

**VARIATION IN HABITAT PREFERENCES  
AMONG CORAL REEF FISHES  
IS EXPLAINED BY BENTHIC COMPOSITION**

by

Jennifer Joseph

A thesis submitted to the Faculty of the University of Delaware in partial fulfillment of the requirements for the degree of Master of Science in Marine Studies

Fall 2019

© 2019 Jennifer Joseph  
All Rights Reserved

**VARIATION IN HABITAT PREFERENCES  
AMONG CORAL REEF FISHES  
IS EXPLAINED BY BENTHIC COMPOSITION**

by

Jennifer Joseph

Approved: \_\_\_\_\_  
Danielle L Dixon, Ph.D.  
Professor in charge of thesis on behalf of the Advisory Committee

Approved: \_\_\_\_\_  
Mark Moline, Ph.D.  
Chair of the School of Marine Science and Policy

Approved: \_\_\_\_\_  
Estella Atekwana, Ph.D.  
Dean of the College of Earth Ocean and the Environment

Approved: \_\_\_\_\_  
Douglas J. Doren, Ph.D.  
Interim Vice Provost for Graduate and Professional Education and  
Dean of the Graduate College

## ACKNOWLEDGMENTS

I would like to thank Dr. Danielle Dixson for this incredible opportunity and all your support along the way. Thank you for trusting my abilities especially with all the obstacles we've faced during this project and helping me become a stronger scientist. Also, thank you to my committee, Dr. Mark Warner and Dr. Aaron Carlisle, for the support and guidance. I want to thank all the administrators at UD, especially Luci and Janis, for being so supportive and helpful especially with so much fieldwork travel.

Thank you to everyone in the Dixson, past and present, for the amazing support and collaboration. Rohan, I am very thankful for your guidance and the amazing fieldwork memories from Carrie Bow. A special thank you to everyone who has helped me in the field and that I've gotten to spend time with on Carrie Bow especially Martha for the incredible food. Thank you to Andy and Olivia for help watching hours of fish videos. I am incredibly thankful for the amazing close-knit group of weirdos, Molly, Lane, Paul, and Emily, that made my time in grad school truly amazing.

Thank you to my parents and family for your constant support and love while being all the way on the other coast. And finally, thank you to Andrew for moving across the country with me and enduring all the time apart while I was doing fieldwork. Your support means the world to me and I appreciate you for being my shamwow.

## TABLE OF CONTENTS

LIST OF TABLES .....	vi
LIST OF FIGURES .....	vii
ABSTRACT .....	x

### Chapter

1	REEF COMMUNITY COMPOSITION AND CURRENT PROFILES SURROUNDING CARRIE BOW CAY, BELIZE.....	1
1.1	Introduction .....	1
1.2	Methods.....	5
1.2.1	Study Sites .....	5
1.2.2	Current Meters .....	6
1.2.3	Reef Transects.....	7
1.3	Results .....	10
1.3.1	Current Meters .....	10
1.3.2	Reef Transects.....	12
1.4	Discussion .....	27
2	HABITAT PREFERENCE OF JUVENILE CORAL REEF FISH .....	36
2.1	Introduction .....	36
2.2	Methods.....	40
2.2.1	Study Site and Species.....	40
2.2.2	Rubble Transects.....	42
2.2.3	Habitat Choice Experiments .....	44
2.2.3.1	Experiment 1: Hard Corals.....	47
2.2.3.2	Experiment 2: Soft Corals .....	48
2.2.3.3	Experiment 2: Macroalgae .....	48
2.2.3.4	Experiment 4: Sponges .....	49
2.2.4	Size Class Observations.....	49

2.3	Results .....	51
2.3.1	Rubble Transects .....	51
2.3.2	Habitat Choice Experiments .....	53
2.3.2.1	Experiment 1: Hard Corals .....	53
2.3.2.2	Experiment 2: Soft Corals .....	56
2.3.2.3	Experiment 3: Algae .....	57
2.3.2.4	Experiment 4: Sponges .....	58
2.3.3	Size Class Observations .....	59
2.4	Discussion .....	61
	REFERENCES .....	67
Appendix		
A	STATEMENT OF ETHICS .....	82
B	REEF TRANSECT ANALYSIS .....	84

## LIST OF TABLES

Table 1:	Functional groups used to categorize fish (based on feeding) and benthic species for transect analysis. ....	10
Table 2:	SIMPER analysis pairwise site comparison of top three benthic species and % contribution to dissimilarities between those sites. Bolded genus corresponds to a higher average at sites at the top of the table compared to comparison site. ....	15
Table 3:	Significant benthic genera influencing fish species, fish species diversity, juvenile fish species, and herbivore species diversity from distance-based redundancy analysis models. ....	25
Table 4:	Linear mixed effects model outputs for benthic groups and genera with a significant influence on fish functional group. ....	27
Table 5:	PERMANOVA output for pairwise comparisons of benthic functional group Bray-Curtis resemblance matrix by sites. ....	84
Table 6:	PERMANOVA output for pairwise comparisons of fish functional groups by sites. ....	85
Table 7:	SIMPER outputs for pairwise comparisons. ....	85
Table 8:	ANOVA outputs for benthic functional groups by site with Tukey post-hoc test of pairwise site comparisons. ....	95
Table 9:	ANOVA outputs for fish functional groups by site with Tukey post-hoc test of pairwise site comparisons. ....	100
Table 10:	Benthic genera used in distance based redundancy analysis models in the order used in the model. ....	105

## LIST OF FIGURES

Figure 1:	Google earth map of Belize with insert highlighting Carrie Bow Cay, South Water Cay and Curlew (Google earth image 2019). .....	5
Figure 2:	Google earth map of study site locations for current meter sites (stars with names adjacent) and reef transect (color coded circles with legend) (Google earth image 2019). .....	6
Figure 3:	Marotte HS drag tilt current meters. ....	7
Figure 4:	Google earth map of current meter sites with rose plots of direction, count, and speed (Google earth image 2019). .....	12
Figure 5:	Non-metric multidimensional scaling (nMDS) plot of Bray-Curtis similarity matrix comparing fish functional groups (Top) and benthic functional group (Bottom) communities across sites. ....	14
Figure 6:	Average count ( $\pm$ SE) of benthic (A) and fish (B) functional group by site. ....	18
Figure 7:	Boxplot of benthic functional groups (A), benthic genus (B), and benthic species (C) diversity index by site. Sites that are significantly different, identified from Tukey post-hoc test, designated by letters. ....	20
Figure 8:	Boxplot of fish functional group (A), genus (B), and species (C) diversity index by sites. Sites that are significantly different, identified from Tukey post-hoc test, designated by letters. ....	21
Figure 9:	Boxplot of herbivore (A) and juvenile fish (B) species diversity index by sites. Sites that are significantly different, identified from Tukey post-hoc test, designated by letters. ....	23
Figure 10:	Constrained analysis of principal coordinates (CAP) the points represent individual surveys. ....	24
Figure 11:	Photos of study species <i>Acanthurus tractus</i> (A), <i>Scarus iseri</i> (B), <i>Sparisoma viride</i> (C), <i>Acanthurus coeruleus</i> (D), and <i>Stegastes diencaeus</i> (E). ....	42

Figure 12:	Picture of Carrie Bow from above showing area where rubble transects were conducted. Orthomosaic was from Open Reef Mapping Society, Citizen Science GIS, The Smithsonian Institute, and University of Central Florida. ....	43
Figure 13:	Experimental design of cafeteria-style choice aquaria with four habitat options (three hard corals and rubble shown), habituation chamber, and air stone.....	45
Figure 14:	Google earth map of size class survey sites (Google earth image 2019). ....	50
Figure 15:	Rubble transects average count ( $\pm$ SE) of benthic organisms for July 2018.....	51
Figure 16:	Rubble transects average count ( $\pm$ SE) of fish genus for July 2018.....	52
Figure 17:	Average count ( $\pm$ SE) of juvenile A) <i>A. tractus</i> and B) <i>S. iseri</i> from rubble transects by month. ....	53
Figure 18:	Percent association ( $\pm$ SE) of hard coral habitat choices for <i>S. iseri</i> (A) and <i>A. tractus</i> (B) individuals (n=20). Habitat choices that are significantly different, identified from Tukey post-hoc test, designated by letters. ....	54
Figure 19:	Percent association ( $\pm$ SE) of hard coral habitat choices for <i>Sparisoma viride</i> (A), <i>Acanthurus coeruleus</i> (B), and <i>Stegastes diencaeus</i> (C) individuals (n=20). Habitat choices that are significantly different, identified from Tukey post-hoc test, designated by letters. ....	56
Figure 20:	Percent association ( $\pm$ SE) of soft coral habitat choices for <i>S. iseri</i> (A) and <i>A. tractus</i> (B) individuals (n=20). Habitat choices that are significantly different, identified from Tukey post-hoc test, designated by letters. ....	57
Figure 21:	Percent association ( $\pm$ SE) of Algae habitat choices for <i>S. iseri</i> (A) and <i>A. tractus</i> (B) individuals (n=20). Habitat choices that are significantly different, identified from Tukey post-hoc test, designated by letters. ....	58
Figure 22:	Percent association ( $\pm$ SE) of sponge habitat choices for <i>S. iseri</i> (A) and <i>A. tractus</i> (B) individuals (n=20). Habitat choices that are significantly different, identified from Tukey post-hoc test, designated by letters. ....	59

Figure 23: Size class survey average count ( $\pm$  SE) of *A. tractus* (A) and *S. iseri* (B) by site. Note the differences in magnitude for average counts and one site difference between species. ....60

## ABSTRACT

Coral reefs are declining dramatically, causing a shift in benthic community composition and a loss of structural complexity. Changes to the benthic community can result in a loss of diversity, ecosystem function, and resilience. A shift in the benthic composition can have a strong influence on fish abundance and diversity. Fishes recruiting as larvae from the pelagic environment to the reef, rely on information provided by the benthos during habitat selection to detect and interpret a suitable location that will enhance survival and growth. Some fishes utilize a nursery habitat during this vulnerable newly settled stage. The availability of adequate juvenile habitat influences population dynamics and connectivity of reefs. Here, I assess community composition of several coral reefs in Belize, identify important benthic components influencing fish communities, and for two common herbivorous fishes assess habitat preferences and habitat use patterns in possible nursery habitats. Surveyed reefs showed differences in communities between sites with several common benthic components driving dissimilarities. In particular, the soft corals *Antillogorgia spp.* significantly influenced several fish functional groups.

Surveys of a shallow rubble habitat showed most fish were in the juvenile phase suggesting this area may be a temporary habitat for some species. Specifically, two common herbivores, *Scarus iseri*, and *Acanthurus tractus*, utilize this backreef and rubble habitats as juveniles. When tested in a cafeteria style choice experiment, these fish exhibit habitat preferences for benthic species found in rubble habitat but also associated with benthic species found on the reef. This information can be used to

help inform lawmakers and conservationists to create more effective strategies when protecting coral reefs. In order to effectively manage the contemporary reefs, it is vital that management strategies consider how the benthic community impacts the fish community and if ecologically important fish display ontogenetic shifts and habitat preferences.

## Chapter 1

### REEF COMMUNITY COMPOSITION AND CURRENT PROFILES SURROUNDING CARRIE BOW CAY, BELIZE

#### 1.1 Introduction

Coral reefs are extremely biodiverse ecosystems however, these reefs and their inhabitants are faced with many threats from a combination of anthropogenic and natural sources (Anthony 2016, Doney et al. 2012, Halpern et al. 2008, Jones et al. 2004). When stressors impact coral reefs, a phase shift can occur transitioning a healthy stable coral dominated system into a degraded alternative stable state. These changes to the reef community composition may alter the ecosystem services they provide, however the functional groups and diversity on a reef can promote resilience (Brandl et al 2019; Hooper et al. 2012). To better understand and predict how changes to community composition may influence reef health and resilience there must be a foundational understanding of the present-day community composition (Hughes et al. 2017; Graham et al. 2015). Therefore, it is extremely important to understand current reef population dynamics and community composition in both healthy and degraded locations.

Most reef organisms have a complex life history beginning with a pelagic larval phase that transitions into a benthic juvenile and adult stage (Shulman & Bermingham 1995, Caley et al. 1996, Cowen & Sponaugle 2009). The pelagic larval duration (PLD) can vary depending species and oceanographic conditions, ultimately influencing the dispersal kernel for each organism. Larval fish use currents, vertical

migration in the water column, and actively swim during their larval phase to select their final settlement location (Stobutzki & Bellwood 1997, Fisher et al. 2002, Leis & Carson-Ewart 1997, Montgomery et al. 2001). The spatial scale of dispersal during the pelagic period is affected by oceanographic processes with the potential for high spatial connectivity between populations, however behavioral mechanisms can also strongly influence fine scale habitat selection (Cowen & Sponaugle 2009). Models investigating the role PLD plays in population connectivity demonstrate that larval behavior is just as important as oceanographic processes when predicting population connectivity (Paris et al. 2007). Once larval fish transition from a pelagic phase to a benthic phase, the small-scale behavioral processes that influence habitat selection are important to consider when investigating population dynamics.

Behavioral decisions during this vulnerable transition to the benthos are critical for survival and growth. Fishes have developed sensory systems to detect and interpret suitable habitat. Settlement and habitat selection acts as a bottleneck for many populations since predation pressure is extremely high these fish must identify proper habitat to survive and grow (Almany 2004, Dixson et al. 2012; Heinlein et al. 2010; White et al. 2010). Settlement typically happens at night during the new moon over a period of a few days, making accurate measurements of recruitment difficult. Transect counts of the juveniles that made it past the extreme predation pressures experienced during the first 24 hours is currently the best method to estimate population replenishment to reefs (Almany & Webster 2006). During habitat selection larvae utilize several of sensory systems when searching for settlement habitat, such as auditory, visual, magnetics, and olfactory cues (Leis et al. 2011). Reef auditory and olfactory cues allow larvae to orient towards the reef community and assess habitat

suitability from a distance (Dixson et al. 2012, Lecchini et al. 2005, Kingsford et al. 2002, Montgomery et al 2001, Sweatman 1988). Larval fish must identify what cues to avoid, such as predators, while detecting the cues attracting them to suitable settlement habitat, such as food availability and benthic community.

In addition to complex interactions between reef organisms, such as predation and competition, benthic habitat structural complexity also organizes a community composition on coral reefs (Bonin et al. 2015; Caley et al. 1996; Doney et al. 2012; Syms & Jones 2000). Predator-prey dynamics and competition between coral reef fish have a strong influence on community assemblage (Geange & Stier 2010; Hixon & Jones 2005; Preisser et al. 2007; Stier et al. 2017). The structural complexity and biodiversity of the benthic community have a strong influence on fish species and functional groups present (Chong-Seng et al. 2012; Coker et al. 2014; Messmer et al. 2011). Community composition is a very important factor for juvenile fish during habitat selection, and juvenile fish have the ability to detect and avoid degraded reef while selecting for healthy reefs (Brooker et al. 2016; Dixson et al. 2014; Feary et al. 2007; McCormick et al. 2010). Changes to the benthic community, shifting from healthy high complexity reefs to degraded reefs, can have a strong impact on future fish replenishment and the functional group assemblages. On coral reefs herbivores are a very important functional group for a healthy reef due to their have direct consumption of algae, which negatively affect the coral community (Adam et al. 2015; Burkepile & Hay 2010; Kuffner et al. 2006; Mumby 2006). These complex interactions between organisms shape the reef community composition, which can indicate the quality of a reef and its resilience potential after disturbances (Bellwood et al. 2006; Duffy et al. 2016). The influence of the benthic community on fish habitat

selection should be considered when managing and restoring these complex ecosystems.

A primary management practice in response to declining coral reef communities is the implementation of marine protected areas and actively restoring reefs using nursery grown corals (Bellwood et al. 2004; Ladd et al. 2019; Mumby & Steneck 2008). Fragments of existing coral colonies are allowed to mature in a nursery before transplanting the fragments directly back onto the reef (Boch & Morse 2012; Levy et al. 2010; Shaish et al. 2010). Conservation groups have taken the lead in coral nursery and transplant activities with programs such as ‘adopt a coral’, however it is important to communicate effective methods for successful coral growth and survival (Bayraktarov et al. 2019; Hein et al. 2017). In the Caribbean, a focal coral used in many restoration efforts is the threatened genus *Acropora spp.*, which historically was a major reef building coral although is no longer abundant (Young et al. 2012). Therefore, restoration efforts may be falling short by focusing on a coral that is no longer a major part of the benthic community and may not provide accurate information during habitat selection for incoming larvae. If we are to effectively manage the current day reefs, it is vital that management strategies consider how fish communities change with benthic communities.

This chapter investigates the roles that benthic composition and fish composition play in the overall reef community structure. Benthic invertebrates and fish communities were surveyed using a series of belt transects at six locations around Carrie Bow Cay, Belize. Current meters were also deployed to determine oceanographic features that may influence larval supply. The research presented here

provides a foundational understanding of the important benthic components required in promoting healthy reef ecosystems for the Caribbean.

## 1.2 Methods

### 1.2.1 Study Sites

This study was conducted at Smithsonian Research Station Carrie Bow Cay (CBC), Belize ( $16^{\circ}48'9.26''N$ ,  $88^{\circ}4'54.87''W$ ). Carrie Bow is located along the Mesoamerican Barrier Reef just south of South Water Cay (Figure 1). The reef transect surveys were conducted on six reefs surrounding CBC and current meters were placed at six separate sites nearby (Figure 2).

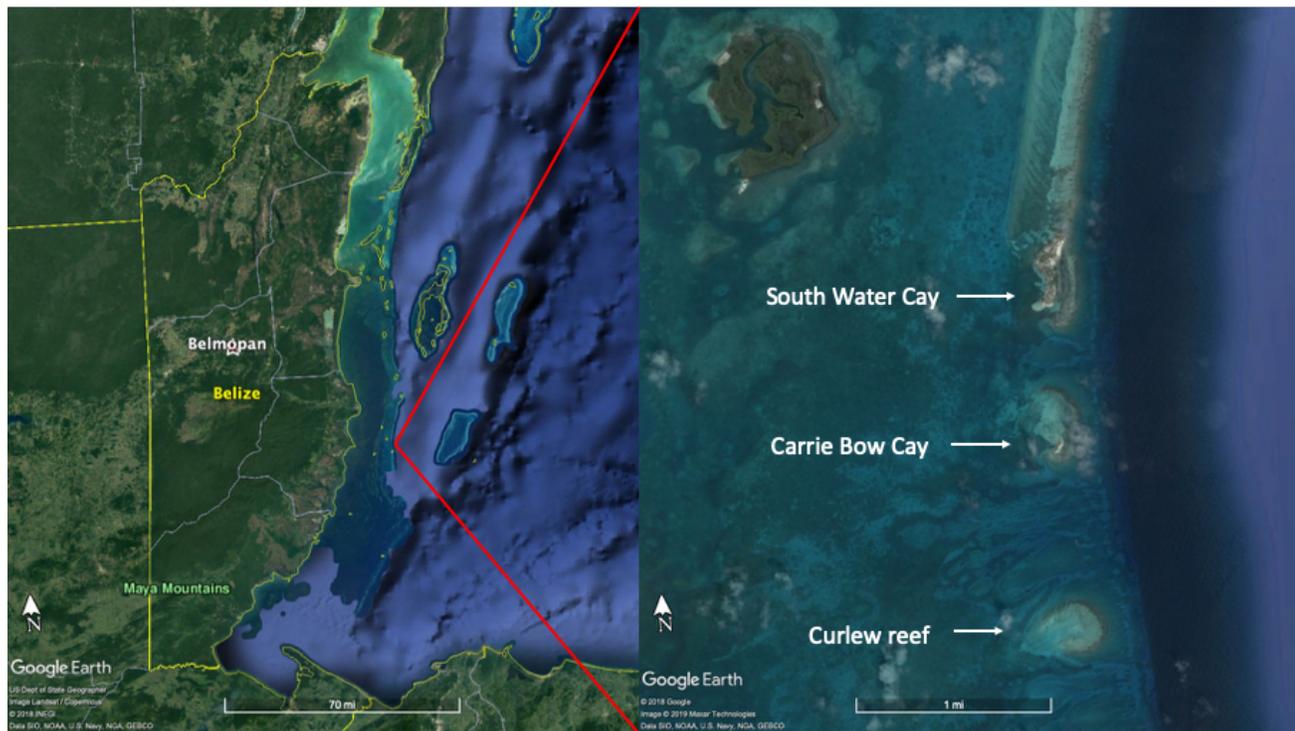


Figure 1: Google earth map of Belize with insert highlighting Carrie Bow Cay, South Water Cay and Curlew (Google earth image 2019).

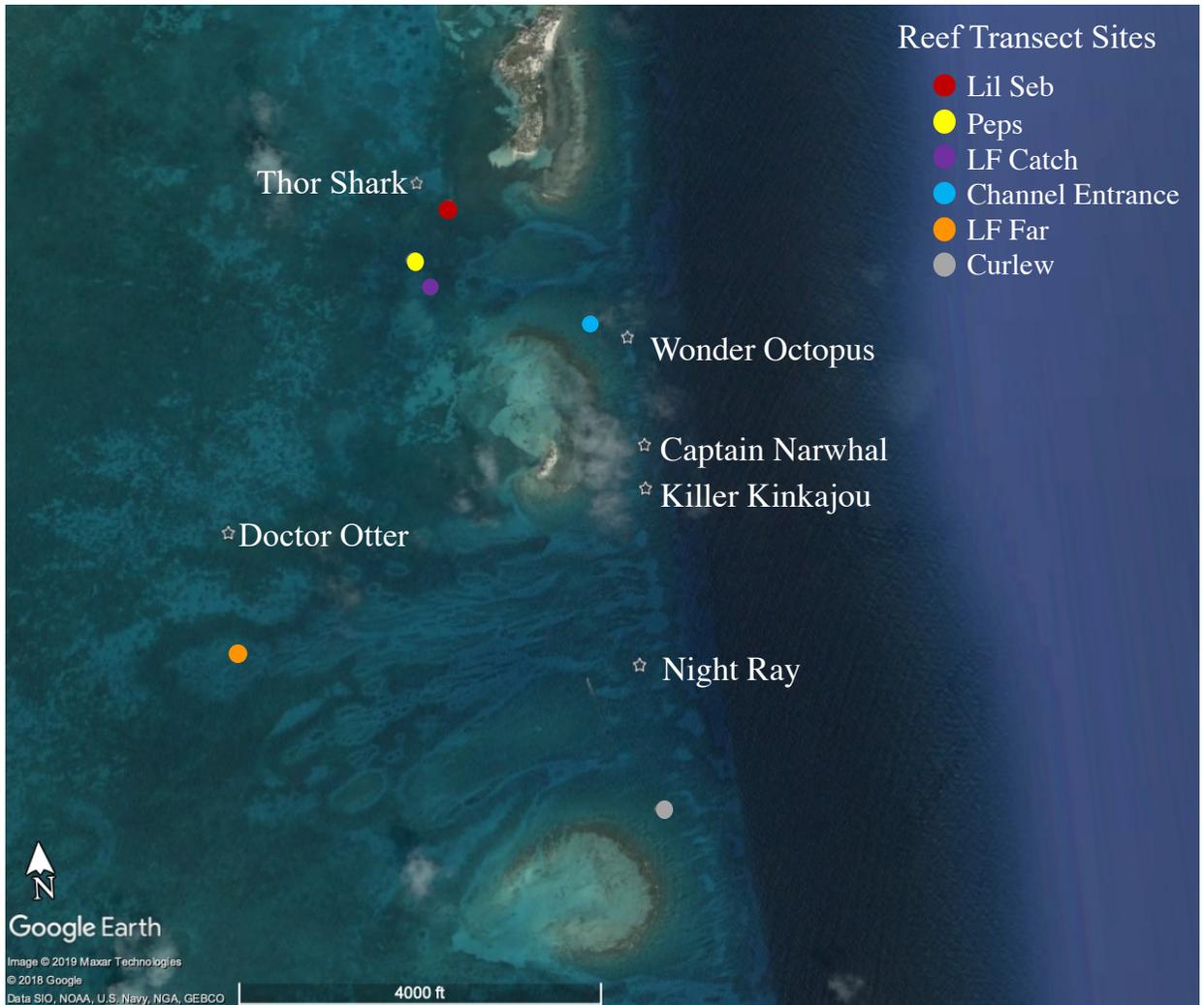


Figure 2: Google earth map of study site locations for current meter sites (stars with names adjacent) and reef transect (color coded circles with legend) (Google earth image 2019).

### 1.2.2 Current Meters

To better understand the current profile in this area, six Marotte HS drag tilt current meters, from James Cook University Marine Geophysics Laboratory, were deployed on cinder blocks just above the benthos from April-September of 2018 (Figure 3). Four current meters were placed on the forereef and two inside the lagoon.

There are two channels entering the lagoon that surround the island of Carrie Bow Cay and two current meters were placed on the forereef near each channel. These sites were chosen to determine how the offshore currents flow onto the reef and through the two channels surrounding CBC. Current meters measured current velocity and direction every second. Upon collection, data were imported into MarotteHSConfig software for post processing, smoothing the data into 10-minute sampling periods. Current profiles were generated and direction, speed, and duration were visualized in rose plot done in R (R Core Team 2019).

### Current Meter: Marotte HS



Figure 3: Marotte HS drag tilt current meters.

#### 1.2.3 Reef Transects

All sites were surveyed at ~ 5 m to account for the influence of depth on coral reef community composition (Goldstein et al. 2016; Pereira et al. 2018). Belt transects were conducted to assess the community composition on six reefs surrounding Carrie Bow Cay during July and August 2017. On each reef, five separate transects were conducted. Surveys were conducted by laying out a 20 m transect tape and waiting

five minutes to begin surveying the fish community. Fish were surveyed by a SCUBA diver slowly swimming the transect while recording the fish community using a GoPro (Hero 5) video camera. The diver took care to record fish in the water column and reef matrix within 1 m of either side of the transect tape. Upon completion, the same transects were surveyed to quantify the benthic community using the linear point intercept method. This was done using 40 random previously marked points along the transect tape and taking photos of the sessile benthic invertebrates that were found underneath each point. Fish and benthic communities were identified to lowest possible taxonomic level using the videos and photos at the University of Delaware. Fish ontogenetic stage (juvenile, intermediate, and adult) was assessed by color phase. Community composition data for both the benthic and fish species were square root transformed. The data were organized into species, genus, and functional group levels for both benthic and fish surveys (Table 1). Shannon diversity index, a commonly reported diversity metric accounting for species abundance and evenness, was calculated for all levels of fish and benthic communities and reported as diversity (Aronson & Precht 1995; Chong-Seng et al. 2012; Duffy et al. 2016). Non-parametric statistics were performed in Primer-e (v7; PERMANOVA+) a Bray-Curtis similarity matrix of square root transformed benthic and fish abundance was used to visualize similarities between sites using non-metric multidimensional scaling (nMDS). An analysis of similarity (SIMPER) was conducted to understand what community components were driving the similarities and dissimilarities between sites. A permutational multivariate analysis of variance (PERMANOVA) was used to compare functional community composition by site.

Further analysis of functional groups and diversity differences between sites were analyzed using ANOVA's with Tukey post hoc tests and assumptions were checked visually. To investigate how specific benthic components influenced the fish communities and fish functional groups a series of Distance-Based Redundancy Analysis and linear mixed effects models were conducted. To do so, Distance-Based Redundancy Analysis (dbra) models using Bray-Curtis matrices were conducted, with ANOVA function, to determine if any benthic genera significantly influenced fish community and diversity. These dbra models accounted for site since each site did have different abundances of functional groups. A forward stepping model selection and the SIMPER output were used to condense and determine the order of benthic variables used in these models (Table 2). From the SIMPER the genera that drove dissimilarities between sites and how often it occurred in all the pairwise comparisons were used to help determine order of variables in model. For these models the benthic genera were grouped by, hard corals, soft corals, sponges, and algae, and analyzed within these categories. A table of benthic genera used and the order for each model can be found in appendix B (Table 10). Fish functional group community, fish species community, and fish species diversity were tested against the four benthic categories. Also, I tested herbivores species diversity, since they are an extremely important functional group for coral reef ecosystems, and juvenile fish species community since the abundance of those incoming juveniles contribute to adult populations. A constrained analysis of principal coordinates (CAP) was used to analyze relationship between variation in the fish and benthic functional groups matrices (Legendre & Anderson 1999). Finally, to investigate if any benthic components significantly influenced fish functional groups a series of linear mixed effects models (package

nlme). These models were used to determine if any of the significant benthic components found from the dbra influenced specific fish functional group, and site was a random effect in the model since benthic communities differed between site. These models were analyzed using R (R Core Team 2019) with packages lme4 and vegan.

Table 1: Functional groups used to categorize fish (based on feeding) and benthic species for transect analysis.

<b>Fish Functional Groups</b>	<b>Benthic Functional Groups</b>
Omnivore	Hard Coral
Herbivore	Soft Coral
Generalist Carnivore	Sponge
Piscivore	Macroalgae
Invertivore	Cyanobacteria
Planktivore	Turf Algae
Cleaner	Sand
Spongivore	

### 1.3 Results

#### 1.3.1 Current Meters

The current meters displayed different current patterns at the six different sites. The patterns varied depending on geographic location on the forereef, within the channel entrances, and inside the lagoon (Figure 4). The two current meters on the forereef (Captain Narwhal and Killer Kinkajou) showed the current primarily coming

from the North East onto the forereef and a stronger current detected by the meter in the south channel (Killer Kinkajou). The Northern channel, between South Water Cay and Carrie Bow Cay, shows the main current is predominantly entering the lagoon (Wonder Octopus). This channel is smaller than the Southern channel between Carrie Bow Cay and Curlew. The larger Southern channel (Night Ray) had the strongest current and the direction flowing in and out of the lagoon indicating the current is tidally driven. Two current meters were also placed inside the lagoon (Doctor Otter and Thor Shark), these were shown to have similar tidal patterns with strong currents flowing both in and out of the lagoon.

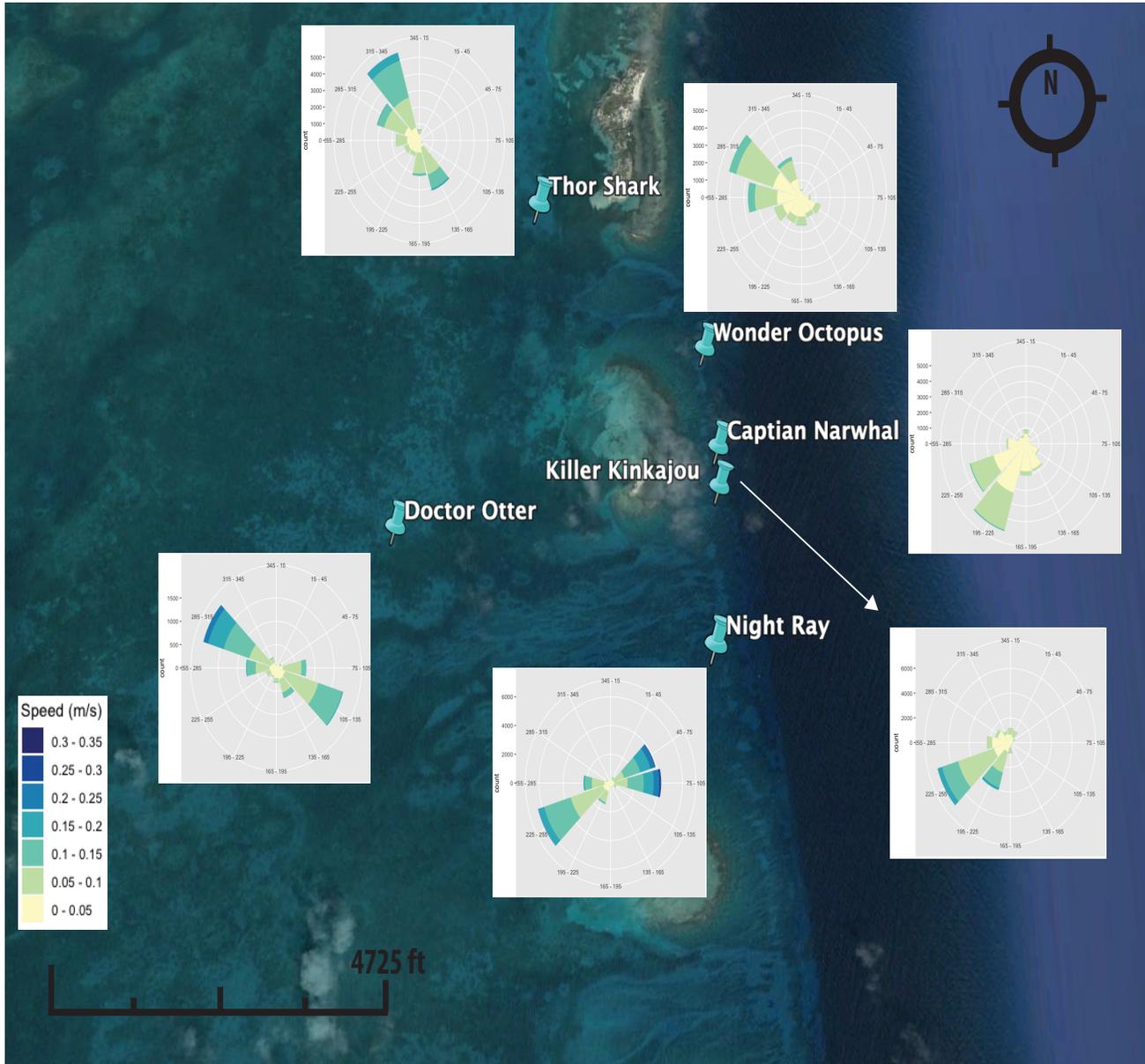


Figure 4: Google earth map of current meter sites with rose plots of direction, count, and speed (Google earth image 2019).

### 1.3.2 Reef Transects

Community composition differed between sites for both fish and benthic functional group data. The nMDS plot of community composition for functional

groups showed the reefs clustered slightly different when comparing the fish and benthic communities. The two sites on the forereef, Channel Entrance and Curlew, clustered close together for the fish functional group community (Figure 5). LF Catch clustered separately while the other reef clustered together when comparing benthic functional community. Benthic functional group communities were significantly different between sites (PERMANOVA pairwise test  $p < 0.01$ ), except between Lil Seb and Peps (PERMANOVA pairwise test  $p = 0.2$ ). Fish functional group communities were significantly different between sites (PERMANOVA pairwise test  $p < 0.01$ ), except between Channel Entrance and Curlew (PERMANOVA pairwise test  $p = 0.196$ ). A complete table with each site pairwise comparison and statistically significant values for both benthic and fish species community are in appendix B (Table 5 & 6).

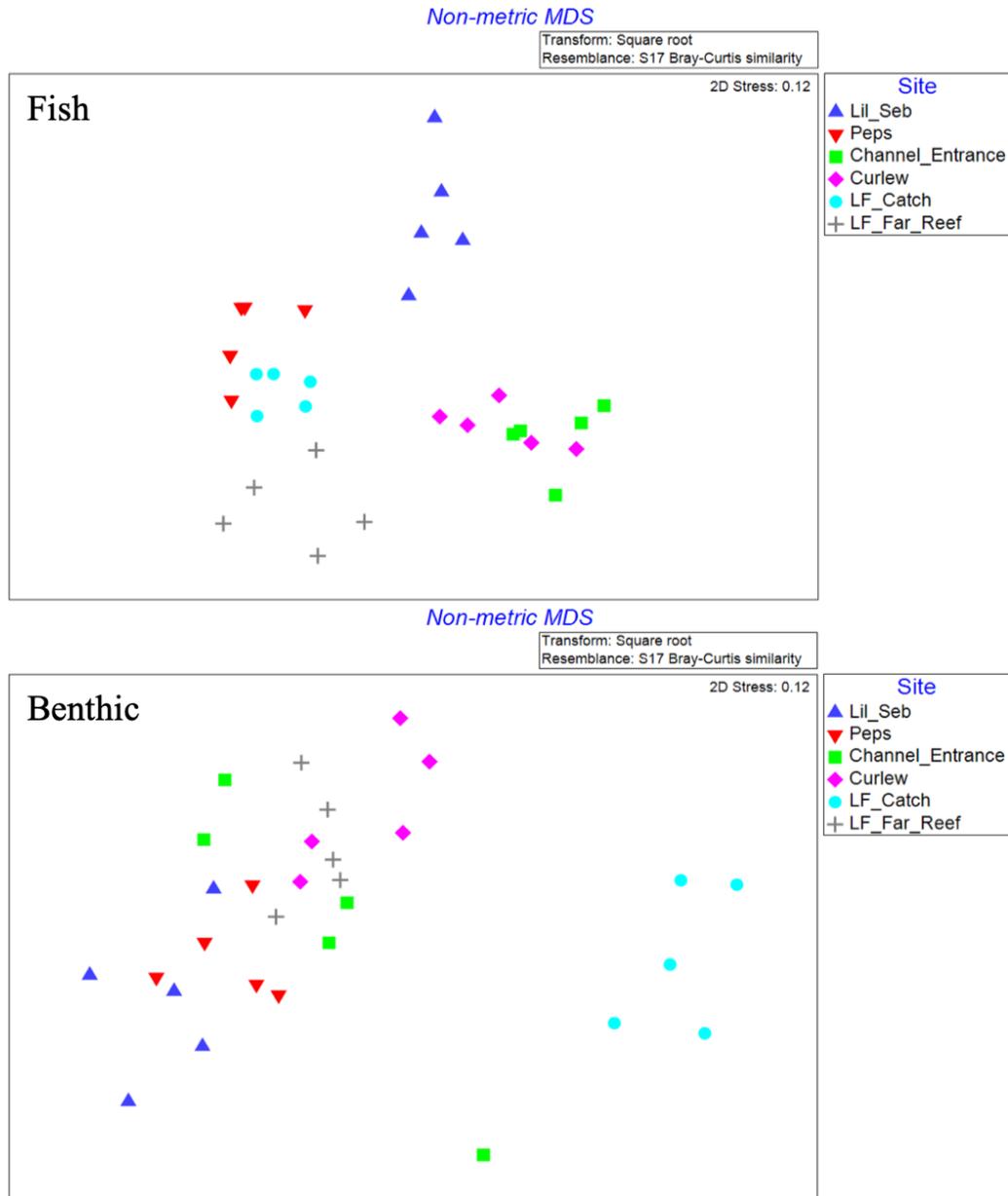


Figure 5: Non-metric multidimensional scaling (nMDS) plot of Bray-Curtis similarity matrix comparing fish functional groups (Top) and benthic functional group (Bottom) communities across sites.

The benthic functional group community had small differences between sites, so benthic genus was used to piece apart what benthic components driving differences between sites. SIMPER analysis was conducted to determine what benthic genera are driving the dissimilarities between sites. The SIMPER identified the main benthic genera contributing to 70% of the dissimilarities between sites and the main three for each comparison cumulatively contributed to between 17.31-29.18% of total dissimilarities (Table 2). The top three genera, *Agaricia spp.* (Hard Coral; 9), *Dictyota spp.* (Algae; 7), and *Antillogorgia spp.* (Soft Coral; 7), were in most of these comparisons driving dissimilarities and were of different functional groups.

Table 2: SIMPER analysis pairwise site comparison of top three benthic species and % contribution to dissimilarities between those sites. Bolded genus corresponds to a higher average at sites at the top of the table compared to comparison site.

Sites	Curlew	Peps	Lil Seb	LF Catch	LF Far
Channel entrance	<i>Dictyota spp.</i> (6.49%) <i>Antillogorgia spp.</i> (6.27%) <b>Turf Algae (5.28%)</b>	<i>Aplysina spp.</i> (7.64%) <b><i>Dictyota spp.</i> (7.10%)</b> <i>Agaricia spp.</i> (6.12%)	<b><i>Dictyota spp.</i> (10.25%)</b> <i>Agaricia spp.</i> (8.95%) <i>Aplysina spp.</i> (7.68%)	Halimeda spp. (9.67%) <i>Agaricia spp.</i> (8.32%) Turf Algae (7.85%)	<b><i>Dictyota spp.</i> (7.11%)</b> <b><i>Actinotrichia spp.</i> (6.33%)</b> <b><i>Orbicella spp.</i> (5.33%)</b>
Curlew		<b><i>Antillogorgia spp.</i> (9.82%)</b> <i>Agaricia spp.</i> (8.19%) <i>Aplysina spp.</i> (6.28%)	<i>Agaricia spp.</i> (10.23%) <b><i>Antillogorgia spp.</i> (9.28%)</b> <b><i>Dictyota spp.</i> (8.92%)</b>	<i>Agaricia spp.</i> (11.09%) <i>Halimeda spp.</i> (10.65%) <b>Sand (7.44%)</b>	<b><i>Actinotrichia spp.</i> (6.09%)</b> <b><i>Orbicella spp.</i> (6.08%)</b> <b><i>Dictyota spp.</i> (5.15%)</b>

Peps			<i>Dictyota spp.</i> <b>(7.81%)</b> Actinotrichia spp. (7.69%) Agaricia spp. (5.88%)	<b>Aplysina spp. (8.30%)</b> Antillogorgia spp. (7.90%) <b>Sand (7.76%)</b>	Antillogorgia spp. (9.54%) Agaricia spp. (6.08%) <b>Orbicella spp. (5.87%)</b>
Lil Seb				Dictyota spp (11.3%) <b>Aplysina spp (8.71%)</b> Antillogorgia spp. (8.28%)	Antillogorgia spp. (8.62%) <b>Agaricia spp (8.22%)</b> <b>Orbicella spp (5.88%)</b>
LF Catch					<b>Halimeda spp (8.58%)</b> Sand (8.07%) <b>Agaricia spp (7.44%)</b>

To determine how functional group abundance differed between sites a series of ANOVA's were run on benthic and fish functional communities against site (Figure 6 A). There was a significant difference between sites for most benthic and fish functional groups. A complete table with each site pairwise comparison and statistically significant values for both each fish and benthic functional group are in appendix B (Table 8 & 9). The general trends from these pairwise comparisons showed Curlew, LF Far Reef, and Channel Entrance have higher hard coral abundance. While soft corals abundance was highest at Peps, Lil Seb, and Channel Entrance. Sponges abundances was highest at Curlew, LF Far Reef, Channel Entrance, and LF Catch. Macroalgae was significantly lower at LF Catch. While turf algal abundance was highest at LF Catch and lowest at Channel Entrance. Cyanobacteria abundance was highest at Curlew and lowest at Lil Seb. LF Catch and Channel

Entrance had the highest sand suggesting these may be patchier reefs than the other sites.

Fish functional group pairwise comparisons detected a lot of variation between sites (Figure 6 B). Omnivores were significantly higher at LF Catch and Peps while lowest at LF Far Reef. Generalist carnivores were significantly higher at Peps. Piscivores were significantly lower at Channel Entrance and Curlew. Invertivores were highest at Lil Seb and then Peps. Cleaners were highest at LF Catch and lowest at LF Far Reef. Planktivores were highest at Peps and LF Far Reef, while Lil Seb and Channel Entrance didn't have any. Spongivores were infrequent on the transects with the most at LF Catch and Lil Seb, and Channel Entrance didn't have any spongivores. It is interesting to note that while abundance of other functional groups fluctuated between sites the herbivore functional groups were similar across all sites. This variation in fish functional group abundance between sites suggests some component of these sites may be driving the differences in fish functional groups.

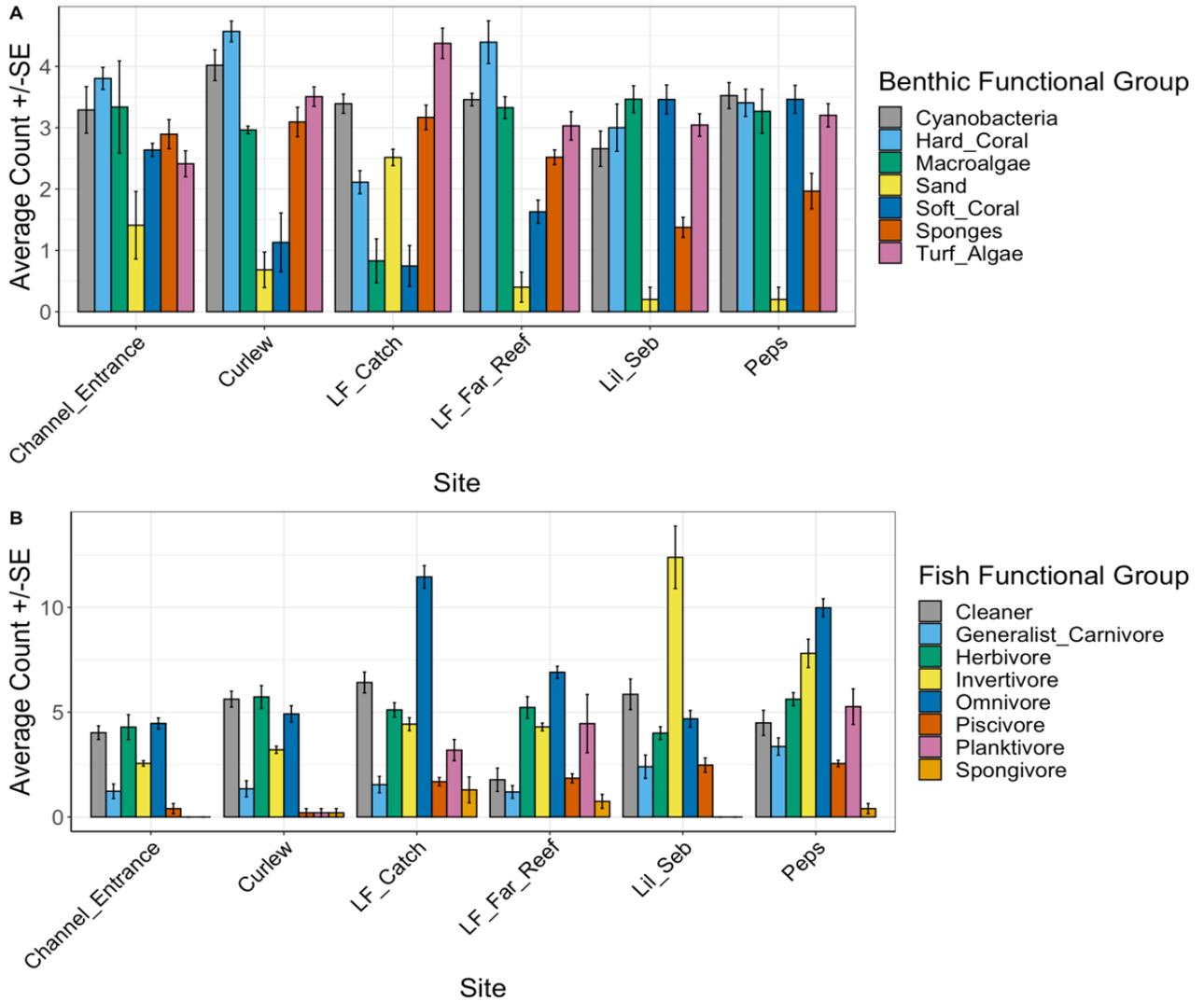


Figure 6: Average count ( $\pm$  SE) of benthic (A) and fish (B) functional group by site.

Diversity indices between sites were examined since fish and benthic abundances varied between sites. Benthic diversity (Figure 7 A) at the functional level was not significantly different between sites. At the genus level (Figure 7 B) benthic diversity index was significantly different between sites (ANOVA;  $F= 7.577$ ;

p=0.0002). Benthic community species diversity (Figure 7 C) was also significantly different between sites (ANOVA; F=6.6834; p<0.0004).

Generally, Channel Entrance, Curlew, LF Far Reef, and Peps had higher benthic diversity than LF Catch and Lil Seb (Figure 7). Looking back at the functional group community of LF Catch and Lil Seb, both generally had less hard corals while having more sponges, turf algae, and sand (Figure 6). When comparing the two reefs against one another, benthic geneses driving dissimilarities found higher averages of a sponge, *Aplysina spp.*, turf algae, or sand on LF Catch and Lil Seb was characterized with more soft coral *Antillogorgia spp.* and algae *Dictyota spp.* (Table 2). LF Catch had more sand, meaning it may be a patchier reef that could be influencing the benthic diversity.

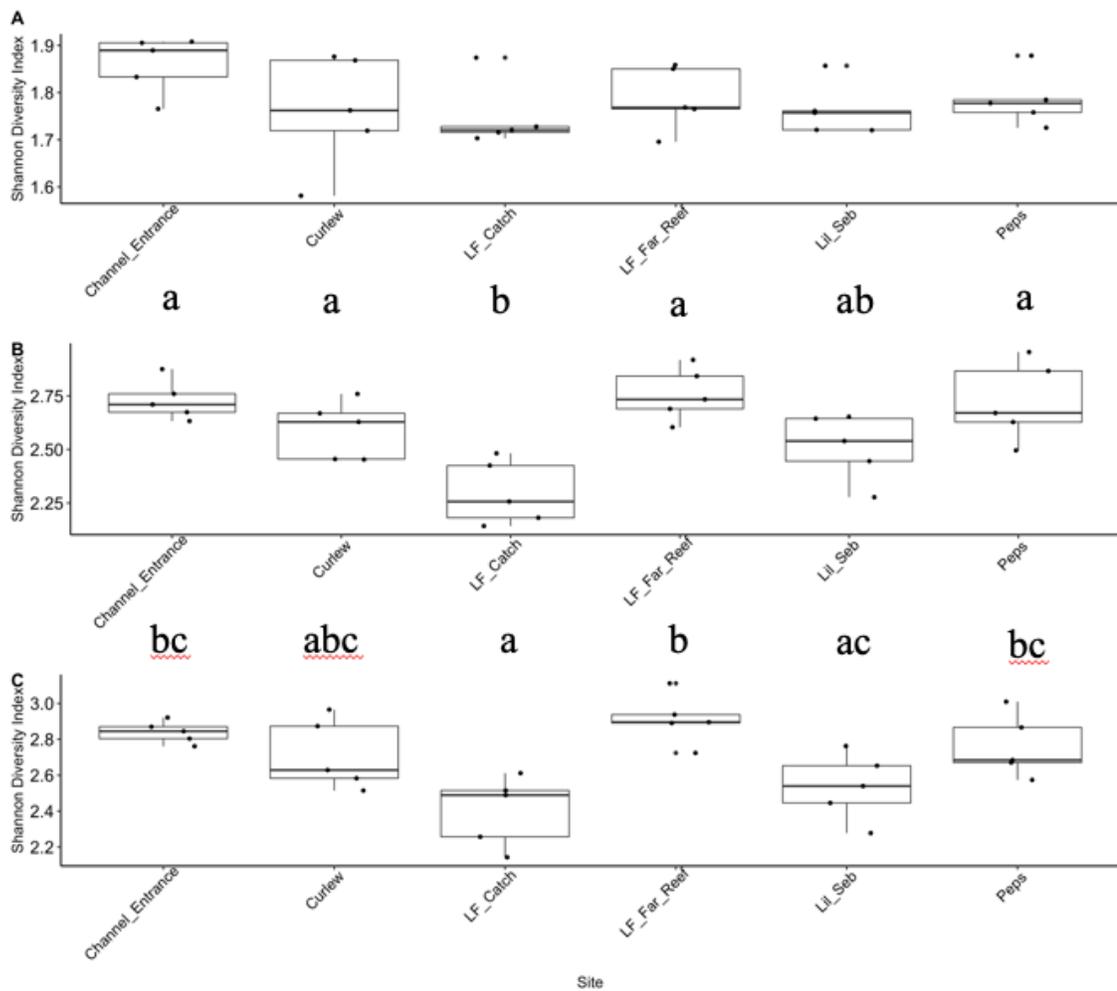


Figure 7: Boxplot of benthic functional groups (A), benthic genus (B), and benthic species (C) diversity index by site. Sites that are significantly different, identified from Tukey post-hoc test, designated by letters.

Fish diversity (Figure 8 A) at the functional level was significantly different between sites (ANOVA  $F= 9.346$ ;  $p<0.0001$ ) with the pairwise comparisons indicated on graphs. Fish genus diversity (Figure 8 B) was significantly different between sites (ANOVA  $F= 5.6944$ ,  $p<0.001$ ). Fish community species diversity (Figure 8 C) was significantly different between sites (ANOVA  $F= 11.148$ ,  $p<0.0001$ ). Fish diversity

was highest at Peps and LF Far Reef, LF Catch and Lil Seb followed, and Channel Entrance and Curlew had the lowest diversity of reefs surveyed. Peps and LF Far Reef were comprised of four main functional groups, omnivores, herbivores, invertivores, and planktivores. Curlew and Channel Entrance had lower abundances of those groups and also have very few piscivores, planktivores, and spongivores driving down their diversity.

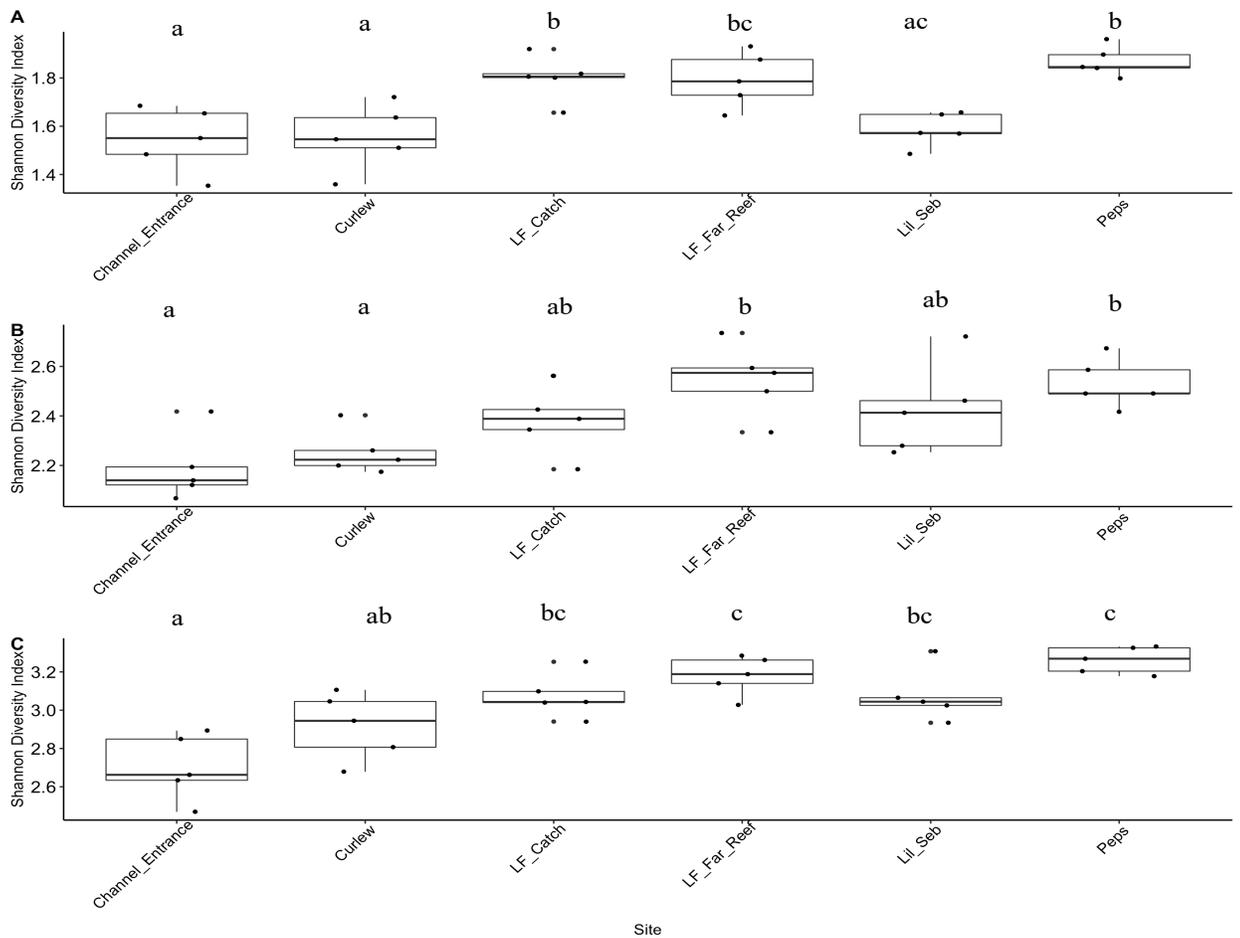


Figure 8: Boxplot of fish functional group (A), genus (B), and species (C) diversity index by sites. Sites that are significantly different, identified from Tukey post-hoc test, designated by letters.

As discussed above herbivores are an extremely important functional group for coral reef ecosystems and algal communities, although diversity was not significantly different between sites (Figure 9 A). Juvenile fish communities are important to consider as well, since this developmental stage is a major bottleneck in reef replenishment. Additionally, a substantial amount of research has been conducted on habitat selection and species interactions during this life stage. The juvenile fish species diversity (Figure 9 B) was significantly different between sites (ANOVA  $F=5.69$ ;  $p=0.001$ ). Juvenile fish species diversity was significantly higher at Peps and LF Catch, with Channel Entrance had the lowest juvenile diversity. Curlew, LF Far Reef, and Lil Seb were in between although no significant difference and had more variation.

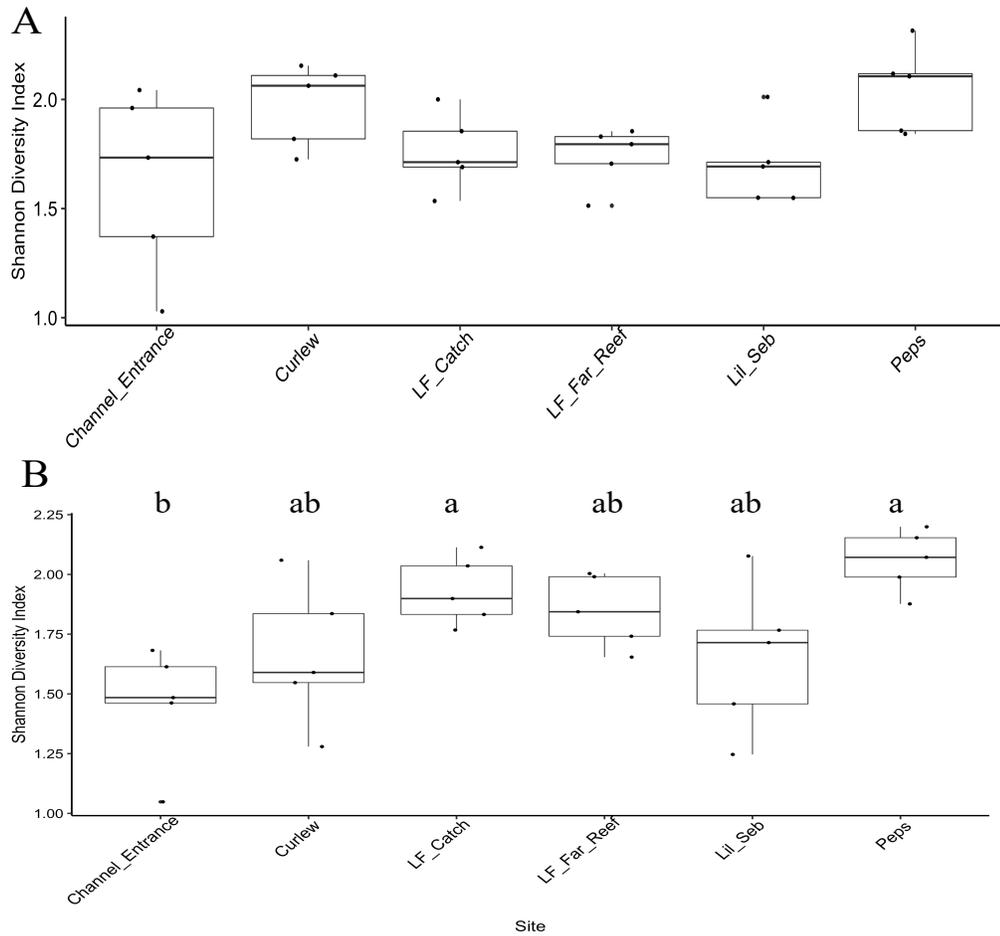


Figure 9: Boxplot of herbivore (A) and juvenile fish (B) species diversity index by sites. Sites that are significantly different, identified from Tukey post-hoc test, designated by letters.

To analyze the relationship fish and benthic functional groups and if the benthic functional groups explain variation in the fish functional groups. The CAP analysis explained a significant proportion of the variance between the fish and benthic functional group matrices which accounted for 41% of the constrained variance ( $F=2.75$ ;  $p=0.001$ ). The location on the CAP plot indicates similarity and functional groups more abundant in sites located nearby in ordination space (Figure

10). The direction and angle of vectors indicate the correlation between the functional groups with a 0° angle is a maximum positive correlation and 180° angle is a maximum negative correlation. Several benthic groups are negatively correlated such as soft corals with sponges, macroalgae with cyanobacteria, and turf algae with hard corals. Fish functional groups farther from the center of the plot indicate stronger relationships with any close by benthic functional groups. Most notably omnivores and slightly less the cleaner fish functional groups are positively correlate with turf algae while invertivores and slightly less piscivore and generalist carnivore fish functional groups positively correlate with soft corals.

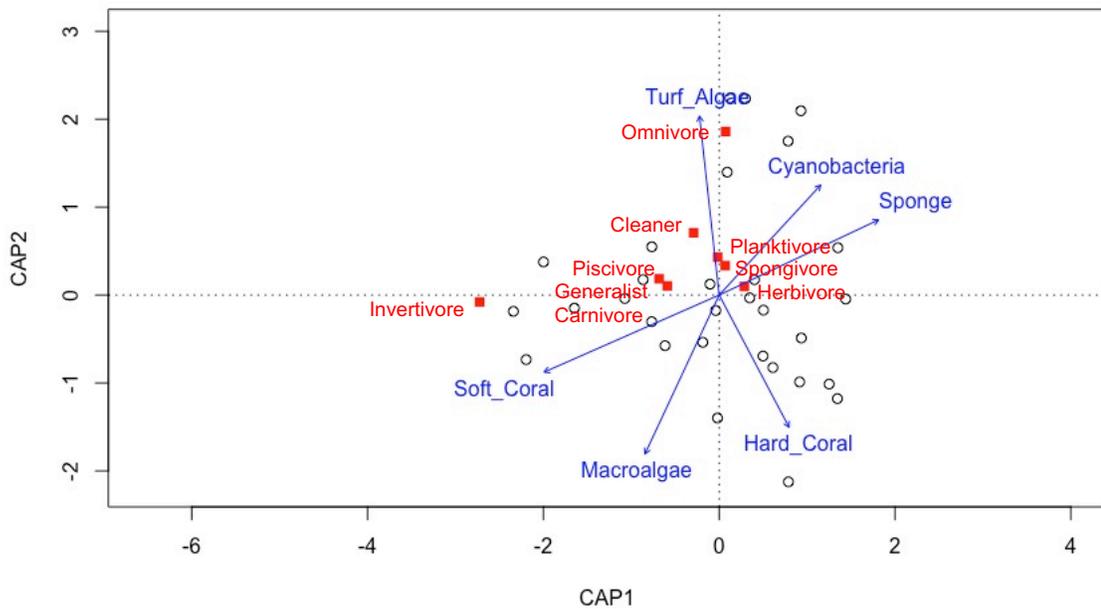


Figure 10: Constrained analysis of principal coordinates (CAP) the points represent individual surveys.

As several sites differed in fish and benthic community composition, it is important to determine how the benthic community may be linked or influencing the fish community. Analyzing by genus also reduced the number of variables with multiple zeros and created a more manageable dataset to investigate models identifying what benthic components influenced fish communities. From the dbra models several benthic genera had a significant effect on fish functional groups, fish species, fish species diversity, juvenile fish species, and herbivore species diversity (Table 3).

Table 3: Significant benthic genera influencing fish species, fish species diversity, juvenile fish species, and herbivore species diversity from distance-based redundancy analysis models.

	Fish Functional Group	Fish Species	Fish Species Diversity	Juvenile Fish Species	Herbivore Species Diversity
Hard Corals	<i>Agaricia spp.</i> (F=5.5523, p=0.006)	<i>Agaricia spp.</i> (F=4.0396, p=0.001)	<i>Agaricia spp.</i> (F=52.99, p=0.013)	<i>Agaricia spp.</i> (F=8.2779, p=0.001) <i>Porites spp.</i> (F=2.3816, p=0.033)	None
Soft Corals	<i>Antillogorgia spp.</i> (F=4.1272, p=0.002)	<i>Antillogorgia spp.</i> (F=4.6054, p=0.001)	<i>Antillogorgia spp.</i> (F=33.67, p=0.003) <i>Briareum asbestinum</i> (F=12.56, p=0.021)	<i>Antillogorgia spp.</i> (F=2.22, p=0.007)	None
Sponges	<i>Aplysina spp.</i> (F=8.7934, p=0.002) <i>Cliona spp.</i>	<i>Aplysina spp.</i> (F=31.77, p=0.001) <i>Cliona spp.</i>	<i>Aplysina spp.</i> (F=19.96, p=0.016)	<i>Aplysina spp.</i> (F=5.83, p=0.001) <i>Cliona spp.</i> (F=2.21,	<i>Aplysina spp.</i> (F=41.61, p=0.006) <i>Cliona spp.</i> (F=21.80, p=0.018) Amphimedon

	(F=3.4014, p=0.017)	(F=18.53, p=0.05)		p=0.02)	compressa (F=26.29, p=0.014) Iotrochota birotulata (F=16.6, p=0.015) <i>Niphates spp.</i> (F=26.09, p=0.017)
Algae	<i>Dictyota spp.</i> (F=10.5894, p=0.001) <i>Halimeda spp.</i> (F=2.922, p=0.04)	<i>Dictyota spp.</i> (F=7.84, p=0.001) <i>Halimeda spp.</i> (F=2.56, p=0.01)	<i>Dictyota spp.</i> (F=8.63, p=0.048) <i>Halimeda spp.</i> (F=7.85, p=0.048)	<i>Dictyota spp.</i> (F=4.54, p=0.001) <i>Halimeda spp.</i> (F=2.0, p=0.036)	None

Overall, *Agaricia spp.* was the main hard coral with a significant effect on three fish community categories at the fish functional group, fish species and fish diversity levels. *Agaricia spp.* and *Porites spp.* had a significant effect on juvenile fish species. *Antillogorgia spp.* was the main soft coral that had a significant effect on three fish community categories at the fish functional group, fish species, and juvenile species levels. Fish species diversity was significantly influenced by the soft corals *Antillogorgia spp.* and *Briareum asbestinum*. The two main algae *Dictyota spp.* and *Halimeda spp.* both had a significant effect on juvenile species, fish species, fish functional groups, and fish diversity. The only category to have significant effect on herbivores was sponges. Surprisingly, five genera of sponges had a significant effect on herbivore diversity. While for fish functional group, fish species, and juvenile species only two had a significant effect *Aplysina spp.* and *Cliona spp.*; *Aplysina spp.* for fish diversity only.

The models investigating the influence of these benthic components on fish functional group communities showed surprising results that soft corals were the main benthic component to significantly effect a variety of functional groups (Table 4).

Omnivores and generalist carnivores were both significantly influenced by soft corals. Looking at the specific soft coral genus *Antillogorgia spp.*, since it had a significant effect on community composition and was a main component in the SIMPER (Table 2 & 4), I tested it against fish functional groups. This showed generalist carnivores, piscivores, and invertivores were significantly influenced by *Antillogorgia spp.* This was surprising as not much research has been done on the influence of soft corals on fish community compositions.

Table 4: Linear mixed effects model outputs for benthic groups and genera with a significant influence on fish functional group.

	Benthic Component
Omnivore	Soft Coral: t-value = 2.127416; P=0.04
Generalist Carnivore	Soft Coral: t-value = 2.372914; P= 0.0264
Generalist Carnivore	<i>Antillogorgia spp.</i> : t-value = 4.676226; P= 0.0001
Piscivore	<i>Antillogorgia spp.</i> : t-value = 2.052923; P=0.05
Invertivore	<i>Antillogorgia spp.</i> : t-value = 2.220279; P=0.0365

#### 1.4 Discussion

This chapter characterized the differences in the benthic and fish communities between six coral reef sites, indicating potential benthic components influencing fish communities on these reefs. Understanding reef community composition and how the benthic community may influence fish diversity and abundance is very important for coral reef ecology as these communities continue to transition from healthy to degraded stable states (Aronson et al. 2002; Pandolfi & Jackson 2006; Norström et al. 2009). At field sites around Carrie Bow Cay, Belize the benthic and fish community

composition differed between sites. An interesting link between soft coral communities significantly influencing multiple fish functional groups was found. Generalist carnivores, piscivores, and invertivores were significantly influenced by the soft coral *Antillologorgia spp.*, and at sites with higher *Antillologorgia spp.* there were higher abundances of these fish functional groups. This was unexpected as very few studies have been done on the influence of soft coral assemblage on fish community. Rather, most research on soft corals look at their secondary metabolite production or linking them with degraded habitats (Harvell et al 1998; Norström et al. 2009; Woolsey et al. 2012). Along with *Antillologorgia spp.*, influencing fish communities, *Briareum asbestinum* was shown to have a significant effect on fish species diversity. Soft corals are a common part of the benthic community especially around Carrie Bow Cay but haven't always been estimated during monitoring and little ecological research has been conducted on the habitat they provide (Lasker & Coffroth 1983; Mumby & Harborne 1999; Williams et al. 2015). Soft corals have become more prevalent in this area with the decline of hard corals; the impact of soft corals detected in this study may underrepresent their influence on fish communities as communities shift to more soft coral dominate (Villamizar et al. 2014). In the Pacific, Syms & Jones (2001), conducted a manipulative experiment removing soft corals and found no impact on fish recruitment or reef fish assemblage. While a more recent study in the Pacific, Epstein & Kingsford (2019), found fish assemblages were similar between hard and soft coral reefs, and there was actually an increase in species richness of fish with increasing soft corals. The role of soft corals on coral reef matrices may be underestimated and these two main studies looking at soft corals on fish assemblages

were both done in the Pacific, emphasizing the need for more research on Caribbean soft coral community.

Throughout the Caribbean there has been a shift from hard coral to soft coral and sponges, but similar to soft coral most research being done on sponges focuses on taxonomy and secondary metabolites. Sponges play a different role in coral reef communities than hard corals and they are important for water filtering and after disturbances help stabilize loose rubble (Diaz & Rützler 2001). Two sponge genera, *Aplysina spp.* and *Cliona spp.*, significantly influenced fish functional groups, fish species community, and juvenile species community. Unexpectedly for herbivore several sponges had a significant influence on species diversity, along with the previous two genera *Amphimedon compressa*, *Iotrochota birotulata*, and *Niphates spp.* had a significant effect on herbivore diversity. Sponges have different strategies influencing their abundance by being chemically defended or fast growing undefended and are a dominant part of the benthic community on coral reefs (Leong & Pawlik 2010; Pawlik 2011). *Aplysina spp.* (encrusting rope or vase sponge) produces secondary metabolites that chemically defended the sponge against predation and *Cliona spp.* are excavating sponges that kill coral tissue and encrust through bioerosion (Chaves-Fonnegra et al. 2015). These *Cliona spp.* excavating sponges are becoming more abundant on Caribbean reefs and are very successful at colonizing corals after bleaching events and disturbances (Chaves-Fonnegra et al. 2018). *Amphimedon compressa* (chemically defended encrusting rope sponge), *Iotrochota birotulata* (variably defended encrusting rope sponge), and *Niphates spp.* (undefended encrusting or vase sponge) are common sponges and have been known to overgrow both hard and soft corals (Loh & Pawlik 2014; Mclean et al. 2015). The CAP analysis

showed soft corals and sponges had a strong negative correlation. For most of the reefs surveyed here, it was unusual to have high abundances of both sponge and soft coral, with the exception of Channel Entrance (Figure 6 B). The two reefs that had higher abundances of soft corals, Peps and Lil Seb, also had higher fish diversity. A shift in this area from hard corals to sponges and soft corals has been reported. This indicates that it is important to understand how sponges compete for space and influence community composition (Bell et al. 2013; Norström et al. 2009; Villamizar et al. 2014). Many sponges are chemically defended influencing competition for space on reefs and bioeroder or ones that over grow corals should be seriously considered when examining a shift in community composition to a higher proportion of sponges.

Two algae genera, *Dictyota spp.* and *Halimeda spp.*, had a significant effect on fish species community, fish diversity and juvenile fish species community. These are both very common macroalgae throughout the Caribbean, *Dictyota spp.* is a fleshy brown alga, while *Halimeda spp.* is a calcareous green alga (Hay et al. 1994; Steneck et al. 2014). *Halimeda spp.* is calcareous to defend against herbivory and can produce secondary metabolites, although it is still consumed by grazing of superficial tissue or bites from large parrotfish (Castro-Sanguino et al. 2017; Paul & Van Alstyne 1992). While *Dictyota spp.* is a chemically defended fleshy brown alga, it is still a primary diet for some herbivores (Hanmer et al. 2017; Hay et al. 1988). Both of these species are known to compete with corals larvae and adults for space on the reef (Kuffner et al. 2006; Paul et al. 2011). Herbivores are ecologically important for managing algal communities to help mediate competition between algae and coral, therefore enhancing ecosystem function (Burkpile & Hay 2010; Topor et al. 2019; Mumby et al. 2006). Changes observed in the benthic community and the corresponding impacts

on fish the community and resilience of each reef may be regionally dependent (Arias-González et al. 2017; Gardner et al. 2003; Graham et al. 2011; Schutte et al. 2010). This information indicates that surveys of reef community composition prior to a disturbance event is extremely important in understanding the health of the reef system.

Throughout the Caribbean *Agaricia spp.* has become a dominant hard coral on coral reefs (Aronson & Precht 1997). On Belizean reefs surveyed here, *Agaricia spp.* had a significant effect on three fish community categories at the fish functional group, fish species, and fish diversity levels. The hard coral *Porites spp.* also had a significant effect on juvenile fish communities. These two corals, *Agaricia spp.* and *Porites spp.*, are fast growing and each genus has an encrusting and branching form that provides structural complexity within interstitial space, but not much vertical structure (Darling et al 2012; Green et al. 2008). It is important to have a diverse assemblage of hard corals, bouldering and branching, to build up the reef matrix that provides structural complexity for fish communities, especially small bodied and juveniles (Coker et al. 2012; Newman et al. 2015). Fish are linked to benthic communities; beginning with juvenile habitat selection, many species actively choose reefs based on specific benthic components indicative of a healthy ecosystem (Dixon et al. 2014). The fish diversity didn't directly correspond to the benthic diversity specifically at Channel Entrance and Curlew, which were generally more diverse and had more hard coral. Fish rely on more than hard corals when selecting a habitat but have to weigh out the community composition of suitable or unfavorable benthic species influencing habitat selection. While hard corals are important for fish communities, the species and type of hard coral is also important and the hard coral at

these sites was primarily *Agaricia spp.*. However, this coral may not provide appropriate habitat that most fish are seeking. Damselfish are aggressive territorial fish that typically farm algae crops within these territories while defending their farm from herbivores (Blanchette et al. 2019; Gibson et al. 2001). The effects of algal farming by damselfish may be playing a role in allowing algae to persist, therefore having a healthy population of predators would be important to regulate damselfish populations and the negative consequences of their algal farming (Lirman 1994; Randazzo et al. 2019; Vermeij et al. 2015). On our transects damselfish were the main fish occupying *Agaricia tenuifolia* and *Agaricia spp.* was higher at Channel Entrance and Curlew but had lower fish diversity and had the lowest abundance of piscivores. It may be beneficial to investigate the role damselfish at these sites play on algal farming and the benthic community as a whole. These complex interactions between reef organisms and the benthic community they live in go beyond just hard corals since coral reefs are diverse ecosystems with other functional groups providing habitat and services.

Coral reef community composition is a delicate balance of competition especially between hard coral and macroalgae competition, this has been exemplified in the Caribbean after *Acropora* disease outbreak, herbivorous urchin *Diadem antillarum* die off, and numerous hurricanes (Aronson et al. 2002; Hughes 1994; Mumby et al. 2007; Nyström et al. 2000). When these phase shifts occur, reefs are not only losing coral and gaining macroalgae, coral can also be replaced with sponges and soft coral, all of which reduce the structural complexity on reefs (Alvarez-Filip et al. 2011; Diaz & Rützler 2001; Norström et al. 2009). Some fish actively avoid reefs due to degradation, which can intensify the degradation process through the loss of ecologically important groups, like herbivores that are required to keep algal

populations in check and prevent further degradation (Dixson et al. 2014, McCormick et al. 2010, Wilson et al. 2006). *Acropora spp.* are widely used in Caribbean coral reef restoration, however these corals went through a die off in the 80's and are uncommon on present day reefs (Young et al. 2012). Fish may not recognize these corals as desirable habitats since they are not abundant on most reefs. Coral reef management strategies are focused on marine protected areas and restoration; however, these strategies may want to consider other important factors that influence coral reef community composition.

Along with the benthic community composition influencing fish community, location and oceanographic processes play a role in these population dynamics. Therefore, it is important to note the locations of these sites (Figure 2). Channel Entrance and Curlew are on the shallow forereefs while Lil Seb, LF Catch, LF Far Reef, and Peps are patch reefs are in the lagoon. The current profiles are important to consider for incoming larval fish if they select for habitat within the lagoon. Since these larval fish are usually coming from offshore if they choose to settle in the lagoon timing would be important for entering the channel. Especially since the current profiles show current speed and direction vary between these sites and that strong currents flow in and out of the lagoon. The four sites within the lagoon were surrounded by other patch reefs, seagrass, and mangroves, while the forereef sites sloped into a steep reef wall (Rützler & Macintyre 1982). When considering population dynamics, it is important to consider adjacent habitats, community functional groups, behavioral and oceanographic processes (Duffy et al. 2016; Paddack et al. 2009; Brandl et al. 2019). In these patch reef systems, fish are able to utilize different habitats within close proximity. Around Carrie Bow within the lagoon

there is a vast network of patch reefs surrounded by seagrass that allow more mobile fish to utilize these reef networks. It has been shown that fish communities benefit from connectivity between these important habitats and can enhance the adult population (Mumby et al. 2004; Green et al. 2015). When considering fish community composition, it is important to consider home ranges of the fish on each reef and consider proximity to nearby reefs.

Fish communities rely on benthic communities for habitat, where more complex and diverse habitats generally support higher abundances of fish species and functional groups, which in turn aids in reef resilience and recovery (Mumby & Steneck 2008; Graham et al. 2015; Wilson et al. 2006). Structural complexity is an important part of coral reef ecosystems and has been shown to impact the species diversity, recruitment potential, and reef fish community (Darling et al. 2017; Ferrari et al. 2016). Considering other benthic components influencing community composition can help management initiatives better protect healthy systems and restore already degraded ones. These changes in ecosystem processes and community structure can then have a negative feedback on these degraded reefs. Coral reefs are complex communities and need to be actively surveyed to understand present day reef communities and ensure preventative measures and effective management strategies against future disturbances. Along with surveying communities while trying to understand and monitor the effects of anthropogenic threats to an ecosystem it is important to conduct robust ecological studies, such as before after control-impact, to provide more accurate results of how community and biodiversity respond (Christie et al. 2019). Coral reefs are dynamic ecosystems and changes to the benthic community and structural complexity of a coral reef impact the communities that live within them.

It is important to recognize how the benthic community impacts the fish community and these are dynamics processes ultimately influencing reef resilience.

## Chapter 2

### HABITAT PREFERENCE OF JUVENILE CORAL REEF FISH

#### 2.1 Introduction

Coral reef organisms have strong habitat preferences for other reef organisms and benthic habitats that influence habitat selection (Coker et al. 2012; Coppock et al. 2013; Lecchini et al. 2013; Öhman et al. 1998). Structural complexity and coral rugosity are extremely important for influencing fish assemblages specifically for small fishes (Harborne et al. 2012). With coral reef ecosystems experiencing declining structural complexity and shifts in community composition it is essential to understand how these changes to reef communities may influence habitat preferences of reef organisms (Alvarez-Filip et al. 2011; Bell et al. 2013; Hughes et al. 2007). The loss of the major reef building coral *Acropora spp.* allowed for a shift in hard corals and an increase in other benthic groups, such as sponges and soft corals (Aronson and Precet 2001; Loh et al. 2015; Norström et al. 2009). This shift in reef community also changed the structural complexity of Caribbean coral reefs (Alvarez-Filip et al. 2009). The loss of major reef building corals and structural complexity of Caribbean reefs has shifted management practices to coral restoration, primarily focusing on *Acropora spp.* (Young et al. 2012). It is important to consider if this strategy alone can be enough to promote recovery in degraded areas by considering the number of corals that must be outplanted to be effective and to monitor the success after corals are outplanted. A lot of planning must go into restoration such as the vulnerability of nursery locations to disturbance, disease, and algal growth, to the required time, effort,

and money for success (Huntington et al. 2017; Ladd et al. 2019; van Woerik et al. 2018). Restoring a reef is not a simple task and most of the effort in the Caribbean has been put into outplanting *Acropora spp.*, but this may not be enough to facilitate the proper fish community required to sustain a healthy reef. It is important to consider the ecosystem dynamics of a healthy reef and what aspects of the benthic community fish may rely on while selecting a reef.

Habitat use and selection are based on behavioral responses to ecological interactions and require the organism to identify the tradeoffs between different habitats for foraging, growth, and predation risk (Grol et al. 2014; Dahlgren and Eggleston 2000). Habitat selection in the early life stages of reef fish is very important for population replenishment and connectivity of reefs. On extremely diverse ecosystems, such as coral reefs, there are complex interactions influencing habitat selection for example predation pressure and competition for space. Predation during settlement onto the reef is a critical time and during the first two days on a reef approximately half of newly settled fish are consumed (Almany & Webster 2006). Competition for space and food, both interspecific and intraspecific, also play an important role in settlement choice and affect survivorship (Almany 2004, Bonin et al. 2009, Carr et al. 2002). These interactions have been widely studied for juvenile fish and how these interactions influence habitat selection and survival (Adam et al. 2011; Benkwitt 2017; Lecchini et al. 2007; Preisser et al. 2007; White et al. 2010). Along with interactions between other reef organisms, many fish seek certain benthic organisms and have specific habitat preferences. Habitat selection is an important part of a reef organism's life, and a better understanding of the factors that play a role in fine scale settlement choices of larval organisms is required.

Many coral reef fishes display ontogenetic habitat shifts to combat strong competition and predation pressure on coral reefs by utilizing nursery habitats during the juvenile phase (Adam et al. 2006; Grol et al. 2011; Kimirei et al. 2013; Lecchini et al. 2007). This is a common strategy for many organisms to reduce tradeoffs between foraging and predation risk to allow for effective growth and survival (Adams et al. 2006; Dahlgren et al. 2006). Mangrove, seagrass, patch reef, and forereef systems allow for ontogenetic habitat movement and can enhance fish communities by providing protection from predators and lessening the population bottleneck (Mumby et al. 2004). Habitat use can change throughout an organism's life history and these nursery habitats can foster growth to certain sizes before requiring movement to an adult habitat. For example, Nassau grouper utilize macroalgal-coral-rubble complexes for juvenile settlement habitat, suggesting an ontogenetic shift to patch reefs then to forereefs (Eggleston 1995; Dahlgren & Eggleston 2000). Quantifying juvenile fish abundances and sizes between different habitats helps indicate what species may be displaying such ontogenetic shifts. By understanding habitat use and habitat preferences at the critical juvenile stage it can help to ensure suitable habitat is available for growth with cascading effects leading to healthy adult populations (Almany & Webster 2006; Carr et al. 2002; Nagelkerken et al. 2017; Öhman et al. 1998). If fish do utilize nursery habitats and ontogenetic shift strategies, then nursery areas must be considered when managing populations.

Herbivores are ecologically important for structuring marine benthic primary producer communities and bioerosion while facilitating coral growth (Adam et al. 2015; Hutchings 1986; Poore et al. 2012). Herbivores often have a strong top down impact on algal cover and succession of algal growth with species specific differences

on grazing effectiveness (Burkepile & Hay 2010; Mumby et al. 2006; Steneck et al. 2014). The community composition of herbivores on a reef enhances ecosystem functioning and resilience, so it is important to consider the diversity of herbivores and how these would respond to a disturbance to ensure each functional role is maintained (Bruno et al. 2019; Nash et al. 2016). The main herbivorous fish on coral reefs are in families Scaridae (parrotfish) and Acanthuridae (surgeonfish), with parrotfish being the dominate grazer (Burkepile & Hay 2008; Lewis and Wainwright 1985; Mumby 2006). Herbivore species, throughout ontogeny and between different species, can have a range of different feeding behaviors, diet preferences, and bite techniques (Bruggemann et al. 1994; Burkepile et al. 2019; Hanmer et al. 2017). Both surgeonfish and parrotfish may shift their feeding behavior and preference across different size classes thereby contributing to herbivore functional diversity and the impact on the benthic community by this functional group (Adam et al. 2018; Duran et al. 2019). Along with differences in feeding preferences, some herbivores such as parrotfish, exhibit differences in habitat use across size classes with some species utilizing nursery habitats (Bell & Kramer 2000; Mumby & Wabnitz 2002; Nagelkerken et al. 2002; Paddack & Sponaugle 2008; Tolimieri 1998). Although more research needs to be done on both parrotfish and surgeonfish to identify habitat preferences between specific benthic components that may contribute to habitat selection. The ecological differences herbivores can perform from feeding behaviors to habitat use across ontogeny by different species is important to consider for management of this critical group and overall reef resilience.

In this chapter, the habitat preferences of juvenile striped parrotfish, *Scarus iseri* and ocean surgeonfish, *Acanthurus tractus* were investigated through surveys and

a series of laboratory experiments. First, identification and abundance of juvenile fish and benthic composition in a rubble reef area were assessed using belt transects. Next, habitat preferences were assessed in the lab by a series of cafeteria-style choice experiments designed to test for preferences between common hard corals, soft corals, algae, and sponges. Finally, patterns of juvenile fish distribution and size class abundance on reefs surrounding Carrie Bow Cay were investigated to determine if habitat mediated ontogenetic shifts were occurring in these two important species.

## **2.2 Methods**

### **2.2.1 Study Site and Species**

This study was conducted at Smithsonian Research Station Carrie Bow Cay (CBC), Belize (16°48'9.26"N, 88° 4'54.87"W) between April 2018 – September 2018 (Figure 1).

The main study species, striped parrotfish *Scarus iseri*, and ocean surgeonfish *Acanthurus tractus*, are common herbivorous fish in the Caribbean and ecologically important for managing algal cover (Figure 11) (Adam et al. 2015; Burkepile & Hay 2010; Mumby 2006; Williams & Polunin 2001). These fish are both found in high abundance in the area and contribute to reef resiliency (Burkepile and Hay 2011; Mumby et al. 2004). *Acanthurus spp.* pelagic larval duration (PLD) ranges from 40 to 70 days, *Scarus spp.* has a similar PLD of approximately 60 days (Robertson et al. 2006; Rocha et al. 2002). *S. iseri* are a smaller bodied parrotfish that commonly school; these fish feed using a scraping method that typically consumes turf algae and some fleshy macroalgae (Adam et al. 2015; Dromard et al. 2015; Mumby and Wabnitz 2002). *A. tractus* are also commonly found in schools. During the juvenile phase this

species typically feeds on macroalgae, such as *Dictyota spp.*, then as adults *A. tractus* feed primarily on turf algae and occasionally consume calcareous algae (Duran et al. 2019; Wolf 1987).

Hard corals are the key building block for habitat structure on a coral reef. The structural complexity hard corals provide heavily influences the overall reef community composition. As a result, specifically for hard coral choice experiments I tested an additional three common fish species found in this area were. *Sparisoma viride*, the stoplight parrotfish, is a larger bodied common parrotfish in the Caribbean generally eating algae over growing coral and occasionally consuming coral and in some places recruit to *Porites spp.* (Bruggemann et al. 1994; Burkepile et al. 2019; Tolimieri 1998). *Acanthurus coeruleus*, blue tang, is a common herbivore typically feeding on turf algae and forming schools (Semmens et al. 2005). *Stegastes diencaeus*, longfin damselfish, is a common territorially damselfish and in adults rarely move territories unless for high quality nest site prompting high intraspecific competition (Cheney & Côté 2003).

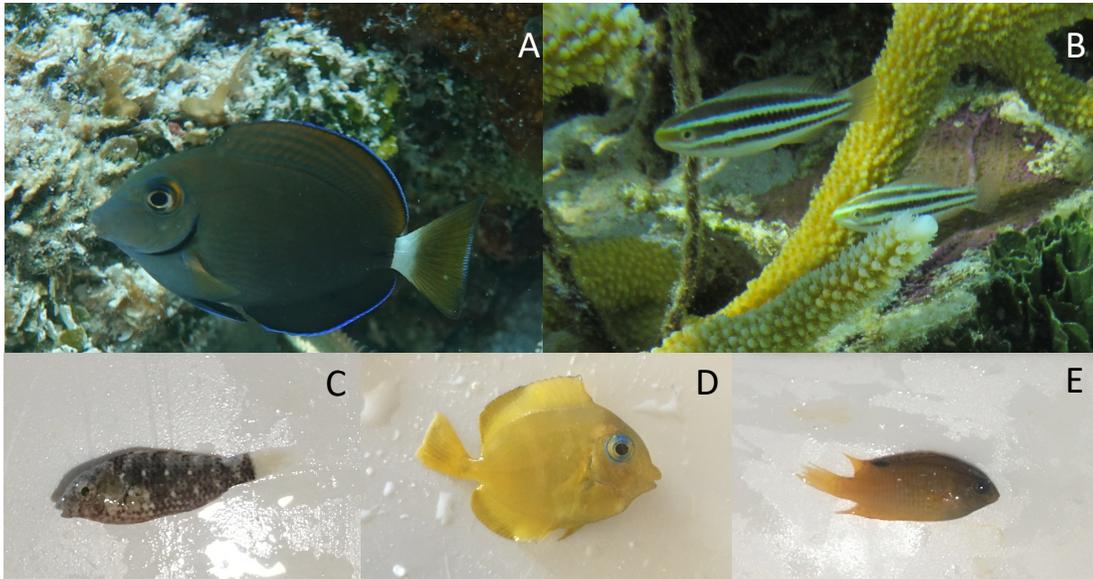


Figure 11: Photos of study species *Acanthurus tractus* (A), *Scarus iseri* (B), *Sparisoma viride* (C), *Acanthurus coeruleus* (D), and *Stegastes dienaecus* (E).

### 2.2.2 Rubble Transects

Assessment of the shallow rubble reef (Figure 12) surrounding Carrie Bow Cay (CBC) was conducted using 20 × 2 m belt transects (n=5). This area was surveyed due to high abundance of juvenile fishes.



Figure 12: Picture of Carrie Bow from above showing area where rubble transects were conducted. Orthomosaic was from Open Reef Mapping Society, Citizen Science GIS, The Smithsonian Institute, and University of Central Florida.

Five transects were conducted once a month between April – September 2018. Using methods similar to those described above, transect tapes were placed in a randomly selected location with care not to overlap previous transect locations, five minutes after being laid out, the fish community was assessed through GoPro (Hero 5) video recording. Upon completion, the same transects were surveyed to assess the benthic community. This was done by recording the benthic species that were found underneath 40 randomly previously marked points along the transect tape and photos were taken of all benthic species. Fish and benthic communities were identified to

lowest possible classification using the videos and photos at the University of Delaware. Fish stage (juvenile, intermediate, and adult) was assessed by color phase. Any benthic species that appeared on the transects less than 5 times were pooled into a category other (*Siderastrea spp.*, *Gorgonia spp.*, *Ircinia spp.*, *Syringodium filiforme*, and *Thalassia testudinum*).

### **2.2.3 Habitat Choice Experiments**

A cafeteria-style choice experiment was used to assess the habitat preferences of *A. tractus* (Standard length range:3.2-5.1cm) and *S. iseri* (Standard length range:2.0-4.2cm). Previous studies have used a similar design to understand behavioral characteristics of fish in the laboratory and field (Brooker et al. 2013, Hoey & McCormick 2004, McCormick et al. 2018, Ruhl & Dixson 2019). Fish were collected from shallow rubble reefs surrounding CBC on snorkel using clove oil and hand nets. Fish were immediately transported to the CBC wet lab where they were held in aquaria (38 L) with flowing seawater and shelter (PVC piece). Fish were held for at least 24 hrs. before use in experiment.

To assess possible habitat preference, a series of choice experiments between common benthic species (hard corals, soft corals, algae, and sponges) was conducted. The benthic species were collected from nearby reefs by searching for individuals at desired size before collection. To minimize the damage to the benthic species, individuals selected for experimental use were chiseled underneath (soft corals and sponges), chiseled off of the colony (hard corals), or dislodged at the base (algae). Organisms were transported back to the laboratory and held in flow-through aquaria (38 L) and given at least 24 hrs. to recover from handling and stress before starting experiments. The size of each benthic species was based on size of aquaria with a

maximum height of ~ 26 cm, but for each experiment benthic organisms use options were size matched for each experimental group tested.

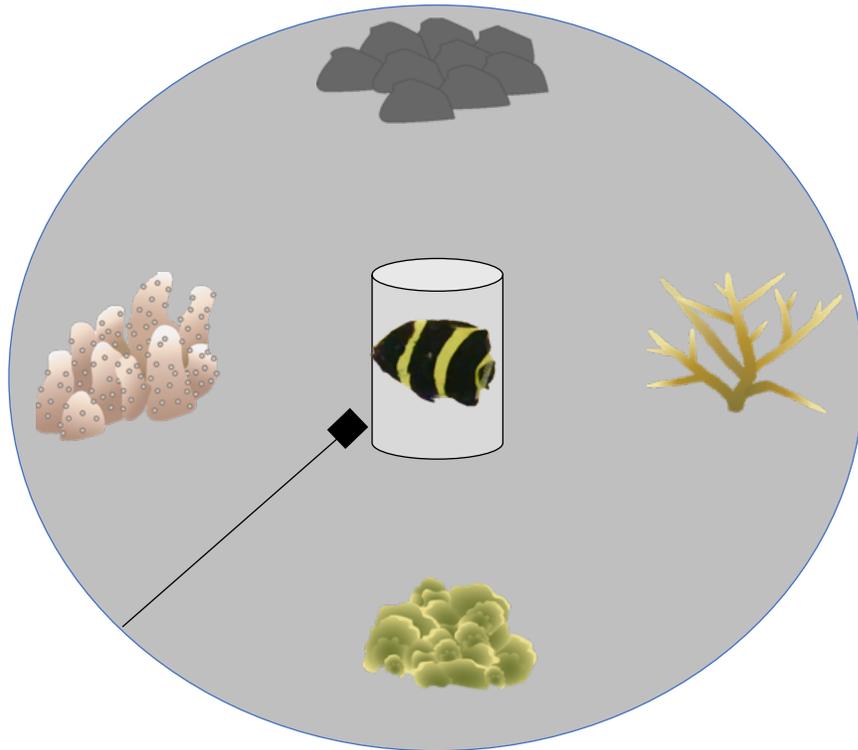


Figure 13: Experimental design of cafeteria-style choice aquaria with four habitat options (three hard corals and rubble shown), habituation chamber, and air stone.

Experiments were conducted in circular aquariums  $1.2 \times 1.2 \times 0.3$  m (340 L) with an air stone secured to the bottom center (Figure 13). Partial water changes were conducted between each trial to ensure similar water conditions and temperature to natural ocean water. Benthic species were spaced an equal distance from each other and positioned vertically at the edge of the aquaria. The position of the benthic species

were haphazardly rotated for each trial. After placement, benthic species were given a one-hour habituation period before the experimental began. At the start of each trial, a single fish was placed in a habituation chamber ~10 cm diameter, constructed from plastic mesh ( $1.27 \times 1.27$  cm) and fly screen ( $1 \times 1$  mm), for 30 minutes. This time frame is typically sufficient for habituation (Brooker et al. 2013; Coker et al. 2009; Ohman et al. 1998). The design of the habituation chamber ensured the sensory cues of the benthic choices were available to the fish, however access was restricted. At the start of each trial, habituation chambers were slowly raised, taking care to not influence the trajectory of the fish. The fish's position was then recorded every 15 sec for 15 minutes and then checked after 30 minutes, 1 hour, 2 hour, and 3 hour time point. During the first 15 minutes and checks afterwards observers remained in one position with minimal disturbance to the fish as possible. Fish were considered associated with a habitat when they were within 14 cm of either four habitat options swimming slowly or stationary, otherwise fish were marked as not associated. Each experiment was run with 3 benthic species habitat choices and rubble as a nonspecific habitat choice (Figure 13). Data were recorded as presence/absence of individuals ( $n=20$  for each experiment) found on each habitat choice at each time point, and the 15-minute observations were pooled and marked for the habitat the fish was found on the most. Individuals were only used once and experiments were conducted between May-September 2018.

Habitat choice associations were not independent and therefore analyzed with a binomial generalized linear mixed effects model conducted in R (R Core Team 2019). The model tested association with treatment and time as fixed effects, fish as a random effect, and family binomial (package lme4). If treatment was significant post-

hoc test (Tukey) was run for pairwise comparison between treatments (package multcomp).

### 2.2.3.1 Experiment 1: Hard Corals

To test for preference between common hard corals, *Agaricia tenuifolia* (Lettuce coral), *Porites furcata* (Finger coral), and *Acropora cervicornis* (Staghorn coral) were used as well as rubble for a nonspecific habitat choice. *A. tenuifolia* is a common branching coral and after *Acropora* die off in the 1980's *A. tenuifolia* became the dominate coral on reefs in this area (Aronson and Precet 2001; Aronson et al. 2002). *P. furcata* is the main branching coral observed in the rubble transects and was found to replace *Acropora* after the die off in the 1980's on <1m shallow reefs (Aronson et al. 1998). Although *Acropora* are no longer major reef building corals, *Acropora cervicornis* is a restoration relevant coral. *A. cervicornis* is also the more structurally complex *Acropora spp.* (Young et al. 2012). Structurally complexity has been shown to influence recruitment of fish larvae and juveniles, as it provides protection during these vulnerable stages (Coker et al. 2012, Geange & Stier 2010, Öhman et al. 1998). Throughout the Caribbean *Acropora spp.*, usually *Acropora cervicornis*, are the main coral outplanted (Huntington et al. 2017; Young et al. 2012). However, if we are to effectively restore reef ecosystems it is vital that we know the species of hard coral that are preferred by ecosystem engineering fish species. This experiment hopes to rectify this by investigating the preferences of two important juvenile herbivorous fishes towards different hard coral habitat options.

### **2.2.3.2 Experiment 2: Soft Corals**

To test for preference between common soft coral, *Antilloorgia americana* (*Slimy sea Plume*), *Briareum asbestinum* (Corky Sea Finger), and *Gorgonia spp.* (Sea Fan) were used as well as rubble for a nonspecific habitat choice. Soft coral such as *Gorgonia spp.* have been shown to produce chemical defenses that may influence habitat use for various organisms (Van Alstyne & Paul 1992, Harvell et al. 1996, Pawlik & Fenical 1992). The Caribbean has seen a shift in benthic communities from hard coral dominance to an increase in other benthic types such as soft coral that can provide structural complexity (Williams et al. 2015). A change in benthic community and ecosystem functioning may influence fish habitat use, therefore, it is important to understand how fish habitat selection is influenced by these soft corals as they make up a large part of the benthic community.

### **2.2.3.3 Experiment 2: Macroalgae**

To test for preference between common macroalgae, *Halimeda spp.* (Calcareous green algae), *Dictyota spp.* (Fleshy brown algae), *Laurencia spp.* (Fleshy red algae), were used as well as rubble for a nonspecific habitat choice. Marine macroalgae are a diverse group, and provide important ecological functions on coral reefs (Fong and Paul 2011). Algae compete with corals through chemical allelopathy or shading for space on coral reefs (McCook et al. 2001; Rasher & Hay 2010). Herbivory plays an important role on the species composition and abundance of both algae and corals (Hay & Fenical 1988). Many characteristics can deter some herbivores, such as morphology, chemical defenses, and dietary preferences (Hanmer et al. 2017). Much of the research to date has focused on investigating herbivore and algal preferences through feeding preferences (Adam et al. 2018; Hanmer et al. 2017).

This experiment aims to identify if juvenile herbivores have any habitat association preferences and if they match their feeding preferences at this stage.

#### **2.2.3.4 Experiment 4: Sponges**

To test for preference between common sponges, *Iotrochota birotulata* (Green finger sponge), *Callyspongia plicifera* (Azure vase sponge), and *Aplysina cauliformis* (Lavender rope sponge) were used as well as rubble for a nonspecific habitat choice. A shift in the benthic communities around the Caribbean has resulted in a decrease in hard coral and increase in other habitat types, such as sponges (Diaz & Rützler 2001, Norström et al. 2009). This increase in sponge abundance changes the structural complexity of these reefs, which may in turn influence habitat use of reef organisms. Sponges mainly use two strategies either producing secondary metabolites to deter predation or chemically undefended sponges allocate resources into faster growing and higher reproduction (Loh & Pawlik 2014; Walters & Pawlik 2005). Most of the research conducted on sponges focuses on taxonomy and secondary metabolites, but not much is known on how a community change to sponge dominant reefs will influence fish habitat use.

#### **2.2.4 Size Class Observations**

After investigating the rubble community composition, and habitat preferences in lab trials, the abundance and size classes of the two fish species were determined at various sites around CBC. This was done to determine if habitat use of these two fish species differs at various size classes. Fish distribution was obtained using data collected for Reef life survey in September 2019 (<https://reeflifesurvey.com>; Duffy et al. 2016; Edgar & Stuart-Smith 2014). These transects were 50 × 10 m, recording fish

to a species level and size classes of total length were recorded (2.5, 5.0, 7.5 10.0, 12.5, 15.0, and 20 cm). These surveys were conducted at five sites, at differing depths depending on the reef (CBC house reef- 4m, CBC lagoon-5 m, Tobacco-10m, CBC reef-10m, and South Reef-10m).

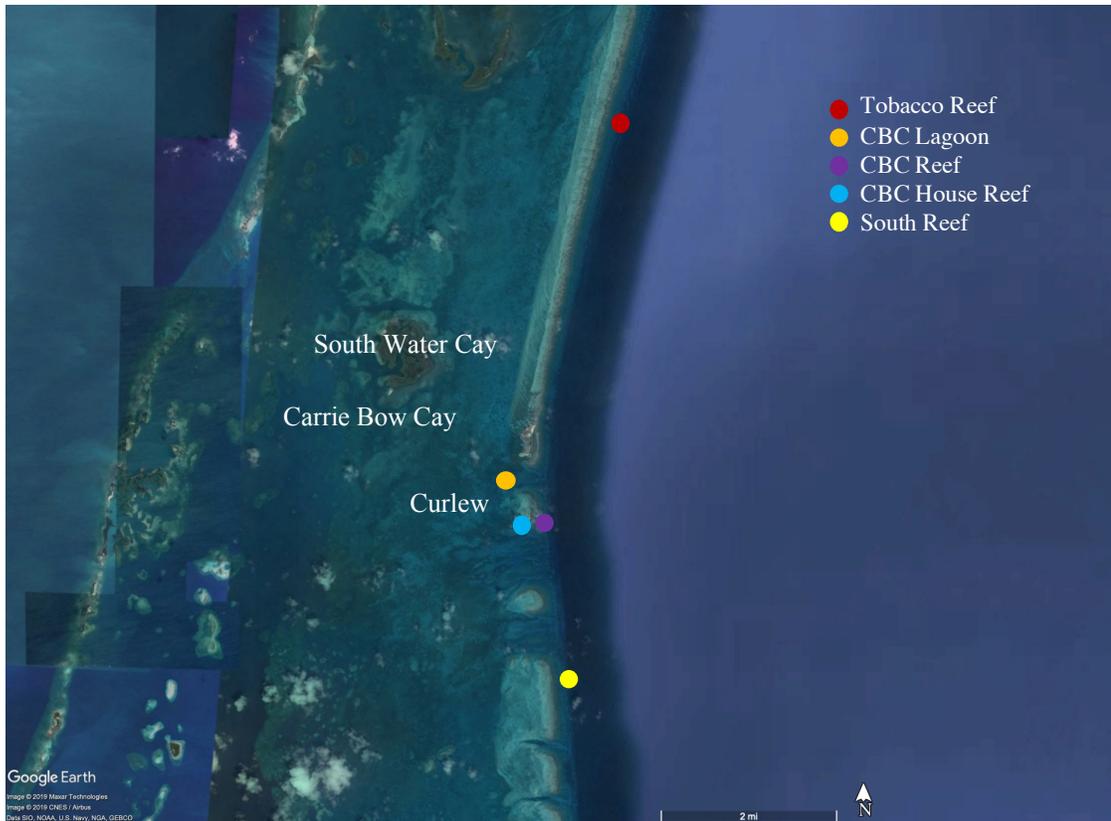


Figure 14: Google earth map of size class survey sites (Google earth image 2019).

## 2.3 Results

### 2.3.1 Rubble Transects

The benthic community was primarily comprised of turf algae, *Dictyota spp.*, *Laurencia spp.*, *Porites furcata*, and sand (Figure 15). The main coral identified was *Porites furcata*, a structurally complex branching coral favorable for small bodied and juvenile fish.

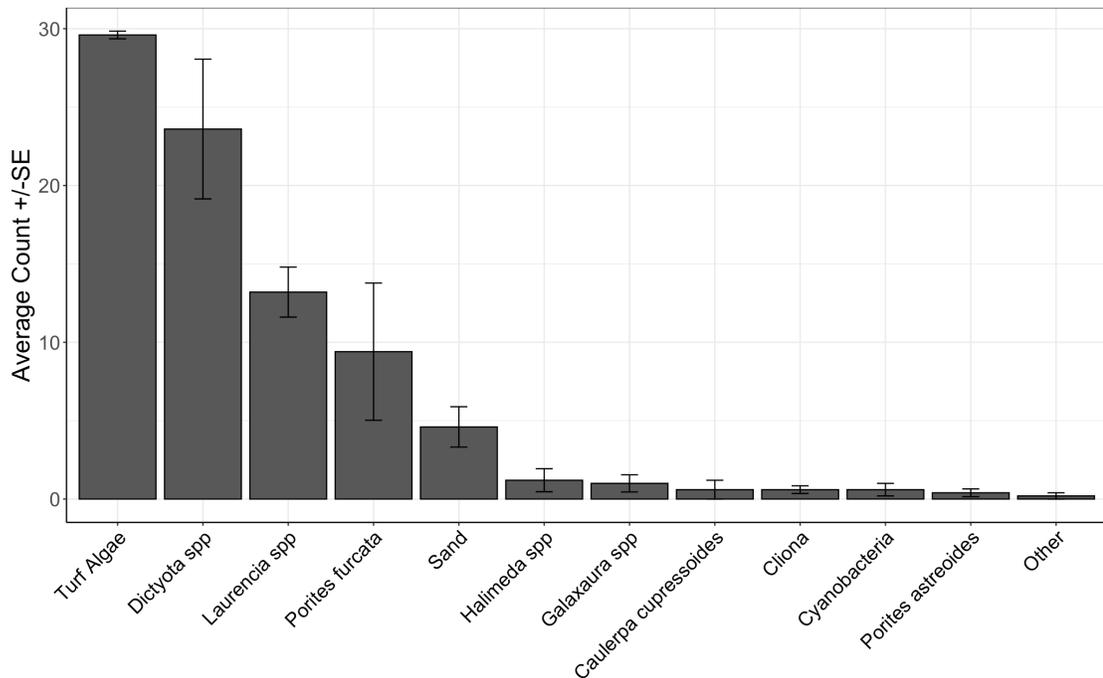


Figure 15: Rubble transects average count ( $\pm$  SE) of benthic organisms for July 2018.

The fish community was primarily composed of Labridae, Scaridae, and Pomacentridae of both juvenile and adult phases (Figure 16). The four most abundant

genera were in the juvenile phase suggesting this area may be a temporary habitat for some fishes.

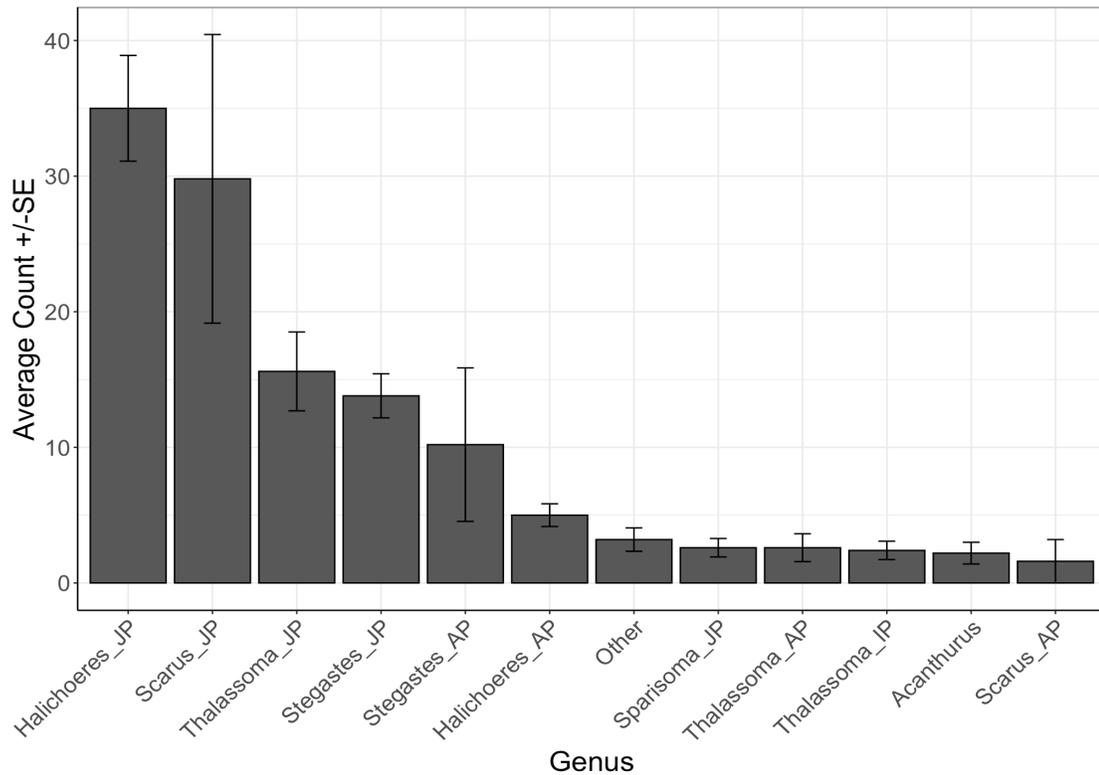


Figure 16: Rubble transects average count ( $\pm$  SE) of fish genus for July 2018.

Specifically focusing on *A. tractus* and *S. iseri* over the six months surveyed show a peak in abundance was detected in June and July (Figure 17). *A. tractus* was less abundant in this area and their abundance peaked in June. *S. iseri* was much more common and their abundance peaked in July. Summer, specifically June and July, is peak time for recruitment and settlement of these fish in this area.

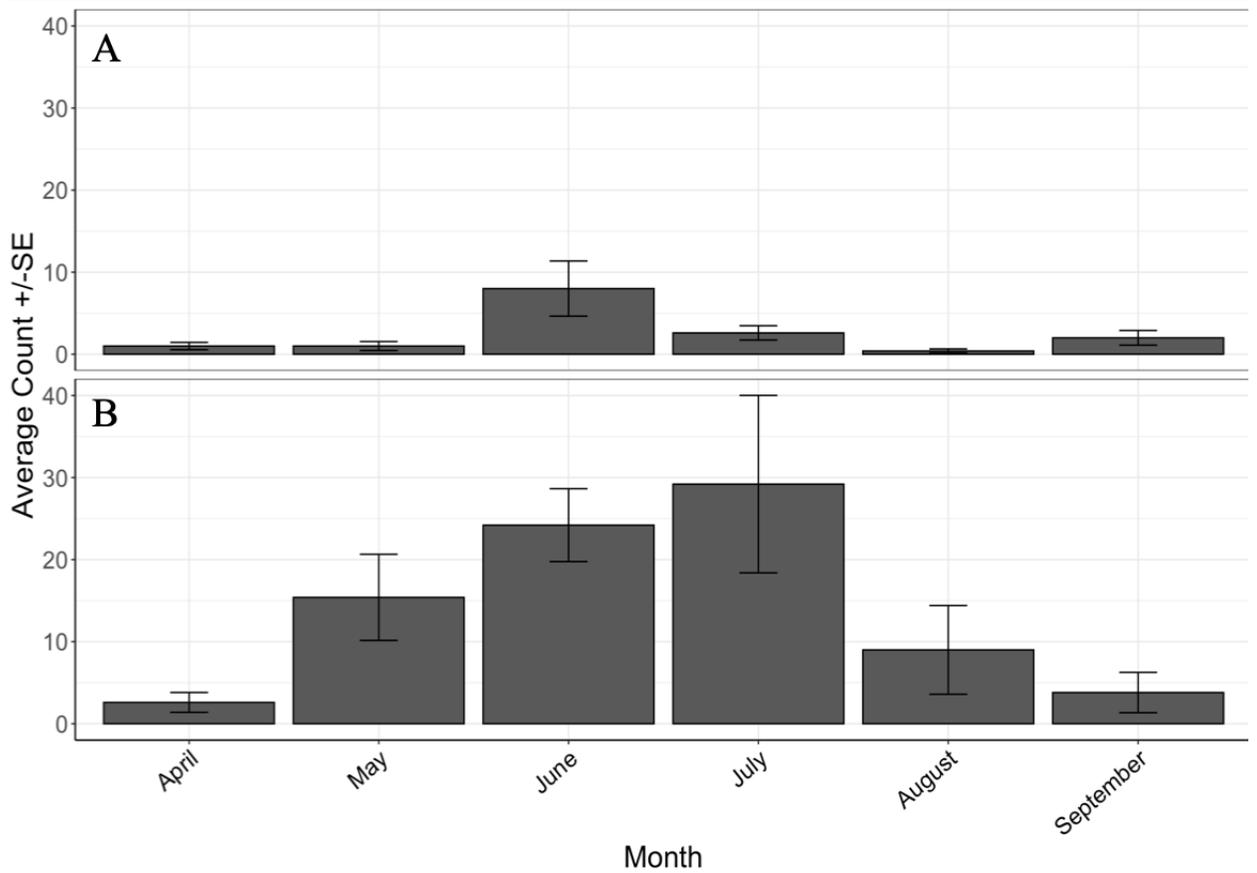


Figure 17: Average count ( $\pm$  SE) of juvenile A) *A. tractus* and B) *S. iseri* from rubble transects by month.

### 2.3.2 Habitat Choice Experiments

#### 2.3.2.1 Experiment 1: Hard Corals

In the habitat preference experiment with common hard corals, *Agaricia tenuifolia* (Lettuce coral), *Porites furcata* (Finger coral), *Acropora cervicornis* (Staghorn coral), and rubble showed time had no significant effect on association for all species. Treatment had a significant effect on association ( $p < 0.001$ ). *S. iseri*

associated preferentially with *P. furcata* significantly more than *Agaricia tenuifolia*, *Acropora cervicornis*, and rubble (Figure 18 A).

*A. tractus* also associated significantly more with *P. furcata* than *A. cervicornis* and rubble (Figure 18 B). They also associated more with *A. cervicornis* over rubble and not associating. *A. tenuifolia* was associated with significantly more than rubble and no association. There was no significant difference between association with *A. tenuifolia* compared to *P. furcata* or *A. cervicornis* was detected although percent association for *A. tenuifolia* was higher than *A. cervicornis* but less than *P. furcata*.

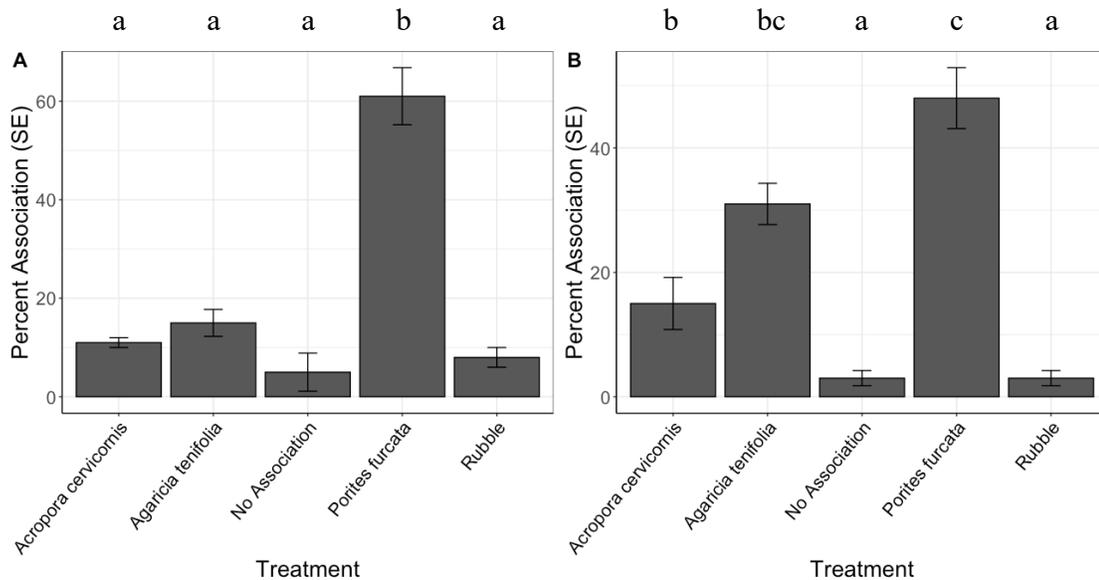


Figure 18: Percent association ( $\pm$  SE) of hard coral habitat choices for *S. iseri* (A) and *A. tractus* (B) individuals (n=20). Habitat choices that are significantly different, identified from Tukey post-hoc test, designated by letters.

The stoplight parrotfish, *Sparisoma viride*, significantly preferred *P. furcata* more than *A. tenuifolia*, *A. cervicornis*, and rubble (Figure 19 A). Meanwhile, the blue tang, *Acanthurus coeruleus*, preferred *P. furcata* over all other habitat choices. The second highest choice was for *A. tenuifolia* which was significantly higher than the rubble and no association choices. However, there was no difference between *A. tenuifolia* and *A. cervicornis* (Figure 19 B). The long fin damsel, *Stegastes diencaeus*, preferred *P. furcata* and *Agaricia tenuifolia* over *A. cervicornis*, rubble, and no association (Figure 19 C).

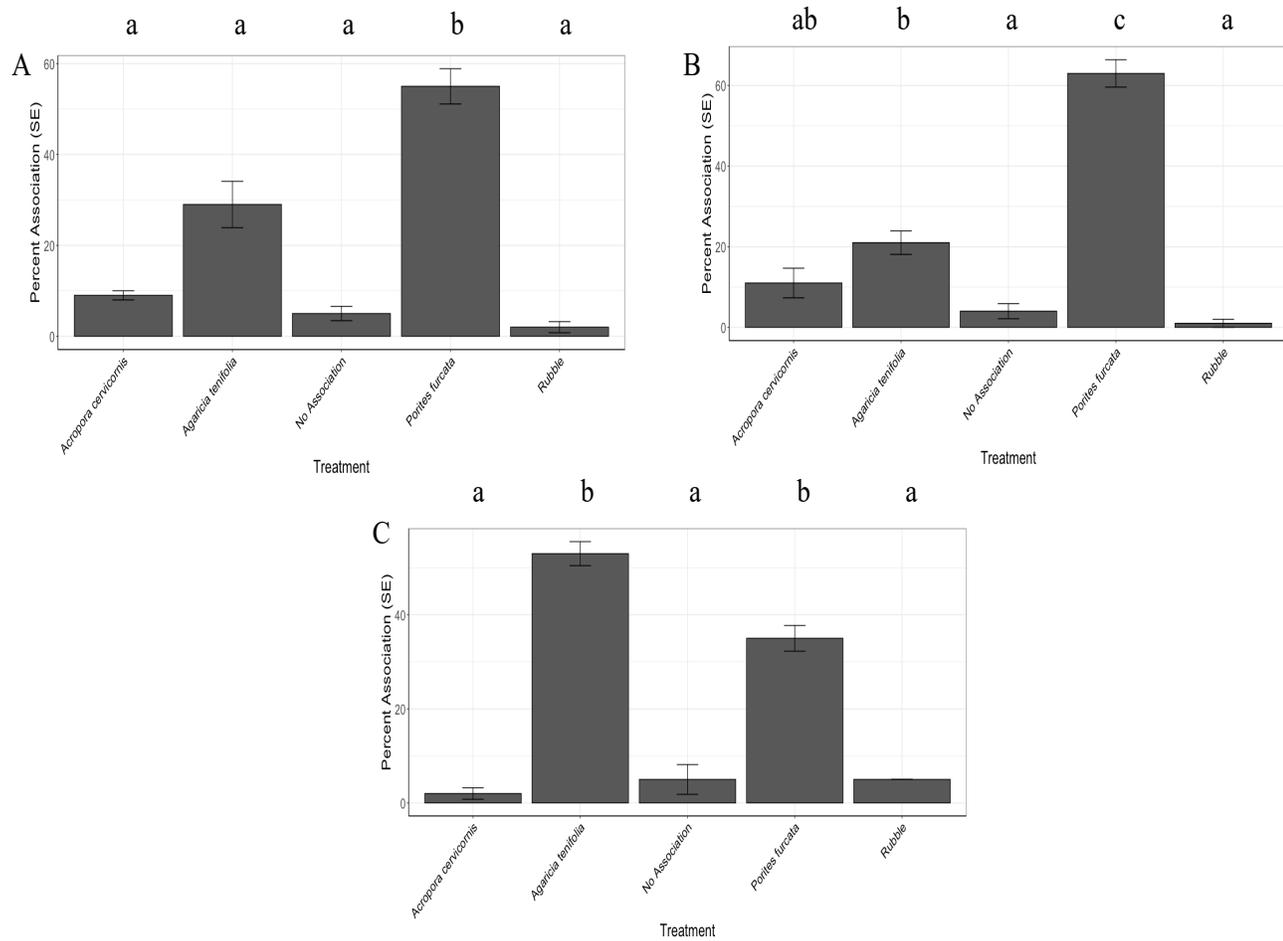


Figure 19: Percent association ( $\pm$  SE) of hard coral habitat choices for *Sparisoma viride* (A), *Acanthurus coeruleus* (B), and *Stegastes diencaeus* (C) individuals (n=20). Habitat choices that are significantly different, identified from Tukey post-hoc test, designated by letters.

### 2.3.2.2 Experiment 2: Soft Corals

In the habitat preference experiment with common soft coral, *Antillologorgia americana* (Slimy sea Plume), *Briareum asbestinum* (Corky Sea Finger), *Gorgonia ventalina*. (Sea Fan), and rubble showed time had no significant effect on association for all species. Treatment had a significant effect on association ( $p < 0.001$ ).

*S. iseri* associated significantly more with *A. americana* and *B. asbestinum* over *Gorgonia ventalina*, rubble, and no association (Figure 20 A).

*A. tractus* significantly associated more with *B. asbestinum* over rubble and no association. Also *A. tractus* associated significantly more with *Gorgonia ventalina* over not associating (Figure 20 B).

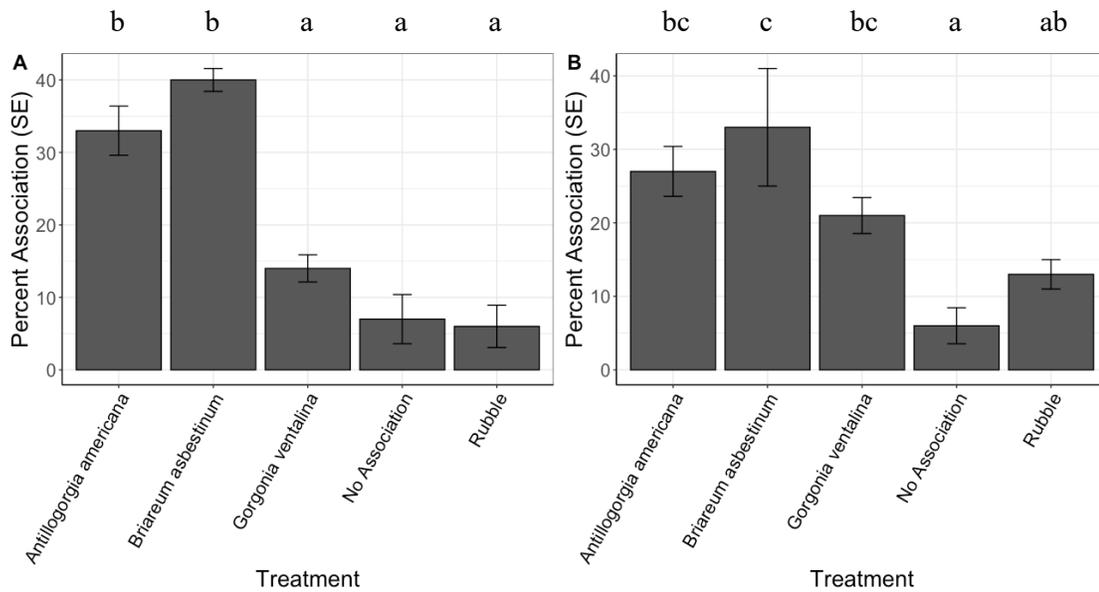


Figure 20: Percent association ( $\pm$  SE) of soft coral habitat choices for *S. iseri* (A) and *A. tractus* (B) individuals (n=20). Habitat choices that are significantly different, identified from Tukey post-hoc test, designated by letters.

### 2.3.2.3 Experiment 3: Algae

In the habitat preference experiment with the common macroalgae, *Halimeda spp.* (Calcareous green algae), *Dictyota spp.* (Fleshy brown algae), *Laurencia spp.* (Fleshy red algae), and showed time had no significant effect on association for all species. Treatment had a significant effect on association ( $p < 0.001$ ). *S. iseri* and *A.*

*tractus* had the same habitat preferences between these choices, associating significantly more with *Dictyota spp.* and *Laurencia spp.* over rubble and no association (Figure 21 A & B). They also associated with *Halimeda spp.* significantly more than no association, but no significant difference between *Dictyota spp.* or *Laurencia spp.* was detected.

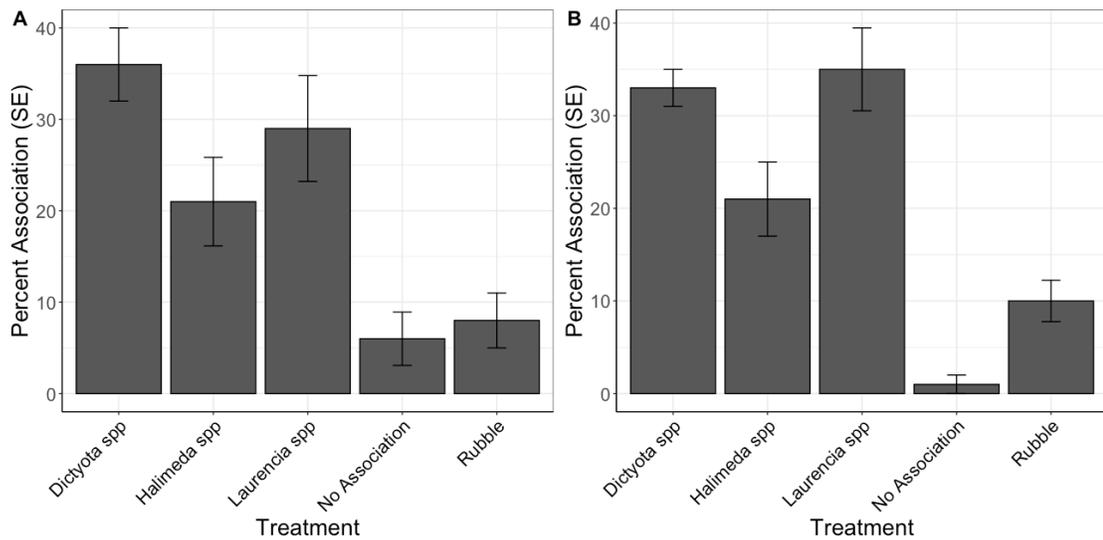


Figure 21: Percent association ( $\pm$  SE) of Algae habitat choices for *S. iseri* (A) and *A. tractus* (B) individuals (n=20). Habitat choices that are significantly different, identified from Tukey post-hoc test, designated by letters.

#### 2.3.2.4 Experiment 4: Sponges

In the habitat preference experiment with the common sponges, *Iotrochota birotulata* (Green finger sponge), *Callyspongia plicifera* (Azure vase sponge), *Aplysina cauliformis* (Lavender rope sponge), and rubble showed time had no significant effect on association for all species. Treatment had a significant effect on association ( $p < 0.001$ ). *S. iseri* associated significantly more with *A. cauliformis* than *I.*

*birotulata*, *C. plicifera*, rubble, and no association. Also *C. plicifera* and rubble were associated with significantly more than *I. birotulata* and no association (Figure 22 A).

*A. tractus* preferentially associated with *C. plicifera* significantly more than all other habitat choice (Figure 22 B).

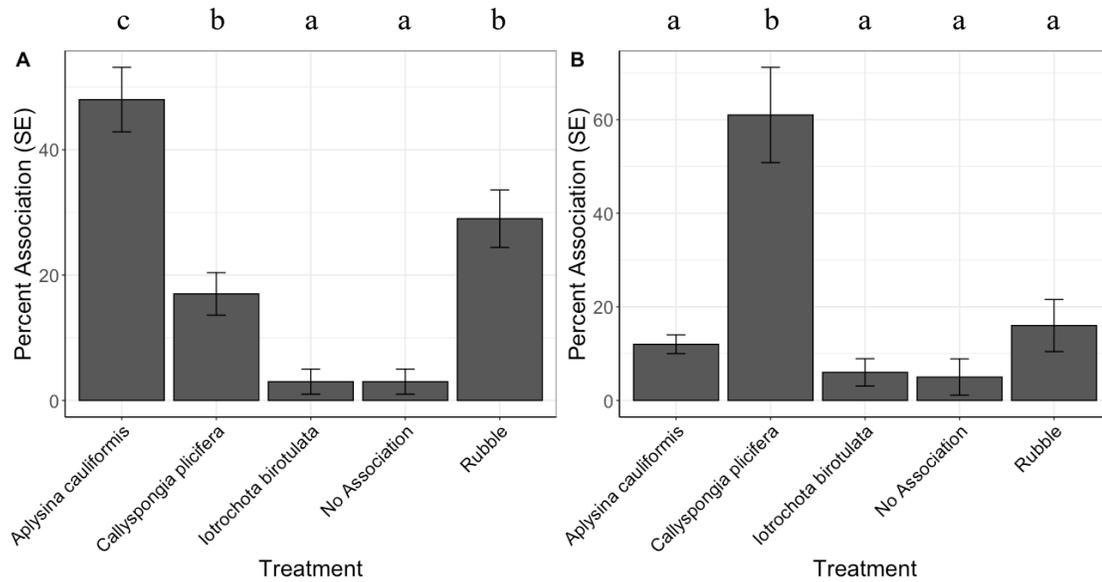


Figure 22: Percent association ( $\pm$  SE) of sponge habitat choices for *S. iseri* (A) and *A. tractus* (B) individuals (n=20). Habitat choices that are significantly different, identified from Tukey post-hoc test, designated by letters.

### 2.3.3 Size Class Observations

The parrotfish and surgeonfish size class surveys revealed interesting trends in size across locations (Figure 23). *A. tractus* was less abundant and more variable, but the majority and most of the size classes were seen at CBC reef. *S. iseri* is more abundant and typically the bigger size classes were found CBC Reef, South Reef, and Tobacco reef which were deeper reefs (10m). The smaller size classes, especially 2.5

cm, were in higher abundance on CBC house reef, which is the closest site to where the rubble transects were conducted (Figure 12 & 14). Based on the size data, *S. iseri* seem to be move onto the deeper reefs once they have grown to 7.5 cm. This suggests this species may be seeking refuge on the shallow areas at the smaller 2.5 and 5 cm size classes and then moving to deeper depths once reaching 7.5 cm.

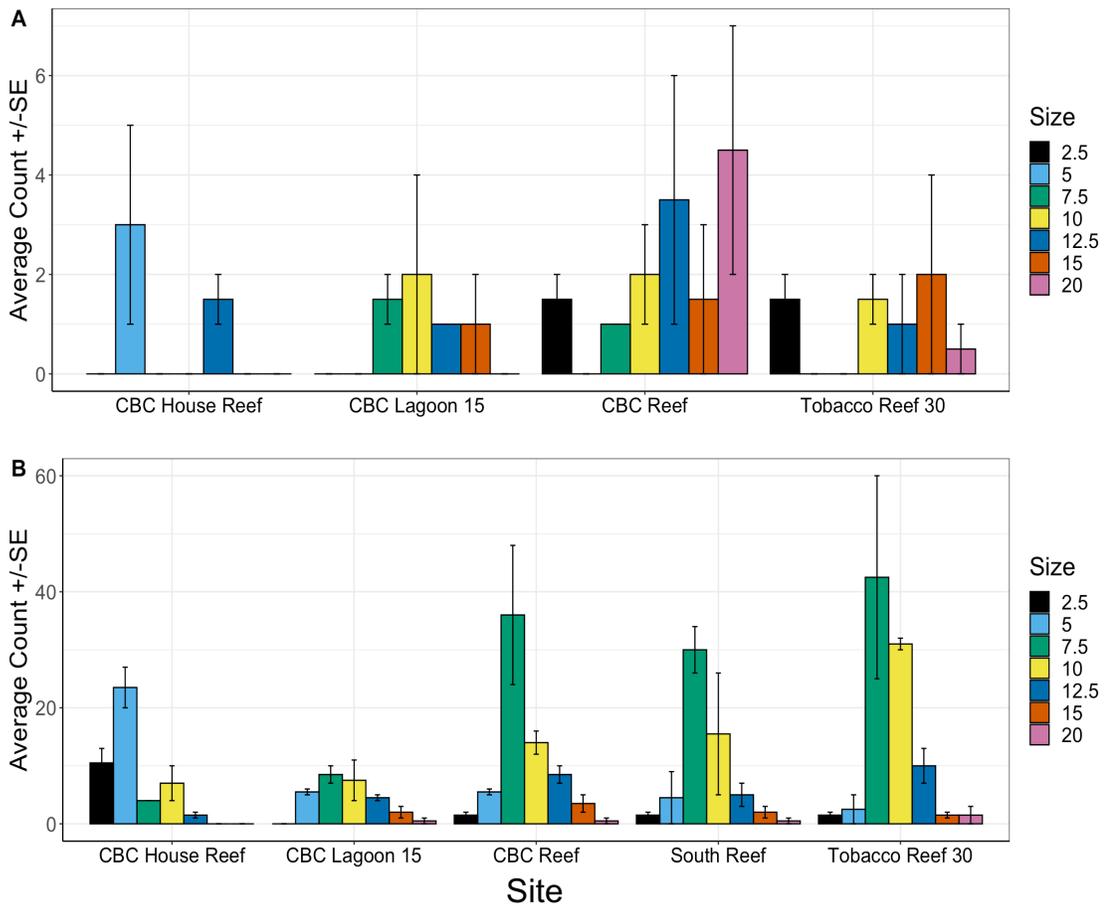


Figure 23: Size class survey average count ( $\pm$  SE) of *A. tractus* (A) and *S. iseri* (B) by site. Note the differences in magnitude for average counts and one site difference between species.

## 2.4 Discussion

Habitat selection is a critical time for juvenile fish. With predation pressure high, fish are faced with tradeoffs in predation risk during foraging to optimize growth and survival during ontogeny (Almany & Webster 2006; Grol et al. 2010). During this time of high predation pressure and high competition, many coral reef fish display ontogenetic habitat use, beginning with nursery habitats as juveniles before moving to adult habitats (Jones et al. 2010; Lefcheck et al. 2019). Along with general habitat selection fish may have preferred habitat that can influence their habitat use on a reef and play a role in habitat selection (Coker et al. 2012; Lecchini et al. 2013; Öhman et al. 1998). Size class observations of *S. iseri* and *A. tractus* shows in this area both species may be using shallow back reef and lagoon habitats at smaller size classes before going onto deeper forereefs. This pattern of habitat shift was particularly apparent for *S. iseri*. *A. tractus* typically form large schools and are more mobile while *S. iseri* have smaller home ranges (Rocha et al. 2002; Mumby & Wabnitz 2002). *S. iseri* abundance on deeper reefs peaked at the size class 7.5 cm, suggesting that size may provide enough predation relief to move onto forereef habitat. The 2.5 cm and 5 cm size classes were abundant on CBC house reef, which is very close to where I conducted my rubble transects and collected all fish for choice experiments that were around 2.5-5 cm (Figure 12 & 14). This shallow rubble area surrounding CBC and adjacent to CBC house reef is likely serving as a temporary habitat for juveniles to grow. The rubble transects showed an abundance of juvenile Labridae, Scaridae, and Pomacentridae, which may indicate that the rubble location provides refuge and food to smaller size classes before moving to the forereef. Eggleston (1995) found that newly settled Nassau groupers in the Bahamas utilized habitats of macroalgal-coral complexes primarily comprised of *Laurencia spp.* and *Porites spp.* during the summer.

Juvenile Nassau groupers exhibited an ontogenetic shift from this macroalgal-coral habitat moving to patch reefs in early fall based on size class abundance patterns at these different habitats. Similar patterns were observed in this study focusing on the rubble habitat surrounding CBC, which had a similar macroalgal-coral habitat and showed a high abundance of juveniles that peaked in June and July. These observed patterns of habitat use from the rubble transects and size class surveys also correspond to some of the preferences these juvenile fish exhibited in laboratory choice experiments.

The hard-coral experiments showed both *S. iseri* and *A. tractus* significantly preferred *P. furcata*. *A. tractus* also preferred *A. tenifolia* as a second choice, and both species preferred *P. furcata* over *A. cervicornis*. *P. furcata* is a shallow water branching coral and was abundant on the rubble transects while *A. tenifolia* is an abundant hard coral on reefs in this area and *A. cervicornis* is infrequent although actively used in coral reef restoration throughout the Caribbean. The preference for *P. furcata* may indicate these juvenile fish select for this coral because it is prevalent in the shallow rubble area and the high structural complexity it provides. *P. furcata* was prevalent on my rubble transects, but reef transects conducted in Chapter 1 showed a similar branching *Porites spp.* was also abundant and significantly influenced the juvenile species community. Juvenile fish may seek out areas with these branching *Porites spp.* that may aid in providing relief from predators. *Sparisoma viride* (stoplight parrotfish) and *Acanthurus coeruleus* (blue tangs) also preferred *P. furcata* while *Stegastes diencaeus* (longfin damsel) had a split preference of *P. furcata* and *A. tenifolia*. The damselfish *S. diencaeus* significantly preferred both *P. furcata* and *A. tenifolia*, unlike most other fish tested preferred *P. furcata*. Overall most of the fish

tested preferred *P. furcata*, followed by *A. tenifolia*, and associated with *A. cervicornis* the least. It is important to consider habitat use and preferences between common benthic habitats, since reef restoration is becoming a normal practice done by both scientists, managers, and nonprofit conservation groups. Reef restoration and coral gardening must be economically viable with proper training of those conducting gardening and restoration techniques for successful restoration (Lirman & Schopmeyer 2016). *A. cervicornis* is a common coral used in restoration, however results found both *S. iseri* and *A. tractus* do not preferentially associate with this coral.

The choice experiment between common soft corals revealed *S. iseri* had a split preference for soft coral and associated significantly more with both *A. americana* and *B. asbestinum* than the other habitat choices. *A. tractus* significantly preferred *B. asbestinum* more than rubble and no association, while *A. americana* and *G. ventalina* association was only significantly different than no association. This was interesting as the reef transects conducted in Chapter 1 revealed soft corals had a significant influence on fish functional group, specifically the genus *Antillologorgia*. Both species did associate with *A. americana*, and *S. iseri* had a stronger preference for both *A. americana* and *B. asbestinum*, although *A. tractus* preferred *B. asbestinum* more. These two soft corals both appeared on the reef transects; However, *B. asbestinum* was not as common and was not found on all reefs surveyed. Although *Gorgonia spp.* was found on the rubble transect it only appeared once and was therefore grouped into the other category. Soft corals are not prevalent in the rubble area where these juveniles are seen in higher abundances, but rather out on the reefs. While these fish are seen in high abundances in non-reef habitats, they still recognize reef components such as soft coral. Both species of fish tested were willing to

associate with soft corals and show preference between the most common soft corals found on reefs.

*S. iseri* and *A. tractus* had the same algal habitat preference split between two choices, associating significantly more with *Dictyota spp.* and *Laurencia spp.* The two algae genera were very common on the rubble transects, while only *Dictyota spp.* was seen on reef transects in Chapter 1. Given both focal fishes are herbivores but of different genera it is interesting that they have the same habitat preferences between algae. Their preferences were for both the fleshy algae *Dictyota spp.* and *Laurencia spp.* rather than the calcareous algae *Halimeda spp.* At this stage both *S. iseri* and *A. tractus* eat fleshy algae, particularly *Dictyota spp.*, matching the habitat preferences found in this experiment (Adam et al. 2018; Duran et al. 2019). Along with corresponding to their feeding preferences the algae they associated with most, *Dictyota spp.* and *Laurencia spp.*, were in high abundances on the rubble transects where many juveniles were found.

The choice experiments between sponges showed both *S. iseri* and *A. tractus* display differing strong preferences for sponges. *S. iseri* associated significantly more with *A. cauliformis* while *A. tractus* associated more with *C. plicifera* Also *S. iseri* showed a second preference for *C. plicifera* and rubble over no association and the third sponge option *I. birotulata*. These fish associated with rubble over *I. birotulata* suggesting they may avoid this sponge. It is important to note *A. cauliformis* and *I. birotulata* are rope sponges, and *C. plicifera* is a vase sponge. It is interesting they both had a very strong preference for sponges since the reef transects showed that sponges significantly influence herbivore species diversity. This choice experiment showed these fish do associate with sponges and have a preference between common

sponges. The rejection of *I. birotulata* may indicate this sponge having an influence on habitat use especially for *S. iseri*.

Overall from these choice experiments fish exhibit some strong habitat preferences or split preferences between the common species within functional groups. These habitat preferences exhibited may be indicative of how these fish would use these as habitats, suggesting the abundance and composition of all these species may play a role while selecting between reefs. Shifts in community composition with coral reef degradation and increased disturbances can have larger impacts on organisms that have strong habitat preferences. Matis et al. (2018), found habitat generalists with no preferred habitat choice at current temperature developed a habitat preference under increased temperature. This change in generalist habitat preference under warming conditions may influence future habitat use and competition. It is important to understand habitat preferences throughout the Caribbean and how habitat use may change with changing conditions. A study done in St. Croix, surveying different lagoon habitat types, found juvenile *Acanthurus spp* and *Scarus iseri* exhibited two different patterns habitat use between lagoon patch reef and rubble habitats (Adam & Ebersole 2002). *Acanthurus spp*, utilized patch reef and rubble habitat as nurseries, while *S. iseri* used mostly back reef with no ontogenetic shift. Species specific habitat use may be regionally dependent, and the potential of ontogenetic shifts may depend on surrounding habitats and environmental conditions.

Herbivorous fish can be vastly different in their morphology, as well as feeding preferences and behaviors (Allgeier et al 2017; Brandl et al. 2015). When examining herbivore diversity on reefs it is important to consider that species even within the same genus may have different feeding preferences, such as eating turf algae vs

macroalgae, and that this may shift with body size (Adam et al. 2018; Duran et al. 2019; Allgeier et al 2017; Burkepile & Hay 2011). Herbivory on coral reefs is critical for maintaining ecosystem functioning and resilience, so it is important to consider the diversity of herbivores and how these would respond to a disturbance to ensure each functional role is maintained (Cheal et al. 2010; Hanmer et al. 2017; Nash et al. 2016). Many coral reef fish utilize nursery habitats by transitioning from mangroves to patch reef systems onto forereefs (Huijbers et al. 2008; Grol et al. 2014; Jones et al. 2010; Mumby et al. 2004). Reefs in close proximity to nursery habitats should be considered when implementing conservation strategies as nursery habitats such as rubble, seagrass, and mangroves can promote juvenile populations and in turn adult populations (Lefcheck et al. 2018; Nagelkerken et al. 2012). Herbivorous fish that use nursery habitats is especially important to consider when trying to understand their population dynamics and their contribution to reef resilience. When implementing management strategies for reef restoration it is critical to consider ontogenetic shifts and habitat preferences of ecologically important species. Backreef and rubble habitats may play a role as a temporary habitat in this area and may utilize the close proximity of patch reefs as fish grow and move to adult habitat. Many management practices look into ways to direct specific fish species to areas that are degraded or starting to degrade. In order to get more fish to an area it is important to consider both functional group level and species level. Habitat preferences influence habitat selection, so it is critical to consider these behavioral choices when trying to manage and restore a reef.

## REFERENCES

- Adams, A. J., Dahlgren, C. P., Kellison, G. T., Kendall, M. S., Layman, C. A., Ley, J. A., ... & Serafy, J. E. (2006). Nursery function of tropical back-reef systems. *Marine Ecology Progress Series*, 318, 287-301.
- Adam, T. C., Burkepile, D. E., Ruttenberg, B. I., & Paddock, M. J. (2015). Herbivory and the resilience of Caribbean coral reefs: knowledge gaps and implications for management. *Marine Ecology Progress Series*, 520, 1-20.
- Adam, T. C., Duran, A., Fuchs, C. E., Roycroft, M. V., Rojas, M. C., Ruttenberg, B. I., & Burkepile, D. E. (2018). Comparative analysis of foraging behavior and bite mechanics reveals complex functional diversity among Caribbean parrotfishes. *Marine Ecology Progress Series*, 597, 207-220.
- Allgeier, J. E., Adam, T. C., & Burkepile, D. E. (2017). The importance of individual and species-level traits for trophic niches among herbivorous coral reef fishes. *Proceedings of the Royal Society B: Biological Sciences*, 284(1856), 20170307.
- Almany, G. R. (2004). Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. *Oecologia*, 141(1), 105-113.
- Almany, G. R., & Webster, M. S. (2006). The predation gauntlet: early post-settlement mortality in reef fishes. *Coral reefs*, 25(1), 19-22.
- Alvarez-Filip, L., Côté, I. M., Gill, J. A., Watkinson, A. R., & Dulvy, N. K. (2011). Region-wide temporal and spatial variation in Caribbean reef architecture: is coral cover the whole story?. *Global Change Biology*, 17(7), 2470-2477.
- Alvarez-Filip, L., Gill, J. A., & Dulvy, N. K. (2011). Complex reef architecture supports more small-bodied fishes and longer food chains on Caribbean reefs. *Ecosphere*, 2(10), 1-17.
- Anthony, K. R. (2016). Coral reefs under climate change and ocean acidification: challenges and opportunities for management and policy. *Annual Review of Environment and Resources*, 41, 59-81.

- Arias-González, J. E., Fung, T., Seymour, R. M., Garza-Pérez, J. R., Acosta-González, G., Bozec, Y. M., & Johnson, C. R. (2017). A coral-algal phase shift in Mesoamerica not driven by changes in herbivorous fish abundance. *PloS one*, *12*(4), e0174855.
- Aronson, R. B., & Precht, W. F. (1995). Landscape patterns of reef coral diversity: a test of the intermediate disturbance hypothesis. *Journal of Experimental Marine Biology and Ecology*, *192*(1), 1-14.
- Aronson, R. B., & Precht, W. F. (1997). Stasis, biological disturbance, and community structure of a Holocene coral reef. *Paleobiology*, *23*(3), 326-346.
- Aronson, R. B. W. F., Precht, W., Toscano, M., & Koltes, K. H. (2002). The 1998 bleaching event and its aftermath on a coral reef in Belize. *Marine Biology*, *141*(3), 435-447.
- Bayraktarov, E., Saunders, M. I., Abdullah, S., Mills, M., Beher, J., Possingham, H. P., ... & Lovelock, C. E. (2016). The cost and feasibility of marine coastal restoration. *Ecological Applications*, *26*(4), 1055-1074.
- Bell, T., & Kramer, D. L. (2000). Territoriality and habitat use by juvenile blue tangs, *Acanthurus coeruleus*. *Environmental Biology of Fishes*, *58*(4), 401-409.
- Bell, J. J., Davy, S. K., Jones, T., Taylor, M. W., & Webster, N. S. (2013). Could some coral reefs become sponge reefs as our climate changes?. *Global change biology*, *19*(9), 2613-2624.
- Bellwood, D. R., Hughes, T. P., Folke, C., & Nyström, M. (2004). Confronting the coral reef crisis. *Nature*, *429*(6994), 827.
- Bellwood, D. R., Hoey, A. S., Ackerman, J. L., & Depczynski, M. (2006). Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Global Change Biology*, *12*(9), 1587-1594.
- Benkwitt, C. E. (2017). Predator effects on reef fish settlement depend on predator origin and recruit density. *Ecology*, *98*(4), 896-902.
- Blanchette, A., Ely, T., Zeko, A., Sura, S. A., Turba, R., & Fong, P. (2019). Damselfish *Stegastes nigricans* increase algal growth within their territories on shallow coral reefs via enhanced nutrient supplies. *Journal of Experimental Marine Biology and Ecology*, *513*, 21-26.

- Boch, C. A., & Morse, A. N. (2012). Testing the effectiveness of direct propagation techniques for coral restoration of *Acropora* spp. *Ecological Engineering*, *40*, 11-17.
- Bonin, M. C., Srinivasan, M., Almany, G. R., & Jones, G. P. (2009). Interactive effects of interspecific competition and microhabitat on early post-settlement survival in a coral reef fish. *Coral Reefs*, *28*(1), 265-274.
- Bonin, M. C., Boström-Einarsson, L., Munday, P. L., & Jones, G. P. (2015). The prevalence and importance of competition among coral reef fishes. *Annual Review of Ecology, Evolution, and Systematics*, *46*, 169-190.
- Brandl, S. J., Robbins, W. D., & Bellwood, D. R. (2015). Exploring the nature of ecological specialization in a coral reef fish community: morphology, diet and foraging microhabitat use. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1815), 20151147.
- Brandl, S. J., Rasher, D. B., Côté, I. M., Casey, J. M., Darling, E. S., Lefcheck, J. S., & Duffy, J. E. (2019). Coral reef ecosystem functioning: eight core processes and the role of biodiversity. *Frontiers in Ecology and the Environment*.
- Brooker, R. M., Munday, P. L., Mcleod, I. M., & Jones, G. P. (2013). Habitat preferences of a corallivorous reef fish: predation risk versus food quality. *Coral reefs*, *32*(3), 613-622.
- Brooker, R. M., Hay, M. E., & Dixon, D. L. (2016). Chemically cued suppression of coral reef resilience: Where is the tipping point?. *Coral reefs*, *35*(4), 1263-1270.
- Bruggemann, J. H., Van Oppen, M. J., & Breeman, A. M. (1994). Foraging by the stoplight parrotfish *Sparisoma viride*. I. Food selection in different, socially determined habitats. *Marine Ecology-Progress Series*, *106*, 41-41.
- Bruno, J. F., Côté, I. M., & Toth, L. T. (2019). Climate change, coral loss, and the curious case of the parrotfish paradigm: Why don't marine protected areas improve reef resilience?. *Annual review of marine science*, *11*, 307-334.
- Burkepile, D. E., & Hay, M. E. (2008). Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proceedings of the National Academy of Sciences*, *105*(42), 16201-16206.
- Burkepile, D. E., & Hay, M. E. (2010). Impact of herbivore identity on algal succession and coral growth on a Caribbean reef. *PloS one*, *5*(1), e8963.

- Burkepile, D. E., & Hay, M. E. (2011). Feeding complementarity versus redundancy among herbivorous fishes on a Caribbean reef. *Coral Reefs*, 30(2), 351-362.
- Burkepile, D. E., Adam, T. C., Roycroft, M., Ladd, M. C., Munsterman, K. S., & Ruttenberg, B. I. (2019). Species-specific patterns in corallivory and spongivory among Caribbean parrotfishes. *Coral Reefs*, 38(3), 417-423.
- Caley, M. J., Carr, M. H., Hixon, M. A., Hughes, T. P., Jones, G. P., & Menge, B. A. (1996). Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics*, 27(1), 477-500.
- Carr, M. H., Anderson, T. W., & Hixon, M. A. (2002). Biodiversity, population regulation, and the stability of coral-reef fish communities. *Proceedings of the National Academy of Sciences*, 99(17), 11241-11245.
- Castro-Sanguino, C., Lovelock, C., & Mumby, P. J. (2017). Factors affecting tolerance to herbivory in a calcifying alga on coral reefs. *Marine biology*, 164(2), 37.
- Chaves-Fonnegra, A., Feldheim, K. A., Secord, J., & Lopez, J. V. (2015). Population structure and dispersal of the coral-excavating sponge *Cliona delitrix*. *Molecular ecology*, 24(7), 1447-1466.
- Chaves-Fonnegra, A., Riegl, B., Zea, S., Lopez, J. V., Smith, T., Brandt, M., & Gilliam, D. S. (2018). Bleaching events regulate shifts from corals to excavating sponges in algae-dominated reefs. *Global change biology*, 24(2), 773-785.
- Cheal, A. J., MacNeil, M. A., Cripps, E., Emslie, M. J., Jonker, M., Schaffelke, B., & Sweatman, H. (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(4), 1005-1015.
- Cheney, K. L., & Côté, I. M. (2003). Habitat choice in adult longfin damselfish: territory characteristics and relocation times. *Journal of Experimental Marine Biology and Ecology*, 287(1), 1-12.
- Chong-Seng, K. M., Mannering, T. D., Pratchett, M. S., Bellwood, D. R., & Graham, N. A. (2012). The influence of coral reef benthic condition on associated fish assemblages. *PLoS One*, 7(8), e42167.
- Christie, A. P., Amano, T., Martin, P. A., Shackelford, G. E., Simmons, B. I., & Sutherland, W. J. (2019). Simple study designs in ecology produce inaccurate estimates of biodiversity responses. *bioRxiv*, 612101.

- Coker, D. J., Graham, N. A. J., & Pratchett, M. S. (2012). Interactive effects of live coral and structural complexity on the recruitment of reef fishes. *Coral reefs*, 31(4), 919-927.
- Coker, D. J., Nowicki, J. P., & Graham, N. A. J. (2017). Influence of coral cover and structural complexity on the accuracy of visual surveys of coral-reef fish communities. *Journal of fish biology*, 90(6), 2425-2433.
- Coppock, A. G., Gardiner, N. M., & Jones, G. P. (2013). Olfactory discrimination in juvenile coral reef fishes: response to conspecifics and corals. *Journal of Experimental Marine Biology and Ecology*, 443, 21-26.
- Cowen, R. K., & Sponaugle, S. (2009). Larval dispersal and marine population connectivity. *Annual review of marine science*, 1, 443-466.
- Dahlgren, C. P., & Eggleston, D. B. (2000). Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology*, 81(8), 2227-2240.
- Darling, E. S., Alvarez-Filip, L., Oliver, T. A., McClanahan, T. R., & Côté, I. M. (2012). Evaluating life-history strategies of reef corals from species traits. *Ecology Letters*, 15(12), 1378-1386.
- Diaz, M. C., & Rützler, K. (2001). Sponges: an essential component of Caribbean coral reefs. *Bulletin of Marine Science*, 69(2), 535-546.
- Dixson, D. L., Pratchett, M. S., & Munday, P. L. (2012). Reef fishes innately distinguish predators based on olfactory cues associated with recent prey items rather than individual species. *Animal Behaviour*, 84(1), 45-51.
- Dixson, D. L., Abrego, D., & Hay, M. E. (2014). Chemically mediated behavior of recruiting corals and fishes: a tipping point that may limit reef recovery. *Science*, 345(6199), 892-897.
- Doney, S. C., Ruckelshaus, M., Duffy, J. E., Barry, J. P., Chan, F., English, C. A., ... & Polovina, J. (2011). Climate change impacts on marine ecosystems.
- Dromard, C. R., Bouchon-Navaro, Y., Harmelin-Vivien, M., & Bouchon, C. (2015). Diversity of trophic niches among herbivorous fishes on a Caribbean reef (Guadeloupe, Lesser Antilles), evidenced by stable isotope and gut content analyses. *Journal of sea research*, 95, 124-131.

- Duffy, J. E., Lefcheck, J. S., Stuart-Smith, R. D., Navarrete, S. A., & Edgar, G. J. (2016). Biodiversity enhances reef fish biomass and resistance to climate change. *Proceedings of the National Academy of Sciences*, *113*(22), 6230-6235.
- Duran, A., Adam, T. C., Palma, L., Moreno, S., Collado-Vides, L., & Burkepile, D. E. (2019). Feeding behavior in Caribbean surgeonfishes varies across fish size, algal abundance, and habitat characteristics. *Marine Ecology*, *40*(4), e12561.
- Eggleston, D. B. (1995). Recruitment in Nassau grouper *Epinephelus striatus*: post-settlement abundance, microhabitat features, and ontogenetic habitat shifts. *Marine Ecology Progress Series*, *124*, 9-22.
- Epstein, H. E., & Kingsford, M. J. (2019). Are soft coral habitats unfavourable? A closer look at the association between reef fishes and their habitat. *Environmental biology of fishes*, *102*(3), 479-497.
- Feary, D. A., Almany, G. R., McCormick, M. I., & Jones, G. P. (2007). Habitat choice, recruitment and the response of coral reef fishes to coral degradation. *Oecologia*, *153*(3), 727-737.
- Ferrari, R., Bryson, M., Bridge, T., Hustache, J., Williams, S. B., Byrne, M., & Figueira, W. (2016). Quantifying the response of structural complexity and community composition to environmental change in marine communities. *Global change biology*, *22*(5), 1965-1975.
- Fisher, R., Bellwood, D. R., & Job, S. D. (2000). Development of swimming abilities in reef fish larvae. *Marine Ecology Progress Series*, *202*, 163-173.
- Gardner, T. A., Côté, I. M., Gill, J. A., Grant, A., & Watkinson, A. R. (2003). Long-term region-wide declines in Caribbean corals. *Science*, *301*(5635), 958-960.
- Geange, S. W., & Stier, A. C. (2010). Priority effects and habitat complexity affect the strength of competition. *Oecologia*, *163*(1), 111-118.
- Gibson, R. N., Barnes, M., & Atkinson, R. J. (2001). Territorial damselfishes as determinants of the structure of benthic communities on coral reefs. *Oceanography and Marine Biology: an annual review*, *39*, 355-89.
- Goldstein, E. D., D'Alessandro, E. K., Reed, J., & Sponaugle, S. (2016). Habitat availability and depth-driven population demographics regulate reproductive output of a coral reef fish. *Ecosphere*, *7*(11), e01542.
- Google Earth. (2019). Belize. <https://www.google.com/earth/index.html>.

- Graham, N. A. J., Nash, K. L., & Kool, J. T. (2011). Coral reef recovery dynamics in a changing world. *Coral Reefs*, 30(2), 283-294.
- Graham, N. A., Jennings, S., MacNeil, M. A., Mouillot, D., & Wilson, S. K. (2015). Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature*, 518(7537), 94.
- Green, A. L., Maypa, A. P., Almany, G. R., Rhodes, K. L., Weeks, R., Abesamis, R. A., ... & White, A. T. (2015). Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews*, 90(4), 1215-1247.
- Green, D. H., Edmunds, P. J., & Carpenter, R. C. (2008). Increasing relative abundance of *Porites astreoides* on Caribbean reefs mediated by an overall decline in coral cover. *Marine Ecology Progress Series*, 359, 1-10.
- Grol, M. G., Nagelkerken, I., Rypel, A. L., & Layman, C. A. (2011). Simple ecological trade-offs give rise to emergent cross-ecosystem distributions of a coral reef fish. *Oecologia*, 165(1), 79-88.
- Grol, M. G., Rypel, A. L., & Nagelkerken, I. (2014). Growth potential and predation risk drive ontogenetic shifts among nursery habitats in a coral reef fish. *Marine Ecology Progress Series*, 502, 229-244.
- Hanmer, J., White, J. W., & Pawlik, J. R. (2017). Application of diet theory reveals context-dependent foraging preferences in an herbivorous coral reef fish. *Oecologia*, 184(1), 127-137.
- Harvell, C. D., Fenical, W., & Greene, C. H. (1988). Chemical and structural defenses of Caribbean gorgonians (*Pseudopterogorgia* spp.). I. Development of an in situ feeding assay. *Marine Ecology Progress Series*, 287-294.
- Harvey, B. J., Nash, K. L., Blanchard, J. L., & Edwards, D. P. (2018). Ecosystem-based management of coral reefs under climate change. *Ecology and evolution*, 8(12), 6354-6368.
- Hay, M. E., Paul, V. J., Lewis, S. M., Gustafson, K., Tucker, J., & Trindell, R. N. (1988). Can tropical seaweeds reduce herbivory by growing at night? Diel patterns of growth, nitrogen content, herbivory, and chemical versus morphological defenses. *Oecologia*, 75(2), 233-245.
- Hay, M. E., Kappel, Q. E., & Fenical, W. (1994). Synergisms in plant defenses against herbivores: interactions of chemistry, calcification, and plant quality. *Ecology*, 75(6), 1714-1726.

- Hein, M. Y., Willis, B. L., Beeden, R., & Birtles, A. (2017). The need for broader ecological and socioeconomic tools to evaluate the effectiveness of coral restoration programs. *Restoration ecology*, 25(6), 873-883.
- Heinlein, J. M., Stier, A. C., & Steele, M. A. (2010). Predators reduce abundance and species richness of coral reef fish recruits via non-selective predation. *Coral Reefs*, 29(2), 527-532.
- Hixon, M. A., & Jones, G. P. (2005). Competition, predation, and density-dependent mortality in demersal marine fishes. *Ecology*, 86(11), 2847-2859.
- Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E., Hungate, B. A., Matulich, K. L., ... & O'Connor, M. I. (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, 486(7401), 105.
- Hughes, T. P. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, 265(5178), 1547-1551.
- Hughes, T. P., Rodrigues, M. J., Bellwood, D. R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., ... & Willis, B. (2007). Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology*, 17(4), 360-365.
- Hughes, T. P., Graham, N. A., Jackson, J. B., Mumby, P. J., & Steneck, R. S. (2010). Rising to the challenge of sustaining coral reef resilience. *Trends in ecology & evolution*, 25(11), 633-642.
- Hughes, T. P., Barnes, M. L., Bellwood, D. R., Cinner, J. E., Cumming, G. S., Jackson, J. B., ... & Palumbi, S. R. (2017). Coral reefs in the Anthropocene. *Nature*, 546(7656), 82.
- Huijbers, C. M., Mollee, E. M., & Nagelkerken, I. (2008). Post-larval French grunts (*Haemulon flavolineatum*) distinguish between seagrass, mangrove and coral reef water: Implications for recognition of potential nursery habitats. *Journal of Experimental Marine Biology and Ecology*, 357(2), 134-139.
- Huntington, B. E., Miller, M. W., Pausch, R., & Richter, L. (2017). Facilitation in Caribbean coral reefs: high densities of staghorn coral foster greater coral condition and reef fish composition. *Oecologia*, 184(1), 247-257.
- Jones, G. P., McCormick, M. I., Srinivasan, M., & Eagle, J. V. (2004). Coral decline threatens fish biodiversity in marine reserves. *Proceedings of the National Academy of Sciences*, 101(21), 8251-8253.

- Jones, D. L., Walter, J. F., Brooks, E. N., & Serafy, J. E. (2010). Connectivity through ontogeny: fish population linkages among mangrove and coral reef habitats. *Marine Ecology Progress Series*, 401, 245-258.
- Kingsford, M. J., Leis, J. M., Shanks, A., Lindeman, K. C., Morgan, S. G., & Pineda, J. (2002). Sensory environments, larval abilities and local self-recruitment. *Bulletin of Marine Science*, 70(1), 309-340.
- Kimirei, I. A., Nagelkerken, I., Trommelen, M., Blankers, P., Van Hoytema, N., Hoeijmakers, D., ... & Rypel, A. (2013). What drives ontogenetic niche shifts of fishes in coral reef ecosystems?. *Ecosystems*, 16(5), 783-796.
- Kuffner, I. B., Walters, L. J., Becerro, M. A., Paul, V. J., Ritson-Williams, R., & Beach, K. S. (2006). Inhibition of coral recruitment by macroalgae and cyanobacteria. *Marine Ecology Progress Series*, 323, 107-117.
- Ladd, M. C., Burkepile, D. E., & Shantz, A. A. (2019). Near-term impacts of coral restoration on target species, coral reef community structure, and ecological processes. *Restoration Ecology*.
- Lasker, H. R., & Coffroth, M. A. (1983). Octocoral distributions at Carrie Bow Cay, Belize. *Marine ecology progress series. Oldendorf*, 13(1), 21-28.
- Lecchini, D., Shima, J., Banaigs, B., & Galzin, R. (2005). Larval sensory abilities and mechanisms of habitat selection of a coral reef fish during settlement. *Oecologia*, 143(2), 326-334.
- Lecchini, D., Osenberg, C. W., Shima, J. S., St Mary, C. M., & Galzin, R. (2007). Ontogenetic changes in habitat selection during settlement in a coral reef fish: ecological determinants and sensory mechanisms. *Coral Reefs*, 26(2), 423-432.
- Lecchini, D., Planes, S., & Galzin, R. (2007). The influence of habitat characteristics and conspecifics on attraction and survival of coral reef fish juveniles. *Journal of Experimental Marine Biology and Ecology*, 341(1), 85-90.
- Lecchini, D., Waqalevu, V. P., Parmentier, E., Radford, C. A., & Banaigs, B. (2013). Fish larvae prefer coral over algal water cues: implications of coral reef degradation. *Marine Ecology Progress Series*, 475, 303-307.
- Lefcheck, J. S., Hughes, B. B., Johnson, A. J., Pfirrmann, B. W., Rasher, D. B., Smyth, A. R., ... & Orth, R. J. (2019). Are coastal habitats important nurseries? A meta-analysis. *Conservation Letters*, e12645.

- Legendre, P., & Anderson, M. J. (1999). Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological monographs*, 69(1), 1-24.
- Leis, J. M., & Carson-Ewart, B. M. (1998). Complex behaviour by coral-reef fish larvae in open-water and near-reef pelagic environments. *Environmental Biology of Fishes*, 53(3), 259-266.
- Leis, J. M., Carson-Ewart, B. M., Hay, A. C., & Cato, D. H. (2003). Coral-reef sounds enable nocturnal navigation by some reef-fish larvae in some places and at some times. *Journal of Fish Biology*, 63(3), 724-737.
- Leis, J. M., Siebeck, U., & Dixon, D. L. (2011). How Nemo finds home: the neuroecology of dispersal and of population connectivity in larvae of marine fishes.
- Leong, W., & Pawlik, J. R. (2010). Evidence of a resource trade-off between growth and chemical defenses among Caribbean coral reef sponges. *Marine Ecology Progress Series*, 406, 71-78.
- Levy, G., Shaish, L., Haim, A., & Rinkevich, B. (2010). Mid-water rope nursery— Testing design and performance of a novel reef restoration instrument. *Ecological Engineering*, 36(4), 560-569.
- Lewis, S. M., & Wainwright, P. C. (1985). Herbivore abundance and grazing intensity on a Caribbean coral reef. *Journal of Experimental Marine Biology and Ecology*, 87(3), 215-228.
- Lewis, S. M., Norris, J. N., & Searles, R. B. (1987). The regulation of morphological plasticity in tropical reef algae by herbivory. *Ecology*, 68(3), 636-641.
- Lirman, D. (1994). Ontogenetic shifts in habitat preferences in the three-spot damselfish, *Stegastes planifrons* (Cuvier), in Roatan Island, Honduras. *Journal of experimental marine biology and ecology*, 180(1), 71-81.
- Loh, Tse-Lynn, and Joseph R. Pawlik. "Chemical defenses and resource trade-offs structure sponge communities on Caribbean coral reefs." *Proceedings of the National Academy of Sciences* 111, no. 11 (2014): 4151-4156.
- McCormick, M. I., & Meekan, M. G. (2010). The importance of attitude: the influence of behaviour on survival at an ontogenetic boundary. *Marine Ecology Progress Series*, 407, 173-185.

- Mclean, E. L., Rützler, K., & Pooler, P. S. (2015). Competing for space: factors that lead to sponge overgrowth when interacting with octocoral. *Open Journal of Marine Science*.
- Messmer, V., Jones, G. P., Munday, P. L., Holbrook, S. J., Schmitt, R. J., & Brooks, A. J. (2011). Habitat biodiversity as a determinant of fish community structure on coral reefs. *Ecology*, *92*(12), 2285-2298.
- Montgomery, J. C., Tolimieri, N., & Haine, O. S. (2001). Active habitat selection by pre-settlement reef fishes. *Fish and Fisheries*, *2*(3), 261-277.
- Mumby, P. J., & Harborne, A. R. (1999). Development of a systematic classification scheme of marine habitats to facilitate regional management and mapping of Caribbean coral reefs. *Biological conservation*, *88*(2), 155-163.
- Mumby, P. J., & Wabnitz, C. C. (2002). Spatial patterns of aggression, territory size, and harem size in five sympatric Caribbean parrotfish species. *Environmental Biology of Fishes*, *63*(3), 265-279.
- Mumby, P. J., Edwards, A. J., Arias-González, J. E., Lindeman, K. C., Blackwell, P. G., Gall, A., ... & Wabnitz, C. C. (2004). Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature*, *427*(6974), 533.
- Mumby, P. J. (2006). The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. *Ecological Applications*, *16*(2), 747-769.
- Mumby, P. J., Dahlgren, C. P., Harborne, A. R., Kappel, C. V., Micheli, F., Brumbaugh, D. R., ... & Buch, K. (2006). Fishing, trophic cascades, and the process of grazing on coral reefs. *Science*, *311*(5757), 98-101.
- Mumby, P. J., Hastings, A., & Edwards, H. J. (2007). Thresholds and the resilience of Caribbean coral reefs. *Nature*, *450*(7166), 98.
- Mumby, P. J., Broad, K., Brumbaugh, D. R., Dahlgren, C. P., Harborne, A. R., Hastings, A., ... & Sanchirico, J. N. (2008). Coral reef habitats as surrogates of species, ecological functions, and ecosystem services. *Conservation Biology*, *22*(4), 941-951.
- Mumby, P. J., & Steneck, R. S. (2008). Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends in ecology & evolution*, *23*(10), 555-563.

- Nagelkerken, I., Roberts, C. V., Van Der Velde, G., Dorenbosch, M., Van Riel, M. C., De La Moriniere, E. C., & Nienhuis, P. H. (2002). How important are mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale. *Marine ecology progress series*, 244, 299-305.
- Nagelkerken, I., Grol, M. G., & Mumby, P. J. (2012). Effects of marine reserves versus nursery habitat availability on structure of reef fish communities. *PloS one*, 7(6), e36906.
- Nagelkerken, I., Huebert, K. B., Serafy, J. E., Grol, M. G. G., Dorenbosch, M., & Bradshaw, C. J. A. (2017). Highly localized replenishment of coral reef fish populations near nursery habitats. *Marine Ecology Progress Series*, 568, 137-150.
- Nash, K. L., Graham, N. A., Jennings, S., Wilson, S. K., & Bellwood, D. R. (2016). Herbivore cross-scale redundancy supports response diversity and promotes coral reef resilience. *Journal of Applied Ecology*, 53(3), 646-655.
- Newman, S. P., Meesters, E. H., Dryden, C. S., Williams, S. M., Sanchez, C., Mumby, P. J., & Polunin, N. V. (2015). Reef flattening effects on total richness and species responses in the Caribbean. *Journal of Animal Ecology*, 84(6), 1678-1689.
- Norström, A. V., Nyström, M., Lokrantz, J., & Folke, C. (2009). Alternative states on coral reefs: beyond coral-macroalgal phase shifts. *Marine ecology progress series*, 376, 295-306.
- Nyström, M., Folke, C., & Moberg, F. (2000). Coral reef disturbance and resilience in a human-dominated environment. *Trends in ecology & evolution*, 15(10), 413-417.
- Öhman, M. C., Munday, P. L., Jones, G. P., & Caley, M. J. (1998). Settlement strategies and distribution patterns of coral-reef fishes. *Journal of Experimental Marine Biology and Ecology*, 225(2), 219-238.
- Paddack, M. J., & Sponaugle, S. (2008). Recruitment and habitat selection of newly settled *Sparisoma viride* to reefs with low coral cover. *Marine Ecology Progress Series*, 369, 205-212.
- Paddack, M. J., Reynolds, J. D., Aguilar, C., Appeldoorn, R. S., Beets, J., Burkett, E. W., ... & Forrester, G. E. (2009). Recent region-wide declines in Caribbean reef fish abundance. *Current Biology*, 19(7), 590-595.

- Pandolfi, J. M., & Jackson, J. B. (2006). Ecological persistence interrupted in Caribbean coral reefs. *Ecology Letters*, *9*(7), 818-826
- Paris, C. B., Chérubin, L. M., & Cowen, R. K. (2007). Surfing, spinning, or diving from reef to reef: effects on population connectivity. *Marine Ecology Progress Series*, *347*, 285-300.
- Paul, V. J., & Van Alstyne, K. L. (1992). Activation of chemical defenses in the tropical green algae *Halimeda* spp. *Journal of Experimental Marine Biology and Ecology*, *160*(2), 191-203.
- Paul, V. J., Kuffner, I. B., Walters, L. J., Ritson-Williams, R., Beach, K. S., & Becerro, M. A. (2011). Chemically mediated interactions between macroalgae *Dictyota* spp. and multiple life-history stages of the coral *Porites astreoides*. *Marine Ecology Progress Series*, *426*, 161-170.
- Pawlik, J. R. (2011). The chemical ecology of sponges on Caribbean reefs: natural products shape natural systems. *Bioscience*, *61*(11), 888-898.
- Pereira, P. H. C., Macedo, C. H., Jose de Anchieta, C. C., de Barros Marangoni, L. F., & Bianchini, A. (2018). Effects of depth on reef fish communities: Insights of a “deep refuge hypothesis” from Southwestern Atlantic reefs. *PloS one*, *13*(9), e0203072.
- Preisser, E. L., Orrock, J. L., & Schmitz, O. J. (2007). Predator hunting mode and habitat domain alter nonconsumptive effects in predator–prey interactions. *Ecology*, *88*(11), 2744-2751.
- Randazzo, A. M., Montero, J. L., McField, M., Myton, J., & Arias González, J. E. (2019). The Effect of Algal-Gardening Damselfish on the Resilience of the Mesoamerican Reef. *Frontiers in Marine Science*, *6*, 414.
- Robertson, D. R., Karg, F., de Moura, R. L., Victor, B. C., & Bernardi, G. (2006). Mechanisms of speciation and faunal enrichment in Atlantic parrotfishes. *Molecular phylogenetics and evolution*, *40*(3), 795-807.
- Rocha, L. A., Bass, A. L., Robertson, D. R., & Bowen, B. W. (2002). Adult habitat preferences, larval dispersal, and the comparative phylogeography of three Atlantic surgeonfishes (Teleostei: Acanthuridae). *Molecular Ecology*, *11*(2), 243-251.
- Ruhl, E. J., & Dixon, D. L. (2019). 3D printed objects do not impact the behavior of a coral-associated damselfish or survival of a settling stony coral. *PloS one*, *14*(8), e0221157.

- Rützler, K., & Macintyre, I. G. (1982). The habitat distribution and community structure of the barrier reef complex at Carrie Bow Cay, Belize. *The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize, I. Structure and communities. Smithsonian Contributions to the Marine Sciences*, 12, 9-45.
- Schutte, V. G., Selig, E. R., & Bruno, J. F. (2010). Regional spatio-temporal trends in Caribbean coral reef benthic communities. *Marine Ecology Progress Series*, 402, 115-122.
- Semmens, B. X., Brumbaugh, D. R., & Drew, J. A. (2005). Interpreting space use and behavior of blue tang, *Acanthurus coeruleus*, in the context of habitat, density, and intra-specific interactions. *Environmental biology of fishes*, 74(1), 99-107.
- Shaish, L., Levy, G., Katzir, G., & Rinkevich, B. (2010). Employing a highly fragmented, weedy coral species in reef restoration. *Ecological Engineering*, 36(10), 1424-1432.
- Shulman, M. J., & Bermingham, E. (1995). Early life histories, ocean currents, and the population genetics of Caribbean reef fishes. *Evolution*, 49(5), 897-910.
- Steneck, R. S., Arnold, S. N., & Mumby, P. J. (2014). Experiment mimics fishing on parrotfish: insights on coral reef recovery and alternative attractors. *Mar Ecol Prog Ser*, 506, 115-127.
- Stier, A. C., Stallings, C. D., Samhuri, J. F., Albins, M. A., & Almany, G. R. (2017). Biodiversity effects of the predation gauntlet. *Coral Reefs*, 36(2), 601-606.
- Stobutzki, I. C., & Bellwood, D. R. (1997). Sustained swimming abilities of the late pelagic stages of coral reef fishes. *Marine Ecology Progress Series*, 149, 35-41.
- Sweatman, H. (1988). Field evidence that settling coral reef fish larvae detect resident fishes using dissolved chemical cues. *Journal of Experimental Marine Biology and Ecology*, 124(3), 163-174.
- Syms, C., & Jones, G. P. (2000). Disturbance, habitat structure, and the dynamics of a coral-reef fish community. *Ecology*, 81(10), 2714-2729.
- Syms, C., & Jones, G. P. (2001). Soft corals exert no direct effects on coral reef fish assemblages. *Oecologia*, 127(4), 560-571.
- Tolimieri, N. (1998). The relationship among microhabitat characteristics, recruitment and adult abundance in the stoplight parrotfish, *Sparisoma viride*, at three spatial scales. *Bulletin of Marine Science*, 62(1), 253-268.

- Topor, Z. M., Rasher, D. B., Duffy, J. E., & Brandl, S. J. (2019). Marine protected areas enhance coral reef functioning by promoting fish biodiversity. *Conservation Letters*, e12638.
- van Woesik, R., Ripple, K., & Miller, S. L. (2018). Macroalgae reduces survival of nursery-reared *Acropora* corals in the Florida reef tract. *Restoration Ecology*, 26(3), 563-569.
- Vermeij, M. J. A., Debey, H., Grimsditch, G., Brown, J., Obura, D., DeLeon, R., & Sandin, S. A. (2015). Negative effect of gardening damselfish *Stegastes planifrons* on coral health depend on predator abundance. *Marine Ecology-Progress Series*, 528.
- Villamizar, E., Díaz, M. C., Rützler, K., & De Nóbrega, R. (2014). Biodiversity, ecological structure, and change in the sponge community of different geomorphological zones of the barrier fore reef at Carrie Bow Cay, Belize. *Marine Ecology*, 35(4), 425-435.
- White, J. W., Samhuri, J. F., Stier, A. C., Wormald, C. L., Hamilton, S. L., & Sandin, S. A. (2010). Synthesizing mechanisms of density dependence in reef fishes: behavior, habitat configuration, and observational scale. *Ecology*, 91(7), 1949-1961.
- Williams, S. M., Mumby, P. J., Chollett, I., & Cortés, J. (2015). Importance of differentiating *Orbicella* reefs from gorgonian plains for ecological assessments of Caribbean reefs. *Marine Ecology Progress Series*, 530, 93-10.
- Williams, S. M., Sánchez-Godínez, C., Newman, S. P., & Cortés, J. (2017). Ecological assessments of the coral reef communities in the Eastern Caribbean and the effects of herbivory in influencing coral juvenile density and algal cover. *Marine ecology*, 38(2), e12395.
- Wilson, S. K., Graham, N. A., Pratchett, M. S., Jones, G. P., & Polunin, N. V. (2006). Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient?. *Global Change Biology*, 12(11), 2220-2234.
- Woolsey, E., Bainbridge, S. J., Kingsford, M. J., & Byrne, M. (2012). Impacts of cyclone Hamish at One Tree Reef: integrating environmental and benthic habitat data. *Marine Biology*, 159(4), 793-803.
- Young, C. N., Schopmeyer, S. A., & Lirman, D. (2012). A review of reef restoration and coral propagation using the threatened genus *Acropora* in the Caribbean and Western Atlantic. *Bulletin of Marine Science*, 88(4), 1075-1098.

## Appendix A

### **STATEMENT OF ETHICS**

The studies were conducted under the under the guidelines of Institutional Animal Care and Use Committee, and the experiments were approved by the University of Delaware's animal ethics committee; IACUC Number: 1313.

University of Delaware  
Institutional Animal Care and Use Committee  
Request to Amend an Animal Use Protocol

RECEIVED  
MAY 05 2017  
IACUC

<b>Title of Protocol:</b> Understanding chemical cues in settlement site selection on coral reefs could lead to more effective marine management	
<b>AUP Number:</b> 1313-2017-A	← (4 digits only)
<b>Principal Investigator:</b> Danielle Dixon	
<b>Requested Changes</b> <b>I am requesting a change to:</b> (Check <u>all</u> that apply) <input type="checkbox"/> Animal Species (Complete Section 1) <input checked="" type="checkbox"/> Animal Numbers (Complete Section 2) <input checked="" type="checkbox"/> Animal Procedures (Complete Section 3) <input type="checkbox"/> Therapeutic or Experimental Agents (Complete Section 4) <input type="checkbox"/> Pain Category (Complete Section 5) <input type="checkbox"/> Use of Biological Material, Hazardous Agents or Radiation (Complete Sections 4 & 6) <input type="checkbox"/> Other (Specify) Click here to enter text. (Complete Section 7)	
Changes MUST NOT be initiated until IACUC approval is granted	

<b>Official Use Only</b>  IACUC Approval Signature: <u>Dr. Taber DVM</u>  Date of Approval: <u>5/30/17</u>
--

## Appendix B

### REEF TRANSECT ANALYSIS

Full statistical analysis outputs for chapter 1 reef transect analysis.

Table 5: PERMANOVA output for pairwise comparisons of benthic functional group Bray-Curtis resemblance matrix by sites.

Benthic Functional Groups	t	P(perm)	Unique perms	P(MC)
Lil_Seb, Peps	1.1981	0.247	126	0.241
Lil_Seb, Channel_Entrance	2.3748	0.006	126	0.013
Lil_Seb, Curlew	3.6946	0.012	126	0.003
Lil_Seb, LF_Catch	5.6531	0.009	126	0.001
Lil_Seb, LF_Far_Reef	3.135	0.013	126	0.004
Peps, Channel_Entrance	1.9374	0.01	126	0.036
Peps, Curlew	3.028	0.007	126	0.001
Peps, LF_Catch	5.344	0.014	126	0.001
Peps, LF_Far_Reef	2.5034	0.017	126	0.005
Channel_Entrance, Curlew	2.2795	0.009	126	0.016
Channel_Entrance, LF_Catch	3.5773	0.006	126	0.001
Channel_Entrance, LF_Far_Reef	1.6991	0.009	126	0.051
Curlew, LF_Catch	4.3176	0.014	126	0.001
Curlew, LF_Far_Reef	1.7411	0.044	126	0.054
LF_Catch, LF_Far_Reef	4.725	0.008	126	0.001

Table 6: PERMANOVA output for pairwise comparisons of fish functional groups by sites.

Fish Functional Groups	t	P(perm)	Unique perms	P(MC)
Lil_Seb, Peps	3.8666	0.012	126	0.003
Lil_Seb, Channel_Entrance	4.3534	0.01	126	0.001
Lil_Seb, Curlew	3.982	0.009	126	0.002
Lil_Seb, LF_Catch	4.8321	0.008	126	0.001
Lil_Seb, LF_Far_Reef	4.2529	0.008	126	0.001
Peps, Channel_Entrance	6.1341	0.009	126	0.001
Peps, Curlew	5.3933	0.01	126	0.001
Peps, LF_Catch	2.7113	0.011	126	0.003
Peps, LF_Far_Reef	2.7844	0.005	126	0.003
Channel_Entrance, Curlew	1.5206	0.075	126	0.111
Channel_Entrance, LF_Catch	5.3648	0.014	126	0.001
Channel_Entrance, LF_Far_Reef	3.8974	0.011	126	0.001
Curlew, LF_Catch	4.2501	0.01	126	0.001
Curlew, LF_Far_Reef	3.5875	0.006	126	0.001
LF_Catch, LF_Far_Reef	2.7873	0.006	125	0.002

Table 7: SIMPER outputs for pairwise comparisons

Groups Lil_Seb & Peps						
Average dissimilarity = 31.86						
	Group Lil_Seb	Group Peps				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum. %
Dictyota_spp	3.22	1.95	2.49	1.82	7.81	7.81
Actinotrichia_spp	0	1.36	2.45	1.75	7.69	15.5
Agaricia_sp	0.55	1.29	1.88	1.34	5.88	21.38
Cyanobacteria	2.66	3.52	1.73	1.44	5.42	26.8
Pseudoplexaura_spp	0.68	1.45	1.63	1.02	5.13	31.93
Halimeda_spp	1.09	1.89	1.49	1.15	4.66	36.59

Cliona_spp	1.31	1.38	1.38	1.34	4.33	40.92
Siderastrea_sp	1.48	1.48	1.37	1.27	4.29	45.21
Millepora_sp	1.23	1.52	1.32	1.27	4.13	49.34
Gorgonia_spp	1.63	1.03	1.31	1.27	4.11	53.45
Coelothrix_spp	0	0.68	1.23	1.15	3.87	57.33
Amphimedon_compressa	0	0.68	1.22	1.16	3.82	61.14
Stephanocoenia_intersepta	0.48	0.4	1.02	1	3.2	64.34
Dichocoenia_stokesi	0.2	0.6	1.01	1.1	3.19	67.53
Plexaurella_sp	0.4	0.28	0.99	0.9	3.11	70.64
Groups Lil_Seb & Channel_Entrance						
Average dissimilarity = 47.05						
	Group Lil_Seb	Group Channel_Entrance				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum. %
Dictyota_spp	3.22	1.46	4.82	3.35	10.25	10.25
Agaricia_sp	0.55	2.83	4.21	2.73	8.95	19.2
Aplysina_sp	0	1.96	3.61	3.25	7.68	26.88
Halimeda_spp	1.09	2.63	2.94	1.8	6.25	33.13
Antillogorgia_sp	2.65	1.31	2.47	1.6	5.25	38.38
Iotrochota_birutulata	0	1.29	2.4	3.33	5.1	43.48
Sand	0.48	1.41	2.22	1.12	4.71	48.19
Gorgonia_spp	1.63	0.48	2.18	1.75	4.63	52.83
Cliona_spp	1.31	0.28	2.01	2.2	4.27	57.1
Ircinia_sp	0	0.97	1.79	1.8	3.8	60.9
Cyanobacteria	2.66	3.29	1.68	1.22	3.58	64.48
Briareum_asbestinum	0	0.88	1.62	1.82	3.44	67.92
Pseudoplexaura_spp	0.68	1.23	1.59	1.31	3.37	71.29
Groups Peps & Channel_Entrance						
Average dissimilarity = 43.52						
	Group Peps	Group Channel_Entrance				

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum. %
Aplysina_sp	0	1.96	3.33	3.2	7.64	7.64
Dictyota_spp	1.95	1.46	3.09	1.7	7.1	14.74
Agaricia_sp	1.29	2.83	2.66	1.63	6.12	20.86
Antillogorgia_sp	2.67	1.31	2.28	1.76	5.24	26.1
Actinotrichia_spp	1.36	0	2.25	1.76	5.18	31.28
Sand	0.2	1.41	2.23	1.13	5.13	36.42
Iotrochota_birotulata	0	1.29	2.21	3.29	5.07	41.49
Cliona_spp	1.38	0.28	2.15	1.41	4.95	46.44
Siderastrea_sp	1.48	0.95	1.61	1.56	3.69	50.13
Halimeda_spp	1.89	2.63	1.59	2	3.64	53.77
Briareum_asbestinum	0	0.88	1.49	1.81	3.42	57.2
Ircinia_sp	0.28	0.97	1.48	1.49	3.4	60.6
Turf Algae	3.2	2.41	1.4	1.51	3.21	63.81
Gorgonia_spp	1.03	0.48	1.36	1.35	3.14	66.94
Pseudoplexaura_spp	1.45	1.23	1.36	1.27	3.13	70.07
Groups Lil_Seb & Curlew						
Average dissimilarity = 53.25						
	Group Lil_Seb	Group Curlew				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum. %
Agaricia_sp	0.55	3.47	5.45	3.03	10.23	10.23
Antillogorgia_sp	2.65	0	4.94	5.83	9.28	19.5
Dictyota_spp	3.22	0.68	4.75	3.2	8.92	28.42
Halimeda_spp	1.09	2.82	3.24	2.45	6.08	34.5
Aplysina_sp	0	1.69	3.16	4.3	5.94	40.44
Iotrochota_birotulata	0	1.56	2.89	3.97	5.43	45.87
Gorgonia_spp	1.63	0.2	2.68	2.5	5.03	50.9
Cyanobacteria	2.66	4.02	2.6	1.73	4.88	55.78
Cliona_spp	1.31	0.68	1.8	1.91	3.39	59.17
Siderastrea_sp	1.48	0.88	1.63	1.33	3.05	62.22
Millepora_sp	1.23	1.68	1.51	1.32	2.83	65.05
Porites_sp	1.6	1.19	1.45	1.34	2.72	67.77
Amphimedon_compressa	0	0.68	1.25	1.16	2.34	70.11

Groups Peps & Curlew						
Average dissimilarity = 46.32						
	Group Peps	Group Curlew				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum. %
Antillogorgia_sp	2.67	0	4.55	10.94	9.82	9.82
Agaricia_sp	1.29	3.47	3.79	2.01	8.19	18
Aplysina_sp	0	1.69	2.91	4.2	6.28	24.28
Iotrochota_birotulata	0	1.56	2.66	3.86	5.75	30.03
Actinotrichia_spp	1.36	0	2.27	1.76	4.9	34.92
Dictyota_spp	1.95	0.68	2.16	1.48	4.66	39.59
Cliona_spp	1.38	0.68	1.96	1.32	4.23	43.82
Pseudoplexaura_spp	1.45	0.4	1.83	1.18	3.95	47.77
Siderastrea_sp	1.48	0.88	1.76	1.28	3.8	51.57
Halimeda_spp	1.89	2.82	1.6	3.11	3.46	55.03
Gorgonia_spp	1.03	0.2	1.56	1.51	3.37	58.4
Orbicella_sp	0.4	0.63	1.2	1.08	2.59	60.99
Cyanobacteria	3.52	4.02	1.17	1.27	2.53	63.52
Coelothrix_spp	0.68	0	1.14	1.15	2.47	65.99
Porites_sp	1.39	1.19	1.14	1.43	2.47	68.46
Millepora_sp	1.52	1.68	1.11	1.26	2.4	70.86
Groups Channel_Entrance & Curlew						
Average dissimilarity = 35.87						
	Group Channel_E ntrance	Group Curlew				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum. %
Dictyota_spp	1.46	0.68	2.33	0.82	6.49	6.49
Antillogorgia_sp	1.31	0	2.25	1.83	6.27	12.76
Turf Algae	2.41	3.51	1.9	1.92	5.28	18.04
Sand	1.41	0.68	1.85	1.05	5.17	23.21
Pseudoplexaura_spp	1.23	0.4	1.71	1.45	4.75	27.96
Cyanobacteria	3.29	4.02	1.66	1.43	4.62	32.59

Briareum_asbestinum	0.88	0.35	1.49	1.8	4.16	36.74
Ircinia_sp	0.97	0.28	1.48	1.5	4.13	40.88
Millepora_sp	1.11	1.68	1.4	1.32	3.89	44.77
Agaricia_sp	2.83	3.47	1.34	1.27	3.74	48.5
Siderastrea_sp	0.95	0.88	1.33	1.34	3.72	52.22
Cliona_spp	0.28	0.68	1.28	0.88	3.56	55.78
Orbicella_sp	0.28	0.63	1.16	0.89	3.23	59.01
Amphimedon_compressa	0	0.68	1.15	1.16	3.19	62.2
Porites_sp	1.31	1.19	1.12	1.33	3.12	65.33
Eunicea_sp	0.8	0.48	1.1	1.36	3.08	68.4
Aplysina_sp	1.96	1.69	1.02	1.31	2.84	71.24
Groups Lil_Seb & LF_Catch						
Average dissimilarity = 61.44						
	Group Lil_Seb	Group LF_Catch				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum. %
Dictyota_spp	3.22	0	6.94	5.78	11.3	11.3
Aplysina_sp	0	2.48	5.35	4.75	8.71	20.01
Antillogorgia_sp	2.65	0.28	5.09	3.21	8.28	28.29
Sand	0.48	2.52	4.33	3.15	7.04	35.34
Gorgonia_spp	1.63	0	3.51	4.07	5.71	41.04
Porites_sp	1.6	0.2	3.02	2.22	4.92	45.96
Turf Algae	3.04	4.38	2.85	2.12	4.63	50.59
Millepora_sp	1.23	0.2	2.36	1.62	3.85	54.44
Niphates_sp	0.2	1.28	2.32	1.96	3.77	58.21
Halimeda_spp	1.09	0.2	2.08	1.49	3.38	61.59
Iotrochota_birotulata	0	0.97	2.05	1.85	3.34	64.93
Cliona_spp	1.31	0.4	1.95	1.6	3.17	68.1
Thalassia_testudinum	0	0.85	1.81	1.19	2.95	71.05
Groups Peps & LF_Catch						
Average dissimilarity = 58.54						
	Group	Group				

	Peps	LF_Catch				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum. %
Aplysina_sp	0	2.48	4.86	4.58	8.3	8.3
Antillogorgia_sp	2.67	0.28	4.63	3.76	7.9	16.21
Sand	0.2	2.52	4.54	4.12	7.76	23.97
Dictyota_spp	1.95	0	3.79	3.23	6.47	30.44
Halimeda_spp	1.89	0.2	3.3	3.53	5.64	36.08
Pseudoplexaura_spp	1.45	0	2.86	1.93	4.88	40.96
Millepora_sp	1.52	0.2	2.52	2.05	4.31	45.27
Porites_sp	1.39	0.2	2.32	2.61	3.97	49.24
Turf Algae	3.2	4.38	2.3	1.82	3.93	53.17
Cliona_spp	1.38	0.4	2.29	1.35	3.91	57.08
Gorgonia_spp	1.03	0	2.02	1.8	3.45	60.53
Iotrochota_birotulata	0	0.97	1.87	1.83	3.19	63.72
Actinotrichia_spp	1.36	0.68	1.85	1.38	3.16	66.87
Agaricia_sp	1.29	0.75	1.77	1.28	3.02	69.9
Niphates_sp	0.4	1.28	1.75	1.38	3	72.89
Groups Channel_Entrance & LF_Catch						
Average dissimilarity = 48.89						
	Group Channel_Entrance	Group LF_Catch				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum. %
Halimeda_spp	2.63	0.2	4.73	2.97	9.67	9.67
Agaricia_sp	2.83	0.75	4.07	2.52	8.32	17.99
Turf Algae	2.41	4.38	3.84	2.8	7.85	25.85
Sand	1.41	2.52	2.77	2.03	5.66	31.51
Dictyota_spp	1.46	0	2.75	0.73	5.63	37.14
Pseudoplexaura_spp	1.23	0	2.42	1.73	4.94	42.08
Antillogorgia_sp	1.31	0.28	2.23	1.48	4.56	46.64
Porites_sp	1.31	0.2	2.19	2.19	4.47	51.11
Millepora_sp	1.11	0.2	1.93	1.6	3.94	55.06
Niphates_sp	0.4	1.28	1.71	1.4	3.5	58.56
Thalassia_testudinum	0	0.85	1.64	1.2	3.36	61.92
Eunicea_sp	0.8	0	1.56	1.95	3.2	65.12

Aplysina_sp	1.96	2.48	1.54	1.53	3.14	68.26
Montastraea_cavernosa	0.48	0.6	1.43	1.01	2.93	71.19
Groups Curlew & LF_Catch						
Average dissimilarity = 48.43						
	Group Curlew	Group LF_Catch				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum. %
Agaricia_sp	3.47	0.75	5.37	2.83	11.09	11.09
Halimeda_spp	2.82	0.2	5.16	5.37	10.65	21.74
Sand	0.68	2.52	3.61	2.78	7.44	29.18
Millepora_sp	1.68	0.2	2.87	2.07	5.93	35.11
Porites_sp	1.19	0.2	2.16	1.35	4.45	39.56
Niphates_sp	0.48	1.28	1.76	1.51	3.64	43.2
Turf Algae	3.51	4.38	1.73	1.57	3.58	46.78
Thalassia_testudinum	0	0.85	1.66	1.2	3.42	50.2
Aplysina_sp	1.69	2.48	1.64	1.54	3.38	53.58
Siderastrea_sp	0.88	1.19	1.63	1.27	3.37	56.95
Cliona_spp	0.68	0.4	1.51	1.07	3.11	60.07
Cyanobacteria	4.02	3.39	1.4	1.38	2.88	62.95
Briareum_asbestinum	0.35	0.6	1.38	1.31	2.86	65.81
Orbicella_sp	0.63	0.4	1.38	1.12	2.86	68.67
Montastraea_cavernosa	0.4	0.6	1.35	0.97	2.78	71.44
Groups Lil_Seb & LF_Far_Reef						
Average dissimilarity = 48.13						
	Group Lil_Seb	Group LF_Far_Reef				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum. %
Antillogorgia_sp	2.65	0.4	4.15	3.33	8.62	8.62
Agaricia_sp	0.55	2.7	3.95	2.7	8.22	16.83
Orbicella_sp	0.2	1.73	2.83	1.98	5.88	22.71
Dictyota_spp	3.22	1.7	2.81	2.05	5.83	28.54

Gorgonia_spp	1.63	0.2	2.64	2.49	5.49	34.03
Halimeda_spp	1.09	2.45	2.52	1.64	5.24	39.27
Actinotrichia_spp	0	1.25	2.31	5.24	4.79	44.06
Iotrochota_birotulata	0	1.05	1.91	1.83	3.96	48.02
Verongula_rigida	0	0.95	1.73	1.68	3.59	51.61
Porites_sp	1.6	1.46	1.66	1.26	3.46	55.07
Amphimedon_compressa	0	0.88	1.62	1.89	3.37	58.43
Briareum_asbestinum	0	0.83	1.57	1.12	3.27	61.7
Cyanobacteria	2.66	3.46	1.56	1.41	3.24	64.95
Aplysina_sp	0	0.77	1.42	1.14	2.94	67.89
Millepora_sp	1.23	1.82	1.3	1.1	2.7	70.59
Groups Peps & LF_Far_Reef						
Average dissimilarity = 40.06						
	Group Peps	Group LF_Far_Reef				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum. %
Antillogorgia_sp	2.67	0.4	3.82	4	9.54	9.54
Agaricia_sp	1.29	2.7	2.44	1.56	6.08	15.62
Orbicella_sp	0.4	1.73	2.29	1.58	5.71	21.33
Pseudoplexaura_spp	1.45	0.2	2.15	1.47	5.36	26.69
Iotrochota_birotulata	0	1.05	1.76	1.83	4.39	31.08
Verongula_rigida	0	0.95	1.59	1.67	3.97	35.05
Cliona_spp	1.38	0.8	1.57	1.37	3.92	38.96
Gorgonia_spp	1.03	0.2	1.54	1.51	3.85	42.82
Siderastrea_sp	1.48	0.97	1.54	1.46	3.84	46.66
Briareum_asbestinum	0	0.83	1.45	1.12	3.61	50.27
Porites_sp	1.39	1.46	1.36	1.17	3.4	53.67
Aplysina_sp	0	0.77	1.3	1.14	3.25	56.93
Dictyota_spp	1.95	1.7	1.17	1.33	2.91	59.84
Coelothrix_spp	0.68	0.2	1.08	1.11	2.69	62.53
Actinotrichia_spp	1.36	1.25	1.07	1.17	2.68	65.2
Eunicea_sp	0.6	0.28	1.07	1.26	2.67	67.88
Halimeda_spp	1.89	2.45	1.02	1.26	2.55	70.42
Groups Channel_Entrance & LF_Far_Reef						

Average dissimilarity = 39.77						
	Group Channel Entrance	Group LF_Far_Reef				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum. %
Dictyota_spp	1.46	1.7	2.83	1.42	7.11	7.11
Orbicella_sp	0.28	1.73	2.52	1.84	6.33	13.44
Actinotrichia_spp	0	1.25	2.12	5.38	5.33	18.77
Sand	1.41	0.4	2.02	1.06	5.07	23.84
Aplysina_sp	1.96	0.77	2.01	1.32	5.05	28.89
Pseudoplexaura_spp	1.23	0.2	1.89	1.56	4.76	33.66
Antillogorgia_sp	1.31	0.4	1.82	1.63	4.58	38.23
Verongula_rigida	0	0.95	1.59	1.69	3.99	42.23
Amphimedon_compressa	0	0.88	1.49	1.89	3.74	45.97
Porites_sp	1.31	1.46	1.39	1.19	3.48	49.45
Eunicea_sp	0.8	0.28	1.3	1.82	3.26	52.72
Cliona_spp	0.28	0.8	1.29	1.83	3.25	55.97
Ircinia_sp	0.97	0.48	1.25	1.28	3.16	59.12
Millepora_sp	1.11	1.82	1.24	1.13	3.12	62.24
Turf Algae	2.41	3.03	1.21	1.29	3.05	65.3
Halimeda_spp	2.63	2.45	1.21	1.49	3.05	68.34
Briareum_asbestinum	0.88	0.83	1.16	1.28	2.92	71.26
Groups Curlew & LF_Far_Reef						
Average dissimilarity = 35.04						
	Group Curlew	Group LF_Far_Reef				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum. %
Actinotrichia_spp	0	1.25	2.13	5.37	6.09	6.09
Orbicella_sp	0.63	1.73	2.13	1.49	6.08	12.17
Dictyota_spp	0.68	1.7	1.8	1.36	5.15	17.31
Porites_sp	1.19	1.46	1.74	1.3	4.98	22.29
Aplysina_sp	1.69	0.77	1.7	1.48	4.84	27.13
Agaricia_sp	3.47	2.7	1.46	1.42	4.18	31.3

Briareum_asbestinum	0.35	0.83	1.46	1.15	4.17	35.48
Cliona_spp	0.68	0.8	1.44	1.84	4.12	39.59
Verongula_rigida	0.2	0.95	1.4	1.39	4.01	43.6
Siderastrea_sp	0.88	0.97	1.3	1.29	3.7	47.3
Cyanobacteria	4.02	3.46	1.08	1.32	3.09	50.39
Iotrochota_birotulata	1.56	1.05	1.05	0.97	3	53.39
Turf Algae	3.51	3.03	1.04	1.49	2.98	56.37
Sand	0.68	0.4	1.03	1.09	2.93	59.29
Millepora_sp	1.68	1.82	1	1.59	2.84	62.14
Amphimedon_compressa	0.68	0.88	0.98	1.09	2.8	64.93
Ircinia_sp	0.28	0.48	0.97	0.89	2.78	67.71
Eunicea_sp	0.48	0.28	0.95	0.89	2.72	70.44
Groups LF_Catch & LF_Far_Reef						
Average dissimilarity = 51.07						
	Group LF_Catch	Group LF_Far_Reef				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum. %
Halimeda_spp	0.2	2.45	4.38	3.38	8.58	8.58
Sand	2.52	0.4	4.12	3.48	8.07	16.65
Agaricia_sp	0.75	2.7	3.8	2.49	7.44	24.09
Aplysina_sp	2.48	0.77	3.34	2.08	6.54	30.63
Dictyota_spp	0	1.7	3.31	2.95	6.49	37.12
Millepora_sp	0.2	1.82	3.13	3.34	6.13	43.25
Turf Algae	4.38	3.03	2.6	1.97	5.08	48.33
Orbicella_sp	0.4	1.73	2.56	1.63	5.01	53.34
Porites_sp	0.2	1.46	2.54	1.35	4.98	58.31
Niphates_sp	1.28	0.2	2.09	1.95	4.09	62.4
Verongula_rigida	0	0.95	1.82	1.69	3.56	65.96
Amphimedon_compressa	0	0.88	1.7	1.89	3.34	69.3
Thalassia_testudinum	0.85	0	1.64	1.19	3.2	72.51

Table 8: ANOVA outputs for benthic functional groups by site with Tukey post-hoc test of pairwise site comparisons.

<b>Hard Coral ANOVA by Site</b>					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Site	5	21.042982	4.2085964	12.172933	6.03E-06
Residuals	24	8.2976153	0.345734	NA	NA
Tukey					
	Site.diff	Site.lwr	Site.upr	Site.p.adj	
Curlew-Channel Entrance	0.7661968	-0.3836257	1.9160194	0.3400987	
LF_Catch-Channel Entrance	-1.6920433	-2.8418658	-0.5422207	0.00162	
LF_Far_Reef-Channel Entrance	0.5908629	-0.5589596	1.7406855	0.613223	
Lil_Seb-Channel Entrance	-0.8025453	-1.9523678	0.3472773	0.2930214	
Peps-Channel Entrance	-0.3976523	-1.5474749	0.7521703	0.8886495	
LF_Catch-Curlew	-2.4582401	-3.6080627	-1.3084175	1.06E-05	
LF_Far_Reef-Curlew	-0.1753339	-1.3251564	0.9744887	0.9967338	
Lil_Seb-Curlew	-1.5687421	-2.7185646	-0.4189195	0.003651	
Peps-Curlew	-1.1638491	-2.3136717	-0.0140266	0.0460868	
LF_Far_Reef-LF_Catch	2.2829062	1.1330837	3.4327288	3.26E-05	
Lil_Seb-LF_Catch	0.889498	-0.2603245	2.0393206	0.1986679	
Peps-LF_Catch	1.294391	0.1445684	2.4442136	0.0210434	
Lil_Seb-LF_Far_Reef	-1.3934082	-2.5432308	-0.2435856	0.0113261	
Peps-LF_Far_Reef	-0.9885152	-2.1383378	0.1613073	0.1215735	
Peps-Lil_Seb	0.404893	-0.7449296	1.5547155	0.8810539	
<b>Soft Coral ANOVA by Site</b>					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Site	5	34.783562	6.9567124	16.804022	3.72E-07
Residuals	24	9.9357816	0.4139909	NA	NA
Curlew-	-1.5068287	-2.7650446	-0.2486127	0.0125643	

Channel_Entrance					
LF_Catch-Channel_Entrance	-1.8904748	-3.1486908	-0.6322588	0.0012797	
LF_Far_Reef-Channel_Entrance	-1.0076321	-2.2658481	0.2505839	0.1709621	
Lil_Seb-Channel_Entrance	0.8237987	-0.4344172	2.0820147	0.3584828	
Peps-Channel_Entrance	0.8264558	-0.4317602	2.0846718	0.3551022	
LF_Catch-Curlew	-0.3836461	-1.6418621	0.8745698	0.9311047	
LF_Far_Reef-Curlew	0.4991966	-0.7590194	1.7574125	0.819636	
Lil_Seb-Curlew	2.3306274	1.0724114	3.5888434	8.88E-05	
Peps-Curlew	2.3332845	1.0750685	3.5915004	8.74E-05	
LF_Far_Reef-LF_Catch	0.8828427	-0.3753733	2.1410587	0.287815	
Lil_Seb-LF_Catch	2.7142736	1.4560576	3.9724895	9.18E-06	
Peps-LF_Catch	2.7169306	1.4587146	3.9751466	9.04E-06	
Lil_Seb-LF_Far_Reef	1.8314308	0.5732149	3.0896468	0.0018297	
Peps-LF_Far_Reef	1.8340879	0.5758719	3.0923039	0.0018005	
Peps-Lil_Seb	0.0026571	-1.2555589	1.260873	1	
<b>Sponge ANOVA by Site</b>					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Site	5	12.523038	2.5046075	10.755152	1.64E-05
Residuals	24	5.5890033	0.2328751	NA	NA
Curlew-Channel_Entrance	0.1996922	-0.7439804	1.1433648	0.9852726	
LF_Catch-Channel_Entrance	0.2748452	-0.6688274	1.2185178	0.942596	
LF_Far_Reef-Channel_Entrance	-0.3753997	-1.3190723	0.568273	0.8180289	
Lil_Seb-Channel_Entrance	-1.5181498	-2.4618224	-0.5744771	0.000568	
Peps-Channel_Entrance	-0.9283544	-1.8720271	0.0153182	0.0556749	
LF_Catch-Curlew	0.075153	-0.8685196	1.0188256	0.9998588	
LF_Far_Reef-Curlew	-0.5750919	-1.5187645	0.3685808	0.4350733	
Lil_Seb-Curlew	-1.717842	-2.6615146	-0.7741693	0.0001131	
Peps-Curlew	-1.1280466	-2.0717193	-0.184374	0.0127677	
LF_Far_Reef-LF_Catch	-0.6502449	-1.5939175	0.2934278	0.3058551	

Lil_Seb-LF_Catch	-1.792995	-2.7366676	-0.8493223	6.19E-05	
Peps-LF_Catch	-1.2031996	-2.1468723	-0.259527	0.0071175	
Lil_Seb-LF_Far_Reef	-1.1427501	-2.0864227	-0.1990775	0.0113995	
Peps-LF_Far_Reef	-0.5529548	-1.4966274	0.3907179	0.4773272	
Peps-Lil_Seb	0.5897953	-0.3538773	1.533468	0.4079169	
<b>Macroalgae ANOVA by Site</b>					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Site	5	25.570689	5.1141378	6.7671673	0.0004586
Residuals	24	18.137472	0.755728	NA	NA
	Site.diff	Site.lwr	Site.upr	Site.p.adj	
Curlew-Channel Entrance	-0.3734424	-2.0734175	1.3265326	0.982614	
LF_Catch-Channel Entrance	-2.508016	-4.207991	-0.8080409	0.0015743	
LF_Far_Reef-Channel Entrance	-0.0097528	-1.7097278	1.6902223	1	
Lil_Seb-Channel Entrance	0.1281501	-1.571825	1.8281251	0.9998923	
Peps-Channel Entrance	-0.0689781	-1.7689532	1.6309969	0.999995	
LF_Catch-Curlew	-2.1345735	-3.8345486	-0.4345984	0.0082133	
LF_Far_Reef-Curlew	0.3636897	-1.3362854	2.0636647	0.984538	
Lil_Seb-Curlew	0.5015925	-1.1983826	2.2015676	0.9395263	
Peps-Curlew	0.3044643	-1.3955107	2.0044394	0.9930881	
LF_Far_Reef-LF_Catch	2.4982632	0.7982881	4.1982382	0.0016446	
Lil_Seb-LF_Catch	2.636166	0.9361909	4.3361411	0.0008855	
Peps-LF_Catch	2.4390378	0.7390628	4.1390129	0.0021435	
Lil_Seb-LF_Far_Reef	0.1379028	-1.5620722	1.8378779	0.9998454	
Peps-LF_Far_Reef	-0.0592254	-1.7592004	1.6407497	0.9999977	
Peps-Lil_Seb	-0.1971282	-1.8971032	1.5028469	0.9991167	
<b>Turf Algae ANOVA by Site</b>					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Site	5	10.640554	2.1281109	10.034793	2.81E-05
Residuals	24	5.0897571	0.2120732	NA	NA

	Site.diff	Site.lwr	Site.upr	Site.p.adj	
Curlew-Channel Entrance	1.0942528	0.1937134	1.9947921	0.0110597	
LF_Catch-Channel Entrance	1.963872	1.0633326	2.8644113	7.73E-06	
LF_Far_Reef-Channel Entrance	0.6180327	-0.2825067	1.518572	0.3099084	
Lil_Seb-Channel Entrance	0.6312692	-0.2692702	1.5318086	0.288759	
Peps-Channel Entrance	0.7900856	-0.1104537	1.690625	0.1093276	
LF_Catch-Curlew	0.8696192	-0.0309202	1.7701586	0.0626837	
LF_Far_Reef-Curlew	-0.4762201	-1.3767595	0.4243193	0.5847457	
Lil_Seb-Curlew	-0.4629836	-1.3635229	0.4375558	0.6127568	
Peps-Curlew	-0.3041671	-1.2047065	0.5963722	0.8979818	
LF_Far_Reef-LF_Catch	-1.3458393	-2.2463787	-0.4452999	0.0013604	
Lil_Seb-LF_Catch	-1.3326028	-2.2331421	-0.4320634	0.0015217	
Peps-LF_Catch	-1.1737863	-2.0743257	-0.273247	0.0057628	
Lil_Seb-LF_Far_Reef	0.0132365	-0.8873028	0.9137759	1	
Peps-LF_Far_Reef	0.1720529	-0.7284864	1.0725923	0.9907077	
Peps-Lil_Seb	0.1588164	-0.7417229	1.0593558	0.9935627	
<b>Cyanobacteria ANOVA by Site</b>					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Site	5	4.8150707	0.9630141	3.1349167	0.0256421
Residuals	24	7.3725529	0.3071897	NA	NA
	Site.diff	Site.lwr	Site.upr	Site.p.adj	
Curlew-Channel Entrance	0.7283848	-0.3554501	1.8122197	0.3313164	
LF_Catch-Channel Entrance	0.1011088	-0.9827261	1.1849436	0.9996933	
LF_Far_Reef-Channel Entrance	0.1676639	-0.916171	1.2514988	0.9965053	
Lil_Seb-Channel Entrance	-0.6318729	-1.7157078	0.451962	0.4827652	
Peps-Channel Entrance	0.2339	-0.8499349	1.3177349	0.9839288	
LF_Catch-Curlew	-0.627276	-1.7111109	0.4565589	0.4905837	
LF_Far_Reef-Curlew	-0.5607209	-1.6445558	0.523114	0.6066044	
Lil_Seb-Curlew	-1.3602577	-2.4440926	-0.2764228	0.0082503	

Peps-Curlew	-0.4944848	-1.5783197	0.5893501	0.7204855	
LF_Far_Reef-LF_Catch	0.0665551	-1.0172798	1.15039	0.9999609	
Lil_Seb-LF_Catch	-0.7329817	-1.8168166	0.3508532	0.3248517	
Peps-LF_Catch	0.1327913	-0.9510436	1.2166261	0.9988484	
Lil_Seb-LF_Far_Reef	-0.7995368	-1.8833717	0.2842981	0.2402166	
Peps-LF_Far_Reef	0.0662361	-1.0175988	1.150071	0.9999618	
Peps-Lil_Seb	0.8657729	-0.218062	1.9496078	0.1729224	
<b>Sand ANOVA by Site</b>					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Site	5	23.169699	4.6339399	19.888355	7.86E-08
Residuals	24	5.5919435	0.2329977	NA	NA
	Site.diff	Site.lwr	Site.upr	Site.p.adj	
Curlew-Channel_Entrance	-1.0363081	-1.9802289	-0.0923873	0.025605	
LF_Catch-Channel_Entrance	1.2036004	0.2596796	2.1475212	0.0071128	
LF_Far_Reef-Channel_Entrance	-0.8363081	-1.7802289	0.1076127	0.1037162	
Lil_Seb-Channel_Entrance	-1.2363081	-2.1802289	-0.2923873	0.005497	
Peps-Channel_Entrance	-1.2363081	-2.1802289	-0.2923873	0.005497	
LF_Catch-Curlew	2.2399085	1.2959877	3.1838293	1.95E-06	
LF_Far_Reef-Curlew	0.2	-0.7439208	1.1439208	0.9851886	
Lil_Seb-Curlew	-0.2	-1.1439208	0.7439208	0.9851886	
Peps-Curlew	-0.2	-1.1439208	0.7439208	0.9851886	
LF_Far_Reef-LF_Catch	-2.0399085	-2.9838293	-1.0959877	8.92E-06	
Lil_Seb-LF_Catch	-2.4399085	-3.3838293	-1.4959877	4.48E-07	
Peps-LF_Catch	-2.4399085	-3.3838293	-1.4959877	4.48E-07	
Lil_Seb-LF_Far_Reef	-0.4	-1.3439208	0.5439208	0.7766644	
Peps-LF_Far_Reef	-0.4	-1.3439208	0.5439208	0.7766644	
Peps-Lil_Seb	-8.88E-16	-0.9439208	0.9439208	1	

Table 9: ANOVA outputs for fish functional groups by site with Tukey post-hoc test of pairwise site comparisons.

<b>Omnivore ANOVA by Site</b>					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Site	5	224.218644	44.8437288	57.2849798	1.48E-12
Residuals	24	18.7876385	0.78281827	NA	NA
	Site.diff	Site.lwr	Site.upr	Site.p.adj	
Curlew-Channel Entrance	0.4547988	-1.2753772	2.18497476	0.96232691	
LF_Catch-Channel Entrance	6.99136353	5.26118756	8.72153949	7.75E-11	
LF_Far_Reef-Channel Entrance	2.44004833	0.70987237	4.1702243	0.00258032	
Lil_Seb-Channel Entrance	0.22304486	-1.5071311	1.95322082	0.99852974	
Peps-Channel Entrance	5.51931546	3.7891395	7.24949142	9.12E-09	
LF_Catch-Curlew	6.53656472	4.80638876	8.26674068	3.12E-10	
LF_Far_Reef-Curlew	1.98524953	0.25507357	3.71542549	0.01803395	
Lil_Seb-Curlew	-0.2317539	-1.9619299	1.49842202	0.99823412	
Peps-Curlew	5.06451666	3.3343407	6.79469262	4.69E-08	
LF_Far_Reef-LF_Catch	-4.5513152	-6.2814912	-2.8211392	3.29E-07	
Lil_Seb-LF_Catch	-6.7683187	-8.4984946	-5.0381427	1.52E-10	
Peps-LF_Catch	-1.4720481	-3.202224	0.2581279	0.12817996	
Lil_Seb-LF_Far_Reef	-2.2170035	-3.9471794	-0.4868275	0.00678981	
Peps-LF_Far_Reef	3.07926713	1.34909117	4.80944309	0.00015399	
Peps-Lil_Seb	5.29627061	3.56609464	7.02644657	2.01E-08	
<b>Herbivore ANOVA by Site</b>					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Site	5	12.3947237	2.47894473	2.43373185	0.06408732
Residuals	24	24.4458622	1.01857759	NA	NA
	Site.diff	Site.lwr	Site.upr	Site.p.adj	
Curlew-Channel Entrance	1.43962136	-0.5339683	3.413211	0.25059121	
LF_Catch-	0.82240065	-1.151189	2.79599029	0.78826572	

Channel_Entrance					
LF_Far_Reef-Channel_Entrance	0.93924366	-1.034346	2.9128333	0.68465463	
Lil_Seb-Channel_Entrance	-0.2847486	-2.2583383	1.68884103	0.99748529	
Peps-Channel_Entrance	1.33274013	-0.6408495	3.30632977	0.32636594	
LF_Catch-Curlew	-0.6172207	-2.5908103	1.35636893	0.92391893	
LF_Far_Reef-Curlew	-0.5003777	-2.4739673	1.47321194	0.96764622	
Lil_Seb-Curlew	-1.72437	-3.6979596	0.24921966	0.11175531	
Peps-Curlew	-0.1068812	-2.0804709	1.86670841	0.99997902	
LF_Far_Reef-LF_Catch	0.11684301	-1.8567466	2.09043265	0.99996736	
Lil_Seb-LF_Catch	-1.1071493	-3.0807389	0.86644037	0.52373182	
Peps-LF_Catch	0.51033948	-1.4632502	2.48392912	0.96483571	
Lil_Seb-LF_Far_Reef	-1.2239923	-3.1975819	0.74959736	0.41622217	
Peps-LF_Far_Reef	0.39349647	-1.5800932	2.36708611	0.98872494	
Peps-Lil_Seb	1.61748874	-0.3561009	3.59107838	0.1537537	
Generalist Carnivore ANOVA by Site					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Site	5	18.7681031	3.75362062	4.52598133	0.00477475
Residuals	24	19.9043894	0.82934956	NA	NA
	Site.diff	Site.lwr	Site.upr	Site.p.adj	
Curlew-Channel_Entrance	0.11715729	-1.6636979	1.89801248	0.999945	
LF_Catch-Channel_Entrance	0.31715729	-1.4636979	2.09801248	0.99326522	
LF_Far_Reef-Channel_Entrance	-0.0343146	-1.8151698	1.74654062	0.99999988	
Lil_Seb-Channel_Entrance	1.17167718	-0.609178	2.95253237	0.35337674	
Peps-Channel_Entrance	2.13400628	0.35315109	3.91486147	0.0124994	
LF_Catch-Curlew	0.2	-1.5808552	1.98085519	0.99924343	
LF_Far_Reef-Curlew	-0.1514719	-1.9323271	1.62938333	0.99980495	
Lil_Seb-Curlew	1.05451989	-0.7263353	2.83537508	0.46604912	
Peps-Curlew	2.01684899	0.2359938	3.79770418	0.02005443	
LF_Far_Reef-LF_Catch	-0.3514719	-2.1323271	1.42938333	0.98923206	
Lil_Seb-LF_Catch	0.85451989	-0.9263353	2.63537508	0.67737301	

Peps-LF_Catch	1.81684899	0.0359938	3.59770418	0.0436707	
Lil_Seb-LF_Far_Reef	1.20599175	-0.5748634	2.98684694	0.32347061	
Peps-LF_Far_Reef	2.16832085	0.38746566	3.94917605	0.01086248	
Peps-Lil_Seb	0.9623291	-0.8185261	2.74318429	0.56273128	
<b>Piscivore ANOVA by Site</b>					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Site	5	25.530776	5.10615519	18.7584541	1.36E-07
Residuals	24	6.53293303	0.27220554	NA	NA
	Site.diff	Site.lwr	Site.upr	Site.p.adj	
Curlew-Channel Entrance	-0.2	-1.2202539	0.82025394	0.98955711	
LF_Catch-Channel Entrance	1.28644408	0.26619014	2.30669802	0.00790079	
LF_Far_Reef-Channel Entrance	1.44920713	0.42895319	2.46946107	0.00238932	
Lil_Seb-Channel Entrance	2.07531793	1.05506399	3.09557187	2.27E-05	
Peps-Channel Entrance	2.15001056	1.12975663	3.1702645	1.32E-05	
LF_Catch-Curlew	1.48644408	0.46619014	2.50669802	0.00181087	
LF_Far_Reef-Curlew	1.64920713	0.62895319	2.66946107	0.00053553	
Lil_Seb-Curlew	2.27531793	1.25506399	3.29557187	5.40E-06	
Peps-Curlew	2.35001056	1.32975663	3.3702645	3.19E-06	
LF_Far_Reef-LF_Catch	0.16276305	-0.8574909	1.18301699	0.995962	
Lil_Seb-LF_Catch	0.78887385	-0.2313801	1.80912779	0.1990802	
Peps-LF_Catch	0.86356648	-0.1566875	1.88382042	0.13154225	
Lil_Seb-LF_Far_Reef	0.6261108	-0.3941431	1.64636474	0.42756605	
Peps-LF_Far_Reef	0.70080343	-0.3194505	1.72105737	0.309027	
Peps-Lil_Seb	0.07469263	-0.9455613	1.09494657	0.99990675	
<b>Invertivore ANOVA by Site</b>					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Site	5	344.222825	68.8445651	28.9598126	2.00E-09
Residuals	24	57.0538761	2.37724484	NA	NA
	Site.diff	Site.lwr	Site.upr	Site.p.adj	
Curlew-	0.65067747	-2.364388	3.66574299	0.98392854	

Channel_Entrance					
LF_Catch-Channel_Entrance	1.87317571	-1.1418898	4.88824123	0.41434146	
LF_Far_Reef-Channel_Entrance	1.74100243	-1.2740631	4.75606795	0.49302811	
Lil_Seb-Channel_Entrance	9.83379726	6.81873174	12.8488628	5.92E-09	
Peps-Channel_Entrance	5.2525416	2.23747608	8.26760712	0.0002051	
LF_Catch-Curlew	1.22249824	-1.7925673	4.23756376	0.80620454	
LF_Far_Reef-Curlew	1.09032496	-1.9247406	4.10539048	0.86908616	
Lil_Seb-Curlew	9.18311979	6.16805427	12.1981853	2.22E-08	
Peps-Curlew	4.60186413	1.58679861	7.61692965	0.00106719	
LF_Far_Reef-LF_Catch	-0.1321733	-3.1472388	2.88289223	0.99999266	
Lil_Seb-LF_Catch	7.96062154	4.94555602	10.9756871	3.08E-07	
Peps-LF_Catch	3.37936589	0.36430037	6.39443141	0.02178656	
Lil_Seb-LF_Far_Reef	8.09279483	5.07772931	11.1078603	2.30E-07	
Peps-LF_Far_Reef	3.51153917	0.49647365	6.52660469	0.0159388	
Peps-Lil_Seb	-4.5812557	-7.5963212	-1.5661901	0.00112438	
<b>Planktivore ANOVA by Site</b>					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Site	5	145.714213	29.1428427	11.8481177	7.53E-06
Residuals	24	59.0328557	2.45970232	NA	NA
	Site.diff	Site.lwr	Site.upr	Site.p.adj	
Curlew-Channel_Entrance	0.2	-2.8669103	3.26691029	0.99994733	
LF_Catch-Channel_Entrance	3.19016892	0.12325863	6.25707922	0.03814345	
LF_Far_Reef-Channel_Entrance	4.45613456	1.38922427	7.52304485	0.00186629	
Lil_Seb-Channel_Entrance	8.88E-17	-3.0669103	3.06691029	1	
Peps-Channel_Entrance	5.26489467	2.19798438	8.33180496	0.00024898	
LF_Catch-Curlew	2.99016892	-0.0767414	6.05707922	0.05898483	
LF_Far_Reef-Curlew	4.25613456	1.18922427	7.32304485	0.00305972	
Lil_Seb-Curlew	-0.2	-3.2669103	2.86691029	0.99994733	
Peps-Curlew	5.06489467	1.99798438	8.13180496	0.00040977	
LF_Far_Reef-LF_Catch	1.26596563	-1.8009447	4.33287593	0.79459915	

Lil_Seb-LF_Catch	-3.1901689	-6.2570792	-0.1232586	0.03814345	
Peps-LF_Catch	2.07472575	-0.9921845	5.14163604	0.32454589	
Lil_Seb-LF_Far_Reef	-4.4561346	-7.5230448	-1.3892243	0.00186629	
Peps-LF_Far_Reef	0.80876011	-2.2581502	3.87567041	0.96181903	
Peps-Lil_Seb	5.26489467	2.19798438	8.33180496	0.00024898	
<b>Cleaner ANOVA by Site</b>					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Site	5	70.9474891	14.1894978	9.9980765	2.89E-05
Residuals	24	34.0613465	1.41922277	NA	NA
	Site.diff	Site.lwr	Site.upr	Site.p.adj	
Curlew-Channel Entrance	1.60172607	-0.7278939	3.93134605	0.30806286	
LF_Catch-Channel Entrance	2.39699236	0.06737238	4.72661234	0.04117677	
LF_Far_Reef-Channel Entrance	-2.245534	-4.575154	0.08408601	0.06340529	
Lil_Seb-Channel Entrance	1.83160433	-0.4980157	4.16122431	0.18542489	
Peps-Channel Entrance	0.4687386	-1.8608814	2.79835859	0.98825131	
LF_Catch-Curlew	0.79526629	-1.5343537	3.12488627	0.89386731	
LF_Far_Reef-Curlew	-3.84726	-6.17688	-1.5176401	0.0004098	
Lil_Seb-Curlew	0.22987826	-2.0997417	2.55949824	0.99959654	
Peps-Curlew	-1.1329875	-3.4626074	1.19663252	0.66525281	
LF_Far_Reef-LF_Catch	-4.6425263	-6.9721463	-2.3129063	3.09E-05	
Lil_Seb-LF_Catch	-0.565388	-2.895008	1.76423195	0.97315318	
Peps-LF_Catch	-1.9282538	-4.2578737	0.40136623	0.14671697	
Lil_Seb-LF_Far_Reef	4.0771383	1.74751832	6.40675828	0.00019292	
Peps-LF_Far_Reef	2.71427257	0.38465259	5.04389256	0.01588739	
Peps-Lil_Seb	-1.3628657	-3.6924857	0.96675425	0.47905759	
<b>Spongivore ANOVA by Site</b>					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Site	5	6.3551549	1.27103098	2.57829516	0.05288068
Residuals	24	11.8313621	0.49297342	NA	NA

	Site.diff	Site.lwr	Site.upr	Site.p.adj	
Curlew-Channel_Entrance	0.2	-1.1730032	1.5730032	0.99736873	
LF_Catch-Channel_Entrance	1.29483569	-0.0781675	2.66783889	0.07253407	
LF_Far_Reef-Channel_Entrance	0.74641016	-0.626593	2.11941336	0.55653735	
Lil_Seb-Channel_Entrance	-9.99E-17	-1.3730032	1.3730032	1	
Peps-Channel_Entrance	0.4	-0.9730032	1.7730032	0.94253132	
LF_Catch-Curlew	1.09483569	-0.2781675	2.46783889	0.17428303	
LF_Far_Reef-Curlew	0.54641016	-0.826593	1.91941336	0.81778511	
Lil_Seb-Curlew	-0.2	-1.5730032	1.1730032	0.99736873	
Peps-Curlew	0.2	-1.1730032	1.5730032	0.99736873	
LF_Far_Reef-LF_Catch	-0.5484255	-1.9214287	0.82457767	0.81554255	
Lil_Seb-LF_Catch	-1.2948357	-2.6678389	0.07816751	0.07253407	
Peps-LF_Catch	-0.8948357	-2.2678389	0.47816751	0.36331544	
Lil_Seb-LF_Far_Reef	-0.7464102	-2.1194134	0.62659304	0.55653735	
Peps-LF_Far_Reef	-0.3464102	-1.7194134	1.02659304	0.96831006	
Peps-Lil_Seb	0.4	-0.9730032	1.7730032	0.94253132	

Table 10: Benthic genera used in distance based redundancy analysis models in the order used in the model.

Hard Coral	Soft Coral	Sponge	Algae
Agaricia spp	Antillogorgia spp	Aplysina spp	Dictyota spp
Porites spp	Briareum asbestinum	Cliona spp	Halimeda spp
Millepora spp	Gorgonia spp	Amphimedon compressa	Turf Algae
Orbicella spp	Pseudoplexaura spp	Iotrochota birotulata	Cyanobacteria
Dichocoenia stokesi	Eunicea spp	Niphates spp	Actinotrichia
	Plexaurella spp	Ircinia spp	Coelothrix spp
		Verongula rigida	