Title
An observational assessment of feeding behavior and preferences of reef fishes: quantifying the driving forces of herbivore foraging

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An observational assessment of feeding behavior and preferences of reef fishes; quantifying the driving forces of herbivore foraging

A Thesis submitted in partial satisfaction of the requirements for the degree
Master of Science

in

Biology

by

Cara Marie Simonsen

Committee in charge:

Professor Stuart Sandin, Chair
Professor Eric Allen
Professor Kaustuv Roy

2013
The Thesis of Cara Marie Simonsen is approved and it is acceptable in quality and form for publication on microfilm and electronically:

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Chair

University of California, San Diego

2013
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Signature Page</td>
<td>iii</td>
</tr>
<tr>
<td>Table of Contents</td>
<td>iv</td>
</tr>
<tr>
<td>List of Figures</td>
<td>v</td>
</tr>
<tr>
<td>List of Tables</td>
<td>vii</td>
</tr>
<tr>
<td>Acknowledgements</td>
<td>iv</td>
</tr>
<tr>
<td>Abstract of Thesis</td>
<td>v</td>
</tr>
<tr>
<td>Introduction</td>
<td>1</td>
</tr>
<tr>
<td>Materials and Methods</td>
<td>9</td>
</tr>
<tr>
<td>Results</td>
<td>17</td>
</tr>
<tr>
<td>Discussion</td>
<td>24</td>
</tr>
<tr>
<td>Figures</td>
<td>33</td>
</tr>
<tr>
<td>Tables</td>
<td>54</td>
</tr>
<tr>
<td>References</td>
<td>57</td>
</tr>
</tbody>
</table>
LIST OF FIGURES

Figure 1. Location of Curaçao................................................................. 33
Figure 2. Benthic cover percentages of functional groups at each site........... 34
Figure 3. Correlation results between turf algae and coral cover................... 34
Figure 4. Correlation results between macroalgae and coral cover................... 35
Figure 5. Average density (ind/m²) of the five functional groups of fish species... 35
Figure 6. Average biomass (grams/m²) of the five functional groups of fish species.. 36
Figure 7a. Average density of *A. bahianus*............................................. 36
Figure 7b. Average density of *A. coerleus*............................................... 37
Figure 7c. Average density of *S. aurofrenatum*......................................... 37
Figure 7d. Average density of *S. taeniopterus*.......................................... 38
Figure 7e. Average density of *S. viride*.................................................. 38
Figure 7f. Average density of the browsers group...................................... 39
Figure 7g. Average density of scraper/excavator group................................ 39
Figure 7h. Average density of the target herbivore guild............................. 40
Figure 8. Average biomass of each of the target species across different reefs...... 40
Figure 9a. Comparison results of the bite rates on the benthic functional groups across sites for *A. bahianus*................................................................. 41
Figure 9b. Relationship between bite rate and density for *A. bahianus*........... 41
Figure 9c. Estimated bite rates (weighted by density) across all species for *A. bahianus*........................................................................................................... 42
Figure 10a. Comparison results of the bite rates on the benthic functional groups across sites for *A. coeruleus* ................................................................. 42

Figure 10b. Relationship between bite rate and density for *A. coeruleus* .......... 43

Figure 10c. Estimated bite rates (weighted by density) across all species for *A. coeruleus* ............................................................................................................. 43

Figure 11a. Comparison results of the bite rates on the benthic functional groups across sites for *S. aurofrenatum* ................................................................. 44

Figure 11b. Relationship between bite rate and density for *S. aurofrenatum* ........... 44

Figure 12c. Estimated bite rates (weighted by density) across all species for *S. aurofrenatum* ............................................................................................................. 45

Figure 12a. Comparison results of the bite rates on the benthic functional groups across sites for *S. taeniopterus* ................................................................. 45

Figure 12b. Relationship between bite rate and density for *S. taeniopterus* ........... 46

Figure 12c. Estimated bite rates (weighted by density) across all species for *S. taeniopterus* ............................................................................................................. 46

Figure 13a. Comparison results of the bite rates on the benthic functional groups across sites for *S. viride* ................................................................. 47

Figure 13b. Relationship between bite rate and density for *S. viride* ........... 47

Figure 13c. Estimated bite rates (weighted by density) across all species for *S. viride* ............................................................................................................. 48

Figure 14a. Estimated bite rates (weighted by density) across all sites for the browsers group ............................................................................................................. 48
Figure 14b. Estimated bite rates (weighted by density) across all sites for the scraper/excavator group……………………………………………………………… 49

Figure 14c. Estimated bite rates (weighted by density) across all sites for the target herbivore guild……………………………………………………………… 49

Figure 15a. Manly’s alpha selectivity index for A. bahianus on six substrate types at the nine different sites………………………………………………………… 50

Figure 15b. Manly’s alpha selectivity index for A. coeruleus on six substrate types at the nine different sites………………………………………………………… 50

Figure 15c. Manly’s alpha selectivity index for S. aurofrenatum on six substrate types at the nine different sites……………………………………………………….. 51

Figure 15d. Manly’s alpha selectivity index for S. taeniopterus on six substrate types at the nine different sites……………………………………………………….. 51

Figure 15e. Manly’s alpha selectivity index for S. viride on six substrate types at the nine different sites……………………………………………………….. 52

Figure 15f. Manly’s alpha selectivity index for the browsers group on six substrate types at the nine different sites…………………………………………………… 52

Figure 15g. Manly’s alpha selectivity index for the scraper/excavator group on six substrate types at the nine different sites…………………………………………………… 53

Figure 15h. Manly’s alpha selectivity index for target herbivore guild on six substrate types at the nine different sites…………………………………………………… 53
LIST OF TABLES

Table 1. Sample sizes of the species and site specific foraging observations…….. 54
Table 2. Analysis of the covariance of fish size and study site......................... 54
Table 3. Manly’s alpha selectivity indices..................................................... 55
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ABSTRACT OF THESIS

An observational assessment of feeding behavior and preferences of reef fishes; quantifying the driving forces of herbivore foraging

by

Cara Simonsen

Master of Science in Biology
University of California, San Diego, 2013
Professor Stuart Sandin, Chair

Coral reefs have undergone major phase shifts in the past three decades resulting in algal dominance. Herbivorous fish are the main force removing algae from Caribbean reefs since the die-off of Diadema antillarum. This study looks to determine the elements controlling herbivorous fish populations on Caribbean coral reefs and their ability to remove turf and erect macroalgae. We asked whether the foraging rates and behaviors at a species, family and guild level changed with context. Over a three-month period, focal observations were conducted on five common herbivorous fish species, three Scarids and two Acanthurids, at nine sites on Curacao that varied in benthic
composition and fish populations. Bite rates, benthic composition and fish assemblages were quantified at each site. The three driving forces of foraging behavior of reef fishes are preferred bite rates, species abundances and diversity, and food availability. An increase in any of these factors increases the foraging intensities. I also found that herbivores have an overwhelming preference for turf algae at every site, regardless of the benthic makeup. Variations of density, estimated bite rates and selectivity all decreased along an inverse taxonomic gradient. These findings suggest that analyzing foraging behavior and intensity at a guild level is the most beneficial to understanding impact of herbivory on coral reefs. The total amount of bites taken on a reef can determine how the herbivorous fish guilds affect both the overall benthic composition and coral reef functionality.
Introduction

Coral reefs are a dynamic ecosystem that support a diverse community of organisms and animals comprising over 25% of all marine life (Spalding 2001) as well as provide a variety of resources to many tropical regions (Hughes et al. 2003). A “healthy” reef is a productive, growing reef with the majority of the benthic coverage comprised of corals and calcifying organisms. Interactions between organisms and populations create a dynamic habitat and ecosystem, including the competitive relationship between algae and coral (Hughes et al. 2007).

Direct competition between coral and algae for benthic space has been studied and recorded across different regions, including the Great Barrier Reef and the Caribbean (Lewis 1986; McCook et al. 2001; Hughes et al. 2007). Corals have a unique calcification process allowing them to deploy a variety of aggressive strategies of including covering and directly ingesting competitive species (Genin et al. 1994). Corals also create rugose and complex habitats for many other living organisms. This is in contrast to the competitive advantage of algae, which is their ability to grow quickly and over many different surfaces. Algal species are very diverse in structure and morphology, varying from filamentous, to fleshy and calcified forms.

In a healthy ecosystem herbivores play a strong mediating role to the benthic competition by limiting algal growth. Herbivore species like echinoids and fish consume and remove algae from the benthos alleviating competitive pressure for corals. In the Caribbean, the echinoid *Diadema antillarum* is a prominent grazer on coral reefs. *D. antillarum* can remove a significant amount of algae, which can free space for the growth of calcifying organisms (Wanders 1977; Hay 1981; Hay et al.)
1983; Foster 1987). Roving herbivorous fish, including the families Scaridae and Acanthuridae, have a larger grazing area but forage at a lower frequency than an individual D. antillarum (Carpenter 1986). Previous studies have shown that herbivorous fish are a direct influence on coral-algae competition on reefs (Carpenter 1986; McCook et al. 2001; Hughes et al. 2007), while experimental herbivore exclusions have effectively measured the significant increase in algal abundance and decrease in coral cover (Lewis 1986; Hughes et al. 2007).

Different species of herbivores affect the benthos in distinguishable ways based on functional and behavioral traits. Among coral reef herbivorous fish there are three different types commonly known as grazers, excavators, and scrapers (Bellwood and Choat 1990). Many Acanthurid species, commonly known as surgeonfish, are considered to be grazers. They have a small gape size relative to body size and often feed selectively by rapidly picking out small algal filaments (Bellwood and Choat 1990; McCook et al. 2001; Semmens et al. 2005). Historically these species have been known to select for turf filaments and epiphytes growing off of the substrate (McAfee and Morgan 1996; Burkepile and Hay 2008).

Fish are able to mediate the coral-algae competition by affecting the algal growth succession without completely removing algae from the reef. Low fish densities and low grazing results in the growth progression: (1) simple filaments, (2) more complex intermediate structure, (3) erect upright algal plant with distinguishable features and morphology (Hixon and Brostoff 1996). In areas of high grazing, succession is deflected and filamentous algae is replaced with low growing, mat-like turf (Wanders 1977; Hixon and Brostoff 1996). A clear difference in herbivore
functionality and behavior has been show through manipulation experiments and observational analysis. Classically, the effect of herbivores on the benthic community has been studied by examining one or two single species and their life history, emphasizing the importance of species-specific behaviors (Bruggemann et al. 1994b; Van Rooij et al. 1998; Bellwood et al. 2003; Semmens et al. 2005; Hoey and Bellwood 2009).

Scarids are a diverse group of herbivores that have specific niches of feeding on tropical marine plants and algae. Two different types of herbivores within Scaridae have evolved: scrapers and excavators. Scrapers scrape and crop the algae leaving a basal portion, which often forms a low growing mat while excavators take deep bites, completely removing the algae and large portions of the underlying substratum leaving a small area for recolonization (Bellwood and Choat 1990).

Different feeding behaviors can significantly change the topography of coral reefs. Scarus taeniopterus is scraping species that grazes on turf patches on many different substrates including dead coral, sediment, and invertebrates (Burkepile and Hay 2010). Most species of Sparisoma are excavators and the majority of species of Scarus are scrapers, however Sparisoma viride is a unique exception because it utilizes both excavating and scraping methods (Bruggemann et al. 1994b). This species is common on Caribbean reefs (Paddock et al. 2006; Sandin et al. 2008), ingesting large amounts of epilithic and crustose algae, including the substrate it grows on (Bruggemann et al. 1994a). S. aurofrenatum while employing scraper/excavator behavior, is an important browser on Caribbean reefs as large parts of their diet may consist of macroalgae species like Halimeda spp (McAfee and Morgan 1996;
Burkepile and Hay 2010). Bellwood and Choat (1990) demonstrated an ecological separation between the two different Scarid groups based on their morphology and functionality.

Disturbances, both natural and anthropogenic may alter competitive interactions between coral and algae (McCook et al. 2001). Disturbances on reefs are often categorized as bottom up and top down effects. Bottom-up effects occur when nutrients and primary producers are the determinants of reef functionality. For example pollution and runoff are elements that amplify the amount of nutrients in the water, providing algae with an abundant source of energy to grow quickly. Common erect macroalgae species including *Dictyota spp* can significantly increase with increased nutrient inputs (Burkepile and Hay 2009). Excluding herbivores, upright macroalgae increased in cover by 65% and in biomass by 150%, subsequently decreasing surviving coral growth by 30-80% (Burkepile and Hay 2009). Although roving herbivores play a key role in reef functionality, herbivory by fishes alone may not be enough to limit the amount of algae on a reef and prevent phase shifts (Paddack et al. 2006; Cheal et al. 2010; Kopp et al. 2010b).

Contrastingly, a disturbance in predation pressure, or top-down effect, can change lower taxonomic levels of fish abundance, distribution, and diversity. For example, overfishing often reduces species density and diversity in a system and consequently decreases the amount of algae removed from a reef. Overfishing not only affects the targeted species, it affects the food web and subsequent trophic levels (Jackson et al. 2001; Mumby et al. 2006). Long term overfishing has significantly reduced fish abundances over the last several decades (Jackson et al. 2001; Hawkins
Previous studies have been shown that low herbivore diversity is linked to phase shifts from coral to algal dominated states (Cheal et al. 2010).

Whether the disturbance is bottom-up or top-down, if it is persistent and forceful reefs can undergo a phase shift. A phase shift occurs when an ecosystem changes from one stable state to another, in this case a coral dominated reef to an algal dominated reef (Done 1992). How long a phase shift will last is determined by the degree of disturbance and the damage done to the community. The Caribbean is a primary example of phase shifts on multiple coral reefs, across different islands. Caribbean reefs have undergone drastic changes in community structure over the past thirty years. Throughout the mid-1980’s a series of massive hurricanes swept through the Caribbean islands, physically destroying many human, terrestrial and marine ecosystems. As a result, sensitive coral reefs were destroyed and left as rubble. The resilience of algae and the fragile structure of corals make reefs vulnerable to massive mechanical and biological perturbations. A second disruption heavily impacting the Caribbean was the die-off of *D. antillarum* due to a disease outbreak, killing almost the entire population (Aronson and Precht 2000). Urchins are a main grazer on the epilithic algae matrix (EAM) comprised of detritus, filamentous algae, and sediment (Foster 1987). Since the die-off, herbivorous fish became the most influential grazer where reefs heavily rely on the removal of erect macroalgae species turf.

The 1980’s also marked the beginning of major coastal development that increased urbanization and tourism on the Caribbean islands. Industrialization and urbanization spread rapidly as the demand for hotels and tourist attractions steadily
increased, bringing in a revenue on each island of over $1 million annually per kilometer of reef (Wielgus 2010; Burke et al. 2011). As both human population and tourism increased, anthropogenic effects became the most prominent detriment on marine environments due to the increase in fishing pressure, industrialization, water temperature and pollution (Vermeij 2012b). Increases in pollution and runoff lead to eutrophication, and commercial and local fishing were imminent threats to fish populations (Best 2001).

The combination of these impacts lead to a drastic change in the composition and functional state of coral reefs on many Caribbean islands. Coral reefs are still experiencing the aftermath of the decline in the 1980’s. Only a select number of reefs have regained any coral cover and the majority is far from a healthy state (Bellwood et al. 2004; Gardner et al. 2005). Although there is little evidence for correlation between the decline of coral reefs and fish populations during this time period, supporting studies in many regions show signs of lag-time between these coinciding events (Jackson et al. 2001; Cote et al. 2005; Graham et al. 2007; Paddack et al. 2009; Wilson et al. 2010)

Curaçao, formerly part of the Netherland Antilles, is a unique island to the Caribbean due to the geographical location and the coral reef communities. Many fringing reef communities surrounding the island are damaged by biological and anthropogenic effects of coastal industrialization and pollution; dredging and landfills contribute to the already present runoff and watershed pollution, increasing pathogens on the reef and infecting fish populations (Burke et al. 2011; Lauretta et al. 2011; Vermeij 2012a). An annual report of Curaçao published in 2012 stated that coral
cover has decreased over 42% in the last 25 years to an average of 23% coral cover (Sandin et al. 2008; Vermeij 2012a). This decrease is synonymous to the overall decline of Caribbean reefs and the increase of human activity.

Despite enduring multiple stressors, Curacao has been able to maintain a surprising amount of healthy coral reefs dispersed along the island. Various assessments reported relatively high coral cover on Curacao from the early 1980’s until the present, providing a possible explanation for the slower decline in coral cover than those seen on other Caribbean reefs (Newman et al. 2006; Sandin et al. 2008; Van Alfen 2010). Curacao reefs have maintained a constant intermediate fish biomass population relative to other islands over the course of three decades (Gardner et al. 2003). The highest fish biomass was found near underdeveloped areas of the island, the extreme west and east ends. The lowest biomass, including the lowest biomass of herbivores, was reported near the largest city on the island (Vermeij 2012b).

Classically, herbivory has been studied by manipulating environmental settings to quantify specific consumption rates and responses to environmental conditions. However, it is useful to examine the behavior of these organisms in a natural setting to understand the total affect of herbivory on coral reefs and how ecosystems change as a whole. The wide range of reef health in such close proximity makes this island a unique location to study contributing factors to reef health. The purpose of this study is to determine the driving factors that control herbivorous fish foraging behavior. To do this, I examined food sources, the foraging rates, and effect of community structure on behavior. We examined the five most abundant species of herbivores on Curacao which were from two families: Acanthuridae (2 species) and Scaridae (3 species).
Questions are addressed in a sequential format, first at a species level, then family level, and finally at a higher taxonomic level of guild behavior. Fish censes and benthic analyses were conducted to quantify fish and benthic communities at nine sites on the leeward coast of Curaçao. Further, selectivity preferences of benthic functional groups were assessed for each species and groups of species. Quantifying the driving factors of foraging behavior will lead to a better understanding of the impact of the herbivore fish guild on reefs.
Materials and Methods

Study Location

This study was conducted on the small country of Curaçao located in the southern Caribbean Sea, approximately 150km off the coast of Venezuela. The island is approximately 60km by 7.5 km and supports a population of about 143,000. The island is situated in a southeast to northwest manner where the north side of the island is windward and the leeward side faces the south. Curaçao became a national park, Stichting Nationale Parken (STINAPA), in 1962 to better manage terrestrial and marine habitats. The Carmabi Foundation, Caribbean Research and Management of Biodiveristy, was started in 1955 to conduct scientific research to address a variety of conservation issues and in 1996, Carmabi and STINAPA fused to monitor nine different natural areas. The Curaçao Underwater Marine Park was established in 1983 and covers 600 hectares (1482 acres) of reef and 436 hectares (1077.4 acres) of inner bays including Eastpoint, which supports some of the healthiest reefs in the Caribbean (Vermeij 2012a). However, Curaçao is at a standstill status of “paper-park” due to the loose and often ineffective enforcement of MPA laws.

The reefs chosen as study sites span the leeward side of the island varying in benthic configuration and fish populations. The leeward side provides more productive, yet calmer waters with a current running westward. Dive sites ranged from very degraded and a high percentage of algal cover, to less degraded with growing calcifiers to support a diverse community. Eastpoint was an unreachable area for our research due to accessibility restrictions implemented by the landowner.
Nine different sites were chosen in a loosely stratified manner based on historical data and observations of benthic health and fish populations. (Fig. 1). At the furthest western part of the island with low population density, Playa Kalki and Playa Grandi have the most rugose and complex benthic structures of the nine study locations (Pers. observ.). Playa Grandi however is a local fishing port where many small motorboats are launched and docked. These two sites also have a considerable amount of macroalgae, majority of which is *Dictyota spp.* (Pers. observ.). Continuing eastward, St. Michel is another fishing port where local fishermen target schooling piscivorous fish inside the inlet. This area is located in Boca Sami, a densely populated residential community. Community members often gather and hold celebrations here, resulting in debris and trash falling onto the beach and into the ocean (Pers. observ.). Located about half a mile east is Snakebay, a small natural beach where locals often frequent, as well as a common SCUBA dive site for tourists.

The study site Blue Bay lies on the outskirts of a man-made beach resort for tourists and residential. It is referred to as the “blue wall” due to the steep sloping nature of the reef. Near Piscaderabaai is the study site Carmabi, located off the shore of Carmabi Research Station and directly in front of the Hilton Hotel. Research experiments are often conducted on this reef due to the accessibility and existing record data. The Waterfactory site is in the shallows in front of a water treatment facility sea wall and a small fishing community. Water is pulled from a nearby entrance, treated and heated then released down current about 250 meters. Although the unusual location and conditions, this reef is known for the relatively high coral cover and typically strong current (Pers. observ.). Still further east is Jan Thiel,
another popular resort and tourist location. The reefs are located on the outside of man-made wave-break. Jan Thiel and the Waterfactory have impressively large and abundant gorgonians and sea fans. The furthest east study site is Caracasbaai, a common docking point for cargo ships. The protected inlet provides calm water and a long shoreline that attracts many locals and beach-goers.

Five sites, Playa Kalki, Snakebay, Blue Bay, Waterfactory, and Jan Thiel had *a priori* expectations based on the natural history to have greater amounts of reef builders (corals, CCA, etc.) and increased reef heath than the other four sites, Playa Grandi, St. Michel, Carmabi and Caracasbaai (M. Vermeij, Pers. comm.; Pers. observ.). All sites experienced periodic strong currents and a small degree of wave action. This is hypothesized to provide water movement and nutrient turnover for many organisms and enhance biodiversity and coral growth (Vermeij et al. 2010).

Study locations are all predetermined SCUBA dive sites that are frequented by tourists and researchers. All dives were shore entries and exits on the fringing reefs 100-200 meters offshore. Observational experiments ranged in depth from 4 meters to 14 meters and all observations were performed on SCUBA.

*Benthic community analysis*

Benthic analysis for each of the nine sites was conducted in order to determine the site makeup and food availability of the study animals. Three 25m transects were laid consecutively at three depths, 4-6m, 7.5-9m, and 12-13m, parallel to shore. Twenty points per transect (ten per side) were randomly chosen previous to the dive where photos were taken. Photos capturing the benthos were taken with a Canon G12 digital camera that was either connected to a “monopod” construction with a capture
frame of 0.6m by 0.9m (0.54m²), or was used to take pictures of a free-floating PVC pipe frame of 0.6m by 0.9m (0.54m²).

Onshore, photos were edited using the computer software program Photoshop CS4 to correct for any color imbalance and photo rotation. The edited photos were then analyzed using a software program Photogrid 1.0 to generate 50-100 randomly stratified points per photo; 40-60 photos were analyzed per depth at each site. Each point under a cross-hair was identified to an order, genus, or species level. Identifications were placed into six functional groups, “Coral”, “CCA”, “Turf”, “Macroalgae”, “Other Inverts” and “Nonbiological”. The main components of each functional group were: Scleractinin hard corals in the coral functional group; live and dying crustose coralline algae in the CCA group; Dictyota spp., Halimeda spp., Lobphora spp., and Amphiroa spp in the macroalgae functional group; turf was considered all to be low growing filamentous algae, EAM, biofilm and cyanobacteria; Other inverts (invertebrates) included sponges, gorgonians, octocorals, and anemones; and sand and limestone in the nonbiological group.

Benthic cover was calculated in percentages at each location for each functional group by dividing the proportion of points on each picture by the sum of all point identifications, which was replicated 40-60 times for every photo at each depth. Percentages were averaged over the three depths to determine a site-specific benthic percent coverage. The six functional groups mentioned earlier summed to a 100% benthic cover in the zone where focal observations occurred.

To determine if benthic compositions differed between sites, a resampling method analogous to an Analysis of Variance was used. Mean benthic percentages of
each substrate (all percentages for each photo summing to 100) of the nine study sites were plotted in multidimensional space. The Euclidian centroids of benthic groups were calculated by taking 10,000 resampled replicates. If the distances between the true mean of individual points and the centroids are in the most extreme percentiles, then the true mean of benthic percentages were significantly different than each other at an $\alpha=0.05$ significance level. This resampling methodology is similar to the statistical approach taken by Barott et al. (2012).

*Fish population assays*

To quantify fish populations of each study site, surveys were conducted of the fish community at each site at three different depths, 4-6m, 7.5-9m, and 12-13m. Three 25 meter transects were laid consecutively at each depth parallel to shore. The total length of the transects was the approximate distance covered by foraging fish individuals. Two divers swam parallel along a transect covering a four meter swath noting quantities and total length of all fish species smaller than 20cm. In the same manner in the opposite direction, divers covered an eight meter swath counting fish quantities and total length (nearest cm) for individuals greater than or equal to 20cm. Smaller fish were counted going eastward to oppose the west flowing current. Each diver was responsible for their own side of the transect, splitting the distance on either side. If a fish crossed from one side of the transect to the other, it was communicated between divers who would count it to avoid over-replication. Methods used are similar to those outlined and executed by Friedlander and DeMartini (2008).

In order to evaluate the community effect, we conducted a census of all fish at every site. We used the fish survey data to calculate the density (the number of fish per
square meter) and biomass (grams of fish per square meter) of each species at each specific study site. Density and biomass were also calculated for each functional group.

**Foraging observations**

To understand the herbivore foraging behavior on different reef communities on Curacao, focal observations were conducted April-June 2012 at each of the nine different sites. Two dives were conducted per site daily, one in the morning and one in the afternoon. Sites were repeated in a cycle to observe the species on different reefs for a balanced experimental design (Table 1). The five most common species to Curacao were chosen for this experiment, two surgeonfish (family *Acanthuridae*) *Acanthurus bahianus* and *Acanthurus coeruleus*, and three parrotfish (family *Scaridae*), *Sparisoma aurofrenatum*, *Scarus taeniopterus*, and *Sparisoma viride*. Foraging behaviors on a family level were also examined, consisting of the two browsing species in *Acanthuridae*: the scraper and the two excavators in *Scaridae*. Because of their population majority on the reef and for all intents and purposes for this study, we will be referring to the group of these five species as the “target herbivore guild”.

Using underwater slates and waterproof writing tools, fish observations were conducted in a general area of 2,250 square meters. Each individual fish was observed for approximately 3-4 minutes, noting total length (to the nearest cm) and life phase (initial phase or terminal phase). Only species that were larger than 10cm were observed in order to capture the individuals that had the most significant affect per capita on the benthos. For each individual, the number of bites taken on a particular
food and the accompanying substrate was tallied for most cases of turf and biofilm. Defecation counts were also taken for each of the fish observed. Bites were then placed into the same functional groups as the benthic groups, “Coral”, “CCA”, “Turf”, “Macroalgae”, “Other inverts” and “Nonbiological”.

A species-specific bite rate was calculated by dividing the total number of bites each individual took by the time observed in minutes, at each site with a standard error of ±1. For each species, bite rates were further broken down to substrate specific bite rates at each of the different sites. To determine the estimated bite rate at each site, we weighted the species-specific bite rate on every substrate by multiplying it by the site-specific density of that species. Estimated bite rates for the excavators/scrapers group, grazers group, and the target herbivore guild across all substrates were calculated in the same manner. Complimentary biomass analysis for each species at each site was also calculated. The comparative analysis between density and biomass informs us about the size profiles of species and the community dynamic.

**Selectivity**

Food selectivity was calculated using a selectivity index, Manly’s Alpha (Manly et al. 1972; Chesson 1983; Price 2010). It was calculated as

\[
\alpha_i = \frac{r_i / n_i}{\sum_{j=1}^{m} r_j / n_j}, i = 1, ..., m
\]

where \( r_i \) is the total bite rate (bites/min/m²) on substrate \( i \) and \( n_i \) is the benthic cover of substrate \( i \) of \( m=6 \) substrates types. The null index, \( \alpha = 0.1667 \), means no food preference indicating the fish foraged evenly and proportional to the availability of each of the food types. Indices above the alpha index indicate preferential feeding
while anything below the alpha line indicates selective avoidance. Indices were calculated for each species and groups of species (Acanthuridae, Scaridae, and target herbivore guild) at each of the nine study sites.

All statistical analyses were computed using the R programming language (R-Core-Team 2012) and JMP statistical software (JMP 2007).
Results

Benthic community analysis

There are significant differences in benthic composition between the nine study sites ($p<<0.001$) (Fig. 2). All pairs of sites were significantly different from each other ($p<0.001$) except for the comparison between Playa Kalki and Blue Bay and between Snakebay and Jan Thiel. Very similar amounts of coral cover and CCA were found between each pair of analogous sites (Fig. 2).

There is a significant negative correlation between turf cover and coral cover ($r(7)=-0.8980$, $p=0.001$), reinforcing a competitive relationship for space between turf and coral (Fig. 3). St. Michel had the lowest coral cover of 3.1% and the highest turf cover of 60%. Waterfactory site had the highest coral cover of 32% and the lowest turf cover of 34%. Each of the nine study locations had higher amounts of turf coverage than any other benthic functional group. The five sites predicted to have a higher abundance of calcifiers had coral cover greater than 18% and four sites had coral cover of 12% or lower. Only two sites, Waterfactory and Snakebay met or exceeded the coral cover average of 23% previously recorded in 2011 (Sandin et al. 2008).

Macroalgae and coral cover are negatively correlated ($r(7)=-0.9285$, $p=0.0399$; (Fig. 4). Playa Grandi had the highest amount of macroalgae dominated by *Dictyota spp*. Jan Thiel has the highest percentage of nonbiological cover of 22%, mainly comprised of sand, reflecting the patchy nature of the reef. Waterfactory had overwhelmingly the highest percentage of other invertebrates with the next highest at Jan Thiel due to the abundance of gorgonians.
Fish population assays

Across the nine study sites, herbivores comprised 16% of the total fish abundance and 38% of the total biomass (Fig. 5, 6). Jan Thiel had the lowest herbivore density (0.3956 fish/m$^2$) (Fig. 5) while Caracasbaai had the highest average density of all herbivores (0.7839 fish/m$^2$). Yet, Caracasbaai had the lowest herbivore biomass (18.379 g/m$^2$) and Playa Kalki had the highest herbivore biomass (41.7808 g/m$^2$) (Fig. 6). Small fish were overwhelmingly abundant on all reefs, 2.3680 fish/m$^2$, where planktivores made up an average of 60% of the total fish assemblage but only 21% of the total biomass across all reefs. Examining the predatory species, only 1% of piscivores and less than 1% of carnivores make up the entire fish population density across the nine study sites. Regarding fish biomass, carnivores stayed low comprising only 1% on average across the nine sites, however piscivores ranged in biomass from 10% at Caracasbaai to 46% at Blue Bay. All nine sites had less than 0.009 fish/m$^2$ for the carnivores resulting in less than 0.7 g/m$^2$ of carnivores for each of the sites.

The five focal species comprised 77% of the entire herbivore guild population across the nine study location sites. These two species of Acanthurids comprised 96% of the surgeonfish population on the nine sites and the three Scarids comprise 68% of all the parrotfish. *A. bahianus* and *S. aurofrenatum* that both had the highest density at Caracasbaai (Fig. 7a, c). *A. coeruleus* had the highest density at Carmabi, while the two scrapers *S. taeniopterus* and *S. viride* had their highest densities at the western sites, Playa Kalki and Playa Grandi respectively (Fig. 7b, d, e). *S. taeniopterus* had the highest average density (0.0478 fish/m$^2$) and *S. aurofrenatum* had the lowest density.
on average (0.0224 fish/m$^2$) across all sites. There was no single species that was consistently the least abundant or the most abundant at all sites.

As a group, grazers have a higher density at the four most east sites, most notably Carmabi (Fig. 7f). The excavator/scrapper group complimented this trend by having a higher density at the western sites and decreasing as the sites move east, with the exception of Jan Thiel (Fig. 7g). This pattern is also seen on a species level where *A. bahianus* increased and *S. taeniopterus* decreased in density as the sites move from west to east sites. The five target species as an herbivore guild are evenly distributed across the southern side of the island with the highest overall density at Playa Grandi and the lowest density at Blue Bay (Fig. 7h).

The biomass within in species was variable and there was no correlation between species’ biomass and species’ density. *S. aurofrenatum* also had the lowest biomass at the majority of sites and *S. viride* had the highest biomass at the majority of the sites (Fig. 8). Smaller fish were more abundant and larger fish were rarely observed; excavators/scrapers were at least twice as abundant and larger than the browser group. For the target herbivore guild, fish density ranged from 6.1 fish/m$^2$ to 2.9 fish/m$^2$ while fish biomass ranged from 118 g/m$^2$ to 56.4 g/m$^2$ (Fig. 7h, Fig. 8). Yet, there was the least amount of variation on the target guild level in density and biomass on the guild level displaying no noticeable trend.

*Foraging observations*

Bite rate and size for each species are not significantly negatively correlated as and the interaction terms between the size and site for each species’ foraging rate are non significant (Table 2).
Each of the five target species foraged in slightly different manners based on the benthic and fish community as each site. *A. bahianus* had a significantly higher bite rate at Playa Grandi and Jan Thiel than the rest of the seven sites, ($F_{(8,498)}=8.9774$, $p<0.0001$; Fig. 9a). Density and bite rate are not significantly correlated, however they demonstrate a mildly negative relationship ($y = -195.78x + 44.344$; $r(7)=-0.3827$, $p=0.3094$; Fig. 9b). *A. bahianus* had an increasing trend in weighted bite rate as the sites moved from west to east (Fig. 9c). This trend paralleled a similar correlation in the density. *A. bahianus* had the highest estimated bite rate at Caracasbaai and the lowest at Blue Bay. *A. bahianus* had a higher overall and estimated bite rate on macroalgal substrates than any other food type at Playa Grandi.

*A. coeruleus* was found to bite at a significantly faster rate at Jan Thiel than at Carmabi or Waterfactory, ($F_{(8,474)}=6.2308$, $p<0.0001$; Fig. 10a). The species also foraged at Waterfactory at a significantly lower rate than the rest of the sites. Although the bite rate and density are not correlated, there is a negative relationship between the two ($y = -147.94x + 28.819$; $r(7)=-0.5293$, $p=0.1428$; Fig. 10b). The estimated bite rate is relatively equal except for the substantially higher bite rate at Carmabi, which notably, has the highest density of *A. coeruleus* (Fig. 10c).

*S. aurofrenatum* had a significantly higher average bite rate at Carmabi than Playa Grandi and St. Michel ($F_{(8,473)}=2.8979$, $p=0.0037$) (Fig. 11a). For this species however, there is a noticeably high bite rate on macroalgae at every site with the highest at Playa Grandi. There seems to be no trending change in density for *S. aurofrenatum*, but the highest estimated bite rates are at the sites furthest west and east, Playa Kalki and Caracasbaai (Fig. 11c). Although the bite rate and density are
not significantly correlated \((y = 15.09x + 8.9691; r(7)=0.1106, p=0.7769; \text{Fig. 11b})\), the density seems to exacerbate the bite rate, widening the gap between the two sites with highest estimated bite rates and the other seven sites.

*S. taeniopterus* had a significantly higher bite rate at Jan Thiel than at Playa Grandi and Caracasbaai, whereas Caracasbaai had a significantly lower bite rate than Playa Kalki, \((F_{(8,509)}=3.2554, p=0.0013; \text{Fig. 12a})\). Bite rate and density are not significantly correlated \((y = 4.8165x + 20.256; r(7)=-0.0588, p=0.8806; \text{Fig. 12b})\).

With the exception of Jan Thiel there is a clear trend moving west to east of estimated bite rates, similar to density (Fig. 12c).

We found that *S. viride* had a significantly higher bite rate at Playa Kalki than at St. Michel and Snakebay, \((F_{(8,471)}=2.5796, p=0.0092; \text{Fig. 13a})\) and bite rate and density are not significantly correlated \((y = 9.993x + 10.364; r(7)=-0.1236, p=0.7515; \text{Fig. 13b})\). Just like the density, St. Michel and Caracasbaai have the lowest estimated bite rate and Playa Kalki, Playa Grandi, and Jan Thiel have the highest estimated bite rate (Fig. 13c). It is worth noting that St. Michel and Caracasbaai have the highest percentage of turf and cyanobacteria cover, while Playa Kalki, Playa Grandi and Jan Thiel have the highest level of rugosity (Pers. observ.).

As a group where *A. bahianus* and *A. coerules* contribute proportionately, the grazers displayed the highest estimated bite rate starting at Carmabi and moving east (Fig. 14a). The highest bite rate weighted by density was at Carmabi and the lowest at Blue Bay, two sites that are geographically very close to each other but very different in benthic composition. Since there is high variation and no trend in the density, the estimated bite rate for the excavator/scrapers group, *S. aurofrenatum*, *S. taeniopterus*,
and *S. viride*, closely resembles the change in density. The most westerly sites have the highest estimated bite rate for the excavator/scraper group (Fig. 14b).

Variation in estimated bite rates and density considerably decreases moving from the species level, to the family level, and finally to the target herbivore guild level (Fig. 14c). Accounting for the density and the bite rate of each species, the estimated bite rates become more homogenous along the island, eliminating any previous geographical trend. The highest estimated bite rates for the herbivore group are at Playa Kalki and Playa Grandi (Fig. 14c).

**Selectivity**

Based on the benthic configuration and the estimated bite rate, a species-specific selectivity index was calculated for each benthic functional group at every site (Table 3).

For *A. bahianus* there was variation in the foraging selectivity on the food types. However turf was exceedingly preferred at every site except at Playa Grandi, where macroalgae was preferred over 3.5 times to turf (Fig. 15a). This preference was also reflected in the higher average and estimated bite rates on macroalgae than on turf at Playa Grandi. Similarly, the selectivity indices for *A. coeruleus* shows that turf was preferred at every site and macroalgae as the second-most preferred food type at five sites (Fig. 15b). At Playa Grandi, macroalgae were selected almost as many times as turf. Playa Grandi has a high cover of *Dictyota spp.*, especially in the shallows (<6m), and was the preferential foraging zone for the species at that site.

*S. aurofrenatum* had the highest preference for macroalgae out of all the species observed; macroalgae was preferred at eight out of nine sites and was
preferred over turf at three different sites (Fig. 15c). *S. aurofrenatum* is considered to be a macroalgavore and the favorite food type is *Halimeda spp.* Other than turf and macroalgae, all other functional groups were always avoided. For *S. taeniopterus*, turf was preferred at every site even though there was a wider preference of food types than any other species (Fig. 15d). At two different sites, St. Michel and Carmabi, other inverts are selected for over turf. These sites have two of the lowest coral cover percentages (>5%) and include larger sponges for fish to feed on. Exhibiting a broad food preference has been found as a foraging characteristic of *S. taeniopterus* (Burkepile and Hay 2010). *S. viride* had the most homogenous selectivity across sites out of the three Scarid species and overwhelmingly preferred turf across all sites (Fig. 15e). This species only selected an alternative food two other times total, “other inverts” at St. Michel and “macroalgae” at Snakebay.

There was less variation for all metrics at a family taxonomic level. Turf is highly preferred for the Acanthurid family, however just like on a finer taxonomic scale, macroalgae was preferred highly at Playa Grandi (Fig. 15f). Scarids distinctly selected turf over any other food type across all sites, however as an excavator/scaper group they selected for a greater variety of food types compared to any of the single species (Fig. 15g). The variety of preferences reflects each species-specific behavior and combines to give a more evenly distributed foraging pattern across multiple sites. At the highest taxonomic level, the target herbivore guild had the least amount of variation in selectivity, preferring turf at every study site and macroalgae at many sites (Fig. 15h). The variation of estimated bite rate and selectivity becomes more homogenous when multiplied across species.
Discussion

The three driving factors of herbivorous fish foraging were (1) species’ abundance and diversity, (2) food availability, and (3) bites rates. By measuring the driving factors, it is possible to estimate the affect of the herbivore fish assemblage on a reef at a given time, increasing our understanding of the future trajectory of coral reef communities. We found that turf is preferred across all sites for the target herbivore guild, regardless of species-specific preferences. Herbivore species and groups of species have context specific foraging behavior based on the benthic and fish community but combine to form a homogenous foraging effort across all sites.

The abundances of fish species and diversity of species within in the community is critical to the foraging behavior. Each of the focal species had variable densities across the study sites. The browser group had low to average densities at the two most west sites, Playa Kalki and Playa Grandi and the highest at the four most east sites. The decrease in human density may allow for Acanthurids to flourish in less structurally dense reefs. This is in contrast to the excavator/scraper group that had a decreasing trend in density moving from west to east. This opposing trend for the two families may be an indication of the human population gradient and the strength of anthropogenic effects. The urbanization of many reefs towards the central part of the island could be decreasing the available habitat for Scarids. This is in comparison to the less human influenced sites, Playa Kalki and Playa Grandi, which have very rugose reefs and might be able to support larger individuals and a more abundant Scarid population.
Foraging intensity directly increases with increasing density. Density exerted a strongly positive influence on the estimated bite rate for the five study species. An increase in foraging intensity with an increase in density has also been found at other locations in the Caribbean (Lewis and Wainwright 1985) and on the Great Barrier Reef (Hoey and Bellwood 2010). Due to the lack of correlation between density and bite rate for the excavator/scrapper group, the estimated bite rate is heavily influenced by the density because it is the most variable factor. Although there is a negative relationship between density and bite rate for the browser group, intra-species competition is not a factor in controlling the fish bite rate.

This study highlights the importance of species richness and diversity to reef functionality. Previous studies show that combinations of parrotfish and surgeonfish are able to remove a significant portion of algae from a reef (Burkepile and Hay 2008; Burkepile and Hay 2010). Although one species can have a significant impact on a particular benthic group (Bellwood et al. 2003; Hoey and Bellwood 2009), the space once occupied by the alga is now available for another rapidly growing alga to potentially take its place. Reefs with diverse communities of herbivorous fish have inherently diverse diets and feeding behaviors. This diversity is essential for controlling the variety of algae present in reef ecosystems. If a reef has a variety herbivorous species and families and a high abundance of each, there will be significant algal removal resulting in a greater chance of increased coral health. When summed across all species to obtain the total amount of bites on the benthos, the combined families display a balanced design in their foraging behavior (Fig. 15h).
Overall the highest bite rate on macroalgae occurs at the site with the highest benthic coverage of macroalgae, Playa Grandi. This is most likely due to certain herbivores preferring the macroalgae that is very abundant, including *Dictyota spp.*, *Lobophora spp.*, and *Halimeda spp.* A study conducted by Francini-Filho et al. (2010) in Belize showed that fish consumed the dominant resource type when it was in large amounts. Despite the relatively high coral cover of 20-33% and variable fish densities at sites such as Waterfactory, Snakebay and Jan Thiel, turf dominates the benthic cover at every study location with an upward abundance of 60%. The highest estimated bite rates overall were on turf and herbivores overwhelmingly preferred turf and had a lesser preference for macroalgae. We can conclude that *S. viride* prefers turf, *S. taeniopterus* prefers turf on variety of substrates, *S. aurofrenatum* prefers *Halimeda spp.* along with other macroalgae species, and *Acanthuridae* species often prefer filamentous turf and epiphytes on macroalgae species. Similar findings support our results (Semmens et al. 2005; Burkepile and Hay 2008; Burkepile and Hay 2010; Francini-Filho et al. 2010). The grazing intensity is determined by an abundance of herbivores feeding on specific available resources.

Similar to other islands in the Caribbean and around the world, Curacao has an excessive amount of algae and benthic food types. The abundance of algae is too great to keep a balanced ecosystem and is creating phase shifts to algal dominance. A source of the algae increase is a surplus of nutrients entering the water from industrialization, watershed pollution and runoff. A study conducted in 2010 on Curacao showed that when nutrients were experimentally increased on a reef, algae were able to out-compete all other organisms for space, including corals, regardless of
the presence of herbivores (Vermeij et al. 2010). Similarly, in the Florida Keys, common macroalgae species have significantly increased abundance as nutrients on the reef increased despite the average abundance of herbivores (Burkepile and Hay 2009). Eutrophication therefore may be heavily influencing selectivity of herbivores.

An increase in macroalgae with a decrease in herbivore foraging creates a positive feedback loop that does not benefit a calcifying reef. Macroalgae species that benefit from eutrophication are not as preferred as turf, often leading to an algal overgrowth and potentially a phase shift (Cheal et al. 2010). If the fleshy erect macroalgae species synthesize the nutrient input for quick growth, blanketing any preferred food type, the herbivores may forage less and decrease grazing rates (McClanahan et al. 2001). Relatively high availability of the preferred food type is necessary in order for grazing intensities to increase (McClanahan et al. 2001; Williams and Polunin 2001). Williams and Polunin (2001) found a strong negative relationship between herbivore biomass and macroalgae abundance, but a positive relationship with turf cover. Although we did not find a link between herbivore biomass and any benthic functional group, the small-scale nature of the study and extreme turf cover at every site may mask any relationship that is present on Curaçao (Sandin et al. 2008). The preferred food type must be available to increase foraging rates. However, if the abundance of algae becomes too great, the herbivores may not be able to control the overgrowth.

The total amount of bites taken by all fishes can be described as the “rain of bites”, which is based on how many individuals are present and the amount of food available (Hamilton in review). This quantifies removal of benthic substrate and top
down pressures on the benthos. Studies on individual species-specific behaviors, abundances, and foraging patterns should not be discounted but applied to an overarching assessment of total herbivore impact. Targeting five different species of fish broadened the experimental ability to examine fish foraging behaviors at three different trophic levels: on a species, family and guild level. By doing so, I can conclude that the “rain of bites” is the most effective way to understand herbivore impact on coral reef functionality and dynamic.

Although scrapers, excavators and grazers belong to the same herbivore guild, their combined herbivory targets all food types to suppress an overgrowth of algae. At the highest taxonomic level, herbivores had the least amount of variation in selectivity, preferring turf at every study site and macroalgae at a minority of sites. The estimated bite rate and selectivity become more homogenous when multiplied across species. Therefore, it is necessary to examine foraging selectivity and intensity on a guild level rather than a species-specific level. This has been supported by another study conducted in Palmyra, an uninhabited island in the Northern Line Islands. The herbivore guild had an overall preference for turf despite individual species preferences for other substrates (Hamilton in review). Observing foraging behavior and surveying benthic and fish populations in two completely different ecosystems, a degraded, anthropogenic influenced Caribbean island, and a remote, predator-dominated atoll, demonstrates that the factors driving foraging are universal (Hamilton in review).

Species within the herbivore guild compliment each other in bite rates and density so that the behavioral foraging is evenly partitioned across a region. Many
reefs on Curaçao and in the Caribbean desperately need foraging redundancy to slow down the excessive overgrowth of turf and macroalgae. A concern of many ecologists is the redundancy of food preferences and bite rates because of disproportionate algal removal and behavioral conflict between species that could potentially arise. (Bellwood et al. 2003; Hoey and Bellwood 2009; Burkepile and Hay 2011), Yet those redundancies are acceptable on a guild level because of the overwhelming abundance of algae on a reef. Competition effects were not specifically accounted for in this study, however non-significant correlation between density and bite rate imply that more individuals on a reef positively influence foraging rates. Similar foraging activities at sites do not act as a limiting factor but instead are a cooperative interaction between individuals.

On an island scale, herbivorous fish display an organizational pattern similar to the ideal free distribution model (IFD) proposed by Fretwell and Lucas (1969). The IFD model proposes that individuals and species organize and distribute themselves to efficiently utilize space and resources at productive sites. Complimentary results show the herbivore guild distributes themselves more frequently at sites with higher productivity (Williams et al. 2001; Semmens et al. 2005). The homogeneity in selectivity and foraging efforts on Curaçao suggest a self organization system to create an average distribution of species population density and foraging activity at every site, diminishing inter and intra species competition.

An understanding of fish foraging behavior should be translated into management strategies of the driving factors of herbivore foraging. Properly regulating fishing practices of multiple trophic levels on coral reefs is a way to sustain
fish abundances and diversity (Hawkins and Roberts 2004). Increased fish abundance and biomass have been linked to marine protected areas where fishing has been reduced. Multiple studies have shown herbivores are positively correlated to apex predators inside or near MPA’s, despite the predation risk, with a reported doubling of herbivore biomass (Mumby et al. 2006; Newman et al. 2006). Marine protected areas in the Caribbean have also significantly reduced the amount of macroalgae due to the doubled amount of grazing (Mumby et al. 2006; Kopp et al. 2010a). The current declining state of Curaçao’s coral reefs and fish assemblage is partially due to the standstill of Curaçao’s “paper park”. Although fishing on Curaçao is small scale and usually conducted by local fisherman using gill nets and spears, enforcement of fishing regulations is lacking and herbivores are still susceptible to reef traps and fishing pressures (Johnson 2010). Sustaining herbivore densities will increase the grazing pressure, removing more algae from a reef. A vital solution is controlling the coastal and anthropological activities directly and indirectly affecting the fringing reef populations.

The rapid urbanization of Curaçao is a cause for concern, where runoff, sedimentation, and watershed pollution are increasing the nutrients in the water (Vermeij 2012a,b). Managing the anthropogenic outflow and runoff into the ocean can help to reduce the amounts of outsourced nutrients available for algal use. Controlling both top down and bottom up factors affecting a reef in a management plan could increase grazing intensity. An example of successful management is Eastpoint, a privately owned area of Curaçao. Fishing pressures, coastal development and pollution are almost nonexistent. Eastpoint subsequently has 70% coral cover in
certain areas, over 50 g/m$^2$ of predatory fish and contains over 70% of all Caribbean species (Newman et al. 2006; Miloslavich et al. 2010). If Eastpoint remains isolated from anthropogenic effects, it may serve as a target goal for recovering reefs.

Although this study is an extensive observational survey of herbivore foraging behavior in different contexts, there were some limitations. All assessments were taken from an herbivore perspective. Growth and production rates of algae were not accounted for. We were unable to analyze the algae quality at each of the different sites, which may be a controlling factor in the dietary preferences of herbivores. Not addressing the growth rates of algae became a limiting factor, when assessing the affect of herbivory. We quantified the rate at which herbivores forage but do not adequately understand the growth rate of algae in relation to herbivore removal. If the algal growth rate exceeds the removal rate of fish, then algae are more likely to overgrow calcifying substrates. Several studies have examined production rates combined with consumption rates (g/m$^2$/d) of fish, which account for the amount of algae removed (Bruggemann et al. 1994c; Van Rooij et al. 1998; Paddack et al. 2006; Kopp et al. 2010b). Sites on Curaçao vary significantly in benthic composition, and it would be worthwhile to analyze the production rates of functional groups combined with the rain of bites of herbivores. Tracking the changes in growth and bite rate would shed light on the trajectory of future coral reefs.

This study is unique in its extensive focal observations on a subset of the herbivore population in different habitat contexts. When we examined three trophic levels, a clear pattern emerged: higher foraging guilds showed increasing homogeneity in estimated bite rates and selectivity. Analyzing bite rates and densities separately
provides an insightful perspective on the mechanisms controlling herbivorous fish foraging behavior. Future studies to include production rates of algae will further help to understand the coral-algae competition and determine whether herbivores are an effective mediator. Although herbivores may not immediately bring a degraded reef to recovery (Kopp et al. 2010b), they may prevent the current state of the reef from degrading further (Paddack et al. 2006). To understand and predict the future health and survivorship of a calcifying coral reef, it is necessary to study herbivory from a guild level.

In order to study influencing factors on herbivorous fish, density and the behavioral bite rate must be measured. Through my observations of natural habitats, I found that herbivory is not static at every site, and species adapt their behaviors to the habitat and other foraging fish. High density within a species and species richness will increase and diversify the foraging on all reefs, regardless of the benthic and taxonomic community assemblage. Understanding that each species has unique foraging and social behaviors will create better management strategies for individual species and for the overall herbivore guild.
Figures

Figure 1. Location of Curaçao. Triangles indicate study sites.
Figure 2. Benthic coverage for the functional groups Nonbiological, Other Invert, Macro Algae, Turf, CCA, and coral are shown in percentages at each of the study sites. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders.

Figure 3. Correlation between the percentage of turf algae and percentage of coral cover across the nine sites.
Figure 4. Correlation between the percentage of turf algae and percentage of coral cover across the nine sites.

Figure 5. Average density (no. individuals/m²) for the five functional groups surveyed at each study site. Fish functional groups are: Planktivores, Piscivores, Omnivores, Herbivores, and Carnivores. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders.
Figure 6. Average biomass (grams/m$^2$) for the five functional groups surveyed at each study site. Fish functional groups are: Planktivores, Piscivores, Omnivores, Herbivores, and Carnivores. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders.

Figure 7a. Average density (no. individuals/m$^2$) for *A. bahianus* at each site. **Indicate sites expected to have a higher amount of reef builders. Sites are listed from west to east. Standard error bars ±1.
Figure 7b. Figure 1b. Average density (no. individuals/m²) for *A. coeruleus* at each site. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders. Standard error bars ±1.

Figure 7c. Figure 1b. Average density (no. individuals/m²) for *S. aurofrenatum* at each site. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders. Standard error bars ±1.
Figure 7d. Figure 1b. Average density (no. individuals/m$^2$) for *S. taeniopterus* at each site. **Indicate sites expected to have a higher amount of reef builders. Standard error bars ±1.

Figure 7e. Figure 1b. Average density (no. individuals/m$^2$) for *S. viride* at each site. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders. Standard error bars ±1.
Figure 7f. Average density (no. individuals/m²) for the grazers *A. bahianus* and *A. coerulescus* at each site. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders. Standard error bars ±1 for the combined species.

Figure 7g. Average density (no. individuals/m²) for the excavators/scrapers *S. aurofrenatum*, *S. taeniopterus* and *S. viride* at each site. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders. Standard error bars ±1 for the combined species.
Figure 7h. Average density (no. individuals/m$^2$) for the target herbivore guild, *A. bahianus*, *A. coerules*, *S. aurofrenatum*, *S. taeniopterus* and *S. viride* combined, at each site. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders. Standard error bars ±1 for the combined species.

Figure 8. Average biomass (grams/m$^2$) for the five target species observed at each study site. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders. Standard error bars ±1 for the combined species.
Figure 9a. The average bite rate (bites/min/ind.) on each substrate type for *A. bahianus* at each site. $F(8, 9774) = 8.9774$, $p < 0.0001$. Letters above bars indicated significant differences by Tukey-HSD post-hoc test. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders. Standard error bars ±1.

Figure 9b. Correlation graph between the densities (no. individuals/m²) and the bite rate (bites/min/ind) for *A. bahianus*. 
Figure 9c. Estimated bite rates (bites/min/m²) weighted by the species density on each substrate type for *A. bahianus* at each site. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders.

Figure 10a. The average bite rate (bites/min/ind.) on each substrate type for *A. coeruleus* at each site. F=(6.2308), p<0.0001. Letters above bars indicated significant differences by Tukey-HSD post-hoc test. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders. Standard error bars ±1.
Figure 10b. Correlation graph between the densities (no. individuals/m²) and the bite rate (bites/min/ind) for *A. coeruleus*.

Figure 10c. Estimated bite rates (bites/min/m²) weighted by the species density on each substrate type for *A. coeruleus* at each site. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders.
Figure 11a. The average bite rate (bites/min/ind.) on each substrate type for *S. aurofrenatum* at each site. $F=(3.2554)$, $p=0.0013$. Letters above bars indicated significant differences by Tukey-HSD post-hoc test. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders. Standard error bars ±1.

Figure 11b. Correlation graph between the densities (no. individuals/m²) and the bite rate (bites/min/ind) for *S. aurofrenatum*.
Figure 11c  Estimated bite rates (bites/min/m$^2$) weighted by the species density on each substrate type for *S. aurofrenatum* at each site. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders.

Figure 12a Figure 1a. The average bite rate (bites/min/ind.) on each substrate type for *S. taeniopterus* at each site. $F=(62.5796)$, $p<0.0092$. Letters above bars indicated significant differences by Tukey-HSD post-hoc test. **Indicate sites expected to have a higher amount of reef builders. Standard error bars ±1.
Figure 12b. Correlation graph between the densities (no. individuals/m²) and the bite rate (bites/min/ind) for *S. taeniopterus*.

Figure 12c. Estimated bite rates (bites/min/m²) weighted by the species density on each substrate type for *S. taeniopterus* at each site. **Indicate sites expected to have a higher amount of reef builders.
Figure 13a. The average bite rate (bites/min/ind.) on each substrate type for *S. viride* at each site. $F=(62.8979)$, $p<0.0037$. Letters above bars indicated significant differences by Tukey-HSD post-hoc test. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders. Standard error bars ±1.

Figure 13b. Correlation graph between the densities (no. individuals/m$^2$) and the bite rate (bites/min/ind) for *S. viride*. 
Figure 13c. Estimated bite rates (bites/min/m$^2$) weighted by the species density on each substrate type for S. viride at each site. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders.

Figure 14a. Estimated bite rates (bites/min/m$^2$) weighted by the species density on each substrate type for the grazer group, A. bahianus and A. coerules combined, at each site. **Indicate sites expected to have a higher amount of reef builders.
Figure 14b. Estimated bite rates (bites/min/m$^2$) weighted by the species density on each substrate type for the scraper/excavator group, *S. aurofrenatatum*, *S. taeniopeterus* and *S. S. viride* combined, at each site. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders.

Figure 14c. Estimated bite rates (bites/min/m$^2$) weighted by the species density on each substrate type for the target foraging guild, *A. bahianus*, *A. coeruleus*, *S. aurofrenatatum*, *S. taeniopeterus* and *S. S. viride*, at each site. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders.
Figure 15a. Selectivity index (Manly’s alpha) for *A. bahianus* for each of the benthic substrate types at each study site. Solid line at 0.1667 is the null foraging index assuming equal selectivity based on substrate availability. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders.

Figure 15b. Selectivity index (Manly’s alpha) for *A. coeruleus* for each of the benthic substrate types at each study site. Solid line at 0.1667 is the null foraging index assuming equal selectivity based on substrate availability. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders.
Figure 15c. Selectivity index (Manly’s alpha) for *S. aurofrenatum* for each of the benthic substrate types at each study site. Solid line at 0.1667 is the null foraging index assuming equal selectivity based on substrate availability. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders.

Figure 15d. Selectivity index (Manly’s alpha) for *S. taeniopterus* for each of the benthic substrate types at each study site. Solid line at 0.1667 is the null foraging index assuming equal selectivity based on substrate availability. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders.
Figure 15e. Selectivity index (Manly’s alpha) for *S. viride* for each of the benthic substrate types at each study site. Solid line at 0.1667 is the null foraging index assuming equal selectivity based on substrate availability. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders.

Figure 15f. Selectivity index (Manly’s alpha) for the browser group of *A. bahianus* and *A. coerules* for each of the benthic substrate types at each study site. Solid line at 0.1667 is the null foraging index assuming equal selectivity based on substrate availability. Sites are listed from west to east. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders.
Figure 15g. Selectivity index (Manly’s alpha) for the excavator/scraper group of *S. aurofrenatum, S. taeniopterus* and *S. viride* for each of the benthic substrate types at each study site. Solid line at 0.1667 is the null foraging index assuming equal selectivity based on substrate availability. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders.

Figure 15h. Selectivity index (Manly’s alpha) for the herbivore guild of the five species *A. bahianus, A. coeruleus, S. aurofrenatum, S. taeniopterus* and *S. viride* for each of the benthic substrate types at each study site. Solid line at 0.1667 is the null foraging index assuming equal selectivity based on substrate availability. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders.
Tables

Table 1. Number of fish per species that were observed at site. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders.

<table>
<thead>
<tr>
<th></th>
<th>A. bahianus</th>
<th>A. coeruleus</th>
<th>S. aurofrenatum</th>
<th>S. taeniopterus</th>
<th>S. viride</th>
<th>Total</th>
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<tbody>
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Table 2. ANCOVA of the differences in Site, Size and interaction term Site x Size. Bold numbers are significantly different based on the 0.05 significance level.

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<th>Fish species</th>
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<th>Site</th>
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Table 3. Selectivity indices for each species, groups of species, and herbivore guild on every substrate across the sites. Bold indices signal a preference for that food type. Sites are listed from west to east. **Indicate sites expected to have a higher amount of reef builders.

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<th>Site</th>
<th>Family</th>
<th>Fish species</th>
<th>Fish type</th>
<th>Substrate type</th>
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<th>Other inverts</th>
<th>Non-biological</th>
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