LSE
Scarus guacamaia	*Scaridae*	LSE
Scarus vetula	*Scaridae*	LSE
Sparisoma viride	*Scaridae*	LSE
Nicholsina usta	*Scaridae*	SSE
Scarus iserti	*Scaridae*	SSE
Scarus sp.	*Scaridae*	SSE
Scarus taeniopterus	*Scaridae*	SSE
Scarus UNK	*Scaridae*	SSE
Sparisoma atomarium	*Scaridae*	SSE
Sparisoma aurofrenatum	*Scaridae*	SSE
Sparisoma chrysopterum	*Scaridae*	SSE
Sparisoma rubripinne	*Scaridae*	SSE
Sparisoma sp.	*Scaridae*	SSE
Sparisoma UNK	*Scaridae*	SSE
Microspathodon chrysurus	*Pomcentridae*	TDF
Stegastes adustus	*Pomcentridae*	TDF
Stegastes diencaeus	*Pomcentridae*	TDF
Stegastes dorsopunicans	*Pomcentridae*	TDF
Stegastes partitus	*Pomcentridae*	TDF
Stegastes species	*Pomcentridae*	TDF
Stegastes variabilis	*Pomcentridae*	TDF

based published studies and online databases (Halpern and Floeter 2008; Froese and Pauly 2011; Edwards et al. 2014). Fish with average length greater than 25 cm were designated as large scrapers/excavators. These lengths were not available for the actual fish data, but were determined from FishBase (Froese and Pauly 2011).

Data Analysis

Benthic cover

Percent macroalgal and coral cover were the response variables in the dataset. Since measurements were of percent cover, they were square root transformed to reduce the mean-variance relationship and meet the assumptions of linear modeling.

Explanatory Variables

The primary explanatory variables tested were the diversity and density within fish functional groups. In addition, the diversity and density of all herbivorous fish was also determined. The Shannon-Weiner diversity index (H') was used as a metric of diversity. The assumption of this index is that all the species in the community are present in the sample (Magurran 2004). The index is structured as follows:

Equation 1: Shannon-Weiner Diversity Index

$$H' = -\Sigma p_i \ln(p_i)$$

where p_i is the proportion of the ith species. Therefore, the diversity of a group will increase with the increase in species richness and the relative abundance of individuals.

This metric is fairly independent of sample sizes (Soetaert and Heip 1990); an important characteristic since sampling effort was not uniform across sites.

The density of the herbivorous fish guild and of the functional groups was calculated by averaging the density of fish across all transects at a particular site and further averaging by depth if the site was sampled at multiple depths. The density is represented as number of fish per m^2.

Statistical Techniques

Multiple linear regressions were used to determine the relationship between the explanatory variables and macroalgal cover. Initial data exploration and preliminary analyses showed heterogeneity in the residual variance when the explanatory variables were being tested were fish density, which was then corrected using natural log transformations of the

density variables. Since the data at the site level are nested within geographic locations, the data points are not assumed to be independent. A linear mixed effect model approach was therefore used to accommodate for this lack of independence using the R package 'nlme'. Location was used as a random factor in the analyses along with the other explanatory variables, which were used as fixed effects. Intraclass correlation coefficients (ICC) were calculated for each model to determine the correlation of sites within location (Zuur et al. 2009).

A high degree of multicollinearity was present between the density of the territorial damselfish and that of small scrapers/excavators and large scrapers/excavators. Since a negative correlation was observed between the densities of LSE and SSE, these two variables were converted into a ratio (LSE/SSE) and then log transformed to satisfy the assumptions of linear modeling. This significantly reduced the correlation between these two variables and TDF density.

Nutrient pollution was tested as an alternate explanation for macroalgal cover. The area of agricultural land as a percentage of total land area was used as a function of nutrient inputs. Land area under cultivation has been used in the previous studies as a proxy for nutrient input (Mora 2008). Since nutrients can affect macroalgal cover, this variable was compared with the fish variables to determine its relative importance. Data for agricultural land were acquired from the World Bank's World Development Indicators Database (http://databank.worldbank.org/data/views/reports/tableview.aspx) and from the United Nations' Department of Economic and Social Affairs Environmental Statistics dataset (http://unstats.un.org/unsd/environment/Questionnaires/country_snapshots.htm).

A manual backwards stepwise procedure was used to determine which variables significantly affected both response variables, using an α=0.05 threshold. Models fit using maximum likelihood were used for variable selection and model ranking. Log-likelihood tests were used to differentiate between candidate models in order to determine the importance of particular variables. The best-fit models were refit using restricted maximum likelihood. The significance of the fixed effects from the final model was confirmed with p-values using the R package 'nlme'. Studies have shown that the indirect effect of increasing the diversity and biomass of herbivorous fish is greater coral cover (Burkepile and Hay 2008; Jackson et al. 2013). Model selection was confirmed using Akaike's information criterion corrected for small sample sizes (AICc) and Akaike weights (w_i).

RESULTS

Benthic Cover

Percent macroalgal cover and coral cover varied across locations and among sites at individual locations (Figure 2). All locations except for St. Croix in the US Virgin Islands

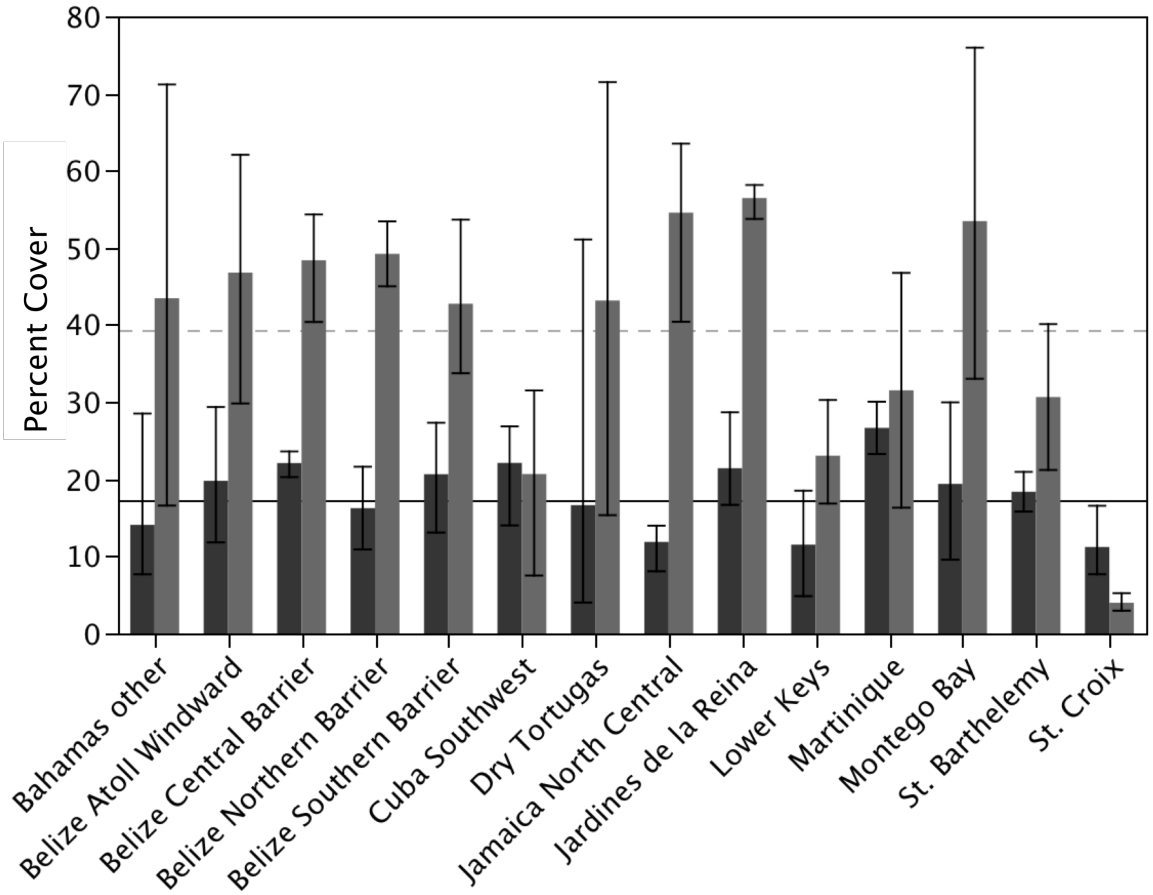

Figure 2: Average percent cover of coral and macroalgae.
Average coral cover and macroalgal cover for the 14 locations used in this study. Error bars represent the range of values at each location. Grey bars represent macroalgae while black bars represent coral. The grey dashed horizontal line is the average macroalgal cover across all locations while the solid horizontal black line is the average coral cover across all locations. See text for means.

and Cuba Southwest showed greater macroalgal cover than coral cover. The average cover of macroalgae across all sites sampled was 39.30±19.27 percent while coral cover was 17.28±8.61 percent. Macroalgal cover ranged from a high of 75.93% at Montego Bay central in Jamaica to 2.95% at Buck Island reef in St. Croix. Coral cover ranged from 51.06% at Loggerhead Key NW in the Dry Tortugas to 4% at Loggerhead Key W in the Dry Tortugas. Coral cover was most variable in the Dry Tortugas with a range of 47.06%, (mean=16.63%, s.d.=17.36, N=6) while the location with the lowest variability was the Belize central barrier with a range of 3.34% (mean=22.09%, s.d.=1.69, N=3). The location with the highest variability in macroalgal cover was the Dry Tortugas with a range of 56/13% (mean=43.16%, s.d.=21.12, N=6) while St. Croix had the least variability with a range 2.26% (mean=3.97%, s.d.=1.15, N=3).

Fish Assemblages

The most conspicuous trend seen across the reefs sampled is the absence of the two species, *Sparisoma radians* and *Archosargus rhomboidalis*. These two species constitute the Browser functional group and feed primarily on macroalgae.

All other functional groups were present on the reefs, but in varying capacity. The average diversity of grazers/detritivores (GD) was 0.73±0.20 (Figure 3) while the average density of this functional group was 0.0056±0.0054 fish/m^2 (Figure 4). Reef locations showed considerable variation in diversity and density. The lowest diversity was seen at Loggerhead NW in the Dry Tortugas (H'=0; note, an H' of 0 implies that there was either 1 or 0 species present) while the highest diversity was seen at Eagle Ray in St. Croix (H'=1.18). The lowest density of grazers/detritivores was seen at site FB in Martinique (density=0.0005 fish/m^2) while Little Harbor in the Bahamas had the highest density (density=0.02 fish/m^2).

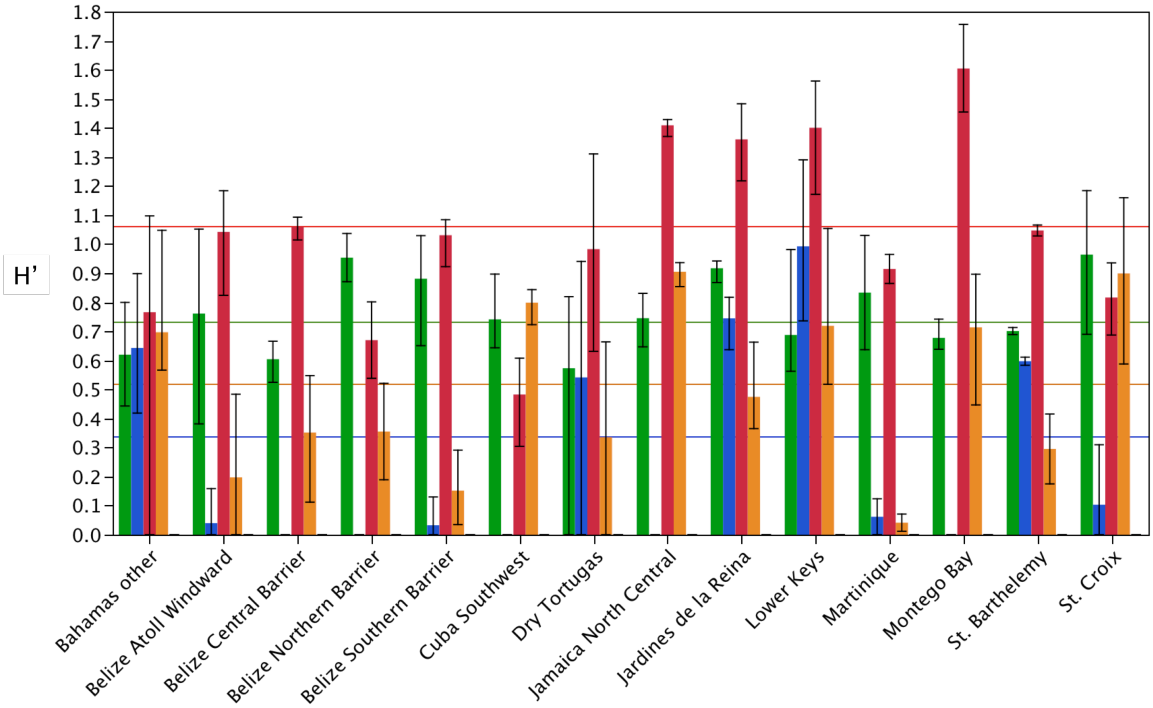

Figure 3: Diversity of the herbivorous functional groups used in this study.
The figure shows the average Shannon-Weiner diversity index (H') for each functional group at the 14 locations analyzed in this study. The error bars represent the range of values at each location showing the variation in the region. Green bars represent the GD functional group, blue bars represent the LSE functional group, red bars represent the SSE functional group, orange bars represent the TDF functional group and yellow bars represent the B functional group. The horizontal lines represent the average H for the functional groups calculated across all locations. The color of the line indicates the functional group. See text for means.

The location with the highest variation in diversity was the Dry Tortugas (Range=0.82, mean=0.57, s.d.=0.3), with minimum diversity seen at Loggerhead NW (H'=0) and maximum diversity seen at Loggerhead E (H'=0.82). St. Barthélemy had the lowest variation in diversity of grazers/detritivores between the two sites sampled (Range=0.02, mean=0.7, s.d.= 0.01, N=2) with minimum diversity of 0.68 at site IC and maximum diversity of 0.71 at site PS. Lowest variation in density of GD was seen at Martinique (Range=0.0005,

mean=0.0007, s.d.=0.0003, N=2) with minimum density of 0.0005 fish/m^2 at site FB and maximum density of 0.0010 fish/m^2 seen at site PB. The highest variation in density was seen in the Bahamas (Range=0.01, mean=0.017, s.d.=0.005, N=6) with the minimum density of 0.007 fish/m^2 found at Rocky Point Reef and maximum density of 0.02 fish/m^2 found at Little Harbor reef.

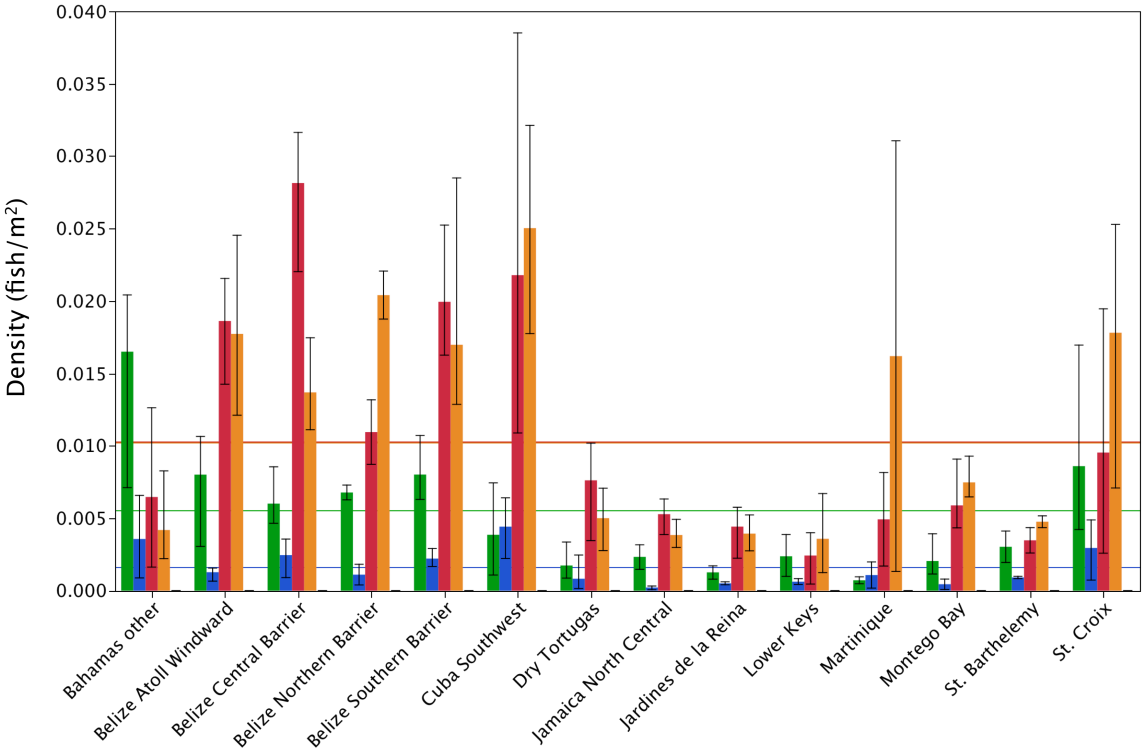

Figure 4: Density of the herbivorous functional groups used in this study.
The figure shows the average density (number of fish/m^2) for each functional group at the 14 locations analyzed in this study. The error bars represent the range of values at each location showing the variation in the region. Green bars represent the GD functional group, blue bars represent the LSE functional group, red bars represent the SSE functional group, orange bars represent the TDF functional group and yellow bars represent the B functional group. The horizontal lines represent the density for the functional groups averaged across all locations. The color of the line indicates the functional group. See text for means.

The average diversity of large scrapers/excavators (LSE) was 0.34±0.39 (Figure 3) while the average density was 0.0016±0.0017 fish/m^2 (Figure 4). Reef locations showed considerable variation in diversity and density. Over half the reefs sampled, including reefs from all the countries except the Bahamas had zero diversity of this group. The highest diversity was found at the lower keys in Florida with a mean diversity of 0.99±0.73. Lowest variation in diversity of LSE was seen at St. Barthélemy (Range=0.03, mean=0.59, s.d.=0.02, N=2) with minimum diversity of 0.58 fish/m^2 at site IC and maximum diversity of 0.61 seen at site PS. The highest variation in diversity was found in the Dry Tortugas (Range=0.94, mean=0.54, s.d.=0.34, N=6). The maximum diversity was found at Loggerhead East (H'=0.94) while the minimum diversity was found at Loggerhead W (H'=0). The maximum density of LSE was found at Fowls Cay in the Bahamas (density=0.0035 fish/m^2) while the minimum density was found at Long Key in the Dry Tortugas (density=0.0001 fish/m^2). The highest variation in density was seen in the Bahamas (Range=0.006, mean=0.004, s.d.=0.002, N=6) with the maximum density of 0.007 fish/m^2 found at site Fowls Cay and minimum density of 0.0009 fish/m^2 found at Rocky Point. The lowest variation in density was found at St. Barthélemy (Range=0.0002, mean=0.0009, s.d.=0.0001, N=2), with maximum density of 0.0009 fish/m^2 found at site PS while the minimum density of 0.0009 fish/m^2 found at site IC.

The average diversity of small scrapers/excavators (SSE) was 1.06±0.35 (Figure 3) while the average density was 0.010±0.009 fish/m^2 (Figure 4). Reef locations showed considerable variation in diversity and density. Rocky Point reef in the Bahamas had zero diversity, which represents the minimum diversity of this group. The highest diversity was found at Montego Bay west in Jamaica with a mean diversity of 0.99±0.73. Lowest variation

in diversity of SSE was seen at St. Barthélemy (Range=0.037, mean=1.05, s.d.=0.03, N=2) with minimum diversity of 1.02 at site IC and maximum diversity of 1.07 seen at site PS. The highest variation in diversity was found in the Bahamas (Range=1.09, mean=0.77, s.d.=0.39, N=6) with maximum diversity at Fowls cay (H'=1.09) and minimum diversity at Rocky Point (H'=0). The maximum density of SSE was found at Cueva Peces in Cuba (density=0.039 fish/m^2) while the minimum density was found at Sand Key in the Lower Keys (density=0.0005 fish/m^2). The highest variation in density was seen at Cuba Southwest (Range=0.03, mean=0.02, s.d.=0.01, N=3) with the maximum density of 0.04 fish/m^2 found at site Cueva Peces and minimum density of 0.01 fish/m^2 found at Ebano. The lowest variation in density was found at St. Barthélemy (Range=0.002, mean=0.003, s.d.=0.001, N=2), with maximum density of 0.004 fish/m^2 found at site IC while the minimum density of 0.002 fish/m^2 found at site PS.

The average diversity of territorial damselfish (TDF) was 0.52±0.31 (Figure 3) while the average density was 0.010±0.008 fish/m^2 (Figure 4). Loggerhead West in the Dry Tortugas and Middle Cay in the Belize Atoll had zero diversity, which represents the minimum diversity of this group. The highest diversity was found at Great Pond in St. Croix (H=1.159). Lowest variation in diversity of TDF was seen at Martinique (Range=0.06, mean=0.04, s.d.=0.04, N=2) with minimum diversity of 0.01 at site FB and maximum diversity of 0.07 seen at site PB. The highest variation in diversity was found in the Dry Tortugas (Range=0.66, mean=0.34, s.d.=0.24, N=6) with maximum diversity at the K Marker (H'=0.66) and minimum diversity at Loggerhead W (H'=0). The maximum density of TDF was found at Punta Perdiz in Cuba (density=0.032 fish/m^2) while the minimum density was found at Nine Foot reef in the Lower Keys (density=0.001 fish/m^2). The highest

variation in density was seen at Martinique (Range=0.03, mean=0.016, s.d.=0.021, N=2) with the maximum density of 0.03 fish/m^2 found at site FB and minimum density of 0.0013 fish/m^2 found at site PB. The lowest variation in density was found at St. Barthélemy (Range=0.001, mean=0.005, s.d.=0.0006, N=2), with maximum density of 0.005 fish/m^2 found at site PS while the minimum density of 0.004fish/m^2 found at site IC.

Model Selection

The global model for both response variables (model 1) contained all the independent variables. The following is a summary of how models were selected for the response variable macroalgal cover. A summary of the relationship of the fixed effects to the response variable showed SSE_{Div} and GD_{Div} to be least significant. Candidate models 2 and 3 were then created respectively by dropping the least significant variables (Table 3). Log likelihood ratio tests of model 1 with 2 showed no significant difference between the models (LLR=0.2899, p=0.5903). Similarly, models 1 and 3 were not significantly different from each other (LLR=0.3434, p=0.5578). The least significant variable (SSE_{Div}) was dropped and model 2 was used as the next full model. An analysis of the coefficients of model 2 showed that GD_{Div} and LSE_{Div} were the least significant. Dropping those variables respectively created models 4 and 5. Models 2 and 4 were not significantly different (LLR=0.2392, p=0.6247). Models 2 and 5 were not significant either (LLR=1.5317, p=0.2158). The least significant variable (GD_{Div}) was dropped. Thus, model 4 was the new full model. LSE_{Div} and $GD_{density}$ were the two least significant variables. Removing these variables respectively created models 6 and 7. Log likelihood ratio tests of model 4 and 6 showed no significant difference (LLR=1.3375, p=0.2475); tests for models 4 and 7 were non significant as well (LLR=3.1562, p=0.0756). The least significant variable (LSE_{Div}) was dropped. Therefore,

model 6 was chosen as the next full model. An inspection of the coefficients of model 6 showed that $GD_{density}$ and TDF_{Div} were the least significant variables. Dropping the former created model 8 and model 9 was created by dropping the latter from model 6. Models 6 and 8 were significantly different (LLR=4.3534, p=0.0369) and models 6 and 9 were significantly different as well (LLR=6.5442, p=0.0105). Since both these comparisons were significantly different, model 6 was determined to be the best model for percent cover of macroalgae. A similar procedure was carried out for percent cover of coral where the final model selected was model 8 (Table 3). Log likelihood test tables are found in Appendix A and B. The

Table 3: Description of models derived from the model selection procedure

Response Variable	Model	Variables
Percent Macroalgae	Model 1	$GD_{Div}+LSE_{Div}+SSE_{Div}+TDF_{Div}+GD_{density}+TDF_{density}+LSE_{density}/SSE_{density}$
	Model 2	$GD_{Div}+LSE_{Div}+TDF_{Div}+GD_{density}+TDF_{density}+LSE_{density}/SSE_{density}$
	Model 3	$LSE_{Div}+SSE_{Div}+TDF_{Div}+GD_{density}+TDF_{density}+LSE_{density}/SSE_{density}$
	Model 4	$LSE_{Div}+TDF_{Div}+GD_{density}+TDF_{density}+LSE_{density}/SSE_{density}$
	Model 5	$GD_{Div}+TDF_{Div}+GD_{density}+TDF_{density}+LSE_{density}/SSE_{density}$
	Model 6	$TDF_{Div}+GD_{density}+TDF_{density}+LSE_{density}/SSE_{density}$
	Model 7	$LSE_{Div}+TDF_{Div}+TDF_{density}+LSE_{density}/SSE_{density}$
	Model 8	$TDF_{Div}+TDF_{density}+LSE_{density}/SSE_{density}$
	Model 9	$GD_{density}+TDF_{density}+LSE_{density}/SSE_{density}$
	Model 10	$Herbivore_{density}+Herbivore_{diversity}$
	Model 11	Null Model
Percent Coral	Model 1	$GD_{Div}+LSE_{Div}+SSE_{Div}+TDF_{Div}+GD_{density}+TDF_{density}+LSE_{density}/SSE_{density}$
	Model 2	$GD_{Div}+SSE_{Div}+TDF_{Div}+GD_{density}+TDF_{density}+LSE_{density}/SSE_{density}$
	Model 3	$GD_{Div}+LSE_{Div}+TDF_{Div}+GD_{density}+TDF_{density}+LSE_{density}/SSE_{density}$
	Model 4	$GD_{Div}+TDF_{Div}+GD_{density}+TDF_{density}+LSE_{density}/SSE_{density}$
	Model 5	$GD_{Div}+SSE_{Div}+TDF_{Div}+GD_{density}+TDF_{density}$
	Model 6	$GD_{Div}+TDF_{Div}+GD_{density}+TDF_{density}$
	Mode 7	$GD_{Div}+GD_{density}+TDF_{density}+LSE_{density}/SSE_{density}$
	Model 8	$GD_{Div}+GD_{density}+TDF_{density}$
	Model 9	$TDF_{Div}+GD_{density}+TDF_{density}$
	Model 10	$GD_{density}+TDF_{density}$
	Model 11	$Herbivore_{density}+Herbivore_{diversity}$
	Model 12	Null Model

goodness of fit for the models was confirmed using AICc and w_i (Table 6). The final models were refit by restricted maximum likelihood (REML) and p-values for individual parameters

were determined. In addition, the response variables were tested against total herbivore diversity and density and with no fixed effects, i.e. a null model (Table 3).

Relationship of the Functional Variables to Macroalgal Cover

Models that split the herbivore guild into functional groups fit better as compared to null model and model with total herbivore density and diversity as fixed effects (Table 6). Herbivore diversity (t= -1.1914, p=0.2415) and density (t= -1.8798, p=0.0685) were negatively associated with macroalgal cover, but the relationships were not significant. Model

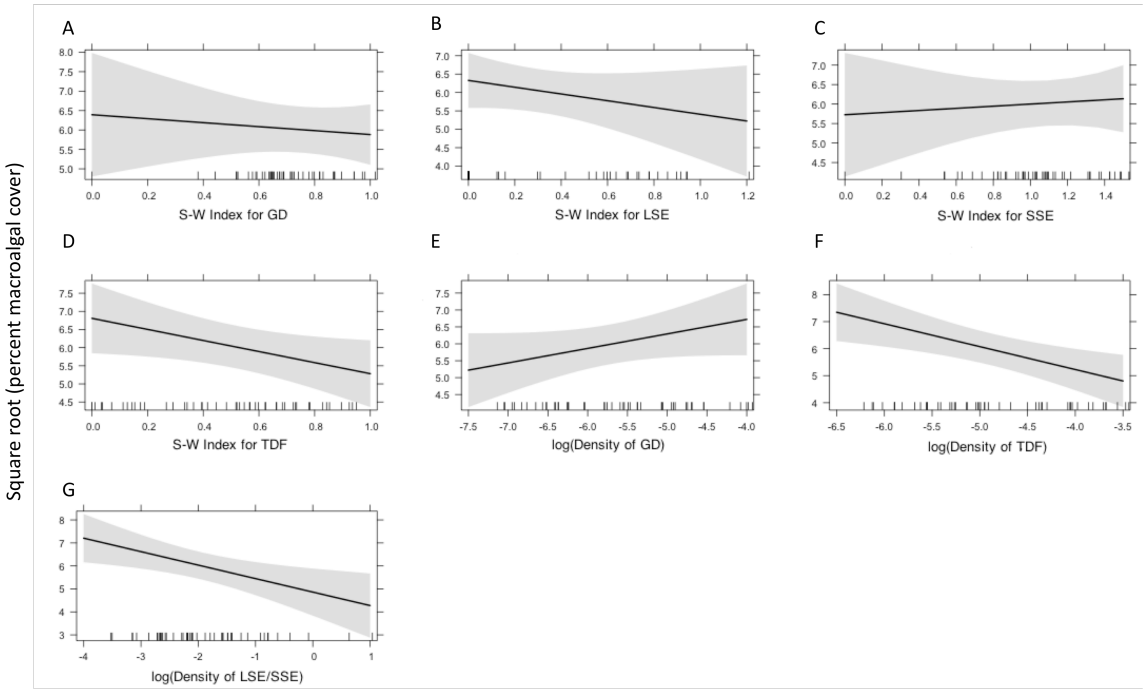

Figure 5: Relationship of the fixed effects to macroalgal cover
Each figure shows the relationship of a particular fixed effect in the model with the square root of macroalgal cover. A shows the diversity of GD, B shows the diversity of LSE, C shows the Diversity of LSE, D shows the diversity of TDF, E shows the log density of GD, F shows the log density of TDF and G shows the log ratio of density of LSE to the density of SSE. Densities are measured in number of fish/m^2; diversity is measured as the Shannon-Weiner Diversity Index. The plots represent the effects from the full model for macroalgal cover, Model 1 (see Table 3 for a description). Grey shaded areas represent 95% confidence intervals.

6 that best predicted the cover of macroalgae (Table 6). The random effect 'Location' had an ICC=0.37 suggesting moderate correlation between sites at the same location. Summary tables showed that the diversity of TDF (Value= -1.7202, S.E.=0.6899, df=33, t= -2.4935, p=0.0178), density of TDF (Value= -0.8391, S.E.=0.2507, df=33, t= -3.3465, p=0.0021) and the ratio of density of LSE to SSE (value= -0.7084, S.E.=0.1874, df=33, t= -3.7794, p=0.0006) were significantly associated with macroalgal cover (Figure 5). The variable $GD_{density}$ was positively associated with macroalgal cover, albeit non-significantly (value=0.4828, S.E.=0.2412, df=33, t=2.0016, p=0.0536) (Figure 5).

Table 4: Comparison of terms from models for macroalgal cover

	Model											
Variable	1	2	3	4	5	6	7	8	9	10	11	6_{agri}
Div_{GD}	-0.5105	-04399			-0.1782							
	0.9835	0.9561			0.9385							
Div_{LSE}	-0.9196	-0.9168	-0.8315	-0.8371			-1.1483					
	0.7661	0.7619	0.7408	0.7352			0.7301					
Div_{SSE}	0.2734		0.2014									
	0.6928		0.6762									
Div_{TDF}	-1.5265*	-1.5226*	-1.5038*	-1.5048*	-1.7362	-1.7202*	-1.3691	-1.6500*				-2.2193**
	0.7274	0.7232	0.7222	0.7163	0.7002	0.6898	0.7294	0.7128				0.7119
log $density_{GD}$	0.4284	0.4246	0.4175	0.4156	0.4884	0.4828			0.4658			0.7094*
	0.2552	0.2536	0.2528	0.2507	0.2453	0.2412			0.2599			0.2660
log $density_{TDF}$	-0.8478**	-0.8711**	-0.8735**	-0.8891**	-0.8299**	-0.8391**	-0.8564**	-0.7723**	-0.8069**			-0.8638**
	0.2727	0.2613	0.2652	0.2558	0.2583	0.2507	0.2601	0.2568	0.2665			0.2419
log($density_{LSE}$/$density_{SSE}$)	-0.5861**	-0.5949**	-0.6081**	-0.6132**	-0.7059***	-0.7084***	-0.5422**	-0.6546**	-0.6374**			-0.7280***
	0.2109	0.2055	0.2035	0.1995	0.1909	0.1874	0.1990	0.1916	0.1960			0.1838
log($Herbivore_{density}$)										-0.8911		
										0.4740		
$Herbivore_{diversity}$										-0.9232		
										0.7749		
Agricultural Land Area												0.02569
												0.01501
Intercept	4.2842	4.3615	3.7063	3.8226*	4.3483	4.1250*	1.7827	1.7801	3.4639	4.3413	6.0126	4.9093**
	2.2066	2.1930	1.8783	1.8337	2.1699	1.7815	1.3769	1.3866	1.9166	2.4135	0.3981	1.7560
Random Intercept (s.d.)	0.8874	0.8878	0.8912	0.8926	0.8462	0.8439	0.9329	0.8668	1.0321	1.4284	1.3189	0.7018
Residual s.d.	1.1012	1.0859	1.0894	1.0756	1.1051	1.0917	1.0899	1.1218	1.1106	1.1782	1.2512	1.1045
ICC	0.39	0.40	0.40	0.41	0.37	0.37	0.42	0.38	0.46	0.59	0.53	0.28

The fixed effects are the diversity of grazers/detritivores (Div_{GD}), diversity of large scrapers/excavators (Div_{LSE}), diversity of small scrapers/excavators (Div_{SSE}), diversity of territorial damselfish (Div_{TDF}), log density of grazers/detritivores (log $density_{GD}$), log density of territorial damselfish (log $density_{TDF}$), the log ratio of the density of large scraper/excavators to small scraper/excavators (log $density_{LSE}$/$density_{SSE}$), agricultural land area. Model 6 modified with agricultural land area is 6_{agri}. S.d. is the standard deviation; ICC=Intraclass correlation coefficient for sites within locations. The random intercept is for the random Location variable. For the fixed effects, the upper value is the coefficient and the lower value is the standard error. *=P<0.05, **=P<0.01, ***=P<0.001.

An independent comparison of the density of SSE with macroalgal cover showed a negative but non-significant relationship (value= -0.2500, S.E.=0.2946, df=36, t= -0.8487, p=0.4017). The significant negative association of the ratio of $LSE_{density}/SSE_{density}$ with macroalgal cover suggests that $LSE_{density}$ is the driving variable in the ratio. The full model (Model 1, Table 3) showed the diversity of GD, LSE and SSE were not significantly associated with macroalgal cover. However, a slight negative association was seen with the diversity of GD and LSE while a slight positive relationship was seen between the diversity of SSE and macroalgal cover (Figure 5). A comparison of model terms is shown in Table 4.

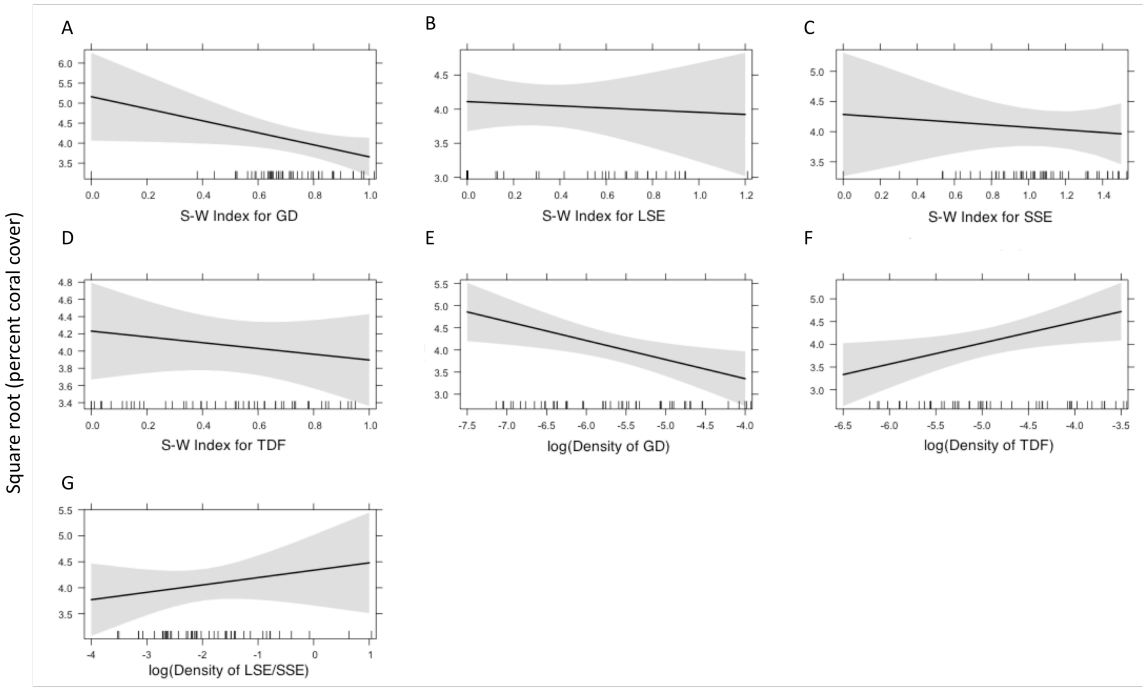

Figure 6: Relationship of the fixed effects to coral cover
Each figure shows the relationship of a particular fixed effect in the model with the square root of coral cover. A shows the diversity of GD, B shows the diversity of LSE, C shows the Diversity of LSE, D shows the diversity of TDF, E shows the log density of GD, F shows the log density of TDF and G shows the log ratio of density of LSE to the density of SSE. Densities are measured in number of fish/m^2; diversity is measured as the Shannon-Weiner Diversity Index. The plots represent the effects from the full model for coral cover, Model 1 (see Table 3 for a description). Grey shaded areas represent 95% confidence intervals.

Alternative hypotheses for Macroalgal Cover

The best-fit model, Model 6, was refit with agricultural land area (as a percentage of total land area). A log-likelihood ratio test between the modified model and model 6 showed no significant difference between the two models (LL=0.2976, p=0.5854). The model summary showed that agricultural land area positively affected macroalgal cover, but this relationship was non significant (value=0.0257, S.E=0.0150, df=12, t=0.7177, p=0.1128).

Relationship of the Functional Variables to Coral Cover

Models that split the herbivore guild into functional groups were better than models that used the entire herbivore guild. Total herbivore density was positively associated with

Table 5: Comparison of terms from models for coral cover

	Model											
Variable	1	2	3	4	5	6	7	8	9	10	11	12
Div_{GD}	-1.5026*	-1.4505*	-1.5572*	-1.5014*	-1.3399	-1.4035*	-1.4885*	-1.3874*				
	0.7059	0.6810	0.6829	0.6606	0.6689	0.6553	0.6580	0.6530				
Div_{LSE}	-0.1564		-0.1834									
	0.4807		0.4698									
Div_{SSE}	-0.2141	-0.2219			-0.3222							
	0.4561	0.4505			0.4298							
Div_{TDF}	-0.3349	-0.3573	-0.3631	-0.3847	-0.3469	-0.3725			-0.3600			
	0.4532	0.4437	0.4423	0.4345	0.4381	0.4299			0.4288			
log $density_{GD}$	-0.4307*	-0.4197*	-0.4123*	-0.4002*	-0.3908*	-0.3565*	-0.4238**	-0.3792*	-0.3435*	-0.3730*		
	0.1589	0.1539	0.1535	0.1488	0.1498	0.1428	0.1521	0.1457	0.1397	0.1435		
log $density_{TDF}$	0.4617*	0.4818*	0.4918*	0.5175**	0.4417*	0.4854**	0.5234**	0.4972**	0.4064*	0.4235*		
	0.1947	0.1828	0.1821	0.1679	0.1749	0.1635	0.1692	0.1642	0.1586	0.1593		
log($density_{LSE}$/$density_{SSE}$)	0.1419	0.1196	0.1613	0.1355			0.1353					
	0.1530	0.1356	0.1459	0.1288			0.1296					
log($Herbivore_{density}$)											0.2879	
											0.2039	
$Herbivore_{diversity}$											-0.6513	
											0.4804	
Intercept	5.7412***	5.7901	5.8649***	5.9202***	5.5349***	5.6582***	5.6146***	5.3891***	4.2935***	0.2107***	6.3390***	4.0611
	1.3683	1.3462	1.3283	1.3084	1.2895	1.2609	1.3156	1.2632	0.9930	0.8928	1.0174	0.1532
Random Intercept (s.d.)	0.3060	0.3010	0.2693	0.2697	0.2798	0.2442	0.3255	0.2886	0.1369	0.2107	$8.4x10^{-5}$	0.2538
Residual s.d.	0.8622	0.8537	0.8609	0.8522	0.8557	0.8581	0.8372	0.8461	0.9069	0.8928	0.9681	0.9685
ICC	0.11	0.11	0.09	0.09	0.10	0.07	0.13	0.10	0.02	0.05	$7.5x10^{-9}$	0.06

The fixed effects are the diversity of grazers/detritivores (Div_{GD}), diversity of large scrapers/excavators (Div_{LSE}), diversity of small scrapers/excavators (Div_{SSE}), diversity of territorial damselfish (Div_{TDF}), log density of grazers/detritivores (log $density_{GD}$), log density of territorial damselfish (log $density_{TDF}$), the log ratio of the density of large scraper/excavators to small scraper/excavators (log $density_{LSE}$/$density_{SSE}$), agricultural land area and coral cover (sqrt coral cover). S.d. is the standard deviation; ICC=Intraclass correlation coefficient for sites within locations. The random intercept is for the random Location variable. For the fixed effects, the upper value is the coefficient and the lower value is the standard error. *=P<0.05, **=P<0.01, ***=P<0.001.

coral cover (t=1.4119, p=0.1668) while herbivore diversity was negatively associated with coral cover (t= -1.3556, p=0.1839). The relationships were not significant. A model that consisted of the diversity of GD, density of GD and density of TDF best predicted the percent cover of coral. The ICC for the model=0.10, showing little correlation between sites at the same location. The diversity of GD (value= -1.3891, S.E.=0.6530, df=34, t= -2.1245, p=0.0410), density of GD (value= -0.3792, S.E.=0.1457, df=33, t= -2.6027, p=0.0136) was negatively associated with coral cover while the density of TDF (value=0.4972, S.E.=0.1643, df=34, t=3.0276, p=0.0047) was positively associated with coral cover (Figure 6). The full model (Model1, Table 3) showed the diversity of LSE, SSE and TDF were negatively associated with coral cover, albeit non-significantly while the ratio of $LSE_{density}/SSE_{density}$ was positively associated with coral cover (Figure 6). However, this relationship was non-significant as well. It is worth noting that the slope of the fixed effects significantly associated with macroalgal cover are the opposite of those associated with coral cover (Figure 5; Figure 6). Only the density of TDF is the common significant variable for both coral and macroalgal cover. A comparison of model terms is shown in Table 5.

Table 6: Model Ranking

Response Variable	Model #	AICc	ΔAICc	w_i	LL
Percent Macroalgae	**6**	**180.6112**	**0.0000**	**0.3353**	**-82.0033**
	4	182.0975	1.4863	0.1595	-81.3345
	8	182.2690	1.6578	0.1464	-84.1800
	7	182.4298	1.8187	0.1351	-82.9126
	5	183.3900	2.7788	0.0836	-81.9807
	9	184.4598	3.8486	0.0490	-85.2754
	2	184.8199	4.2087	0.0409	-81.2148
	3	184.8734	4.2623	0.0398	-81.2416
	1	187.6397	7.0286	0.0100	-81.0699
	10	194.842	14.2291	0.0003	-91.7534
	11	195.1012	14.4900	0.0002	-94.2953

Percent Coral	**8**	**142.1122**	**0.0000**	**0.3342**	**-64.1016**
	10	143.7464	1.6342	0.1476	-66.2065
	6	143.7469	1.6347	0.1476	-63.5711
	7	143.7756	1.6643	0.1454	-63.5859
	4	145.4195	3.3073	0.0640	-62.9954
	9	145.4505	3.3382	0.0630	-65.7707
	5	146.0451	3.9329	0.0468	-63.3082
	3	148.0171	5.9049	0.0174	-62.8134
	2	148.1940	6.0817	0.0160	-62.9019
	11	149.6619	7.5497	0.0077	-69.1643
	12	150.0128	7.9006	0.0064	-71.7511
	1	150.9892	8.8770	0.0039	-62.7446

AICc=Akaike Information Criterion corrected for small sample sizes, ΔAICc=delta AICc, w_i=Akaike weights, LL=log likelihood. Models with the lowest AICc score and highest w_i are the best models. The best-fit models are shown in bold.

DISCUSSION

This study explored the associations between the herbivorous fish and benthic cover on Caribbean coral reefs. The diversity and density of four herbivorous functional groups was tested against macroalgal and coral cover in an effort to determine which functional group is most responsible for controlling the function of herbivory and which characteristic of that functional group drives this function.

The reefs on average had almost twice as much macroalgal cover as coral cover. Only the reefs on St. Croix and Cuba Southwest had more coral cover than macroalgal cover. Smaller species of fish like the damselfish and small parrotfish were more abundant than the large parrotfish or the surgeonfish. These results can be explained by the fact that large parrotfish are more susceptible to fish traps, which has been shown to significantly decrease their populations (Mumby et al. 2006). Reefs also showed a considerable amount of variation in the diversity of functional groups.

Both density and diversity were good predictors of macroalgal and coral cover as shown by the final models. But benthic cover variables were predicted by different functional groups. In general, models that divided the herbivorous guild into functional groups were better at predicting benthic cover than models that included the entire guild.

The findings of these models show that the density of large scrapers/excavators and the density and diversity of territorial damselfish are significantly negatively associated with the cover of macroalgae. The results also show that coral cover, an indirect proxy for

herbivory, is significantly negatively associated with the diversity and density of grazers/detritivores and positively with the density of territorial damselfish.

Herbivory on Caribbean Reefs: Size Matters

Previous studies have shown the importance of parrotfish in reducing macroalgal cover in the Caribbean (Williams and Polunin 2001; Paddack et al. 2006; Burkepile and Hay 2008; Cardoso et al. 2009; Burkepile and Hay 2010, 2011). The linear models showed that macroalgal cover was negatively associated with the ratio of the densities of large scrapers/excavators to small scrapers/excavators. Both these groups consist exclusively of parrotfish. In other words, as the number of large parrotfish increased with respect to the number of small parrotfish, macroalgal cover decreased. Both the density of large and small parrotfish was negatively correlated with macroalgal cover, but the significance of the ratio variable suggests that the large parrotfish play a more important role. While it can be hypothesized that the patterns seen are merely a result of habitat preference, parrotfish in the Caribbean do not show any such habitat preference (Rotjan and Lewis 2006). Therefore, the association between parrotfish density and macroalgal cover is more likely due to increased grazing intensity on reefs driven by the high density of large parrotfish.

The importance of large parrotfish in ecosystem functioning has been previously established in the Caribbean and in the Pacific (Bruggemann et al. 1996; Bonaldo and Bellwood 2008). On unfished reefs in the Caribbean, where the density of large parrotfish is high, macroalgal cover is significantly lower than that on fished reefs, where the density of large parrotfish is low (Mumby et al. 2006). The density of small bodied parrotfish is seen to remain fairly unchanged across both fished and unfished reefs, further supporting the idea that large bodied parrotfish are key to the effective removal of macroalgae on reefs (Mumby

et al. 2006). Out of the five potential species that constitute the large scraper and excavator functional group, only four were present in relatively high densities on the surveyed reefs with only 2 reefs having four species. *Scarus coelestinus* was present on one reef in very low densities. An examination of the contribution of each species to the total diversity of large scrapers/excavators revealed that two species were disproportionately contributing to the total density-*Sparisoma viride* and *Scarus vetula* (Figure 7). It has been suggested before

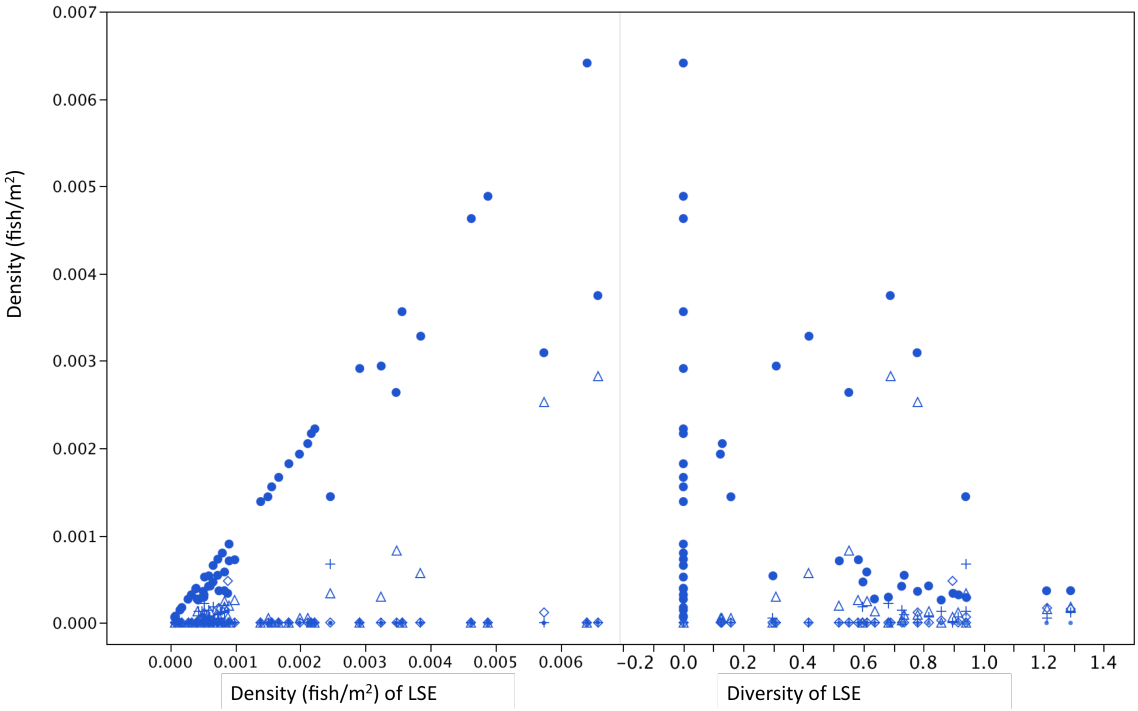

Figure 7: Relationship of the densities of individual species within the LSE to total density and diversity. The left panel shows the contribution of individual species to the total density of LSE. The right panel shows how the diversity of LSE is related to the densities of individual species within the group. Small dots=*Scarus coelestinus*, plus signs=*Scarus coeruleus*, open diamonds=*Scarus guacamaia*, open triangles=*Scarus vetula* and closed large circles=*Sparisoma viride*.

that these two species play a very important role in keeping macroalgal cover down on coral reefs (Mumby et al. 2006) and recent observational studies have shown that both species ingest large quantities of macroalgae along with other algal turfs (Cardoso et al. 2009).

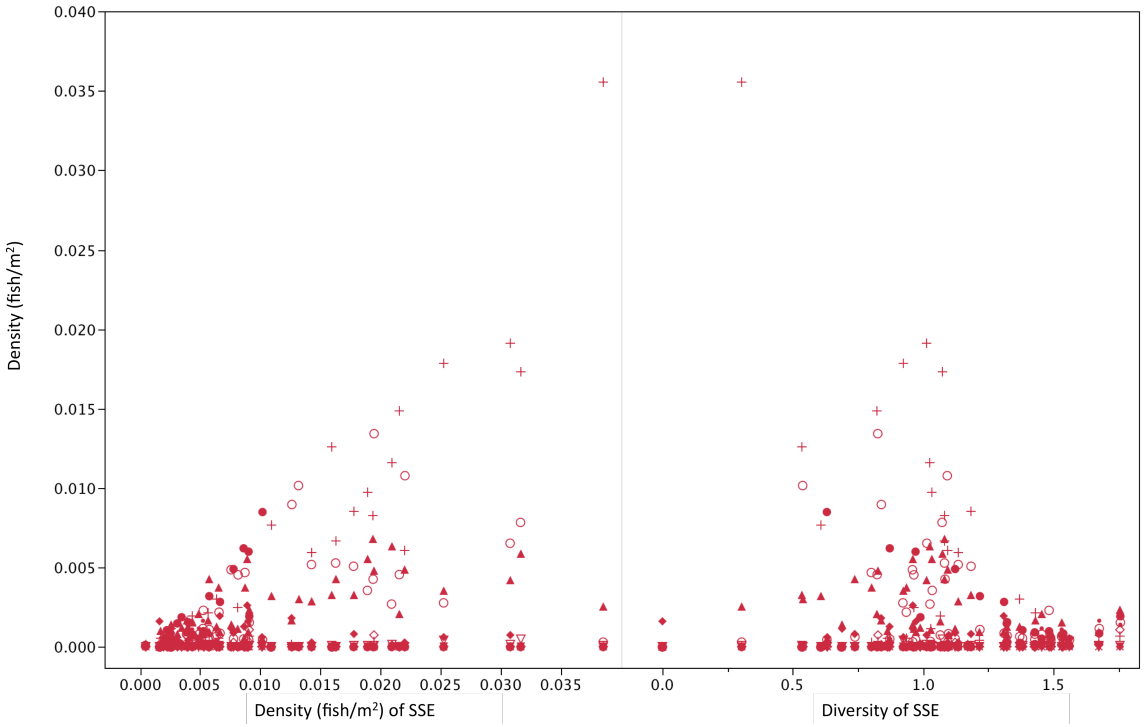

Figure 8: Relationship of the densities of individual species within the SSE to total density and diversity. The left panel shows the contribution of individual species to the total density of SSE. The right panel shows how the diversity of SSE is related to the densities of individual species within the group. Open circles=*Scarus iserti*, closed circles=*Scarus* sp., plus signs=*Scarus taeniopterus*, crosses=*Scarus* UNK, open diamonds=*Sparisoma automarium*, closed triangles=*Sparisoma aurofrenatum*, open inverted triangles=*Sparisoma chrysopterum*, closed diamonds=*Sparisoma rubipinne*, small dots=*Sparisoma* sp., inverted closed triangles=*Sparisoma* UNK.

Scarus taeniopterus, *Scarus iserti* and *Sparisoma aurofrenatum*, the three most abundant small parrotfish (Figure 8) contribute the most to the overall density of the small scraper/excavator functional group. The lack of significance between the density of small parrotfish and macroalgal cover is likely due to the fact that small parrotfish do not

completely remove macroalgae from the substrate; they reduce the height of the macroalgae, but not overall cover (Bonaldo and Bellwood 2008; Burkepile and Hay 2008). The two most abundant species seen on these reefs, *Scarus taeniopterus* and *Scarus iserti* generally feed on more turf algae than macroalgae (Cardoso et al. 2009). Species like *Sparisoma rubipinnae* and *Sparisoma chrysopterum* that have been seen to feed on macroalgae (Cardoso et al. 2009) were in very low densities on the reefs (Figure 8). Experimental studies have shown that *Sparisoma aurofrenatum* is able to reduce the cover of macroalgae on established substrates while *Sparisoma taeniopterus* is more efficient at reducing early successional macroalgae (Burkepile and Hay 2010). *S. taeniopterus* has also been shown to be unable to curb the growth of macroalgal cover on established algal communities (Burkepile and Hay 2010). The relatively low densities of *Sparisoma aurofrenatum* and high densities of *Scarus taeniopterus* suggests that established macroalgae are not being grazed effectively by this group, explaining the negative association, but lack of significance between the density of small parrotfish and macroalgal cover.

These findings point to the importance of the size of herbivorous fish in the process of herbivory on the reefs surveyed in this study. The importance of size in ecosystem functioning is seen in other systems as well. Studies on burrowing bivalves have shown that within the same species, larger individuals are more efficient at nutrient and oxygen cycling (Norkko et al. 2013). According to previous studies, biomass of parrotfish, an indicator of size, has been negatively associated with macroalgal cover (Williams and Polunin 2001). The biomass metric also shows that smaller fish are unable to graze as efficiently as large fish, again highlighting the importance of the size of the species responsible for the function of macroalgal grazing.

Coral cover, which can be viewed as an indirect proxy for herbivory was not significantly related with the density of large scrapers and excavators, but a positive relationship was seen. This relationship seen in the model is likely not significant because coral recruitment depends on a number of factors besides macroalgal cover, such as diseases, hurricanes and climate change (Aronson and Precht 2006; Mumby and Steneck 2008). This indicates that while coral cover has not rebounded completely, the effects of macroalgal grazing by large parrotfish are likely facilitating coral recruitment. The positive effects of grazing on coral recruitment have been shown experimentally and observationally in the Caribbean (Burkepile and Hay 2008; Burkepile and Hay 2010; Jackson et al. 2013). The findings of this study add to the body of evidence that large herbivores are important for grazing macroalgae and maintaining reef health.

Diversity and the Function of Herbivory

While reefs with high density of large parrotfish had low macroalgal cover, reefs with a more diverse assemblage did not show this relationship. In order to understand why diversity did not show a negative relationship with macroalgal cover, we need to take a closer look at the Shannon-Weiner Diversity Index.

On its own, the index does not provide much biological or ecological information. It must be interpreted in the context of the species richness, evenness of abundance and total abundance of the functional group in question. The index is based on information theory whereby it measures the uncertainty of picking the same species from a list of species after knowing the identity of the first species. Thus, the index increases as the richness and evenness of an assemblage increases. As the richness increases, the probability of drawing a new species at random increases. As evenness increases, the numerical dominance decreases,

increasing the odds of drawing a new species. Additionally, for a given level of species richness, if the density of the individual species is low, but more even, the index will be high but the index will be low if species richness decreases while keeping the proportions of each species constant and will be low if one species becomes disproportionately more abundant.

Since the density of large scrapers/excavators significantly influences macroalgal cover, increasing diversity will only be significantly related to macroalgal cover if both the species richness and evenness increases proportionally with increasing density of individual species in the functional group such that reefs with a high diversity of large scrapers and excavators also have a high density of these fish.

The diversity of both LSE and SSE was not significantly related to macroalgal cover on the reefs surveyed. The diversity of LSE was negatively related to macroalgal cover while the diversity of SSE was slightly positively related to macroalgal cover. For the large scrapers/excavators, the lowest diversity of 0 is associated with both very low and very high densities of one species, *Sparisoma viride* (Figure 7). Since macroalgal cover is negatively related to density, macroalgal cover at low diversity is very variable. After this point, diversity tends to increase with density at intermediate levels of diversity (Figure 8), explaining the slight negative relationship with macroalgae, but at the highest levels of diversity, overall density of each of the four species is very low, resulting in low levels of grazing. This variability in total density with diversity is likely the reason the diversity of LSE does not significantly affect macroalgal cover.

For the small scrapers/excavators, low diversities are associated with either high or low total densities (Figure 8). From a diversity level of 0.5 to about 1.25, the total density increases with diversity, but, from 1.25 to about 1.75, total density decreases (Figure 8).

Thus, there is a great amount of variability in the relationship with macroalgal cover and the low total density associated with very high diversity resulting in the slight positive relationship. Thus, increasing the species richness or evenness in these groups did not have an impact on functioning. The function of herbivory was more influenced by the density of two highly functioning species.

Absence of the Browsers

A very interesting finding of this study is the conspicuous absence of the browser functional group at all the reefs sampled. This group consists of only two species-*Sparisoma radians* and *Archosargus rhomboidalis*. These species are specialized macroalgal feeders (Lobel and Ogden 1981; Halpern and Floeter 2008; Holzer et al. 2013). A possible explanation for this absence is that these species are more often found in sea grass beds than on coral reefs (Ogden and Lobel 1978; Lobel and Ogden 1981). The absence of a specialized browser functional group from the reefs might be a reason why macroalgal cover has not returned to the pre-1983 levels. In contrast, Pacific reefs that generally do not encounter these phase shifts have a number of species that preferentially feed on macroalgae (Mantyka and Bellwood 2007).

Associations between Grazers/Detritivores and Benthic Cover

The reefs surveyed had a depauperate assemblage of grazers/detritivores. Out of a total of ten species, only four, *A. bahianus*, *A. coeruleus*, *A. chirurgus* and *Melichthys niger* were present on the majority of the reefs. (Figure 9). *Nicholsina usta* was present in very low densities on one reef. All other species were absent. None of the associations between the grazers/detritivores and macroalgae were significant. But, the density of GD was positively associated with macroalgal cover, while the diversity showed a slight negative correlation.

These results are in contrast to previous studies on this group which have shown that the biomass of acanthurids is significantly negatively correlated with macroalgal cover (Lewis and Wainwright 1985; Williams and Polunin 2001; Heenan and Williams 2013; Mumby et al. 2013). The two numerically dominant species in this functional group, *Acanthurus bahianus* and *Acanthurus coeruleus* are known to be capable of reducing macroalgal growth at early successional stages (Burkepile and Hay 2008; Burkepile and Hay 2010, 2011). However,

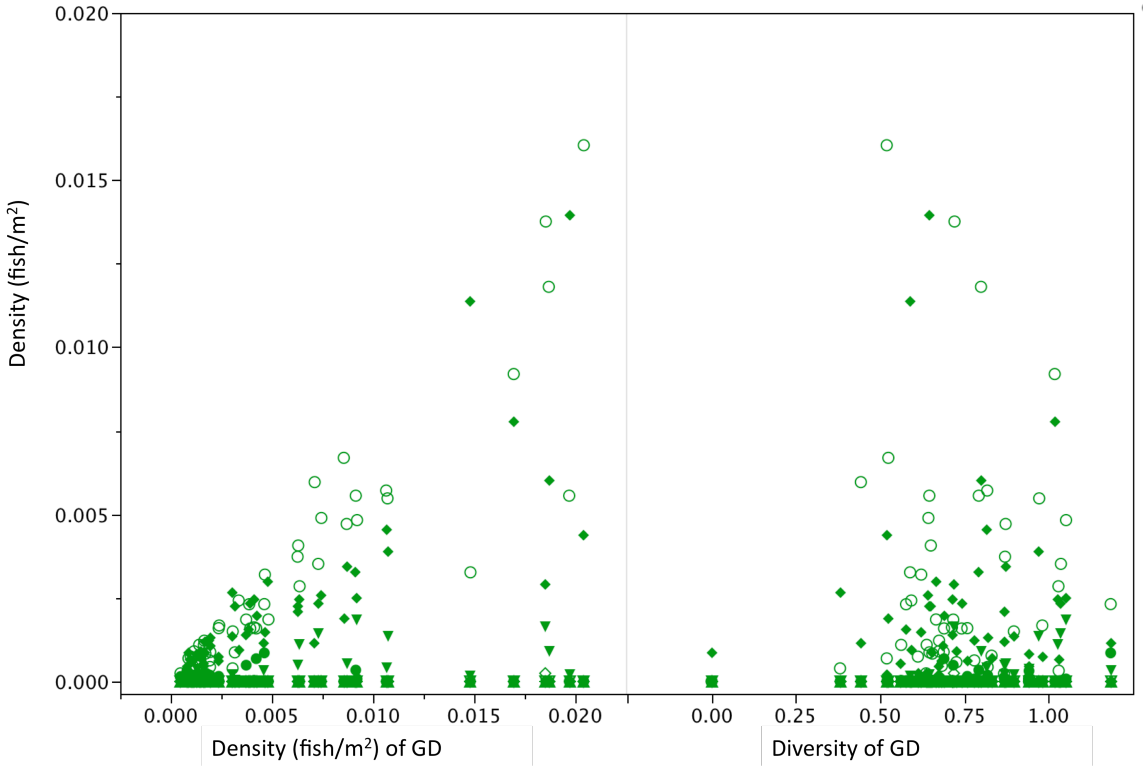

Figure 9. Relationship of the densities of individual species within the GD to total density and diversity.
The left panel shows the contribution of individual species to the total density of GD. The right panel shows how the diversity of GD is related to the densities of individual species within the group. Open circles=*Acanthurus bahianus*, closed circles=*Acanthurus chirurgus*, closed diamond=*Acanthurus coeruleus*, plus sign=*Acanthurus* UNK, small dot=*Centropyge argi*, open triangles=*Coryphopterus eidolon*, closed triangles=*Cryptotomus roseus*, inverted open triangle=*Gnatholepis thompsoni*, inverted closed triangle=*Melichthys niger*.

these studies correlate the biomass of the acanthurids with macroalgal cover. In this study, density and diversity were measured instead of biomass. Two hypotheses can explain the observed trends. 1) Grazers and detritivores are responsible for controlling turf algae instead of macroalgae. *Acanthurus bahianus* and *Acanthurus coeruleus* feed on large quantities of filamentous turf algae and do not impact macroalgae as much as parrotfish (Burkepile and Hay 2011). Reefs with high densities of grazers and detritivores might be associated with low cover of turf algae while reefs with low densities of this group are associated with high turf cover; the gradient in macroalgal cover might be coincidental. Further investigations with other algal functional groups will help resolve this hypothesis. And 2) Where densities of this functional group are low, it is possible that the biomass of this groups is high, resulting in more macroalgae being grazed. Conversely, reefs with high densities might have small individuals that are incapable of effectively grazing macroalgae. Reefs with low diversity of GD had high densities of *A. bahianus* and *A. coeruleus*. Similarly, it is probable that these individuals are very small and incapable of efficiently grazing macroalgae. Further investigation with the biomass of this group will shed light on these curious patterns.

Both the density and diversity of the grazers/detritivores were significantly related to coral cover. Coral cover was negatively associated with density and positively with diversity. Grazers/detritivores do not feed on coral itself. That function is performed by parrotfish species such as *Scarus vetula* and *Sparisoma viride*. Therefore, these associations might be due to the fact that reefs with more macroalgae tend to have less coral cover. But, within the constraints of the dataset being used in this study the findings for this group are inconclusive and further study is required to fully understand the role of grazers and detritivores in the function of herbivory.

Habitat Preference of the Territorial Damselfish

Reefs with a high density of territorial damselfish are significantly associated with high coral cover and low macroalgal cover. These trends are similar to those shown by the large scrapers and excavators, but the cause of these trends is different. An examination of the individual species that comprise this group reveals that *Stegastes partitus* is the numerically

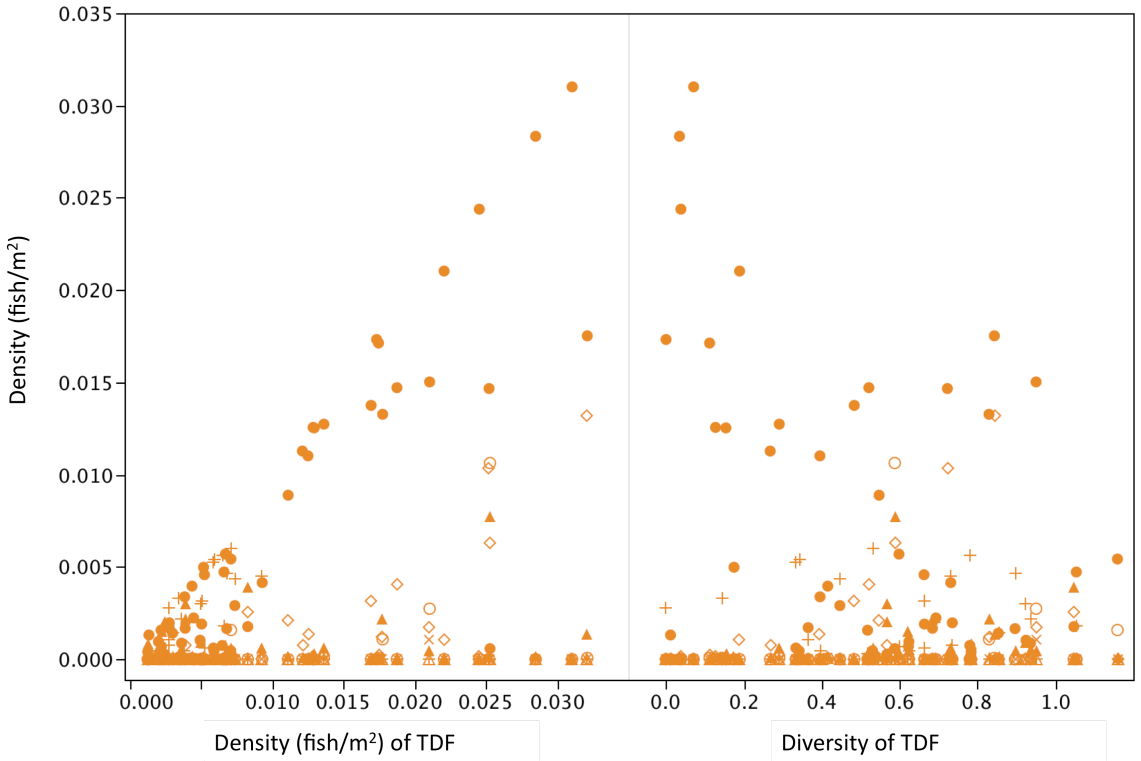

Figure 10: Relationship of the densities of individual species within the TDF to total density and diversity. The left panel shows the contribution of individual species to the total density of TDF. The right panel shows how the diversity of TDF is related to the densities of individual species within the group. Open diamonds=*Stegastes adustus*, open circles=*Stegastes diencaeus*, open triangle=*Stegastes dorsopunicans*, closed circle=*Stegastes partitus*, plus sign=*Stegastes* sp., cross=*Stegastes variabilis*, closed triangles=*Microspathodon chrysurus*.

dominant species followed by *Stegastes adustus* (Figure 10). Studies have shown that *Stegastes partitus* does not weed out macroalgae from its territories and prefers to live on substrates

that are dominated by massive coral species while *Stegastes adustus* prefers to live on habitat that comprises of branching corals (De Ruyter van Steveninck 1984; Chaves et al. 2012). Neither species prefers substrates dominated by macroalgae (Chaves et al. 2012). Experimental and observational studies have also shown that the density of *S. partitus* increases significantly as structural cover increases with respect to macroalgal cover (Williams et al. 2001; Precht et al. 2010).

Macroalgal cover was also negatively associated with reefs that had a more diverse assemblage of territorial damselfish. However, the relationship with coral cover was not significant and slightly negative. Total density increases with total diversity after an H' of 0.4, thus allowing for the significant association with macroalgal cover since we know that diversity will only significantly relate to macroalgal cover if there is a proportional increase in total density. It is likely that the incomplete recovery of corals is causing the lack of significant for the relationship between the diversity of TDF and coral cover. The lack of macroalgal weeding by the dominant species and the habitat preferences show that the patterns seen with benthic cover are most likely the result of habitat specificity rather than herbivory.

Alternative Explanations for Benthic Cover

A number of studies have suggested that nutrients have a significant effect on the growth of macroalgae (Lapointe 1997). This is still a highly debated area of study (Littler et al. 2006). A number of recent studies have shown that top-down control by herbivores is more important than the bottom-up control by nutrients (Burkepile and Hay 2009) but other studies suggest the opposite (Vermeij et al. 2010). This study used agricultural land area as a proxy for nutrient input to determine whether this factor has a significant impact on

macroalgal cover. The results show that while a positive trend was seen, this factor did not significantly affect macoalgal cover. Since this variable is a proxy, the results must be interpreted with caution. Agricultural runoff will affect the reefs only if the rivers that collect the runoff drain directly into the reef system (pers. comm.. Jeremy Jackson, 2014). Also, some islands like the Florida Keys have very little agriculture, but the proxy for these islands was developed using the agricultural land area of the United States as a percentage of total land area. Therefore, these values are highly exaggerated compared to the true percent of agricultural land area in the Keys. Further work is required to develop better proxies for nutrients in the Caribbean.

Coral cover is also influenced by factors such as sedimentation, hurricanes and bleaching events and coastal development (Rogers 1983; Rogers 1990; Gardner et al. 2005; Mora 2008; Pandolfi et al. 2011; Jackson et al. 2013). Enough data could not be collected in this study to test the effects of these factors on coral cover along with the functional characteristics.

Conclusion

The reefs studied here represent highly degraded ecosystems. The fish densities on these reefs are strikingly low. Despite these low densities, large parrotfish still seem to be able to keep macroalgal cover low on some reefs. Indeed, the reefs with the lowest cover of macroalgae and relatively high cover of coral also have the highest densities of large parrotfish, eg: reefs in St. Croix and Cuba Southwest. An interesting effect of the shift from coral domination to macroalgal domination is the loss of territorial damselfish on reefs. These fish prefer coral dominated habitats as it offers them refuge from predatory fish

(Chaves et al. 2012) . More work is needed to determine whether the trends seen with the acanthurids are because of variation in biomass across the reefs.

From a management point of view, a ban on the trapping or spear fishing of large parrotfish has the potential to make the reefs more resistant and resilient to coral-macroalgal phase shifts. Management practices that favor the drivers of the function of herbivory will also help increase the densities of *S. partitus*. In a seemingly hopeless situation, the fact that very low densities of large parrotfish are keeping macroalgae in check suggests that robust conservation efforts might still be able to help these reefs recover to their former coral dominated states.

APPENDICES

Appendix A: Log-Likelihood Ratio Test Tables for Model Selection for Models with Macroalgal Cover as the Response Variable

	df	AIC	BIC	LL	L Ratio	p-value
Model 1	10	182.1397	201.458	-81.0698		
Model 2	9	180.4827	197.8161	-81.2148	0.2899	0.5903

	df	AIC	BIC	LL	L Ratio	p-value
Model 1	10	182.1397	201.458	-81.0698		
Model 3	9	180.4832	197.8696	-81.2415	0.3434	0.5578

	df	AIC	BIC	LL	L Ratio	p-value
Model 2	9	180.4297	197.8161	-81.2148		
Model 4	8	178.6689	194.1235	-81.3344	0.2392	0.6247

	df	AIC	BIC	LL	L Ratio	p-value
Model 2	9	180.4297	197.8161	-81.2148		
Model 5	8	179.9614	195.4160	-81.9801	1.5317	0.2158

	df	AIC	BIC	LL	L Ratio	p-value
Model 4	8	178.6689	194.1235	-81.3344		
Model 6	7	178.0065	191.5293	-82.0032	1.3375	0.2475

	df	AIC	BIC	LL	L Ratio	p-value
Model 4	8	178.6689	194.1235	-81.3344		
Model 7	7	179.8252	193.3480	-82.9162	3.1562	0.0756

	df	AIC	BIC	LL	L Ratio	p-value
Model 6	7	178.0065	191.5293	-82.0032		
Model 8	6	180.3599	193.3480	-84.1799	4.3530	0.0369

	df	AIC	BIC	LL	L Ratio	p-value
Model 6	7	178.0065	191.5293	-82.0032		
Model 9	6	179.8252	193.3480	-85.2753	6.5442	0.0105

df=degrees of freedom, AIC=Akaike Information Criterion, BIC=Bayesian Information Criterion, LL=Log Likelihood, L Ratio= Likelihood Ratio

Appendix B: Log-Likelihood Ratio Test Tables for Model Selection for Models with Coral Cover as the Response Variable

	df	AIC	BIC	LL	L Ratio	p-value
Model 1	10	145.4891	164.8074	-62.7445		
Model 2	9	143.0837	161.1901	-62.9018	0.3145	0.5749

	df	AIC	BIC	LL	L Ratio	p-value
Model 1	10	145.4891	164.8074	-62.7445		
Model 3	9	143.6269	161.0133	-62.8134	0.1377	0.7106

	df	AIC	BIC	LL	L Ratio	p-value
Model 2	9	143.0837	161.1901	-62.9018		
Model 4	8	143.9909	157.4455	-62.9945	0.1871	0.6653

	df	AIC	BIC	LL	L Ratio	p-value
Model 2	9	143.0837	161.1901	-62.9018		
Model 5	8	142.6165	158.0711	-63.3082	0.1827	0.3673

	df	AIC	BIC	LL	L Ratio	p-value
Model 4	8	141.9909	157.4455	-62.9945		
Model 6	7	141.1427	154.6650	-63.5711	1.1513	0.2833

	df	AIC	BIC	LL	L Ratio	p-value
Model 4	8	141.9909	157.4455	-62.9945		
Model 7	7	141.1718	154.6946	-63.5859	1.1809	0.2772

	df	AIC	BIC	LL	L Ratio	p-value
Model 6	7	141.1427	154.6650	-63.5711		
Model 8	6	140.2031	151.7941	-64.1015	1.0608	0.3030

	df	AIC	BIC	LL	L Ratio	p-value
Model 6	7	141.1427	154.6650	-63.5711		
Model 9	6	143.5431	155.1323	-65.7706	4.3991	0.036

	df	AIC	BIC	LL	L Ratio	p-value
Model 8	6	140.2031	151.7941	-64.1015		
Model 10	5	142.4130	152.0722	-66.2065	4.2099	0.0402

df=degrees of freedom, AIC=Akaike Information Criterion, BIC=Bayesian Information Criterion, LL=Log Likelihood, L Ratio= Likelihood Ratio

REFERENCES

Anderson, J. E., and R. S. Inouye. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. Ecological Monographs 71:531-556.

Arnold, S. N., R. S. Steneck, and P. J. Mumby. 2010. Running the gauntlet: inhibitory effects of algal turfs on the processes of coral recruitment. Marine Ecology Progress Series 414:91-105.

Aronson, R., and W. Precht. 2001. White-band disease and the changing face of Caribbean coral reefs. Pp. 25-38 *in* J. Porter, ed. The Ecology and Etiology of Newly Emerging Marine Diseases. Springer Netherlands.

Aronson, R. B., and W. F. Precht. 2006. Conservation, precaution, and Caribbean reefs. Coral Reefs 25:441-450.

Arthur, R., T. J. Done, and H. Marsh. 2005. Benthic recovery four years after an El Nino-induced coral mass mortality in the Lakshadweep atolls. Current Science 89:694-699.

Bellwood, D., and J. H. Choat. 1990. A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. Environmental biology of fishes 28:189-214.

Bellwood, D. R., A. S. Hoey, and J. H. Choat. 2003. Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. Ecol. Lett. 6:281-285.

Bellwood, D. R., T. P. Hughes, C. Folke, and M. Nystrom. 2004. Confronting the coral reef crisis. Nature 429:827-833.

Bellwood, D. R., T. P. Hughes, and A. S. Hoey. 2006. Sleeping functional group drives coral-reef recovery. Current Biology 16:2434-2439.

Bonaldo, R. M., and D. R. Bellwood. 2008. Size-dependent variation in the functional role of the parrotfish Scarus rivulatus on the Great Barrier Reef, Australia. Marine Ecology Progress Series 360:237-244.

Bruggemann, J., A. Van Kessel, J. Van Rooij, and A. Breeman. 1996. Bioerosion and sediment ingestion by the Caribbean parrotfish Scarus vetula and Sparisoma viride: implications of fish size, feeding mode and habitat use. Marine ecology progress series. Oldendorf 134:59-71.

Bruggemann, J. H., M. W. M. Kuyper, and A. M. Breeman. 1994. Comparative-Analysis of Foraging and Habitat Use by the Sympatric Caribbean Parrotfish Scarus-Vetula and Sparisoma-Viride (Scaridae). Marine Ecology Progress Series 112:51-66.

Bueno, R. S., R. Guevara, M. C. Ribeiro, L. Culot, F. S. Bufalo, and M. Galetti. 2013. Functional Redundancy and Complementarities of Seed Dispersal by the Last Neotropical Megafrugivores. PLoS One 8:e56252.

Burkepile, D. E., and M. E. Hay. 2008. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. Proc. Natl. Acad. Sci. U. S. A. 105:16201-16206.

Burkepile, D. E., and M. E. Hay. 2009. Nutrient versus herbivore control of macroalgal community development and coral growth on a Caribbean reef. Marine Ecology Progress Series 389:71-84.

Burkepile, D. E., and M. E. Hay. 2010. Impact of herbivore identity on algal succession and coral growth on a Caribbean reef. PLoS One 5:e8963.

Burkepile, D. E., and M. E. Hay. 2011. Feeding complementarity versus redundancy among herbivorous fishes on a Caribbean reef. Coral Reefs 30:351-362.

Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, G. M. Mace, D. Tilman, D. A. Wardle, A. P. Kinzig, G. C. Daily, M.

Loreau, J. B. Grace, A. Larigauderie, D. S. Srivastava, and S. Naeem. 2012. Biodiversity loss and its impact on humanity. Nature 486:59-67.

Cardinale, B. J., K. L. Matulich, D. U. Hooper, J. E. Byrnes, E. Duffy, L. Gamfeldt, P. Balvanera, M. I. O'Connor, and A. Gonzalez. 2011. The functional role of producer diversity in ecosystems. American Journal of Botany 98:572-592.

Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran, and C. Jouseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443:989-992.

Cardoso, S. C., M. C. Soares, H. A. Oxenford, and I. M. Côté. 2009. Interspecific differences in foraging behaviour and functional role of Caribbean parrotfish. Marine Biodiversity Records 2:1-6.

Carpenter, R. C., and P. J. Edmunds. 2006. Local and regional scale recovery of Diadema promotes recruitment of scleractinian corals. Ecol. Lett. 9:271-280.

Ceccarelli, D. M., G. P. Jones, and L. J. McCook. 2005. Effects of territorial damselfish on an algal-dominated coastal coral reef. Coral Reefs 24:606-620.

Ceccarelli, D. M., G. P. Jones, and L. J. McCook. 2011. Interactions between herbivorous fish guilds and their influence on algal succession on a coastal coral reef. Journal of Experimental Marine Biology and Ecology 399:60-67.

Chaves, L. d. C. T., C. G. A. Ormond, E. S. McGinty, and B. P. Ferreira. 2012. Space partitioning among damselfishes in the Caribbean coast of Panama: the role of habitat preferences. Neotropical Ichthyology 10:633-642.

Cheal, A. J., M. A. MacNeil, E. Cripps, M. J. Emslie, M. Jonker, B. Schaffelke, and H. Sweatman. 2010. Coral-macroalgal phase shifts or reef resilience: links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. Coral Reefs 29:1005-1015.

Choat, J. H. 1991. The Biology of Herbivorous Fishes on Coral Reefs. Pp. 120-155. Sale, P. F.

Davis, G. E. 1982. A Century of Natural Change in Coral Distribution at the Dry Tortugas: A Comparison of Reef Maps from 1881 and 1976. Bulletin of Marine Science 32:608-623.

De Ruyter van Steveninck, E. D. 1984. The composition of algal vegetation in and outside damselfish territories on a Florida reef. Aquatic Botany 20:11-19.

Duffy, J. E. 2002. Biodiversity and ecosystem function: the consumer connection. Oikos 99:201-219.

Duffy, J. E., and M. E. Hay. 1990. Seaweed Adaptations to Herbivory. Bioscience 40:368-375.

Eakin, C. M., J. A. Morgan, S. F. Heron, T. B. Smith, G. Liu, L. Alvarez-Filip, B. Baca, E. Bartels, C. Bastidas, C. Bouchon, M. Brandt, A. W. Bruckner, L. Bunkley-Williams, A. Cameron, B. D. Causey, M. Chiappone, T. R. L. Christensen, M. J. C. Crabbe, O. Day, E. de la Guardia, G. Díaz-Pulido, D. DiResta, D. L. Gil-Agudelo, D. S. Gilliam, R. N. Ginsburg, S. Gore, H. M. Guzmán, J. C. Hendee, E. A. Hernández-Delgado, E. Husain, C. F. G. Jeffrey, R. J. Jones, E. Jordán-Dahlgren, L. S. Kaufman, D. I. Kline, P. A. Kramer, J. C. Lang, D. Lirman, J. Mallela, C. Manfrino, J.-P. Maréchal, K. Marks, J. Mihaly, W. J. Miller, E. M. Mueller, E. M. Muller, C. A. Orozco Toro, H. A. Oxenford, D. Ponce-Taylor, N. Quinn, K. B. Ritchie, S. Rodríguez, A. R. Ramírez, S. Romano, J. F. Samhouri, J. A. Sánchez, G. P. Schmahl, B. V. Shank, W. J. Skirving, S. C. C. Steiner, E. Villamizar, S. M. Walsh, C. Walter, E. Weil, E. H. Williams, K. W. Roberson, and Y. Yusuf. 2010. Caribbean Corals in Crisis: Record Thermal Stress, Bleaching, and Mortality in 2005. PLoS One 5:e13969.

Edmunds, P. J., and R. C. Carpenter. 2001. Recovery of Diadema antillarum reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. Proc. Natl. Acad. Sci. U. S. A. 98:5067-5071.

Edwards, C. B., A. M. Friedlander, A. G. Green, M. J. Hardt, E. Sala, H. P. Sweatman, I. D. Williams, B. Zgliczynski, S. A. Sandin, and J. E. Smith. 2014. Global assessment of the status of coral reef herbivorous fishes: evidence for fishing effects. Proc Biol Sci 281:20131835.

Fox, R. J., and D. R. Bellwood. 2007. Quantifying herbivory across a coral reef depth gradient. Marine Ecology Progress Series 339:49-59.

Froese, R., and D. Pauly. 2011. FishBase, World Wide Web electronic publication.

Fründ, J., C. F. Dormann, A. Holzschuh, and T. Tscharntke. 2013. Bee diversity effects on pollination depend on functional complementarity and niche shifts. Ecology 94:2042-2054.

Gardner, T. A., I. M. Cote, J. A. Gill, A. Grant, and A. R. Watkinson. 2003. Long-term region-wide declines in Caribbean corals. Science 301:958-960.

Gardner, T. A., I. M. Côté, J. A. Gill, A. Grant, and A. R. Watkinson. 2005. Hurricanes and Caribbean Coral Reefs: Impacts, Recovery Patterns, and Role in Long-Term Decline. Ecology 86:174-184.

Gilmour, J. P., L. D. Smith, A. J. Heyward, A. H. Baird, and M. S. Pratchett. 2013. Recovery of an isolated coral reef system following severe disturbance. Science 340:69-71.

Green, A. L., and D. R. Bellwood. 2009. Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience - A practical guide for coral reef managers in the Asia Pacific Region. Pp. 70. . IUCN working group on Climate Change and Coral Reefs, IUCN, Gland, Switzerland.

Halpern, B. S., and S. R. Floeter. 2008. Functional diversity responses to changing species richness in reef fish communities. Marine Ecology-Progress Series 364:147-156.

Hay, M. E. 1984. Patterns of Fish and Urchin Grazing on Caribbean Coral Reefs: Are Previous Results Typical? Ecology 65:446-454.

Hay, M. E., and P. R. Taylor. 1985. Competition between herbivourous fishes and urchins on Caribbean reefs. Oecologia 65:591-598.

Heenan, A., and I. D. Williams. 2013. Monitoring Herbivorous Fishes as Indicators of Coral Reef Resilience in American Samoa. PLoS One 8:e79604.

Hinds, P. A., and D. L. Ballantine. 1987. Effects of the Caribbean threespot damselfish, Stegastes Planifrons (Cuvier), on algal lawn composition. Aquatic Botany 27:299-308.

Hoey, A. S., and D. R. Bellwood. 2008. Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. Coral Reefs 27:37-47.

Hoey, A. S., and D. R. Bellwood. 2009a. Damselfish territories as a refuge for macroalgae on coral reefs. Coral Reefs 29:107-118.

Hoey, A. S., and D. R. Bellwood. 2009b. Limited Functional Redundancy in a High Diversity System: Single Species Dominates Key Ecological Process on Coral Reefs. Ecosystems 12:1316-1328.

Holzer, K. K., D. A. Seekell, and K. J. McGlathery. 2013. Bucktooth parrotfish Sparisoma radians grazing on Thalassia in Bermuda varies seasonally and with background nitrogen content. Journal of Experimental Marine Biology and Ecology 443:27-32.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setala, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs 75:3-35.

Hooper, D. U., M. Solan, A. J. Symstad, S. Diaz, M. O. Gessner, N. Buchmann, V. Degrange, P. Grime, F. Hulot, F. Mermillod-Blondin, J. Roy, E. Spehn, and L. van Peer. 2002. Species diversity, functional diversity and ecosystem functioning. Pp. 195-281 *in* M. Loreau, S. Naeem, and P. Inchausti, eds. Biodiversity and Ecosystem Functioning: Synthesis and Perspectives. Oxford University Press, Oxford, UK.

Hughes, T. P. 1994. Catastrophes, Phase-Shifts, and Large-Scale Degradation of a Caribbean Coral-Reef. Science 265:1547-1551.

Hughes, T. P., A. H. Baird, D. R. Bellwood, M. Card, S. R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J. B. C. Jackson, J. Kleypas, J. M. Lough, P. Marshall, M. Nystrom, S. R. Palumbi, J. M. Pandolfi, B. Rosen, and J. Roughgarden. 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301:929-933.

Hughes, T. P., N. A. J. Graham, J. B. C. Jackson, P. J. Mumby, and R. S. Steneck. 2010. Rising to the challenge of sustaining coral reef resilience. Trends Ecol. Evol. 25:633-642.

Hughes, T. P., D. C. Reed, and M.-J. Boyle. 1987. Herbivory on coral reefs: community structure following mass mortalities of sea urchins. Journal of Experimental Marine Biology and Ecology 113:39-59.

Hughes, T. P., M. J. Rodrigues, D. R. Bellwood, D. Ceccarelli, O. Hoegh-Guldberg, L. McCook, N. Moltschaniwskyj, M. S. Pratchett, R. S. Steneck, and B. Willis. 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. Curr Biol 17:360-365.

Idjadi, J. A., S. C. Lee, J. F. Bruno, W. F. Precht, L. Allen-Requa, and P. J. Edmunds. 2006. Rapid phase-shift reversal on a Jamaican coral reef. Coral Reefs 25:209-211.

Jackson, J. B. 1997. Reefs since Columbus. Coral Reefs 16:S23-S32.

Jackson, J. B., M. K. Donovan, K. L. Cramer, and V. Lam. 2013. Status and Trends of Caribbean Coral Reefs: 1970-2012. Global Coral Reef Monitoring Network, Global Marine and Polar Program, Washington, DC, USA.

Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629-638.

Johansson, C. L., I. A. Leemput, M. Depczynski, A. S. Hoey, and D. R. Bellwood. 2013. Key herbivores reveal limited functional redundancy on inshore coral reefs. Coral Reefs 32:963-972.

Knowlton, N., and J. B. C. Jackson. 2008. Shifting baselines, local impacts, and global change on coral reefs. Plos Biology 6:215-220.

Kuffner, I. B., L. J. Walters, M. A. Becerro, V. J. Paul, R. Ritson-Williams, and K. S. Beach. 2006. Inhibition of coral recruitment by macroalgae and cyanobacteria. Marine Ecology Progress Series 323:107-117.

Lapointe, B. E. 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. Limnology and Oceanography 42:1119-1131.

Lefevre, C. D., and D. R. Bellwood. 2011. Temporal variation in coral reef ecosystem processes: herbivory of macroalgae by fishes. Marine Ecology-Progress Series 422:239-251.

Lessios, H. A. 1988. Mass Mortality of Diadema Antillarum in the Caribbean: What Have We Learned? Annu. Rev. Ecol. Syst. 19:371-393.

Lewis, S. M. 1985. Herbivory on coral reefs: algal susceptibility to herbivorous fishes. Oecologia 65:370-375.

Lewis, S. M. 1986. The Role of Herbivorous Fishes in the Organization of a Caribbean Reef Community. Ecological Monographs 56:184-200.

Lewis, S. M., and P. C. Wainwright. 1985. Herbivore abundance and grazing intensity on a Caribbean coral reef. Journal of Experimental Marine Biology and Ecology 87:215-228.

Littler, M. M., D. S. Littler, and B. L. Brooks. 2006. Harmful algae on tropical coral reefs: Bottom-up eutrophication and top-down herbivory. Harmful Algae 5:565-585.

Lobel, P. S. 1980. Herbivory by Damselfishes and their Role in Coral Reef Community Ecology. Bulletin of Marine Science 30:273-289.

Lobel, P. S., and J. C. Ogden. 1981. Foraging by the herbivorous parrotfish Sparisoma radians. Marine Biology 64:173-183.

Loreau, M., and A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412:72-76.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. Science 294:804-808.

Lubchenco, J., and S. D. Gaines. 1981. A Unified Approach to Marine Plant-Herbivore Interactions. I. Populations and Communities. Annu. Rev. Ecol. Syst. 12:405-437.

Magurran, A. E. 2004. Measuring Biological Diversity. Blackwell Publishing, Oxford, UK.

Mantyka, C. S., and D. R. Bellwood. 2007. Macroalgal grazing selectivity among herbivorous coral reef fishes. Marine Ecology Progress Series 352:177-185.

Marshell, A., and P. J. Mumby. 2012. Revisiting the functional roles of the surgeonfish Acanthurus nigrofuscus and Ctenochaetus striatus. Coral Reefs 31:1093-1101.

McAfee, S. T., and S. G. Morgan. 1996. Resource use by five sympatric parrotfishes in the San Blas Archipelago, Panama. Marine Biology 125:427-437.

McClanahan, T. R., and N. A. Muthiga 1998. An ecological shift in a remote coral atoll of Belize over 25 years. Environmental Conservation 25:122-130.

Mora, C. 2008. A clear human footprint in the coral reefs of the Caribbean. Proc Biol Sci 275:767-773.

Mora, C., O. Aburto-Oropeza, A. Ayala Bocos, P. M. Ayotte, S. Banks, A. G. Bauman, M. Beger, S. Bessudo, D. J. Booth, E. Brokovich, A. Brooks, P. Chabanet, J. E. Cinner, J. Cortés, J. J. Cruz-Motta, A. Cupul Magaña, E. E. DeMartini, G. J. Edgar, D. A. Feary, S. C. A. Ferse, A. M. Friedlander, K. J. Gaston, C. Gough, N. A. J. Graham, A. Green, H. Guzman, M. Hardt, M. Kulbicki, Y. Letourneur, A. López Pérez, M. Loreau, Y. Loya, C. Martinez, I. Mascareñas-Osorio, T. Morove, M.-O. Nadon, Y. Nakamura, G. Paredes, N. V. C. Polunin, M. S. Pratchett, H. Reyes Bonilla, F. Rivera, E. Sala, S. A. Sandin, G. Soler, R. Stuart-Smith, E. Tessier, D. P. Tittensor, M. Tupper, P. Usseglio, L. Vigliola, L. Wantiez, I. Williams, S. K. Wilson, and F. A. Zapata. 2011. Global Human Footprint on the Linkage between Biodiversity and Ecosystem Functioning in Reef Fishes. PLoS Biol 9:e1000606.

Mora, C., S. Andrèfouët, M. J. Costello, C. Kranenburg, A. Rollo, J. Veron, K. J. Gaston, and R. A. Myers. 2006. Coral Reefs and the Global Network of Marine Protected Areas. Science 312:1750-1751.

Mumby, P. J., S. Bejarano, Y. Golbuu, R. S. Steneck, S. N. Arnold, R. Woesik, and A. M. Friedlander. 2013. Empirical relationships among resilience indicators on Micronesian reefs. Coral Reefs 32:213-226.

Mumby, P. J., C. P. Dahlgren, A. R. Harborne, C. V. Kappel, F. Micheli, D. R. Brumbaugh, K. E. Holmes, J. M. Mendes, K. Broad, J. N. Sanchirico, K. Buch, S. Box, R. W. Stoffle, and A. B. Gill. 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. Science 311:98-101.

Mumby, P. J., A. Hastings, and H. J. Edwards. 2007. Thresholds and the resilience of Caribbean coral reefs. Nature 450:98-101.

Mumby, P. J., and R. S. Steneck. 2008. Coral reef management and conservation in light of rapidly evolving ecological paradigms. Trends Ecol. Evol. 23:555-563.

Naeem, S., J. E. Duffy, and E. Zavaleta. 2012. The Functions of Biological Diversity in an Age of Extinction. Science 336:1401-1406.

Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1995. Empirical-Evidence That Declining Species-Diversity May Alter the Performance

of Terrestrial Ecosystems. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 347:249-262.

Naeem, S., and J. P. Wright. 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. Ecol. Lett. 6:567-579.

Newman, M. J., G. A. Paredes, E. Sala, and J. B. Jackson. 2006. Structure of Caribbean coral reef communities across a large gradient of fish biomass. Ecol. Lett. 9:1216-1227.

Norkko, A., A. Villnas, J. Norkko, S. Valanko, and C. Pilditch. 2013. Size matters: implications of the loss of large individuals for ecosystem function. Sci. Rep. 3.

Ogden, J. C., and P. S. Lobel. 1978. The role of herbivorous fishes and urchins in coral reef communities. Environmental biology of fishes 3:49-63.

Paddack, M. J., R. K. Cowen, and S. Sponaugle. 2006. Grazing pressure of herbivorous coral reef fishes on low coral-cover reefs. Coral Reefs 25:461-472.

Paddack, M. J., J. D. Reynolds, C. Aguilar, R. S. Appeldoorn, J. Beets, E. W. Burkett, P. M. Chittaro, K. Clarke, R. Esteves, A. C. Fonseca, G. E. Forrester, A. M. Friedlander, J. Garcia-Sais, G. Gonzalez-Sanson, L. K. Jordan, D. B. McClellan, M. W. Miller, P. P. Molloy, P. J. Mumby, I. Nagelkerken, M. Nemeth, R. Navas-Camacho, J. Pitt, N. V. Polunin, M. C. Reyes-Nivia, D. R. Robertson, A. Rodriguez-Ramirez, E. Salas, S. R. Smith, R. E. Spieler, M. A. Steele, I. D. Williams, C. L. Wormald, A. R. Watkinson, and I. M. Cote. 2009. Recent region-wide declines in Caribbean reef fish abundance. Current biology 19:590-595.

Pandolfi, J. M., R. H. Bradbury, E. Sala, T. P. Hughes, K. A. Bjorndal, R. G. Cooke, D. McArdle, L. McClenachan, M. J. Newman, G. Paredes, R. R. Warner, and J. B. Jackson. 2003. Global trajectories of the long-term decline of coral reef ecosystems. Science 301:955-958.

Pandolfi, J. M., S. R. Connolly, D. J. Marshall, and A. L. Cohen. 2011. Projecting coral reef futures under global warming and ocean acidification. Science 333:418-422.

Pandolfi, J. M., and J. B. Jackson. 2006. Ecological persistence interrupted in Caribbean coral reefs. Ecol. Lett. 9:818-826.

Paul, V. J., and M. E. Hay. 1986. Seaweed Susceptibility to Herbivory - Chemical and Morphological Correlates. Marine Ecology Progress Series 33:255-264.

Philpott, S. M., O. Soong, J. H. Lowenstein, A. L. Pulido, D. T. Lopez, D. F. B. Flynn, and F. DeClerck. 2009. Functional richness and ecosystem services: bird predation on arthropods in tropical agroecosystems. Ecological Applications 19:1858-1867.

Precht, W. F., R. B. Aronson, R. M. Moody, and L. Kaufman. 2010. Changing Patterns of Microhabitat Utilization by the Threespot Damselfish, *Stegastes planifrons*, on Caribbean Reefs. PLoS One 5:e10835.

Rogers, C. S. 1983. Sublethal and lethal effects of sediments applied to common Caribbean Reef corals in the field. Marine Pollution Bulletin 14:378-382.

Rogers, C. S. 1990. Responses of coral reefs and reef organisms to sedimentation. Marine ecology progress series. Oldendorf 62:185-202.

Rotjan, R. D., and S. M. Lewis. 2006. Parrotfish abundance and selective corallivory on a Belizean coral reef. Journal of Experimental Marine Biology and Ecology 335:292-301.

Schutte, V. G. W., E. R. Selig, and J. F. Bruno. 2010. Regional spatio-temporal trends in Caribbean coral reef benthic communities. Marine Ecology Progress Series 402:115-122.

Shulman, M. J., and D. R. Robertson. 1996. Changes in the coral reefs of San Blas, Caribbean Panama: 1983 to 1990. Coral Reefs 15:231-236.

Soetaert, K., and C. Heip. 1990. Sample-Size Dependence of Diversity Indexes and the Determination of Sufficient Sample-Size in a High-Diversity Deep-Sea Environment. Marine Ecology Progress Series 59:305-307.

Steneck, R. S. 1993. Is herbivore loss more damaging to reefs than hurricanes? Case studies from two Caribbean reef systems (1978–1988). Pp. 220-226. Proceedings of the Colloquium on Global Aspects of Coral Reefs: Health, Hazards and History.

Steneck, R. S., and M. N. Dethier. 1994. A functional group approach to the structure of algal-dominated communities. Oikos 69:476-498.

Tilman, D. 1997. The Influence of Functional Diversity and Composition on Ecosystem Processes. Science 277:1300-1302.

Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379:718-720.

Vergés, A., M. A. Vanderklift, C. Doropoulos, and G. A. Hyndes. 2011. Spatial Patterns in Herbivory on a Coral Reef Are Influenced by Structural Complexity but Not by Algal Traits. PLoS One 6:e17115.

Vermeij, M. J. A., I. van Moorselaar, S. Engelhard, C. Hörnlein, S. M. Vonk, and P. M. Visser. 2010. The Effects of Nutrient Enrichment and Herbivore Abundance on the Ability of Turf Algae to Overgrow Coral in the Caribbean. PLoS One 5:e14312.

Weil, E., and C. Rogers. 2011. Coral Reef Diseases in the Atlantic-Caribbean. Pp. 465-491 *in* Z. Dubinsky, and N. Stambler, eds. Coral Reefs: An Ecosystem in Transition. Springer Netherlands.

Williams, I., and N. Polunin. 2001. Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. Coral Reefs 19:358-366.

Williams, I. D., N. V. C. Polunin, and V. J. Hendrick. 2001. Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. Marine Ecology Progress Series 222:187-196.

Wilson, S. K. 2009. Diversity in the Diet and Feeding Habits of Blennies. Pp. 139-162. The Biology of Blennies. Science Publishers.

Wilson, S. K., R. Fisher, M. S. Pratchett, N. A. J. Graham, N. K. Dulvy, R. A. Turner, A. Cakacaka, N. V. C. Polunin, and S. P. Rushton. 2008. Exploitation and habitat degradation as agents of change within coral reef fish communities. Global Change Biology 14:2796-2809.

Woodley, J. D., E. A. Chornesky, P. A. Clifford, J. B. C. Jackson, L. S. Kaufman, N. Knowlton, J. C. Lang, M. P. Pearson, J. W. Porter, M. C. Rooney, K. W. Rylaarsdam, V. J. Tunnicliffe, C. M. Wahle, J. L. Wulff, A. S. G. Curtis, M. D. Dallmeyer, B. P. Jupp, M. A. R. Koehl, J. Neigel, and E. M. Sides. 1981. Hurricane Allen's Impact on Jamaican Coral Reefs. Science 214:749-755.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed Effects Models and Extensions in Ecology with R. Springer New York, New York.