Spring 2013

Fine-Scale Behavior of Coral Reef Fishes in a Small Floridian Marine Reserve

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FINE-SCALE BEHAVIOR OF CORAL REEF FISHES IN A SMALL
FLORIDIAN MARINE RESERVE

A Thesis
Presented to the
Faculty of the
Division of Science and Environmental Policy
California State University Monterey Bay

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
in
Coastal and Watershed Science and Policy

by
Jessica Watson
May 2013
CALIFORNIA STATE UNIVERSITY MONTEREY BAY

The Undersigned Faculty Committee Approves the

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FINE-SCALE BEHAVIOR OF CORAL REEF FISHES IN A SMALL

FLORIDIAN MARINE RESERVE

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“The sea, once it casts its spell, holds one in its net of wonder forever.”

- Jacques Yves Cousteau
DEDICATION

I dedicate this thesis to the following people who are most important to me:

My supportive partner, Nick, who stood by me throughout my entire academic career and believed in me when my confidence waned; my parents Bernice and Terry, who instilled in me a strong work ethic and have supported me through all my life decisions; my antagonistic brother Josh who has always made me strive to be the best I could possibly be; and to all those who have ever dealt with the perils and strife of pursuing a master’s degree in marine science.
ABSTRACT

Fine-Scale Behavior of Coral Reef Fishes in a Small Floridian Marine Reserve
by
Jessica Watson
Master of Science in Coastal Watershed Science and Policy
California State University Monterey Bay, 2013

Foraging is a fundamental ecological process. Foraging patterns are not only related to the spatial distribution of prey, but are also important in understanding which habitats are utilized in the acquisition of prey. In the present study, we provide context to previous telemetric work by exploring the inter- and intra-specific differences in foraging behavior and habitat utilization of three representative species from different feeding guilds in a small marine reserve at Conch Reef. Field work was conducted during a saturation mission to the Aquarius Undersea Laboratory in November of 2008. The results of this study clearly depict inter- and intra-specific variation of fine-scale foraging behaviors and habitat utilization for these three species of coral reef fishes. New insights into the foraging behavior were observed for hogfish (Lachnolaimus maximus), which were observed to winnow primarily over sand and continuous reef habitats, and for blue parrotfish (Scarus coeruleus) which were observed to bite primarily over sand and continuous reef habitats. Black grouper (Mycteroperca bonaci) as expected were found to be the only species to display ram/suction feeding. Given the increasingly wide application of small marine reserves world wide, including the reserve in which the study was conducted, enhanced understanding of fine-scale foraging behaviors of fishes targeted for protection by reserves will be needed to improve spatial management efforts. Though this study only provides information for adults of these species at Conch Reef, it still provides details on the landscape features that these three species utilize while foraging. Since foraging is a basic ecological process that directly influences movement patterns, the relative proportions of these foraging habitats should be included by managers when evaluating and establishing new marine reserves dedicated to protecting this species within the Florida Keys Reef Tract.
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ACKNOWLEDGEMENTS

I would like to thank my thesis committee members: Dr. James Lindholm, Dr. Fred Watson, and Dr. Peter Auster for all their support and guidance through this thesis process. To James; thank you for all the opportunities and support you have provided me throughout my academic career both as my advisor and as the fearless leader of IfAME. You have provided me with more experience and opportunities than I could have ever dreamed possible, and I am forever in your debt. Fred, thank you for the statistical insight you have provided during my graduate career, it is a skill set that I will continue to improve upon in the future. Peter, thank you for your straight forward candor and constructive feedback. You have helped me grow during this thesis process and I am immensely grateful. To Jon Detka, thank you for the statistical refresher course that you provided. I would also like to thank Frank Degnan for inspiring me to explore the ocean from underneath the waves and providing me with the training to be the best diver I could be.

I would like to acknowledge all those who helped with the data collection during the 2008 Aquarius mission. I would like to thank the Aquarius Reef Base team for keeping scientists’ safe and allowing us to live and conduct science on the reef. I would also like to thank all those at the National Marine Sanctuary Program for providing a northern California foothill girl with the opportunity to participate as an Aquanaut in the 2010 Aquarius mission “If Reefs Could Talk”. That opportunity not only allowed me to live with the species I was studying for ten days, but also let me gain incomparable insight into the environment I was studying.

I would like to thank all those who have read my thesis and provided feedback specifically members of the “peanut gallery”. Thank you for your tireless and endless support and reading and editing multiple thesis drafts. Lastly, I would like to thank all those who have provided moral support during this process: my family, Nicholas Sherman, Arley Muth, Monica Galligan, Heather Kramp, Leora Martin, and Jessica Sullivan.
INTRODUCTION

Many of the basic ecological processes that drive fish population dynamics are influenced directly by behavioral responses (Sutherland 1996). To fully understand these fundamental ecological processes, including predator-prey interactions, interference competition, dispersal, and patterns in habitat use, knowledge of specific behavioral responses is required (Sutherland 1996). In particular, habitat use by fishes specifically integrates behavior with population dynamics and community structure (Levin 2000). Further, behavioral responses related to habitat use may reflect decisions of mobile animals as to how they balance the requirements associated with foraging for prey and avoiding predation (Dahlgren and Eggleston 2000).

Though the associations between marine fishes and habitat attributes of the seafloor have been well-documented worldwide (Jones 1988; Carr 1989; García-Charton and Perez-Ruzafa 2001; Yoklavich et al. 2002; Knight 2012), and in coral reef ecosystems in particular (Roberts and Ormond 1987; Green 1996; Friedlander and Parrish 1998; Tolimieri 1998; McClanahan and Arthur 2001; Gratwicke and Speight 2004), important questions still remain with respect to the fine-scale habitat use of most fishes. The effects of habitat patch use and the spatial heterogeneity of resources has been a fundamental concept in studies of behavioral ecology (Levin 2000). Since foraging patterns are related to the spatial distribution of prey (Iwasa et al. 1981), it is not only important to understand what behaviors are used in acquiring prey but also the habitat utilization that accompanies these foraging behaviors. Foraging and the behaviors associated with the act of finding prey have a direct influence on habitat associations which drive fine-scale movement patterns (Hansson and Fahrig 1995). Given the increasing use of spatial approaches to management in the marine environment (including marine protected area; Botsford et al. 1997; Murray et al. 1999; Brodziak and Link 2002; Claudet and Pelletier 2004; Pomeroy et al. 2005), more precise information on fish-habitat associations will be critical for successful management.

Not unlike habitat utilization, foraging, including the suite of behaviors associated with the act of finding prey, is a fundamental ecological process (Stephens and
Krebs 1986) for which a great deal remains to be identified for many fish species. Foraging strategy can be characterized by describing the morphologies and behaviors associated with different prey acquisition techniques. Coral reef fishes employ several foraging strategies during the acquisition of prey that are indicative of specific morphological attributes. Fish morphology plays a major role in foraging and determining diet because physical attributes such as gape, jaw mechanics, body size and shape affect feeding ability (Wainwright and Bellwood 2002). For example, the acquisition of prey associated with hard bottom substrates requires predators to be morphologically equipped to employ suction or biting techniques to capture prey (Wainwright and Bellwood 2002). Biting force is directly related to morphological jaw-closing ratios, while rapid-strike and ram-suction feeding require species to have morphological features that allow the expansion of the mouth during the strike and increased speed when closing the mouth in order to acquire prey (Wainwright and Richard 1995). Other reef prey are associated with soft unconsolidated substrates like sand and therefore successful predators have morphological adaptations such as barbels and the ability to winnow in order to find prey and extract it from the substrate (Gosline 1984).

Morphology is not the only factor determining foraging strategy. Behavior also plays an integral role in foraging, allowing species with similar feeding morphologies to display different patterns of prey consumption (Bellwood and Choat 1990). Many animal species adjust their feeding behavior in order to balance increasing food intake with the risk of predation (Lima and Dill 1990), which can have ecological consequences through trophic interactions (Abrams 1984).

While species-specific information on habitat use and foraging behavior advances our understanding of particular species and/or species complexes, our ability to scale up information is enhanced by apportioning species into guilds. A guild is defined as a "group of species, regardless of taxonomic position, that exploit the same class of environmental resources in a similar way" (Root 1967, Simberloff and Dayan 1991). The two basic feeding guilds within reef fish communities are carnivores and herbivores
Representatives from each of these feeding guilds have differences in diet, physiology, and morphology.

In this study three species were chosen to capture attributes of each of the two primary guilds among coral reef fishes in order to explore inter-specific and intra-specific variations in behavior. Hogfish (*Lachnolaimus maximus*, Walbaum 1792) are benthivorous, a subclass of the carnivore feeding guild, whose diet consists of a varied array of benthic invertebrates (Clifton and Motta 1998). *L. maximus* are found in subtropical and tropical waters from South Carolina to Brazil, including the Gulf of Mexico, at depths of 3 to 30 m (Randall 1983; Robins et al. 1999). They associate primarily with shallow, low relief (<1.5 m) mixed substrates and patch reef environments (Robins et al. 1999; Ault et al. 2003). Worldwide, fishing pressure has reduced many populations of *L. maximus* to critically low levels, such that the species has been identified as vulnerable to extinction by the International Union for Conservation of Nature (IUCN 2000).

Black grouper (*Mycteroperca bonaci*, Poey 1860) are piscivorous, another subclass of the carnivore feeding guild. *M. bonaci* feed mainly on other fishes and inhabits coral reef habitats and rock ledges from North Carolina to southern Brazil (Jory and Iversen 1989). They are generalist piscivores that occupy trophic positions near the top of the food web (Chiappone et al. 2000). *M. bonaci* populations are showing signs of overfishing which could have negative effects on reef ecosystem functions (Jory and Iversen 1989; Chiappone et al. 2000; Ault et al. 2001).

Blue parrotfish (*Scarus coeruleus*, Bloch 1786) are part of the herbivore feeding guild. *S. coeruleus* distribution extends from Maryland to southeast Brazil, from depths of 3 to 25m (Lieske and Myers 1994). They are coral reef dwelling fish that have been known to be hesitant to swim over expansive areas of bare sand (Lindholm et al. 2006b). *S. coeruleus* were chosen for this study due their potential ecological importance as bio-eroders and since they are among the least studied of the common Caribbean Scarids (Molina-Ureña 2009), rather than for their limited commercial importance.

This study was sited at Conch Reef in southeast Florida, in order to capitalize on telemetric studies conducted there to describe the small scale (i.e. 100's of meters)
movements of \textit{M. bonaci}, \textit{L. maximus}, and \textit{S. coeruleus} (Lindholm et al. 2005a,b, 2006a,b). In 2001 telemetry studies indicated that the majority of \textit{M. bonaci} showed limited movement at Conch Reef and the adjacent Davis Reef (Lindholm et al. 2005b). In 2002 and 2003, a similar study was conducted at Conch Reef, which described \textit{L. maximus} as having high site fidelity within specific areas on Conch Reef (Lindholm et al. 2006a) while \textit{S. coeruleus} showed movement across Conch Reef (Lindholm et al. 2006b). On-going research at Conch Reef (Lindholm et. al., unpublished) found that \textit{M. bonaci}, while showing high overall fidelity to the reef, were quite mobile across the reef, moving outside the reserve boundaries thus becoming vulnerable to exploitation. \textit{L. maximus} and \textit{S. coeruleus} were found to have higher residencies to specific locations within the reef complex and were less vulnerable to exploitation.

While these telemetric studies have provided insight into the movements of fishes, the underlying rationale for those movements remain uncertain. To that end direct underwater observation of the fine-scale behaviors of these fishes was conducted to provide context to the broader movement patterns observed in previous studies by exploring foraging behavior and fine scale habitat associations. Specifically, foraging behavior was classified using a combination of feeding and swimming behaviors, and our goal was to identify inter-specific and intra-specific differences between coral reef fishes from different feeding guilds. The three ecological questions addressed in this study were:

a) To what extent does habitat utilization of selected coral reef fishes differ between feeding guilds?

b) To what extent are patterns in swimming behaviors of selected coral reef fishes in different feeding guilds correlated with variation in habitat attributes?

c) To what extent are patterns in diurnal feeding behaviors of selected coral reef fishes in different feeding guilds correlated with variation in habitat attributes?
MATERIALS AND METHODS

Conch Reef

Field work was conducted during a saturation mission to the Aquarius Undersea Laboratory in November of 2008. Aquarius is located at Conch Reef, approximately nine miles south of Key Largo, within the Conch Reef Research Only Area (24°59'N, 80°25'W) and the Florida Keys National Marine Sanctuary (Figure 1). It is a fringing reef characterized by relatively small (1-2m) spur and groove formations that extend from the reef crest then break up into a number of isolated patch reefs that lead to the sand plain which extends into the deep channel of the Florida Straits (Leichter et al. 1996). Like other reefs around the world, the community at Conch Reef is moving from a live coral dominated system towards an algal dominated system (Beach et al. 2003; Herren et al. 2006).

Figure 1: Map of the study area, including the boundaries of both the Conch Reef Research Only Area, the location of the Aquarius Undersea Laboratory, and the “line highway” around Aquarius Undersea Laboratory that was used for the navigation during the study. The location of the study site within the Florida Keys National Marine Sanctuary is included in the inset. The 30 m buffer around the line highway depicts areas of the reef that were accessible by saturation divers.
Observations

A total of 148 SCUBA surveys were conducted during the Aquarius mission to collect observational data on the habitat utilization, swimming, and feeding behaviors of three coral reef species; *S. coeruleus* (n=53 individuals), *M. bonaci* (n=49 individuals), and *L. maximus* (n=46 individuals). Observations were made primarily by three saturation divers and augmented by two surface divers using Nitrox (36% O₂).

All data were collected during daylight hours (from 1 hour after sunrise to 1 hour before sunset). Surveys consisted of 10 minute sampling periods during which observations of individual fish behavior, and the primary habitat type over which that behavior was observed, were recorded every 20 seconds on a waterproof datasheet (Appendix A). Divers remained stationary 1-2 m above the substrate, far enough away from the subject under observation to minimize diver effects on behavior and movement of fishes, but close enough to identify reef landscape attributes and fish behavior.

Efforts were made to avoid duplicate observations of the same individual within a 24-hour period. These efforts included dive teams avoiding the same species at the same location in the same hour, unless a school was observed and divers could consecutively survey different individuals. Other efforts to reduce pseudo-replication included dive teams avoiding sampling the same location multiple times on the same day.

Although a 10 minute observation period was the goal, there were instances when individuals were followed for less time and, rarely, for longer, due to constraints on diver movement. Video imagery collected during the 2002 and 2005 missions to Aquarius, was used to supplement diver observations. Imagery was recorded on mini-DV format tape. Data were extracted from the imagery for the same three coral reef species; *S. coeruleus* (N= 10 individuals), *M. bonaci* (N= 4 individuals), and *L. maximus* (N= 11 individuals) using the same protocol as was used for the *in situ* observations. A programmable keyboard (P.I. Engineering, Williamston, MI, USA) was used to denote the feeding and movement behaviors as well as substrate type.
CLASSIFICATION OF VARIABLES

Response Variables

Swimming behaviors were divided a priori into two categories (active swimming and station keeping) to broadly encompass the movements of coral reef fishes on the reef. Active swimming was defined as directed swimming in a single direction, while station keeping was defined as maintaining position, either over a particular habitat feature or in the water column.

Three distinct classifications were delineated a priori to encompass the feeding behaviors of the species included in the study: biting, winnowing, and ram-suction feeding. Biting was defined as the process in which a predator takes individual directed bites that remove tissue and/or skeletal structure (Liem 1980). Winnowing was defined as a mode of foraging behavior in which the predator takes mouthfuls of substrate in search of edible prey and separates the two to feed on the prey at which point the remaining undesired material is ejected from the mouth (Schmitt and Coyer 1982; Laur and Ebeling 1983). Suction feeding is the process in which the predator draws in water and the prey into the mouth by flaring the operculum (Liem 1980). Ram feeding is the process in which the predator overtakes the prey with forward movement of the body or protruding jaws (Liem 1980). Since ram feeding can only be distinguished in practice from suction feeding based on the relative role of forward mouth movement (ram) and water flow toward the mouth (suction) in moving the prey into the oral cavity (Liem 1980), the two categories were grouped.

The reef landscape was divided a priori into four broad habitat classes and three relief sub-classifications. Habitat classes consisted of seafloor features ranging from 10s of meters to 1 meter in scale (Greene et al. 1999). The heterogeneous reef formations at Conch Reef have previously been classified using several microhabitat categories (Leichter et al. 1996; Auster and Lindholm 2002; Lindholm et al. 2005b). The categories used in previous works to classify habitat type were also used for this study and included continuous reef (CRe), sand (SD), water column (WC), and coral rubble (Cru). The continuous reef habitat patch classification consists of coral/reef hard substrates and...
included spur formations as well as their associated epifauna, while coral rubble habitat patches are primarily characterized as transitional zones between continuous reef and the sand plain. The water column classification was used when an individual’s altitude was greater than three body lengths off the bottom. The relief of each habitat class was binned into three categories, High (> 1m), Moderate (0.5 – 1 m), and Low (< 0.5m).

Time of day was a discrete variable classified *a priori* into three categories (i.e. morning, midday, and afternoon) to encompass the entire time period in which data were collected and because diurnal reef-dwelling fish have a predictable succession of behaviors that correspond with specific times of day (Collette and Talbolt 1972; Hobson 1972, McFarland et al. 1979; Rickel and Genin 2004). These categories represent times of day that have significant increases and decreases in light level, as well as high light levels throughout the specified time duration (Collette and Talbolt 1972; Hobson 1972; McFarland et al. 1979; Rickel and Genin 2004). Morning was therefore defined as 0600 hours to 1000 hours, midday represented 1000 hours to 1400 hours, and afternoon represents 1400 hours to 1800 hours.

**Predictor Variables**

For this study the three species that were chosen to represent each of the basic feeding guilds which include *M. bonaci* (BG), *L. maximus* (HG), and *S. coeruleus* (BP) were used as predictor variables.

**STATISTICAL ANALYSES**

Inter-specific differences were compared using either a Pearson’s chi-square contingency table analysis or a Fishers exact test (*α* = 0.05). The Pearson’s chi-square contingency table was conducted on sample sizes greater than five and in cases where the sample size was less than five, a Fishers exact test was used. Both tests were used to test numerous comparisons of null-vs-alternative hypotheses to explore the inter-specific differences in foraging behaviors and habitat utilization. These included comparisons of the three different feeding behavior classifications, comparisons of the two swimming behaviors, and comparisons of the four habitat classifications. In all these cases,
comparisons were made with respect to representative species from different feeding
guilds. For each comparison, pairs of null-vs-alternative hypotheses were posed using the
following basic format:

\[ H_{F,0}: BG_F = HG_F = BP_F \]
\[ H_{F,1}: BG_F \neq HG_F \neq BP_F \]

\[ H_{S,0}: BG_S = HG_S = BP_S \]
\[ H_{S,1}: BG_S \neq HG_S \neq BP_S \]

\[ H_{H,0}: BG_H = HG_H = BP_H \]
\[ H_{H,1}: BG_H \neq HG_H \neq BP_H \]

\[ H_{SH,0}: BG_{SH} = HG_{SH} = BP_{SH} \]
\[ H_{SH,1}: BG_{SH} \neq HG_{SH} \neq BP_{SH} \]

Each variable represents a proportion of time a given species (BG, HG, or BP) spent
displaying a given behavior (F or S) or utilizing a given habitat type (H). Where the
following terminology was used to describe foraging behavior and habitat utilization:

- **F**: The predefined feeding behaviors ram/suction, winnowing, and biting.
- **S**: The predefined swimming behaviors station keeping and active swimming.
- **H**: The predefined habitat classifications continuous reef, coral rubble, water
column, and sand.
- **SH**: The predefined swimming behaviors that were observed over each of the
  habitat classifications.
The alternative hypotheses specify that there is a relationship between the variables but does not specify the nature of this relationship. When $H_{X1}$ was accepted, the strength of associations was determined by qualitatively comparing proportions. This rejection of the null hypothesis is evidence for either selective utilization or non-uniform availability of habitat. We cannot know which, because data were not available on the distribution of available habitat. However, since the same habitat distribution was available to all species, we consider a rejection of the null hypothesis in this case to be evidence that different species were using the available habitat differently. Therefore, at least one of species was using the habitat selectively. Yet it remains quantitatively unclear which particular species was or were being selective.

Since we have a qualitative understanding of habitat availability, some qualitative inference was possible in regard to evidence for selective utilization. Since surveys were restricted to divers attached to the “line highway” of *Aquarius* by reels it is assumed that surveys were never more than 30m from an anchor line. With this in mind a 30m buffer was created around the “line highway” which represents that total area in which a survey could be conducted (Figure 1). Using a digital elevation model with 2 meter resolution vector ruggedness measure (VRM) grids were created using the Terrain Tools toolbox for ArcGIS (Young et al. 2010). Vector ruggedness use the slope and aspect of the grid cells in a DEM to classify substrate rugosity with harder substrates having higher values and soft substrates lower values. Once created, VRM threshold values representing the given habitat types used in this study were assigned using a visual classification method. The zonal statistics toolbox was then used to subjectively estimate the availability of each representative habitat type in order to qualitatively compare the estimates of available habitat to the proportions of habitat utilized by each species surveyed.

Intra-specific differences were analyzed using descriptive statistics comparing means and standard errors. The mean proportion of time a given behavior was observed as well as the proportion of time spent over a given habitat was calculated for each individual within a species as well as for the entire species. These proportions were
compared between individuals in order to describe the variation in foraging behaviors as well as habitat utilization.

All observational data were assumed to be part of the same statistical population since all data were collected during the same time period along the same section of the reef tract. Behavioral data often violate the assumptions of independence due to the nature in which the data are collected (Mattson et al. 2005). Therefore, the data were tested for temporal autocorrelation, using the autocorrelation function plot display in the R statistical package. This function displays graphical representations of the correlation coefficient for a given lag time. Response variables in our dataset were auto correlated at \( \leq 40 \) seconds. Therefore, the data were sub-sampled out at 40 second intervals (n = 3869 observations). This sub-sampled data set was used in the following Pearson’s chi-square contingency table statistical analyses. All statistical analyses in this study were conducted using the R statistical package (R Core Development Team).

RESULTS

A total of one hundred and forty eight surveys were completed, totaling approximately 21.5 hours of observation. Of the 148 surveys 49 were \textit{M. bonaci}, 53 were \textit{S. coeruleus}, and 46 were \textit{L. maximus}. The depth range of the surveys ranged from 12 m – 30 m with the majority of the surveys conducted between 18 m – 27 m. The numbers of surveys conducted in each of the depth zones were comparable between species.

Of the 148 surveys, 60 were conducted in the morning, 29 in mid-day, and 59 in the afternoon. For all three species comparable numbers of surveys were conducted during the morning (\textit{M. bonaci} N= 21 individuals, \textit{S. coeruleus} N= 20 individuals, \textit{L. maximus} N= 16 individuals) and the afternoon (\textit{M. bonaci} N= 18 individuals, \textit{S. coeruleus} N= 20 individuals, \textit{L. maximus} N= 20 individuals). During midday fewer surveys were conducted (\textit{M. bonaci} N= 10 individuals, \textit{S. coeruleus} N= 13 individuals, \textit{L. maximus} N= 6 individuals).

The three species used sand habitat (33.4%) and continuous reef (47.8%) predominantly, while coral rubble and the water column combined accounted for less
than 20% of habitats utilized. Continuous reef habitats were also classified by vertical relief, including 30% high, 40% moderate, and 30% low.

An additional 25 surveys were conducted using the supplementary video footage totaling approximately 1.7 hours. Due to the short observational periods and small sample sizes the video-derived data were not used in the analyses and instead were used as a reference for classification of fish behaviors and habitat types.

**Inter-specific Differences**

There were significant differences in habitat utilization among the three species ($\chi^2=189.2$, df = 6, p < 0.001).

![Figure 2: The proportion of time spent by M. bonaci (BG), S. coeruleus (BP) and L. maximus (HG) utilizing a given habitat type (sand (SD), continuous reef (CRe), coral rubble (Cru) and water column (WC)) during this observational study and the subjective estimate of habitat availability using a VRM calculation in ArcGIS of the study region of this observational study. Standard error of the proportion of time spent utilizing a habitat type is depicted by the error bars.](image)

The habitat availability estimates suggest that the study area was composed primarily of continuous reef habitats. Sand and coral rubble accounted for approximately 17% and 11% of the available habitat respectively. The water column was continuously available since it is the vertical space in the water column above the substrate and
therefore was potentially available for utilization 100% of the time. Given these available habitat proportions, observational surveys showed that *L. maximus* and *M. bonaci* had similar habitat utilization patterns, though the frequency with which these patterns occurred was not similar. The proportion of time spent by *L. maximus* over continuous reef and sand substrates combined was 0.95 (Figure 2). *M. bonaci* spent a combined proportion of time of 0.86 over continuous reef and sand habitats (Figure 2). Since continuous reef and sand habitats account for 82% of the estimated available habitat, both these patterns of habitat utilization coincided with the available habitat. However, both species seem to be utilizing sand habitats more than the estimated percentage that is available, potentially implying that these species show selectivity to sandy habitats (Figure 2).

Even though *L. maximus* and *M. bonaci* spent the highest proportion of time utilizing continuous reef habitats, the relief sub-classifications that they were utilizing were not similar (Table 1). *L. maximus* spent more time over continuous reef habitats and were approximately two times more likely to utilize continuous reef habitats with moderate reliefs (Table 1). While *M. bonaci* spent approximately 70% of the time utilizing continuous reef habitats with moderate and high reliefs (Table 1).

*S. coeruleus* split the proportion of their time rather evenly between the two primary utilized habitats and secondary utilized habitats (Figure 2). These patterns of utilization show strong evidence that *S. coeruleus* were partitioning their time between these habitats selectively due to the significant differences in availability and time spent in these habitats. *S. coeruleus* also differed from the other two species in this study in that the proportion of time spent over continuous reef habitats with low relief was approximately 46% while time over moderate and high relief substrate accounted for 54% (Table 1).
Table 1: The observed percentage of each relief classification for continuous reef (CRe) habitats observed during this study for each species

<table>
<thead>
<tr>
<th></th>
<th>CRe with Low Relief Utilized</th>
<th>CRe with Moderate Relief</th>
<th>CRe with High Relief Utilized</th>
</tr>
</thead>
<tbody>
<tr>
<td>M. bonaci</td>
<td>7.3%</td>
<td>13.4%</td>
<td>14.0%</td>
</tr>
<tr>
<td>S. coeruleus</td>
<td>12.6%</td>
<td>7.8%</td>
<td>6.7%</td>
</tr>
<tr>
<td>L. maximus</td>
<td>9.5%</td>
<td>19.2%</td>
<td>9.4%</td>
</tr>
<tr>
<td>TOTAL</td>
<td>29.4%</td>
<td>40.5%</td>
<td>30.1%</td>
</tr>
</tbody>
</table>

There were significant differences in swimming behaviors among the three species ($\chi^2 = 66.2$, df = 2, $p < 0.001$). L. maximus and M. bonaci had similar swimming behaviors though the frequency at which these patterns occurred differed. Both species spent the highest proportion of time displaying station keeping movement behaviors (Figure 3). The proportion of time each species spent displaying station keeping movement behaviors were similar (L. maximus SK = 0.62, M. bonaci SK = 0.68). Just as the proportion of time spent station keeping was similar for these two species so was the time spent active swimming (Figure 3). These patterns however were the opposite with regards to the proportion of time S. coeruleus spent displaying these two movement behaviors (Figure 3). S. coeruleus spent more time active swimming than station keeping (Figure 3).
Figure 3: The proportion of time spent by *M. bonaci* (BG), *S. coeruleus* (BP) and *L. maximus* (HG) displaying active swimming (AS) and station keeping (SK) during this observational study. Standard error of the proportion of time spent displaying a swimming behavior is depicted by the error bars.

Due to small expected values for feeding behaviors, a Fisher’s exact test was used to investigate the inter-specific differences instead of the Pearson’s chi-square test. The Fisher’s exact test revealed significant differences in feeding behaviors among the three species ($\chi^2 = 677.9, df = 4, p < 0.001$). *M. bonaci* were the only species observed to ram/suction feed. *S. coeruleus* spent the highest proportion of time biting (Figure 4). *L. maximus* spent the highest proportion of time winnowing (Figure 4). *S. coeruleus* were also observed winnowing for a proportion of time of 0.06 and *L. maximus* were observed biting for a proportion of time of 0.26.
There were significant differences in percent time each species spent displaying station keeping over the four habitat types ($\chi^2 = 47.82$, df = 6, $p < 0.001$). The total of all swimming behaviors observed showed that for all three trophic guilds, station keeping accounted for 56.6% of the movement behaviors observed. Of this 56.6%, 30% occurred over continuous reef habitats and 22.8% over sand habitats with the remaining 3.8% consisting of coral rubble and water column habitats. All three species spent highest percent of time station keeping over continuous reef and sand habitats (Table 2). Active swimming was more evenly distributed between habitat types than was the case with station keeping (Table 2).

*M. bonaci* were observed to station keep 67.3% of the time. Of that 67.3%, 34.7% occurred over continuous reef habitats and 28.7% occurred over sand habitats with the remaining 3.9% occurring over coral rubble and water column habitats. Active swimming accounted for 32.7% was displayed relatively similar across all habitats except for coral rubble (Table 2). Station keeping accounted for 42.2% of the time *S. coeruleus* displayed swimming behavior, however it was more concentrated over continuous reef and sand habitats (Table 2). *S. coeruleus* were observed active swimming the majority of the time.
Of this 57.8% time observed active swimming *S. coeruleus* spent a similar amount of time utilizing all four habitat types (Table 2) *L. maximus* were observed to exhibit station keeping swimming behaviors for 61.9% of the time. Of the time observed station keeping, 23.4% of observations occurred over sand habitats while 37.6% occurred over continuous reef habitats. *L. maximus* were observed to active swim for 38.1% of the time. Active swimming over continuous reef habitats accounted for approximately 66% of the observations with the rest of the observations occurring over the other three habitat types (Table 2). The proportion of time spent by *M. bonaci* station keeping was similar to that of *L. maximus* over both continuous reef and sand habitats (Table 2). *M. bonaci* and *S. coeruleus* were the only species observed to station keep in the water column (Table 2).

There were significant differences in active swimming over the four habitat types among the three species ($\chi^2 = 116.22, df = 6, p < 0.001$). *M. bonaci* and *S. coeruleus* spent a similar proportion of time active swimming over continuous reef habitats, while *L. maximus* spent a larger proportion active swimming over ominous reef habitats (Table 2). *S. coeruleus* spent the highest proportion of time active swimming over coral rubble habitats (Table 2). *M. bonaci* and *L. maximus* spent a similar proportion of time actively swimming over coral rubble and sand habitats (Table 2).

**Table 2:** The number of observations of all individuals of each species displaying movement behaviors (active (AS) and station keeping (SK)) over the different habitat types (sand, coral rubble, continuous reef, and water column).

<table>
<thead>
<tr>
<th>Species (sample size)</th>
<th>Swimming Movements</th>
<th>Habitat Type</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Sand</td>
<td>Rubble</td>
<td>Reef</td>
<td>Column</td>
<td></td>
</tr>
<tr>
<td><em>M. bonaci</em> (N = 49)</td>
<td>AS</td>
<td>411</td>
<td>104</td>
<td>10</td>
<td>173</td>
<td>124</td>
<td></td>
</tr>
<tr>
<td></td>
<td>SK</td>
<td>847</td>
<td>361</td>
<td>39</td>
<td>437</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td><em>S. coeruleus</em> (N = 53)</td>
<td>AS</td>
<td>792</td>
<td>196</td>
<td>158</td>
<td>208</td>
<td>230</td>
<td></td>
</tr>
<tr>
<td></td>
<td>SK</td>
<td>579</td>
<td>232</td>
<td>78</td>
<td>260</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td><em>L. maximus</em> (N = 46)</td>
<td>AS</td>
<td>453</td>
<td>101</td>
<td>9</td>
<td>304</td>
<td>39</td>
<td></td>
</tr>
<tr>
<td></td>
<td>SK</td>
<td>737</td>
<td>279</td>
<td>11</td>
<td>447</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>
Of all the feeding behaviors observed in this study 60.4% were biting and 39.2% were winnowing. Ram/suction feeding accounted for less than 1% of all feeding behaviors observed. Biting occurred most often over continuous reef habitats (Table 3) However, biting also occurred over sand, coral rubble, and water column (Table 3). Of the winnowing events observed the majority occurred in sand and continuous reef habitats with less than 1% occurring in coral rubble habitats (Table 3).

*M. bonaci* were the only species in this study to be observed displaying ram/suction feeding. Ram/suction feeding was only observed over continuous reef and sand habitats. Of these observations 80% occurred over continuous reef habitats. The proportion of time spent *M. bonaci* feeding was less than 0.01 showing that observation of feeding event was not common occurrence.

*S. coerules* were observed biting 96.4% of the time, with the remainder spent winnowing (Table 3). Biting occurred over all habitat types with the majority occurring evenly over sand, continuous reef, and coral rubble (Table 3). *S. coerules* were also observed biting in the water column but this was less than 1% of total observations. *S. coerules* were observed to winnow for approximately 3.6% of the time observed. Ninety-four percent of the winnowing observations for *S. coerules* occurred in sand habitats with the remainder occurring in coral rubble (Table 3). Winnowing consisted of 74.2% of all *L. maximus* feeding behaviors observed during this study. Of the 25.8% percent time *L. maximus* were observed biting 96% occurred while utilizing continuous reef habitats. *L. maximus* also displayed biting in sand and coral rubble habitats (Table 3).

*L. maximus* and *S. coerules* spent a similar proportion of time biting over continuous reef habitats (Table 3). However, a disproportionate amount of time was spent biting over sand habitats for these two species (Table 3). Sand and continuous reef habitats were the primary habitats used by *L. maximus* when winnowing. Sand accounted for 37% and continuous reef 35.8% of the time when winnowing was observed for *L. maximus* with the balance occurring over coral rubble. The proportion of time spent winnowing by *L. maximus* was similar over continuous reef and sand habitats (Table 3).
Table 3: The number of observations of individuals of each species displaying feeding behaviors (biting (B), winnowing (W), ram/suction (RS)) over the different habitat types (sand, coral rubble, continuous reef, and water column).

<table>
<thead>
<tr>
<th>Species (sample size)</th>
<th>Feeding Behavior</th>
<th>Total</th>
<th>Coral Rubble</th>
<th>Continuous Reef</th>
<th>Water Column</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Sand</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M. bonaci (N = 49)</td>
<td>B</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>RS</td>
<td>5</td>
<td>1</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>S. coeruleus (N = 53)</td>
<td>B</td>
<td>616</td>
<td>199</td>
<td>183</td>
<td>228</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>23</td>
<td>22</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>RS</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>L. maximus (N = 46)</td>
<td>B</td>
<td>169</td>
<td>5</td>
<td>1</td>
<td>163</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>487</td>
<td>243</td>
<td>9</td>
<td>235</td>
</tr>
<tr>
<td></td>
<td>RS</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Of the five ram/suction feeding events that were observed for M. bonaci, two occurred while station keeping and three while active swimming. The proportion of the time spend ram/suction feeding while station keeping and active swimming was thus similar for these swimming behaviors as was the occurrence of witnessing these two types of feeding strategies.

S. coeruleus were only observed station keeping swimming when a winnowing feeding event was observed (Table 4). A much smaller proportion of time was spent winnowing and station keeping by S. coeruleus than biting while station keeping (Table 4). A higher proportion of time was spent by S. coeruleus station keeping when biting than when active swimming and biting (Table 6).

While winnowing, L. maximus spent the highest proportion of time station keeping (Table 4). Station keeping was also observed while L. maximus were biting and the proportion of time spent was greater than when they were biting while active swimming (Table 4). A much smaller proportion of time was spent winnowing and active swimming by L. maximus than winnowing while station keeping (Table 4).
Table 4: The total number of observations for individuals of each species displaying movement behaviors (active (AS) and station keeping (SK)) while displaying a feeding behavior (biting, winnowing, and ram/suction).

<table>
<thead>
<tr>
<th>Species</th>
<th>Swimming Movements</th>
<th>Total</th>
<th>Feeding Behavior</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Biting</td>
</tr>
<tr>
<td>M. bonaci</td>
<td>AS 3 (N = 49)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>SK 2 (N = 49)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>S. coeruleus</td>
<td>AS 245 (N = 53)</td>
<td>245</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>SK 393 (N = 53)</td>
<td>370</td>
<td>23</td>
</tr>
<tr>
<td>L. maximus</td>
<td>AS 111 (N = 46)</td>
<td>63</td>
<td>48</td>
</tr>
<tr>
<td></td>
<td>SK 571 (N = 46)</td>
<td>106</td>
<td>465</td>
</tr>
</tbody>
</table>

Intra-specific Differences

There was little intra-specific variation in *M. bonaci* utilization of coral rubble and water column habitats (Table 5). All but one individual *M. bonaci* were observed to utilize coral rubble habitats greater than 25% of the time. Approximately 84% of all the *M. bonaci* spent less than 25% of the time utilizing the water column. Continuous reef habitats and sand habitats show more intra-specific variation among *M. bonaci* (Table 5). Intra-specific variation within *M. bonaci* with respect to sand habitat utilization was polarized with individuals either utilizing the habitat for less than 25% of the time or spending a higher percent (>50%) of time utilizing this habitat.

Habitat use varied among *S. coeruleus* (Table 5). A common trend however was that across all habitats there were only 1-2 individual *S. coeruleus* which utilized a given habitat more than 75% of the time. Similar to *M. bonaci* coral rubble and water column habitat utilization were similar, with the majority of individuals spending less than 25% of the time utilizing these habitats (Table 5). Intra-specific variation of *S. coeruleus* utilization of sand and continuous reef habitats were similar (Table 5). Ninety-two percent of the individual *S. coeruleus* observed utilized sand habitats 25% and 75% of the time, while 90% utilized continuous reef habitats over that same interval.
There was little intra-specific variation in *L. maximus* utilization of coral rubble and water column habitats (Table 5). Only eight individual *L. maximus* were observed utilizing coral rubble habitat and all of these individuals spent less than 25% of the time utilizing this specific habitat type. Of all the individual *L. maximus* observed 97% spent 25% of the time utilizing the water column (Table 5). Intra-specific variation with respect to sand and continuous reef habitats were almost perfect reciprocals (Table 5).

**Table 5**: Intra-specific variation depicted by the number of individuals of each species that spent a specific percentage of time spent utilizing a given habitat type (sand, coral rubble, continuous reef, and water column). The number of individuals in the "None" category represent those individuals of a species that were never observed to utilize the corresponding habitat type.

<table>
<thead>
<tr>
<th>Species (sample size)</th>
<th>Percent Time Observed</th>
<th>Habitat Type</th>
<th>Coral Rubble</th>
<th>Continuous Reef</th>
<th>Water Column</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Sand</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>M. bonaci (N = 49)</strong></td>
<td>None</td>
<td>13</td>
<td>41</td>
<td>8</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td>&gt;0 - 25%</td>
<td>12</td>
<td>7</td>
<td>7</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>25% - 50%</td>
<td>9</td>
<td>0</td>
<td>10</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>50% - 75%</td>
<td>5</td>
<td>0</td>
<td>8</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>75% - 100%</td>
<td>10</td>
<td>1</td>
<td>16</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>49</td>
<td>49</td>
<td>49</td>
<td>49</td>
</tr>
<tr>
<td><strong>S. coeruleus (N = 53)</strong></td>
<td>None</td>
<td>3</td>
<td>21</td>
<td>3</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>&gt;0 - 25%</td>
<td>19</td>
<td>18</td>
<td>16</td>
<td>29</td>
</tr>
<tr>
<td></td>
<td>25% - 50%</td>
<td>18</td>
<td>9</td>
<td>20</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>50% - 75%</td>
<td>12</td>
<td>4</td>
<td>12</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>75% - 100%</td>
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<td>1</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>53</td>
<td>53</td>
<td>53</td>
<td>53</td>
</tr>
<tr>
<td><strong>L. maximus (N = 46)</strong></td>
<td>None</td>
<td>14</td>
<td>38</td>
<td>3</td>
<td>29</td>
</tr>
<tr>
<td></td>
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<td>12</td>
<td>8</td>
<td>6</td>
<td>16</td>
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<tr>
<td></td>
<td>25% - 50%</td>
<td>6</td>
<td>0</td>
<td>5</td>
<td>1</td>
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<tr>
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<td>50% - 75%</td>
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<td>0</td>
<td>6</td>
<td>0</td>
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<tr>
<td></td>
<td>75% - 100%</td>
<td>9</td>
<td>0</td>
<td>26</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>46</td>
<td>46</td>
<td>46</td>
<td>46</td>
</tr>
</tbody>
</table>
Individual movement behaviors varied among *M. bonaci*. Even though there was variation in the proportion of the time *M. bonaci* spent station keeping, 44% of individuals spent a high percentage (75% - 100%) of the time station keeping (Table 6). *M. bonaci* also showed intra-specific variation in the proportion of time individuals spent active swimming. Few individuals spent a high percentage of time (75% - 100%) active swimming.

There was little intra-specific variation between active swimming and station keeping for *S. coeruleus* individuals (Table 6). Approximately, 54% of individual *S. coeruleus* observed split the percent of the time (0% - 75%) between active swimming and station keeping rather evenly (Table 6). The main intra-specific difference was that 25% *S. coeruleus* individuals spend a high percentage of time (75% - 100%) displaying active swimming while less than 1% spent this amount of time station keeping (Table 6).

There was little intra-specific variation between *L. maximus* individuals while displaying movement behavior (Table 6). It appears that the majority of individuals are splitting the percentage of time displaying movement behaviors relatively evenly between active swimming and station keeping with the highest percentage of time being spent station keeping.

*M. bonaci* showed no intra-specific variation in feeding. Ram suction feeding was the only feeding strategy employed by individuals. Observing a feeding event never exceeded a percentage of time greater than 25% which was expected since feeding events were rarely observed.

*S. coeruleus* showed intra-specific variation in the percent time utilizing biting while individuals displaying winnowing behavior showed little intra-specific variation. Variation in the amount of time individuals spent biting seemed to be evenly represented among the different classifications that ranged from 0% - 75% (Table 6) with 81% of the individuals sampled being encompassed in this group. As was expected, there was no intra-specific variation with ram/suction feeding since this behavior was not observed for this species.
L. maximus showed intra-specific variation in the percent time biting. Approximately, 73% of individuals were observed biting for 0% - 25% percent of the time. Variation in the amount of time individuals spent winnowing seemed to be evenly represented among the different classifications that ranged from 25% - 100% (Table 6) with 58% of the individuals sampled being encompassed in this group. As was expected, there was no intra-specific variation with ram/suction feeding since this behavior was not observed for this species.

Table 6: Intra-specific variation depicted by the number of individuals of each species that spent a specific percentage of time spent displaying movement behaviors (active and station keeping) and feeding behaviors (biting, winnowing, and ram/suction). The number of individuals in the “None” category represent those individuals of a species that were never observed to display the corresponding behavior.

<table>
<thead>
<tr>
<th>Species (sample size)</th>
<th>Percent Time Observed</th>
<th>Swimming Behavior</th>
<th>Feeding Behavior</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Active Swimming</td>
<td>Station Keeping</td>
</tr>
<tr>
<td>M. bonaci (N = 49)</td>
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<td></td>
</tr>
<tr>
<td>None</td>
<td>9</td>
<td>1</td>
<td>49</td>
</tr>
<tr>
<td>&gt;0 - 25%</td>
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<tr>
<td>25% - 50%</td>
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<td>0</td>
</tr>
<tr>
<td>50% - 75%</td>
<td>15</td>
<td>12</td>
<td>0</td>
</tr>
<tr>
<td>75% - 100%</td>
<td>4</td>
<td>22</td>
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</tr>
<tr>
<td>Total</td>
<td>49</td>
<td>49</td>
<td>49</td>
</tr>
<tr>
<td>S. coeruleus (N = 53)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>None</td>
<td>2</td>
<td>11</td>
<td>4</td>
</tr>
<tr>
<td>&gt;0 - 25%</td>
<td>3</td>
<td>3</td>
<td>12</td>
</tr>
<tr>
<td>25% - 50%</td>
<td>19</td>
<td>16</td>
<td>12</td>
</tr>
<tr>
<td>50% - 75%</td>
<td>16</td>
<td>19</td>
<td>19</td>
</tr>
<tr>
<td>75% - 100%</td>
<td>13</td>
<td>4</td>
<td>6</td>
</tr>
<tr>
<td>Total</td>
<td>53</td>
<td>53</td>
<td>53</td>
</tr>
<tr>
<td>L. maximus (N = 46)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>None</td>
<td>3</td>
<td>8</td>
<td>24</td>
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<td>&gt;0 - 25%</td>
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<tr>
<td>25% - 50%</td>
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<td>75% - 100%</td>
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</tr>
<tr>
<td>Total</td>
<td>46</td>
<td>46</td>
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</tr>
</tbody>
</table>
DISCUSSION

The results of this study clearly depict inter-specific and intra-specific variation of fine-scale foraging behaviors and habitat utilization for three species of coral reef fishes at Conch Reef in the Florida Keys. While selected aspects of these results could have been predicted based on existing knowledge of each species, other aspects provide new insights into each species and their respective interactions with the reef environments in which they occur. *L. maximus* were observed to winnow primarily over sand and continuous reef habitats, and *S. coeruleus* were observed to bite primarily over sand and continuous reef habitats. *M. bonaci* as expected were found to be the only species to display ram/suction feeding.

Given the increasingly wide application of small marine reserves world wide (Gell and Roberts 2003), including the reserve in which this study was conducted, enhanced understanding of fine-scale foraging behaviors of fishes targeted for protection by reserves will be needed to improve spatial management efforts. Though this study only provides information for adults of these species at Conch Reef it still provides details on the landscape features that these three species utilize while foraging. Since foraging is a basic ecological process that directly influences movement patterns the relative proportions of these foraging habitats should be considered by managers when evaluating and establishing new marine reserves dedicated to protecting this species throughout Florida Keys.

Habitat Utilization

Our results expand on the current knowledge of habitats utilized during feeding bouts for each of the species in this study. *L. maximus* have previously been reported to primarily utilize sand and coral rubble habitat types when foraging (Clifton and Motta 1998). Our findings concur, and provide additional insight into the habitats utilized by adult *L. maximus* when foraging. We found that sand and continuous reef habitats were the primary habitats used by *L. maximus* when winnowing, with the remainder of the time winnowing occurring in coral rubble. Based on our subjective estimates of habitat availability, the lack of utilization coral rubble habitat by *L. maximus* does not derive
from a lack of coral rubble habitat availability. Coral rubble habitats and sand habitats had similar proportions of availability based on our estimates, yet *L. maximus* winnowing events clearly differed between continuous reef and sand habitats compared to coral rubble habitats.

Previous literature has reported that *M. bonaci* have been observed to feed near rock ledges (Smith et al. 1961; Jory and Iversen 1989). These findings were supported by our study as we found that the majority of feeding events occurred when individuals were utilizing continuous reef habitats. We also observed *M. bonaci* to associate with biologic and abiotic structures that were not specifically analyzed using the current methodology. Specifically, some *M. bonaci* were observed to be associated with gorgonian species during the observation periods, while others were observed to utilize reef ledges and overhangs. Due to these observations, we postulate that substrate type may not be the only driving force mediating foraging behaviors, but rather, these behaviors may be determined by a combination of substrate type and abiotic and biotic structure.

Adult *S. coeruleus* are thought to be specialized sand suckers that forage directly from sandy bottoms (Longley and Hildebrand 1941). This generalization however does not hold true across all life stages of this species. Overholtzer and Motta (1999) found juveniles were never observed to utilize sand substrates when feeding and instead were found to be specialized in their consumption of upright, foliose macroalgae on hard substrates. Our findings showed that *S. coeruleus* partitioned their time foraging over hard substrates as well as sand habitats.

Variation among individual *S. coeruleus* could be due to ontogenetic shifts in habitat and resource utilization during the sub-adult to adult life stages. Ontogenetic shifts in foraging behavior allow for limiting resources to be allocated differently among conspecifics. Comparing our findings to previous literature there is evidence that suggests a potential ontogenetic shift with juvenile *S. coeruleus* feeding on a variety of foods and specialization occurring as sub-adults shift to adult phases and begin feeding primarily from the sand. These shifts in utilization associated with size could be due to predation risk as well. Werner et al. 1983 investigated behavioral responses of potential prey to risk
of predation and found that prey changed patterns of habitat use to avoid predation. This pattern could be influencing the habitat utilization of different life stages of *S. coeruleus* where increasing size reduces the risk of predation due to gap limitations, potentially allowing larger individuals to utilize habitats that have a higher risk of predation to smaller individuals.

Patterns due to intra-specific variation for these three species would benefit in the future by noting the size and sex of individuals in order to identify if the sex of the individual is the contributing factor on determining individual variation in behavior and habitat utilization and identify ontogenetic shifts. Hoffman (1983) found that male hogfishes (*Bodianus* spp) minimized foraging time since their reproductive success depends more upon the time spent in social and mating activities than upon net energy gains. However, the opposite was the true for females which were found to spend more time foraging in order to gain the energy needed for gamete production (Hoffman 1983). Gender related difference in allocations of foraging effort could be the determining factor of the observed intra-specific differences in individuals of the same species utilization of habitat types as well as display in feeding and movement behaviors. Thus, the driving factor determining the intra-specific variation in the number of individuals observed feeding could be resulting from the male to female sex ratio observed in this study.

This study demonstrated that inter-specific variations in habitat utilization exist for these three trophically different species. The similarities and differences in habitat utilization can be explained by feeding guild classification with similarities between the two carnivorous species and differences occurring with the representative herbivore species. Though the reasoning for these variations are probably due to a variety of factors, the use of feeding guild as a proxy for describing habitat utilization of species within a guild could influence future management measures for conservation at a species complex level rather than individual species level at the Conch Reef marine reserve.

**Foraging**

Foraging has direct influence on habitat associations. Therefore, just as inter-specific differences were found for habitat utilization, inter-specific differences were also
found for foraging behaviors. Our results support the theory that just as morphology influences foraging strategy so does feeding behavior. These results expand on the current knowledge of feeding behaviors utilized by these three representative species and the habitats utilized during these feeding bouts.

Morphology is the primary indicator of feeding behavior, with species possessing morphological adaptations that aide in the acquisition of prey. Our results found direct examples where morphology was not the only factor determining foraging strategy, and demonstrated how behavior also plays an integral role by allowing species with similar feeding morphologies to display different patterns of prey consumption. Parrotfish have a beak that is morphologically suited to bite and scrape from hard substrates. Parrotfish in general are considered important grazers on coral reefs to the morphological features of their beak allowing for biting and scraping of hard substrates (Bellwood and Choat 1990; Molina-Ureña 2009), yet we observed S. coeruleus continually feeding in sandy habitats. Possible resources that could be utilized during these feeding bouts explaining the behavior are infaunal and epifaunal invertebrates or algal mats. This provides further support confirming the theory that even though adult S. coeruleus are morphologically specialized to bite and scrape prey from hard substrates they have developed behavioral adaptations as adults to become sand suckers that forage directly from sandy bottoms (Longley and Hildebrand 1941).

We know from previous literature that the main feeding behaviors employed by L. maximus are biting and winnowing (Clifton and Motta 1998). Our results support the previous literature that found L. maximus to be a focal species during group foraging bouts. As a focal species over continuous reef habitats through biting and winnowing feeding behaviors L. maximus has the potential to be ecologically important in group foraging bouts. Group foraging is a common type of species interaction that occurs on coral reef communities (Auster and Lindholm 2002). Since group foraging allows individuals to acquire more prey resources, while decreasing search time, and increasing predator vigilance it has potential to not only enhance the fitness of the individuals in the group, but also community composition and diversity (Auster and Lindholm 2002).
Black grouper were observed to feed only 5 times during the surveys and employed ram/suction feeding which is expected based on their morphology and previous literature. During several missions divers observed individual *M. bonaci* holding a stationary position in the spur and groove formations orienting themselves in currents at twilight. This could be a feeding strategy and twilight surveys should be conducted in the future to investigate the possible ecological forces driving these behaviors.

**Implications**

Globally most marine management is based on generalizations since there is not enough information available during the implementation process. With the current push towards marine spatial management, effective management requires the reduction of scientific uncertainty through monitoring and research that is directed at filling the gaps in the scientific knowledge (Nagelkerken 2009). Specifically, to be effective as a fisheries enhancement tool, a marine reserve requires detailed knowledge of the movement behavior of a fish species in order to decide which proportion of suitable habitat needs to be protected in order to conserve the exploited stock and justify the effect of closing that area to fishing (Roberts and Polunin 1991).

When determining the boundaries for no-take marine reserves, like that at Conch Reef, it is important to identify the associations between fish populations and their habitats. The need to identify essential fish habitat (EFH), or the area required for a species to sustain its life processes, has been described as critically important in efforts to rebuild depleted stocks (Fogarty 1999). When creating no-take marine reserves boundaries it is a logical progression to consider EFH because optimal reserve design requires that the boundaries include habitats that are essential to the sustainability of the species targeted for protection.

Though this study only provided information for adults of these species at Conch Reef it still provides a basic understanding of the habitats that are needed to mediate fine scale behaviors of two federally managed species. The Atlantic fish stocks in federal waters (3-200 miles offshore) are managed by the South Atlantic Fisheries Management Council (SAFMC). Specifically, *M. bonaci* and *L. maximus* are managed under the
Snapper Grouper Fishery Management Plan (FMP) (SAFMC 1983). The FMP was established in 1983 and is amended as needed to protect stocks from overexploitation (SAFMC 1983). As part of the FMP, Stock Assessments Fishery Evaluation (SAFE) reports are created periodically to summarize the best available scientific information concerning the status of the stocks and their predicted future condition given the management efforts (50 CFR 600.10).

In the most recent SAFE report (2005) *M. bonaci* adults were reported as being “found over hard bottom such as coral reefs and rocky ledges”, while *L. maximus* were reported as being “found over open bottom or coral reefs” these are extremely broad habitat classifications when creating management measures such as marine reserves. This study identifies landscape features potentially driving feeding behaviors not only will the SAFE report be informed, but so will the classification of EFH for these two species.

Since foraging has direct links to utilization and influences movement patterns, the relative proportions of these foraging habitats should be included by managers when evaluating and establishing new marine reserves dedicated on protecting these species. Since previous telemetric data showed that *L. maximus* and *S. coeruleus* have higher residencies to specific locations inside Conch Reef reserves boundaries it is likely that adequate proportions of foraging habitat are contained in the boundaries of this reserve. However, *M. bonaci* were found to move across the reef and becoming vulnerable to exploitation by leaving the protection of the reserves boundaries. Previous telemetric work conducted by Lindholm (2005a, 2005b, 2006b, 2006a) could benefit from the integration of behavioral work into future sampling designs. By combining foraging behavioral observation with telemetric work simultaneously ambit and activity budgets could be calculated for these species as well as other key species in MPA planning. This would provide insight to the area that it utilized when foraging as well as the time spent in this area and the respective habitat types being utilized.

Although the reserves in the FKNMS are mostly comprised of relatively small areas (several km2), many can encompass areas that contain a variety of distinct ecosystem features (Jeffery 2004). Thus we suggest for future studies a combined
methodology of coupling benthic habitat maps with geo-referenced observations of feeding guild foraging behavior data. This coupling would allow for greater extrapolation throughout the Florida Reef Tract on the habitat types that are used when foraging and the specific habitat characteristics that are driving these patterns. This is similar to reef fish abundance work conducted by Jeffery (2004) where benthic maps were used to explore how fish assemblages are affected by underlying habitats, and show that particular species and guilds occur more frequently in particular habitat types. By using this technique of extrapolation EFH required during foraging across the entire reef tract inside and outside marine reserves can be informed across feeding guilds.
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## APPENDIX A

Data Sheet

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### OBSERVATIONS

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APPENDIX B

Policy Applications

The Sustainable Fisheries Act of 1996 was the first step towards implementing a more holistic approach to fisheries management. This act was monumental since it began requiring Fisheries Management Councils (FMC) to describe and identify Essential Fish Habitat (EFH) in Fishery Management Plans (FMPs). The reauthorized Magnuson Stevens Fisheries Management and Conservation Act (MSFMCA) defines EFH as, “those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity” (MSFCMA, 2006). The goal of the act was to minimize adverse effects from anthropogenic fishing impacts on habitat, and to identify the habitats that fisheries depend on (MSFCMA, 2006).

The most recent step towards marine spatial management is through the establishment of Marine Protected Areas (MPAs), which seek to enhance fisheries by regulating specific human activities at specific given locations (Botsford et al. 1997, Murray et al. 1999, Brodziak and Link 2002, Claudet and Pelletier 2004, Pomeroy et al. 2005). The FKNMS in itself is a MPA since it is a spatially explicit area that regulates human uses and was established under the National Marine Sanctuaries Act (NMSA).

To achieve the goals of the NMSA of protecting national resources, each sanctuary must be able to effectively manage the resources within its boundaries (NMSA). In efforts to accomplish this goal, on July 1, 1997, a new approach to marine spatial management went into effect in the FKNMS that included a large-scale marine zoning plan (Miller et al. 2000). This plan established 23 comparatively small no-take zones (1-2 km$^2$) along the Florida Keys reef tract (Miller et al. 2000). These no take zones are the most restrictive of Marine Protected Areas (MPAs) since the directly impact fisheries take through restricting the commercial and recreational take of species within a given area (Miller et al. 2000). With the implementation of no take marine reserves as tools for fishery management, it is important to have a complete knowledge of these species movement patterns, which will ultimately determine the efficacy of these
areas protecting these species from further exploitation (Gell and Roberts 2003; Sale et al. 2005).

The key to success of no take MPAs (marine reserves) is that the size of the marine reserve corresponds with the movements of the species it is intended to protect (Gell and Roberts 2003, Sale et al. 2005). Specifically, an effective marine reserve must encompass enough area to not only protect an adequate proportion of individuals from exploitation, but still be small enough to allow for production in the reserve to supplement surrounding populations (Rowley 1994; Sale et al. 2005). Due to the economic impacts of closing fishing areas, it is important to understand the potential scales at which supplemental spillover of adults occurs (McClanahan and Mangi 2000). Since spillover is a function of perimeter length (Sale et al. 2005), in order to fully understand spillover potential of marine reserves we must understand the extent to which individual species move while maintaining basic life processes (McClanahan and Mangi 2000; Gell and Roberts 2003; Sale et al. 2005). Given the importance of spillover from a management perspective, information on fish movements and the identification of the interactions between fish and habitat attributes of the seafloor influencing these movements is important to evaluating marine reserve design (Sale et al. 2005).

The Conch Reef reserve is a no take zone which is the most restrictive of Marine Protected Areas (MPAs) and has direct impacts on fisheries take through restricting the commercial and recreational take of species within a given area (Miller et al. 2000). With the implementation of no take marine reserves as tools for fishery management, it is important to have a complete knowledge of these species movement patterns, which will ultimately determine the efficacy of these areas protecting these species from further exploitation (Gell and Roberts 2003; Sale et al. 2005).

Though this study specifically provides information for these three species at the Conch Reef Marine Reserve, these species are also present throughout the Florida Keys Reef Tract. The Atlantic fish stocks in federal waters (3-200 miles offshore) are managed by the South Atlantic Fisheries Management Council (SAFMC). Specifically, *M. bonaci* and *L. maximus* are managed under the Snapper Grouper Fishery Management Plan.