

Distribution of Roving Herbivorous Fishes on Coral Reefs at Multiple Spatial Scales

By

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A dissertation submitted in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY
in
MARINE SCIENCES

UNIVERSITY OF PUERTO RICO
MAYAGUEZ CAMPUS
2013

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Abstract

Roving herbivorous fishes are an integral part of the biodiversity of coral reefs due to their high abundance and ecological role as grazers of benthic algae. The present study examined the ecology of surgeonfish (Acanthuridae) and parrotfish (Scaridae) in three parts: (1) their distribution on fore-reefs in relation to transect scale characteristics, (2) the spatial pattern in the interaction between fish and algae, and (3) the relative importance of composition and configuration seascape metrics to determine how these help explain spatial patterns at a large scale. At the transect scale across three depths and six reefs herbivorous fish distribution exhibited an inverse relationship with depth and a positive one with topographic relief. A complex interaction between the two was also present. Across the inshore-offshore gradient the fish distribution pattern suggests that habitat use on inner-shelf reefs is skewed toward shallower depths. Non-metric multidimensional scaling revealed that the most distinct herbivorous fish and algal community occurred at three meters on reefs with higher topographic relief. Three species crustose coralline algae (CCA) were positively correlated with the biomass of herbivorous fish, and the highest abundance of both fish and CCA was found on the shallow fore-reef. The primary PCA axis of water quality parameters revealed a cross-shelf water quality gradient driven by higher turbidity and lower light penetration inshore. The inner-shelf and mid-shelf reefs differed in the composition of CCA species, suggesting an interaction with herbivorous fish and the cross-shelf water quality gradient. A multi-scale seascape approach correlating composition and configuration metrics to 810 random fish surveys confirmed topographic relief as an important factor positively related to herbivorous fish biomass. A model of preferred feeding habitat for

herbivores that combined depth and rugosity explained significant variability in fish distribution, with higher biomass at shorter distances from the modeled polygons.

Overall the results suggest that the distribution of roving herbivorous fishes is influenced by habitat characteristics related to preferred feeding sites that can be described by a combination of in-situ and seascape scale metrics.

Resumen

Los peces herbívoros son una parte integral de la biodiversidad de los arrecifes coralinos por su abundancia y su rol como consumidores de las algas bentónicas. Este estudio examina la ecología de los peces cirujanos (Acanthuridae) y cotorros (Scaridae): (1) su distribución en el ante-arrecife en relación a la escala de transectos, (2) el patrón espacial en la interacción entre los peces y las algas, y (3) la importancia relativa de métricas de composición y configuración paisajistas para determinar como estas ayudan a explicar los patrones espaciales a gran escala.

A la escala de transectos y a través de tres profundidades en seis arrecifes la distribución de peces herbívoros demostró una relación inversa con profundidad y una positiva con relieve topográfico. Además, se encontró una interacción compleja entre estos dos factores y la distribución de peces. A través del gradiente costero-oceánico el patrón de distribución sugiere que el uso de hábitat en arrecifes en la plataforma interior favorece las profundidades someras. Los resultados del análisis de medidas multidimensionales no métricas demostraron que las comunidades más distintas de peces herbívoros y algas ocurrieron al nivel de 3 metros en los arrecifes con alto relieve topográfico. El grupo de algas 'CCA' y tres especies correlacionaron positivamente con la biomasa de peces herbívoros, y la abundancia máxima de ambos ocurrió sobre el ante-arrecife somero.

El primer eje del análisis de componentes principales de parámetros de calidad de agua indica un gradiente a través de la plataforma dominado por una mayor turbidez y una baja penetración de luz cercana a la costa. Los arrecifes en la plataforma interior difirieron de los de la plataforma media en su composición de especies de 'CCA', que

sugiere una interacción con peces herbívoros y el gradiente de calidad de agua a través de la plataforma. El análisis paisajista de datos en múltiples escalas para correlacionar métricas composicionales y de configuración de 810 sondeos aleatorios de peces, confirmó al relieve topográfico como un factor importante y que está positivamente relacionado a la biomasa de los peces herbívoros. Un modelo espacial de los hábitáculos preferidos de alimentación para los herbívoros que combina la profundidad y topografía explicó la distribución de los peces mostrando una biomasa más alta a distancias cortas de los polígonos del modelo. En conjunto, estos resultados sugieren que la distribución de peces herbívoros móviles es influenciada por características del hábitáculo relacionado a lugares preferidos de alimentación, los cuales pueden ser descritos por una combinación de métricas in-situ y a escala paisajista.

Dedication

To my mother Mayra L. Nemeth Feliciano who introduced me to the world of natural history and science; and to my father Gabriel P. Nemeth Farrington who always had time to take me fishing and get our feet wet.

Acknowledgements

First and foremost I would like to thank Michelle T. Schärer Umpierre because without her technical assistance, critical review and unconditional support this work could not have been possible.

I gratefully acknowledge the longtime support of my professor and chairman Richard S. Appeldoorn for professional guidance and providing an opportunity to work on this and the many other lab research projects. I would like to thank my past and present committee members Dannie Hensley (RIP), Paul Yoshioka, Ernesto Otero, Alberto Sabat, and Nikoloas Schizas for their help with this dissertation. I am indebted to Manuel Valdez-Pizzini from CIEL and Ruperto Chapparo from Seagrant for providing invaluable assistance and exciting discussions during my time as a graduate student.

I acknowledge the invaluable assistance provided by the staff members of the Department of Marine Science at the University of Puerto Rico. In particular Godoberto Lopez (RIP), Milton Carlo, Neftali Figueroa, Negrito, Lalo, Anibal Santiago who made field work and marine logistics safe and never denied a request for help. My many thanks to Zulma Martinez, Lilivette Valle, Nereida Santiago, Monserrate Cassiano and Linette Mercado for their professional support with administrative issues.

I am indebted to the group of students, researchers and professors in the CRES program who provided long hours of spirited field assistance, companionship and critical discussions about ecology. Hector Ruiz is co-author on the fish-algae publication and provided the algal community data as well as spectacular photographs. Emmanuel Irizarry, Francisco Pagan, Katie Flynn, Carlos Prada, Alex Mercado, Jorge Pinzon, Ernesto Weil, David Ballantine and Aldo Croquer and others provided help with field

work and helpful discussions on coral reef ecology. I also acknowledge the support of my lab partners and other students from the department who made student life a valuable experience.

The NOAA Biogeography Branch and the researchers who worked in La Parguera graciously provided the data that made the analyses in Chapter 3 possible. This research was funded by NOAA grant NA17OP2919 (CRES).

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1 Introduction

This study provides information aimed at improving our understanding of the ecology of roving herbivorous fishes, a group that plays a critical role on coral reefs by grazing on benthic algae. The interaction between algae and fish grazing has been shown to be a determinant factor in maintaining coral dominance on reefs or being part of a shift to algal cover when absent (Hughes et al. 2007; Mumby 2009). The conservation and management of coral reefs requires maintaining this ecosystem process to provide resilience to human and natural disturbances (Hughes et al. 2007; Mumby and Steneck 2008). These reef fishes also provide important income to coral reef fisheries that require the implementation of sustainable management. The conservation of coral reefs and associated fisheries benefits from an ecosystem approach that involves a spatial component; therefore ecological processes of reef fishes should be presented at the multiple scales pertinent to the needs of management.

This dissertation presents three separate but related studies to examine patterns in the habitat use by roving herbivorous fishes in La Parguera, Puerto Rico. The studies are presented in the following three chapters titled:

1. The Distribution of Herbivorous Coral Reef Fishes within Fore-reef Habitats: the Role of Depth, Light and Rugosity.
2. Variation in the Interaction Between Herbivorous Fish and Algal Communities on Fore-Reef Habitats.

3. Contrasting seascape factors that influence the distribution of roving herbivorous fishes on coral reefs.

Significant changes have occurred in Caribbean coral reefs in the past decades involving the association between herbivorous reef fishes and algal communities, with resulting effects to the persistence and dominance of scleractinian corals on reefs (Bellwood et al. 2004). Strong interactions exist between herbivorous reef fishes and algal communities on coral reefs and the complex processes that structure these two assemblages remain an important focus of investigation (Smith et al. 2001; Paddock and Cowen 2006; Mumby 2009). The distribution and abundances of these two groups on coral reefs are strongly intertwined although the association has been found to be variable spatially at scales from several kilometers to 100 km (Albert et al. 2007; Fox and Bellwood 2007; Hoey and Bellwood 2010). Understanding the patterns of distribution and abundance of both herbivorous fish assemblages and algal communities under varying biophysical conditions will provide useful information for managing these valuable coral reef resources.

Coral reefs in the Caribbean have experienced wide spread degradation in the past 20-30 years. Throughout the region coral cover has declined an average of 80% (Gardner et al. 2003) and reefs that were previously dominated by scleractinian corals are experiencing a phase shift toward macroalgal dominated communities. Such a decline in the abundance of reef building corals has serious implications regarding the ecological and economic services that coral reefs provide. The causes of this widespread change in coral reefs are complex but known to be influenced by a suite of

natural and human caused disturbances that may act synergistically. Natural disturbances include disease outbreaks, bleaching and hurricanes, punctuated by the die-off of the herbivorous urchin *Diadema antillarum* and the decrease in the abundance of Acroporid corals due to an outbreak of white-band disease. These events have opened up reef surfaces for the colonization by macroalgae. The system's resilience to these disturbances is being compromised throughout the region by anthropogenic impacts including overfishing, sedimentation, and eutrophication (Bellwood et al. 2004). These impacts affect the corals directly as well as disrupt important ecological processes, such as the removal of herbivorous fishes through overharvesting. It is evident that grazing by reef fish is an important process and needs to be incorporated into the science of management and conservation of coral reefs (Mumby et al. 2006).

Fishes from the family Acanthuridae (surgeonfishes) and Scaridae (parrotfishes) are important herbivorous fish on Caribbean coral reefs in terms of density and biomass (Lewis and Wainwright 1985). Acanthurids and Scarids are commonly harvested with fish traps, nets, and spears in the Caribbean. High fishing intensity has led to a reduction in abundance and mean size in these groups and has been correlated with decreased grazing intensity (Williams and Polunin 2001). The spatial variability in fish-algal interactions on coral reefs have often been studied across inshore to offshore environmental gradients (Albert et al. 2007). Reef fish abundance and distribution is driven by processes that occur at varying spatial scales. Fish populations are controlled at different life history processes such as settlement, post-recruitment mortality and growth (Tolimieri 1998).

Knowledge of the association between herbivorous fishes and their habitat provides tools to design marine reserves and develop effective monitoring research to assess population trends (Appeldoorn et al. 2003; Mumby et al. 2007). In order to provide useful information the study of fish-habitat associations should evaluate the relative importance of measurable ecosystem characteristics (i.e. depth, rugosity) at multiple spatial scales. The interaction between algae and fish grazing has been shown to be a determinant factor in maintaining coral dominance on reefs or conversely being part of a shift to increased algal cover. In this context the present study examined this relationship in three sections:

1. The distribution of roving herbivorous fish on fore-reefs in relation to transect scale characteristics.
2. The spatial patterns and the taxa principally involved in the association between fish and algae.
3. Examining the relative importance of composition and configuration seascape metrics to understand how these help explain spatial patterns at large spatial scale.

Mapping the distribution of fish species across the seascape is essential for obtaining robust estimates of population abundance and developing successful natural resource management strategies. Since reef fish species have complex life cycles and sampling in the marine realm is costly, there is a need for approaches that make efficient use of the available information to understand distribution patterns. The recent availability of large scale marine habitat maps provide an opportunity to test how multiple habitat and environmental variables help explain the way that fish use the

seascape. The use of GIS tools provides a framework to relate the geographic variables to fish distribution under a multiple conditions and spatial scales (Pittman and Brown 2011).

Throughout different life stages reef fish respond to the immediate environment due to physiological adaptations and requirements for feeding, refuge and reproduction. These associations shape the way species utilize the available environment but certain features of the habitat can play a disproportionate role. For example topographic complexity is one the most important variables structuring fish distribution (Friedlander and Parrish 1998). Additionally interactions among variables can add a level of complexity to using habitat to understand spatial patterns (Pittman and Brown 2011).

Landscape level patterns of habitats may influence the distribution and abundance of demersal fishes on coral reefs. Habitat characterization has often been used as a proxy for describing spatial patterns in reef fish assemblages (Friedlander and Parrish 1998; Pittman et al. 2007). Across a seascape habitats occur as a mosaic where extent and connectivity of habitat types can influence how fishes are distributed. Spatial patterns in abundance of *Haemulon flavolineatum*, an invertebrate feeding reef fish, are correlated to the distance between feeding and refuge habitats (Kendall et al. 2003). The daytime occurrence of this species was found to be restricted to reef areas within 500 m of seagrass areas that are used as nighttime feeding habitat. The requirement of different habitats for feeding and refuge is likely to occur for other reef fishes. Understanding how the distribution and abundance of reef fishes is affected by the connectivity among habitat types can help explain spatial variability observed by reef fish monitoring studies and aid in the design of marine reserves.

Grazing by herbivorous fishes varies spatially from nearshore reefs to offshore reefs and among the different habitats within a reef. On the Great Barrier Reef demographics of Acanthurids and Scarids showed differences on offshore shelf edge reefs compared to similar nearshore bank reefs (Gust et al. 2001). This information indicates that the growth and survivorship of Acanthurids and Scarids can vary at scales of tens of kilometers. Within a reef grazing is highest in the physically complex fore-reef habitat compared to the reef flat, back reef, and sand areas (Lewis and Wainwright 1985; Hixon and Brostoff 1996). Reef fish populations experiencing large spatio-temporal environmental variability suggest that habitat quality can affect the growth and reproductive ecology of parrotfish (Clifton 1995).

2 The Distribution of Herbivorous Coral Reef Fishes Within Fore-Reef Habitats: The Role of Depth, Light and Rugosity

2.1 Abstract

Examining the relationship between habitat characteristics and utilization patterns by herbivorous fishes on coral reefs will add to our understanding of the factors that influence the abundance and distribution of this important group. The abundances of parrotfishes (Scaridae) and surgeonfishes (Acanthuridae) on fore-reef habitats were sampled along an inshore-offshore gradient to provide for within reef and cross-shelf comparisons in relation to the environmental parameters of depth and topographic relief. Temporally replicated visual surveys were conducted along permanent belt transects (100m²) at three depth intervals (3, 10, 15 m) to obtain data on fish species density and lengths, which were used to calculate biomass. The roving herbivorous fish assemblage was dominated by three species of parrotfishes (*Scarus iseri*, *Sparisoma aurofrenatum* and *S. viride*) and three surgeonfishes (*Acanthurus bahianus*, *A. chirurgus* and *A. coeruleus*). Overall the biomass of both families was highest at 3m compared to 10 or 15m ($p < 0.05$). However, the relative decrease in biomass across depths for both families was greatest at inshore reefs where water transparency is lowest. The mean biomass for both families differed between inner and mid-shelf reefs at 10 and 15 m ($p < 0.05$) but not at 3m. Fish biomass was correlated to reef topographic relief at 3m for parrotfishes ($p < 0.05$) and at all three depth intervals for surgeonfishes ($p < 0.05$). Overall patterns of herbivore biomass across the shelf reflect differences in

light penetration, suggesting that fish may be responding to algal productivity. Thus, within fore-reef habitats along a cross-shelf gradient water transparency and topographic relief may interact to structure biomass patterns.

2.2 Introduction

Algal grazing by reef fishes is an important ecological process with practical significance to the management and conservation of coral reefs (Mumby et al. 2006, Hughes et al. 2007). The process of herbivory has been shown to play a key role in structuring the benthic community on coral reefs (Hixon and Brostoff 1996; Smith et al. 2001; Belliveau and Paul 2002). In areas of high grazing on benthic algae, the algal assemblage is dominated by crustose coralline algae with cropped algal turfs (Littler et al. 2006). This affects the interaction between macroalgae and corals, particularly in enhancing coral recruitment, and is seen as a fundamental determinant of coral reef resilience (Mumby et al. 2007).

Fishes from the family Acanthuridae (surgeonfishes) and Scaridae (parrotfishes) are important herbivores on Caribbean coral reefs in terms of biomass (Lewis and Wainwright 1985) and are found commonly on fore-reef habitats from 1 to 30 m. Surgeonfishes and parrotfishes are commonly harvested with fish traps, nets, and spears in the Caribbean (Munro 1983). High fishing intensity has led to a reduction in abundance and mean size in these groups, and in some locations has been correlated with increased macroalgal cover (Williams and Polunin 2001). Understanding the distribution of the herbivorous fish assemblage is important because the consequences

of grazing depend in part on spatial abundance patterns (Mumby et al. 2006, Paddock et al. 2006).

The abundance and distribution of herbivorous coral reef fishes can vary spatially along a cross-shelf gradient, by depth and among the different habitats within a reef. On the Great Barrier Reef the abundance, at the family level, of surgeonfishes and parrotfishes was higher on offshore reefs compared to near shore reefs (Russ 1984a, Gust et al. 2001). Within a reef, studies have shown that the highest densities of roving herbivorous fishes are often found on the shallow fore-reef and reef crest (Russ 1984b, Lewis and Wainright 1985, Fox and Bellwood 2007, Hoey & Bellwood 2008). This pattern may be related to food availability and quality since the biomass of roving herbivores has been found to be positively correlated to algal productivity (Russ 2003). The topographic relief of reef habitat is also a major factor in structuring fish communities (Friedlander and Parrish 1998) since fish benefit from abundant reef crevices to escape predation. Yet, this relationship has typically been studied across a wide variety of habitats, from relatively flat sand and algal plains to emergent coral reefs. Little work has investigated what role rugosity plays in structuring fish distributions on finer, within habitat scales.

It is clear that roving herbivorous fishes are not randomly distributed over coral reefs and that spatial patterns may be related to preferences in habitat characteristics in order to meet requirements for feeding and refuge. This study examines the importance of depth, cross-shelf reef position and topographic relief in structuring the distribution of roving herbivorous fishes in Southwest Puerto Rico. The study focuses on topographic relief only within the fore reef habitat on coral reefs, and examines trends across

multiple species within the surgeonfishes and parrotfishes. The resulting spatial and depth related patterns are then used to infer underlying processes structuring herbivorous fish distributions and community structure on fore-reef habitats.

2.3 Methods

The density of parrotfishes and surgeonfishes was quantified at six reef sites stratified into inner-shelf (3) and mid-shelf reefs (3) to allow for within reef (across depths) and among reef (cross-shelf) comparisons (Figure. 2.1). The study was conducted on the fringing coral reefs off of La Parguera, Puerto Rico (N 17° 58.3', W 67° 02.6'). A water quality gradient generally exists from inshore to offshore with inner shelf reefs having higher turbidity resulting from local land-based runoff and upstream sources that are carried by the alongshore current. Published values for water transparency ($K_d \text{ PAR}$) at the study reefs were used to relate water quality to cross-shelf reef position (Table 2.1, Bejarano Rodríguez 2006). The study sites were located on the fore-reef along a series of emergent reefs that occur from 1 to 5 km offshore and rise from surrounding unconsolidated bottom at 15-18 meters depth. The general fore-reef profile slopes gently from the surface to ~6 m where the slope becomes steeper down to the reef base.

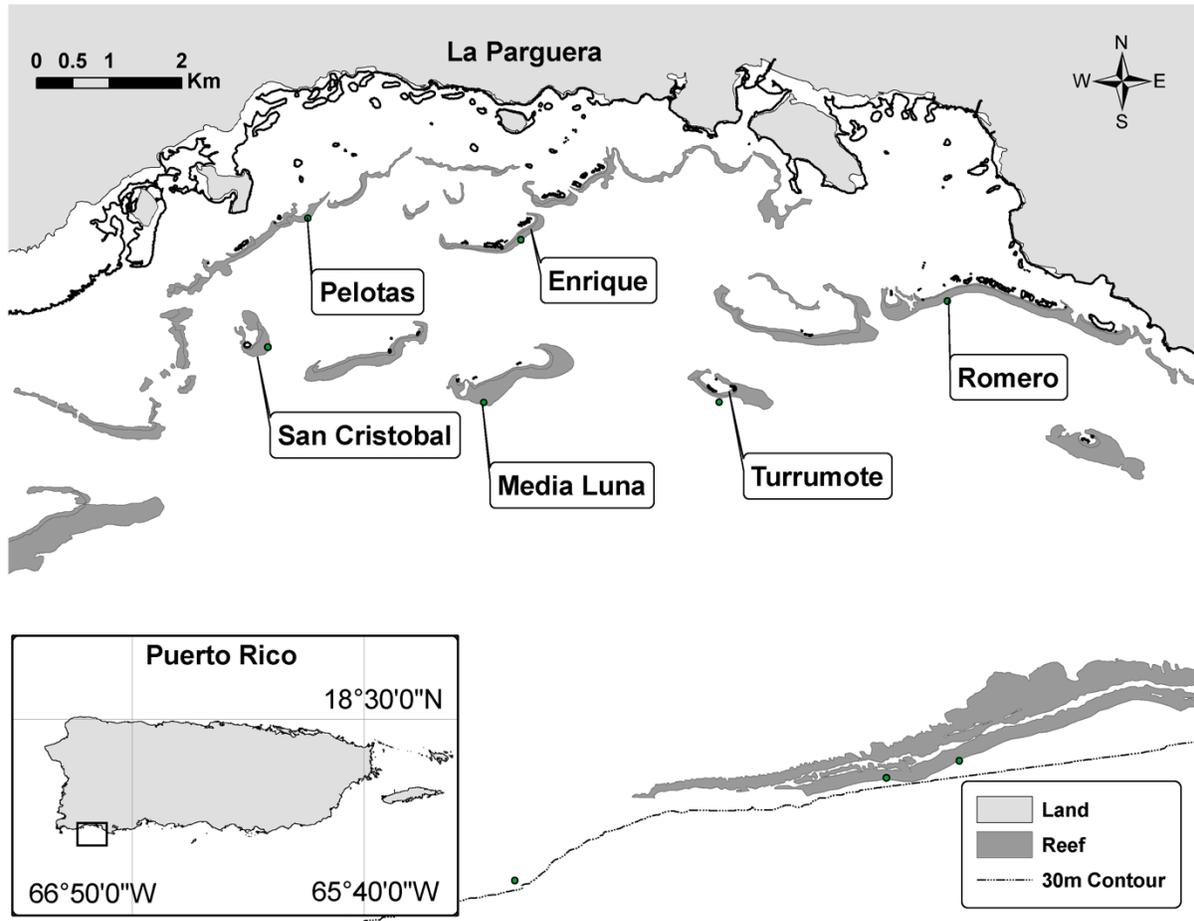


Figure 2.1 Map of the study area showing the 6 study reefs, which are divided into two cross-shelf strata for purposes of analyses: inner-shelf (Romero, Enrique, Pelotas) and mid-shelf (Turrumote, Media Luna, San Cristobal).

Table 2.1 Reef sites with cross-shelf strata designation, minimum distance from mainland shoreline and light extinction coefficient. Extinction coefficient estimates from Bejarrano Rodríguez (2006).

Reef Site	Shelf Strata	Offshore	Light Extinction
		Distance (km)	Coefficient (Mean K_d PAR)
Romero	Inner-shelf	1.2	0.19
Enrique	Inner-shelf	1.8	0.20
Pelotas	Inner-shelf	1.5	0.19
Turumote	Mid-shelf	3.8	0.17
Media Luna	Mid-shelf	4.0	0.17
San Cristobal	Mid-shelf	3.1	0.16

To determine fish abundance, visual surveys were conducted using SCUBA along belt transects measuring 25 x 4m. At each study reef three depth intervals were selected: 3 (3-5m), 10 (8-10m), and 15 (12-15m). Three replicate transects were established per depth interval and permanently marked with rebar stakes for repeated sampling of the same reef area. Transects were sampled four times per year, corresponding to the four seasons, from 2004 to 2007. All surgeonfishes and parrotfishes within transects were counted, identified to species and their fork length estimated visually. Prior to beginning surveys the observers were trained in estimating fish fork lengths underwater using wooden fish models (Rooker and Recksiek 1992). Topographic relief was sampled once along 10 m of all transects with the chain method to calculate a rugosity index. A light chain was draped loosely over the bottom following the topography. The rugosity index is expressed as the ratio of the chain distance to the linear distance.

Fish length data were used to calculate mean sizes, and biomass was derived utilizing published parameters for length-weight relationships (Bohnsack and Harper 1988). Data were analyzed for differences across depth intervals and between inner and mid-shelf reef strata at the family level. Homoscedasticity of the data was tested with Levene's test. The fish density and biomass data did not meet assumptions of equal variance even after log and square-root transformations. Therefore the non-parametric Kruskal-Wallis test with the multiple comparisons of mean ranks routine was used to test for significant differences across depth intervals. The Mann-Whitney test was used to compare between inner and mid-shelf strata within each of the three depth intervals. Since data did not meet parametric assumptions the Spearman rank correlation was used to examine the relationship between fish abundance and rugosity. All tests were implemented using Statistica (2005) software. Annual and seasonal patterns in the abundance data were examined as part of another study and no temporal patterns were evident at the family or species level.

2.4 Results

The roving herbivorous fish assemblage on fore-reef habitats in La Parguera is predominantly made up of three species from the surgeonfish family (Acanthuridae) and eight species from the parrotfish family (Scaridae). The surgeonfishes are represented by *Acanthurus bahianus*, *A. chirurgus* and *A. coeruleus* with the latter having the highest frequency of occurrence. The parrotfishes are numerically dominated by *Scarus iseri*, *Sparisoma aurofrenatum* and *S. viride* with *S. iseri* having the highest overall density for parrotfish. Other species of parrotfish were present in the samples but in low abundances, and therefore they were not included in species level analyses. Overall the densities of both families pooled within reef position and across depth intervals were slightly higher on mid-shelf reefs (surgeonfishes: 9.4 versus 10.9 fish/100m² for inner and mid-shelf respectively, parrotfishes: 19.7 versus 23.4 fish/100m² for inner and mid-shelf respectively).

The abundances of parrotfishes and surgeonfishes were distinctly structured in relation to depth on the fore-reef habitat. The overriding pattern is a maximum in density and biomass on the shallow fore-reef with lower abundances deeper on the reef (Figure 2.2). Pooling across all reef sites the mean biomass of both families for the 3m interval was significantly higher than at the 10 and 15m intervals which did not differ significantly (K-W multiple comparisons $p < 0.05$). A greater relative difference in biomass was observed between the 3 m interval and the other two depth intervals for the surgeonfishes than for the parrotfishes (Figure 2.2).

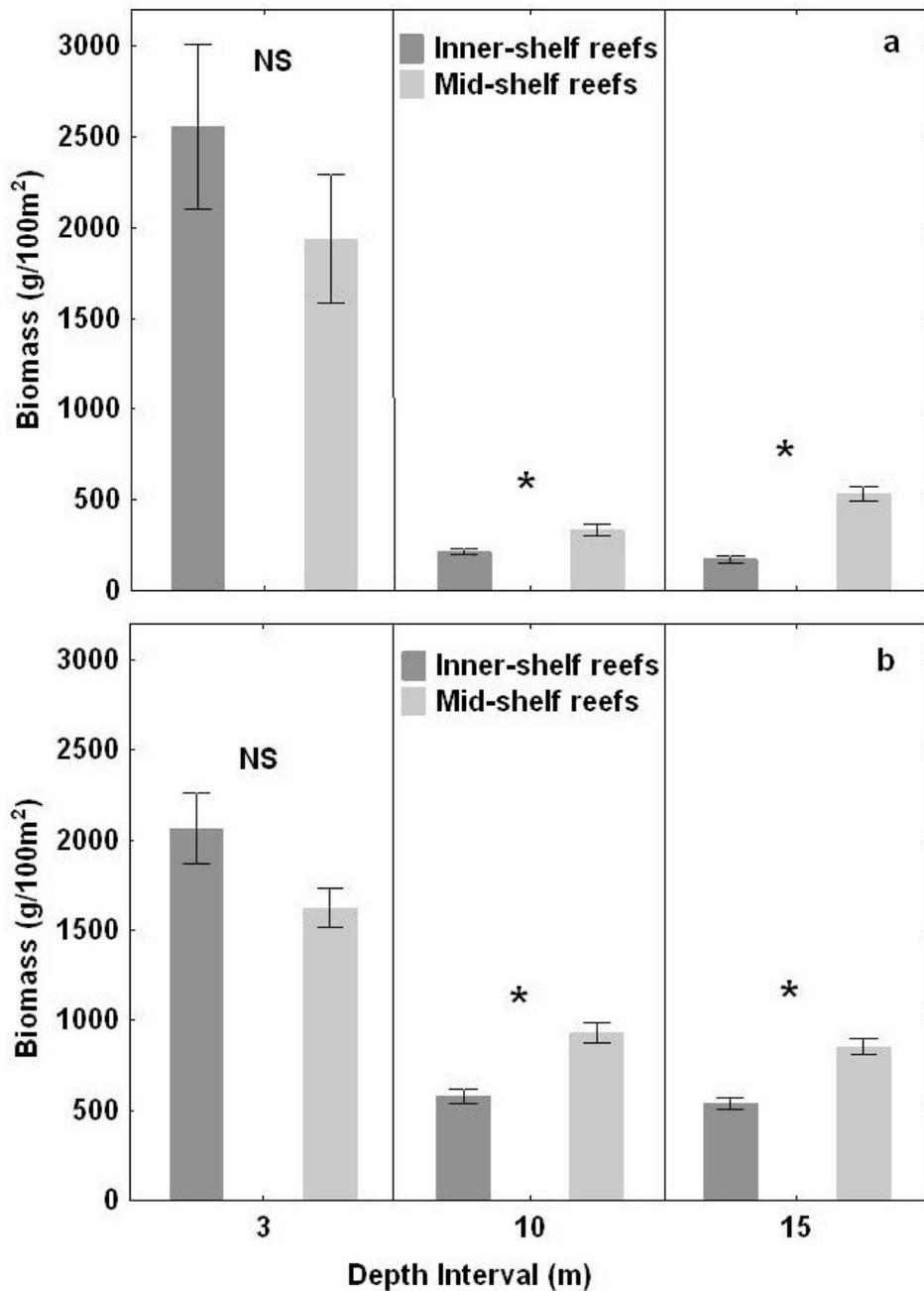


Figure 2.2 Mean (\pm SE) Biomass of (a) surgeonfishes and (b) parrotfishes by depth interval for the two cross-shelf reef strata. Asterisks (*) represent significant differences for comparison between reef position within a depth interval (Mann-Whitney test, $p < 0.05$, $n = 108$).

Comparing the biomass of both families within depth intervals and between inner-shelf and mid-shelf reefs revealed that the general trend of decreasing abundances with depth varies between the two reef strata. The overall pattern of higher biomass at 3m than at 10 and 15m was not the same between inner and mid-shelf reefs. The decline in biomass of fish across the depth gradient was of a greater magnitude at the inner shelf reefs when compared to the mid shelf reefs (Figure 2.2). At the 3 m depth interval the mean biomass for both families did not differ significantly between inner and mid-shelf reef groupings. However, for both the 10 and 15m depth intervals the biomass of both surgeonfishes and parrotfishes was significantly higher on mid-shelf reefs than inner-shelf reefs (Mann-Whitney test, $p < 0.01$).

Individual species exhibited varying degrees of deviation from the general trend of decreasing biomass with depth seen at the family level when pooling all reefs. The three species of surgeonfish all showed highest densities at 3m with a decrease at 10 and 15m (K-W multiple comparisons $p < 0.01$, Figure 2.3). One species of parrotfish, *Scarus iseri* exhibited a significant decline in density when comparing the 3m to the 10m depth interval but the 15m interval was not significantly different from the 3 or 10m intervals (K-W multiple comparisons $p < 0.01$, Figure 2.3). The decrease in density with depth for *Sparisoma aurofrenatum* and *S. viride* was of a lesser magnitude although still evident.

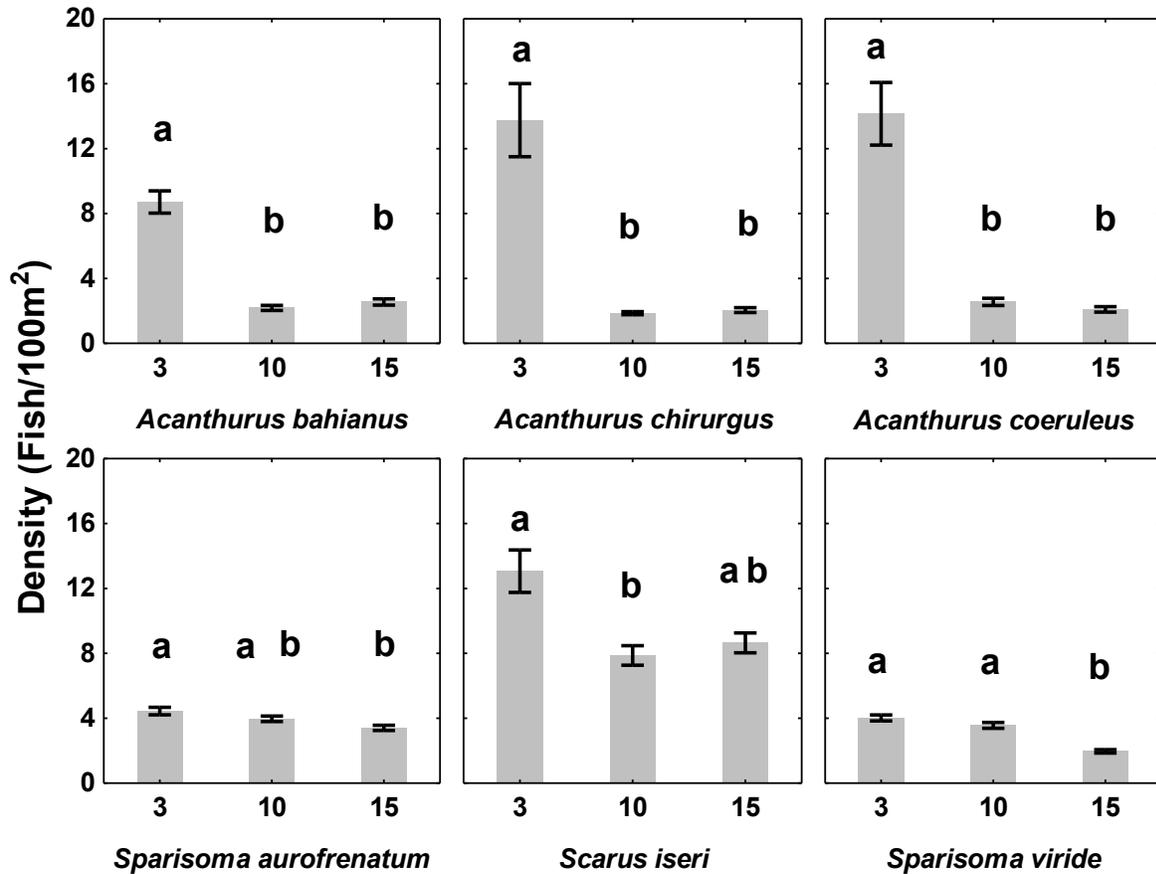


Figure 2.3 Mean (\pm SE) density of most common surgeonfishes (top row) and parrotfishes (bottom row) by depth interval pooled across all reefs. Letters represent groupings of non-significant differences provided by Kruskal-Wallis multiple comparison routine ($p < 0.05$, $n = 216$).

The mean biomass of either family was not significantly correlated to rugosity when pooling all reefs and depth intervals (Spearman Rank Order Correlation = 0.22 for surgeonfishes and 0.07 for parrotfishes). However, when grouping the data at the individual depth intervals rugosity was positively correlated to the biomass of both surgeonfishes and parrotfishes at the 3 m interval (Spearman=0.59 and 0.57 respectively, $p < 0.05$) but only to surgeonfishes at the 10 and 15 m intervals (Spearman=0.68 and 0.67 respectively, $p < 0.05$, Figure 2.4).

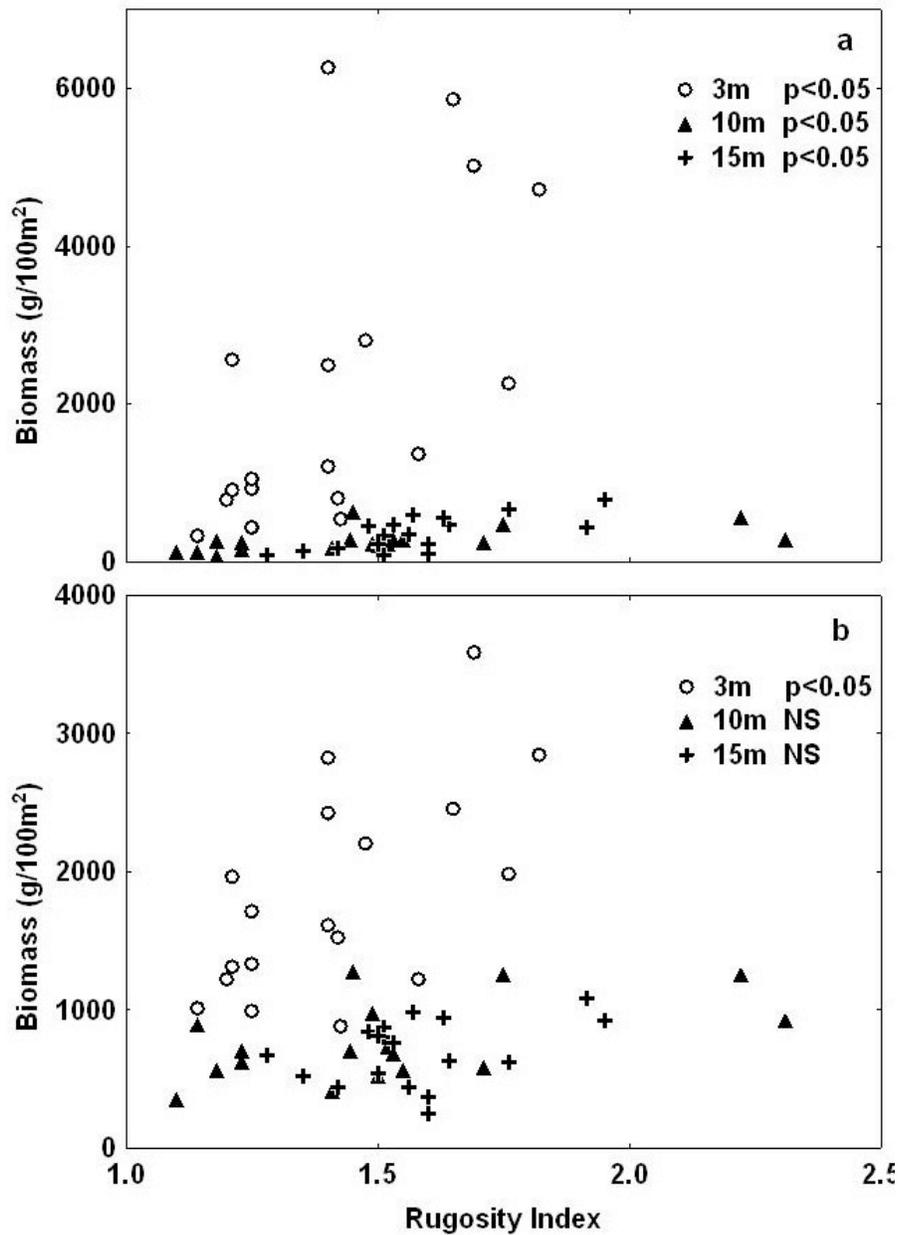


Figure 2.4 Correlation between the rugosity index and the mean biomass of (a) surgeonfishes and (b) parrotfishes for the three depth intervals. The p-values are from Spearman Rank Correlation. The mean biomass for each of the fixed transects within each depth at each reef is based on the mean of 12 transects sampled across the 3 year period.

2.5 Discussion

Understanding fish distribution patterns in relation to habitat characteristics will provide insight into the processes involved in structuring the fish assemblages across the seascape. The general pattern of highest abundances of roving herbivores on the shallow fore-reef (Lewis and Wainright 1985, Russ 1984b, Fox and Bellwood 2007, Hoey & Bellwood 2008) was also observed in this study indicating that depth is an important descriptor in the distribution of roving herbivores on the fore-reef. Due to large sample size we were able to detect similar but distinct patterns at the species level, even with the high variability typical of visual survey counts of reef fish. Our results also show that the relative intensity of the depth related effect varied by species, so the family level response to depth will depend on the relative abundance and proportions of the species present.

The difference in the depth related pattern between the two families may be due to the predominance of surgeonfishes to form large schools. These schools are most common in shallow fore-reef areas (unpublished data), which may reflect a feeding strategy to overcome the high density of territorial damselfish by overwhelming their ability to defend their territories. Parrotfishes seem to have a slightly different strategy in that, while also forming schools to feed in shallow areas, number of fish per school is lower (unpublished data), and proportionally more fish were found deeper compared to surgeonfishes.

It is likely that the physical changes in depth are not affecting the fishes directly, but rather they are responding to some environmental factor that co-varies with depth.

The most compelling evidence is that productivity of the algal turf assemblage in shallow habitats correlates positively with the biomass of roving herbivorous fishes (Russ 2003). The usefulness of grouping abundances at higher taxonomic or trophic groupings has been demonstrated previously where the pooled biomass of all species of parrotfish and surgeonfish was inversely correlated to algal cover (Williams and Polunin 2001). Also, the total biomass of herbivores was used to examine patterns in this assemblage within and among reefs (Wismer et al. 2009).

Although the cross-shelf scale of this study (1-4 km) is limited in an absolute sense compared to previous works from the Great Barrier Reef (5-50km), the cross shelf differences in environmental parameters from open ocean to coastal fringe are the same and should result in even steeper spatial gradients. Cross-shelf variability in community structure similar to that observed on the Great Barrier Reef has previously been documented for La Parguera (Kimmel 1985). In the present study the herbivorous fish assemblage also exhibited a cross-shelf response to reef position that was evident within the overall depth related pattern. Inner-shelf reefs had relatively lower abundances of both surgeonfishes and parrotfishes on the deeper fore-reef compared to mid-shelf reefs, while shallower areas were similar throughout.

Herbivorous fish biomass has been shown to correlate positively with algal turf productivity (Russ 2003), fish may be selecting for areas that have higher food quality. One important factor affecting algal productivity is the availability of light. Clifton (1995) showed spatial differences in turbidity to affect algal turf productivity, with corresponding differences in parrotfish growth and fecundity. In La Parguera, existing data on light availability (Bejarano Rodríguez 2006) show that cross-shelf reef position is related to

reef water quality, with inshore reefs having higher coefficients of extinction (Table 2.1).

This is consistent with inner-shelf reefs generally having higher turbidity (unpublished data). Turbidity and light differences would be expected to cause differences in the algal productivity (Clifton 1995, Klumpp and McKinnon 1989). The differences in herbivore biomass at 10 and 15m between inner and mid-shelf strata is seen as a result of fish responding to lower algal productivity in the inshore reefs. Since the amount of light reaching the reef surface may affect benthic primary productivity, water transparency has the potential to influence the algal resources available to herbivorous fishes and thus affect their distribution. This was demonstrated in La Parguera, where the extinction coefficient of light was directly correlated to the density and abundance of herbivorous fishes (Bejarano-Rodríguez 2006).

Topographic relief can influence the distribution of herbivorous fish over reef habitat (Friedlander and Parrish 1998), but separating this factor from depth effects is difficult because they can often co-vary. In this study rugosity was not correlated to fish biomass when samples from all depths were included in the analysis. When separated into discrete depth intervals the confounding effects were minimized and this revealed that habitat areas of high topographic relief are positively correlated with biomass. These results indicate that over the entire fore-reef slope roving herbivorous fishes may be responding more strongly to depth related habitat conditions, such as light level or productivity, than to topographic relief.

In this study, surgeonfishes and parrotfishes did not utilize the entire fore reef habitat equally but instead showed preference for certain habitat characteristics within the fore-reef habitat. The reefs in this study provide a continuous topographically

complex habitat patch that extends from the surface to 15m wherein fish can select for optimum habitat characteristics. If herbivores are able to choose optimum habitat in terms of depth, water quality and topographic relief, their distribution patterns and resulting ecological impacts may be related to the spatial mosaic of these characteristics.

3 Variation in the Interaction Between Herbivorous Fish and Algal Communities on Fore-Reef Habitats

3.1 Introduction

A strong interaction exists between herbivorous reef fishes and the algal community on coral reefs involving complex processes that play a role in structuring the entire reef community (Lewis & Wainwright 1985; Littler et al. 2006; Burkepile & Hay 2006). Understanding the variation in the distribution and abundance of these two groups as well as the key species involved can provide insight into the factors that drives this important ecological process. The ongoing increase of algal abundance on coral reefs has been attributed to the loss of herbivores, increase in nutrients, the loss of coral cover or a combination of these (McClanahan et al. 2002). Research on the influence of herbivorous fishes on algal communities has progressed from observational descriptions (Steneck 1988; Lewis & Wainwright 1985; Littler et al. 2006) to manipulative experiments, to parse out the importance of the factors involved (Albert et al. 2007; McClanahan et al. 2000; Belliveau & Paul 2002; Smith et al. 2001). However, manipulative experiments may be too limited in spatial scope to fully understand the variability in biophysical factors that can influence the interaction between herbivorous fish and the algal community, therefore large spatial scale studies continue to be necessary to test experimental studies.

The top-down effect of fish herbivores is a factor that can determine where particular functional groups of algae are able to establish and persist in coral reef habitats (Littler et al. 2006), although bottom-up processes may also play an important

role in some circumstances (Lapointe 1997). Models developed to explain the distribution of algal communities on coral reefs have included herbivory, nutrient availability, turbidity and wave action (McCook 1999). The widely cited relative dominance model (RDM) categorizes the algal community according to nutrient availability and the magnitude of herbivory (Littler et al. 2006). High nutrient load and low herbivory should result in a reef dominated by frondose macroalgae; whereas low nutrients and a high grazing rate will yield an algal community dominated by crustose coralline algae (CCA) and cropped algal turfs. At high rates of herbivory calcareous algae and cropped turfs, both of which are resistant to grazing pressure, dominate the algal community (Burkepile & Hay 2006). High grazing and a cropped algal community may promote coral recruitment and growth by limiting smothering of young corals by frondose macro algae (Mumby et al. 2006). In manipulative experiments conducted in Hawaii with the four combinations of nutrient availability and herbivory, the results supported the RDM (Smith et al. 2001). In the Indo-Pacific grazing by herbivorous fish had a stronger influence over algal community taxonomic structure (species and functional group composition), while both herbivory rate and nutrient availability were shown to be important in determining overall algal biomass (Albert et al. 2007). It is clear that grazing by reef fishes is an important ecological process in the resilience of coral reefs (Hughes et al. 2007; Mumby et al. 2007).

The distribution of roving herbivorous coral reef fishes from the families Acanthuridae and Scaridae is influenced by settlement processes (Tolimieri 1998), ontogenetic migration (Aguilar-Perera & Appeldoorn 2007; Cervený 2006; Mumby & Hastings 2008), intraspecific social interactions (Bruggemann et al. 1994), interspecific

interactions (Hixon & Brostoff 1996), and preference for particular habitat characteristics (Friedlander & Parrish 1998; Russ 2003; Hoey & Bellwood 2010). One of the most important factors may be the productivity of the algal community and the selectivity of herbivorous fishes for feeding within these reef zones (Russ 2003; Bruggemann et al. 1994).

In this study we examined algal community structure and the biomass of herbivorous fishes on the fore-reef habitat on coral reefs to look at spatial patterns in their association. Since algal productivity has been shown to influence grazing processes, the importance of the factors depth and reef position along an inshore to offshore gradient were examined to describe the relationship between algae and herbivores under different environmental conditions (Russ 2003; Albert et al. 2007). The objectives of the present study included: (1) evaluating the RDM relative to field observations, (2) determining where fish-algae interactions are prevalent, (3) identifying which algal species are indicators of spatial variability and (4) examining the role of reef water quality in structuring the interaction between the algal community and herbivorous fish.

3.2 Methods

This study was conducted on the coral reefs off of La Parguera, Puerto Rico (N 17° 58.3', W 67° 02.6') (Figure 3.1). A water quality gradient generally exists from inshore to offshore with inner shelf reefs having higher turbidity resulting from local land-based runoff and upstream sources that are carried by the alongshore current (Otero 2009). The study sites were located on the fore-reefs at six emergent reefs that occur from 1 to 5 km offshore and rise from surrounding unconsolidated bottom at 15-18 meters depth (Figure 3.1). The six reefs were stratified into inner-shelf (3) and mid-shelf reefs (3) to allow for within reef (across depths) and among reef (cross-shelf) comparisons. The general fore-reef profile of these reefs is a gradual slope from the surface to ~6 m where the slope becomes steeper down to the reef base (Yoshioka 2009). At each study reef three depth intervals were selected: 3 (2-5m), 10 (6-10m), and 15 (11-15m). Three 25 m long replicate transects were established parallel to the depth contour per depth interval and permanently marked with rebar stakes for repeated sampling.

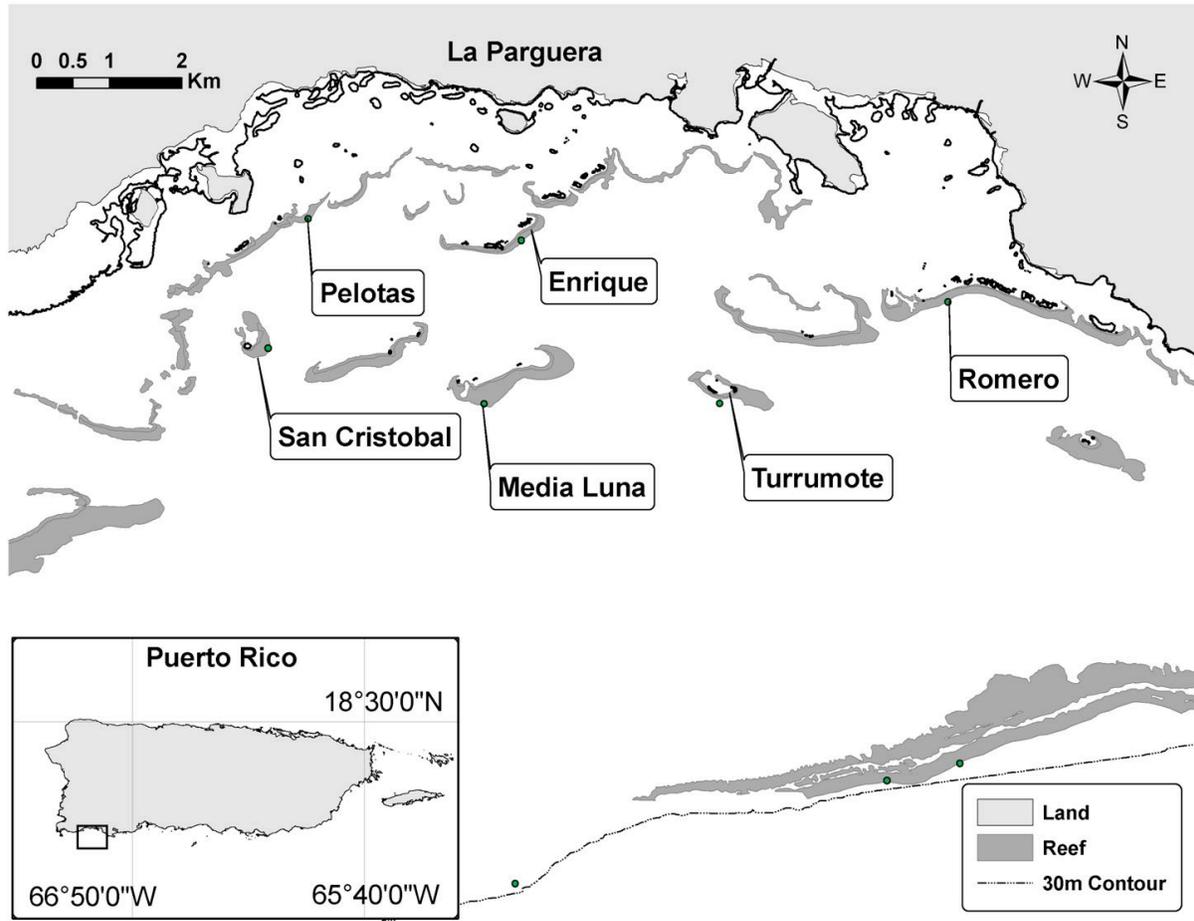


Figure 3.1 Map of the study reefs off La Parguera, Puerto Rico.

The percent cover of algae was quantified within permanent quadrats photographically sampled annually from 2003 to 2007. At the study reefs six 0.25 m² quadrats were photographed at each of the three depth intervals (N=72 quadrats per reef). Each quadrat was labeled with an identification number for reference. At each sampling period, photographs of each quadrat were taken with a digital camera (Canon Rebel 300D, 6 megapixel, 18-55mm lens) fitted with a strobe. For each digital photograph, percent cover of recognizable algal elements was calculated by overlaying with 100 (randomly stratified points) using Coral Point Count with Excel extension

(CPCe) (Kohler & Gill 2006). Algae were identified to the lowest possible taxon and subsequently placed into six functional groups (Steneck 1988).

To quantify the abundance of roving herbivorous fishes, visual census surveys were conducted using SCUBA along belt transects measuring 25 x 4m (Brock 1954; Pittman et al. 2010). Three surveys were conducted at each depth interval utilizing the same transects that were permanently marked for the algae quadrats. Transects were sampled four times per year corresponding to the seasons, from 2004 to 2007. All surgeonfishes and parrotfishes within transects were counted, identified to species and their fork length estimated visually. Fish length data were used to calculate biomass utilizing published parameters for length-weight relationships (Bohnsack & Harper 1988). Fish biomass data were pooled across years and seasons for a total of 48 transects per depth interval at each reef. Previous analyses showed that significant differences do not exist among seasons or years (Nemeth & Appeldoorn 2009). Prior to beginning surveys the observer (MN) practiced to estimate fish fork lengths underwater using wooden fish models (Rooker & Recksiek 1992).

Non-parametric statistics were used to analyze the algal community and herbivorous fish data since these remained non-normal after applying transformations. Multivariate analyses utilizing Primer statistical software were used to examine patterns in the algal community and herbivorous fish assemblage data to examine their relationship among the coupled algae fish transects. Similarity among sites for both algae and fish was examined for each reef/depth interval combination (n=18) using Non-metric multidimensional scaling (MDS). Analysis of similarities (ANOSIM) was utilized to determine if significant dissimilarity exists in the algal data when categorized

by the factors reef, shelf position (inner or mid-shelf) and depth interval. The similarity percentages (SIMPER) routine ranked the algal species that contributed the most to the patterns provided by ANOSIM. Correlation analysis with Spearman correlation coefficient was utilized to determine the relationship between fish biomass and percent cover of algae. The fish variables included the biomass of total herbivores, Acanthuridae, Scaridae and the most abundant species in these families. The algal variables included the percent cover of the algal species indicated as important from the multivariate analyses and the six algal functional groups following Steneck (1988).

Data to examine the water quality gradient were obtained for the study area from samples collected at the same reefs as fish and algae data. The water quality parameters include turbidity, salinity, temperature, N15 stable isotope, chlorophyll a, dissolved organic matter (DOMFI), bacterial production (BP), bacterioplankton counts (PB), bacterial abundance (DAPI) and sediment accumulation rate (Otero 2009). Published values for water transparency (K_d) at the study reefs were used to relate water quality to cross-shelf reef position (Bejarano 2006). Means of the water quality data at each reef were square-root transformed to normalize, and a Principal Component Analysis (PCA) was conducted to discern patterns among the study reefs (Primer 6 statistical software). Water quality data were not available for Turrumote reef so it was not included in the analysis.

The mean percent cover of the indicator algae species and functional groups were plotted in bar graphs categorized by depth interval and reef position. Differences in the percent cover of the important algal species between inner and mid-shelf reefs were

tested for each of the three depth intervals utilizing the Mann-Whitney U non-parametric test.

3.3 Results

Multivariate analyses revealed that the herbivorous fish assemblage (Table 3.1) exhibits distinct spatial patterns at both fore-reef (10s of meters) and cross-shelf scales (kilometers). The non-metric multidimensional scaling (MDS) plot shows study site (reef and depth) groupings according to the similarity in the fish assemblage structure (Figure 3.2). A stress value of 0.02 indicates a meaningful separation of groups (Clarke and Warwick 2001). In particular, the 3m depth interval sites at San Cristobal, Enrique and Pelotas reefs show the greatest separation, indicating a relatively distinct assemblage; while the 3 m sites at Turrumote, Romero and Media Luna reefs were less distinct from the deeper depth intervals. To a lesser magnitude the herbivorous fish assemblage at 10 and 15 m is grouped according to position of the reef on the inner or mid-shelf location. These patterns demonstrate that for the herbivorous fish assemblage, grouping of sample sites is related to the depth interval and reef position along the inshore-offshore gradient.

Table 3.1 The mean biomass (g/100m²) for roving herbivorous fishes, families and the most abundant species; classified by reef and depth (m) interval.

Reef Name	Depth Interval	Total Herbivores	Acanthuridae	Scaridae	<i>Acanthurus coeruleus</i>	<i>Acanthurus bahianus</i>	<i>Acanthurus chirurgus</i>	<i>Sparisoma aurofrenatum</i>	<i>Scarus iseri</i>	<i>Sparisoma viride</i>
Enrique	3	5511	2963	2549	1588	74	170	435	1053	812
Enrique	10	869	178	692	24	289	511	333	128	230
Enrique	15	698	120	578	5	202	397	316	141	95
Media Luna	3	1404	444	960	124	214	27	597	117	202
Media Luna	10	1121	246	875	156	184	21	409	236	197
Media Luna	15	1264	485	779	316	83	51	371	235	133
Pelotas	3	5611	3264	2347	1892	51	734	49	466	729
Pelotas	10	683	199	484	18	30	573	266	64	130
Pelotas	15	855	171	684	65	42	229	273	270	140
Romero	3	2725	1433	1292	591	178	150	557	435	203
Romero	10	815	259	555	101	181	174	273	123	154
Romero	15	578	227	351	23	190	331	225	72	53
San Cristobal	3	6439	4306	2133	2475	446	568	369	878	600
San Cristobal	10	852	197	655	64	469	595	274	186	191
San Cristobal	15	1384	495	889	100	144	136	357	354	178
Turumote	3	2824	1058	1766	348	556	31	682	512	352
Turumote	10	1813	555	1258	284	363	31	468	370	411
Turumote	15	1507	618	889	192	406	21	410	324	133

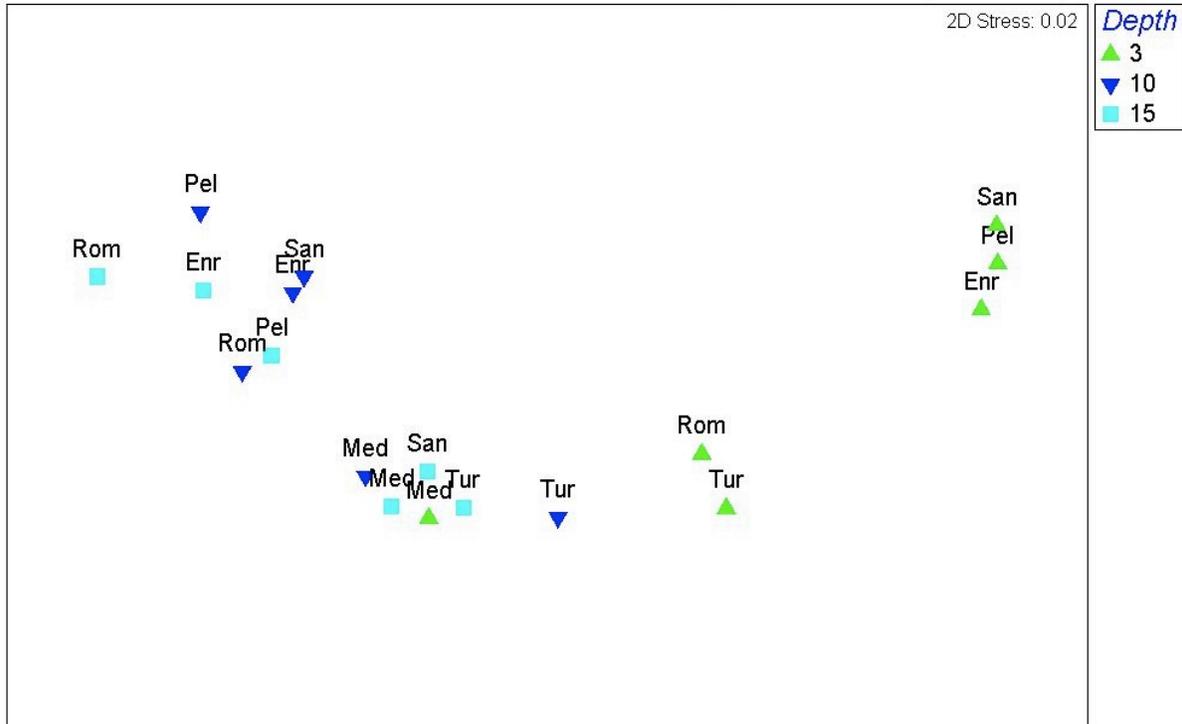


Figure 3.2 Non-metric multidimensional scaling plot of the herbivorous fish assemblage data with points representing the location of the 18 reef-depth combinations. The symbols represent depth interval and reefs (see Fig. 3.1) and are abbreviated using the first three letters of the name.

The MDS analysis of the benthic algal community reveals a similar pattern as the fish for the 3 m depth interval, but with a less distinct grouping at Enrique, San Cristobal and Pelotas (Figure 3.3). These results indicate that the most revealing pattern of the association between roving herbivorous fishes and the algal community is the grouping of the reefs Enrique, Pelotas and San Cristobal at the 3 m depth interval, which suggests the strongest interaction between the two groups occurs on the habitat common to these three sites. These three sites are shallow with high rugosity and had the highest density and biomass of fish and highest cover of CCA.

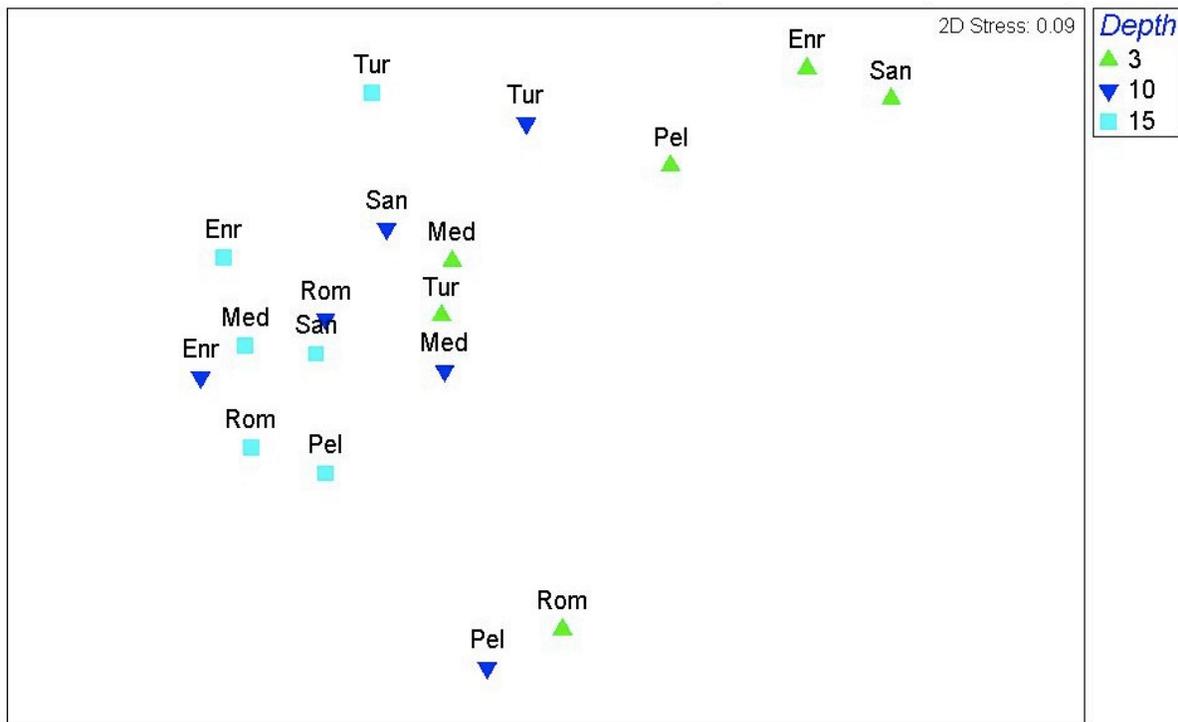


Figure 3.3 Non-metric multidimensional scaling plot of the algal community data with points representing the location of the 18 reef-depth combinations. The symbols represent depth interval and reefs (see Fig. 3.1) and are abbreviated using the first three letters of the name.

The ANOSIM analysis of the algal community data revealed that among the three factors of reef, cross-shelf position and depth interval, there was significant dissimilarity at the multivariate level only for depth; between the 3 and 15 m intervals (Table 3.2). Since depth resulted as the only statistically significant factor it was further utilized to examine its relationship with algal community composition. SIMPER analysis identified ten algal species responsible for the difference in community composition between the 3 and 15 m depth intervals, and these species explained 90% of the dissimilarity (Table 3.3). The average dissimilarity for all study reefs between these two depths is 50.61 %.

Four of these species are CCA, two are foliose macroalgae, one is an articulated macroalgae, one is a microalgae; the higher taxonomic groupings include filamentous algae and endolithic chlorophyta following the functional groups of Steneck (1988). These ten algal taxa, including six functional groups, were utilized to examine potential correlations between herbivorous fish biomass and the algal percent cover at the different reefs and depth intervals.

Table 3.2 Results from an ANOSIM analysis of algal community data from all study reefs utilizing depth interval as the grouping factor. Values in bold show significant differences between groups for the pairwise tests.

Global R: 0.173		Global Significance
		level: 3.7%
Pairwise Tests	R Statistic	Significance Level %
3, 10	0.093	17.7
3, 15	0.387	0.4
10, 15	-0.002	42.9

Table 3.3 Dissimilarity in algal community structure between the 3 and 15 m depth intervals resulting from a SIMPER analysis. The algal species that contributed 90% of the dissimilarity are listed by rank of percent contribution. The average dissimilarity for all study reefs is 50.61 %.

Species	Depth 3 m	Depth 15 m	Average Dissim.	Percent Contrib.	Cumm. Percent
	Average Cover	Average Cover			
Turf	15.7	13.5	7.4	14.7	14.7
<i>Schizothrix</i> sp.1	7.7	13.6	7.3	14.5	29.2
<i>Halimeda opuntia</i>	5.7	2.9	5.4	10.6	39.8
<i>Porolithon pachydermum</i>	6.1	0.0	4.9	9.8	49.5
<i>Dictyota</i> sp.1	3.6	0.3	3.9	7.8	57.3
<i>Neogoniolithon accretum</i>	6.4	7.4	3.9	7.6	64.9
<i>Metapeyssonnelia corallepida</i>	4.6	0.1	3.9	7.6	72.6
<i>Dictyota humifusa</i>	2.4	3.1	3.6	7.2	79.7
Endolithic Chlorophyta	4.4	0.5	3.5	6.9	86.6
<i>Metapeyssonnelia</i> sp.2	2.8	0.3	2.2	4.4	91.0

Correlation analysis utilizing Spearman's non-parametric coefficient (R_s) revealed that some of the algal functional groups and a subset of algal species were significantly correlated to the biomass of herbivorous reef fishes (Table 3.4). The most evident pattern is the positive correlation between CCA percent cover and the fish variables: total herbivorous fish, Acanthuridae, Scaridae, as well as the species *Acanthurus coeruleus*, *Scarus iseri*, and *Sparisoma viride*. These are three of the most abundant species of roving herbivorous fish on the study reefs (Table 3.1). Three other abundant species, *A. bahianus*, *A. chirurgus* and *Sparisoma aurofrenatum* did not exhibit a relationship with any of the algal variables. Three out of the four species of CCA and endolithic chlorophyta are significantly correlated to the same fish variables as the whole of the CCA functional group (Table 3.4). The fish variables Scaridae, *S. iseri*, and *S. viride* are positively correlated to the articulated algae functional group and *Halimeda opuntia*. *Sparisoma viride* is positively correlated to the microalgae functional group and to *Schizothrix* sp.1.

Table 3.4 Spearman's non-parametric correlation coefficient (R_s) between algal cover and herbivorous fish biomass. Algae are categorized by functional group as well as by species; and fish by total herbivores, families and important species. Coefficients in bold show significant correlations at the $p < 0.05$ level.

Functional Group/Species	Herbivores	Acanthuridae	Scaridae	<i>Acanthurus coeruleus</i>	<i>Scarus iseri</i>	<i>Sparisoma viride</i>
Articulated	0.46	0.39	0.47	0.35	0.51	0.49
<i>Halimeda opuntia</i>	0.44	0.39	0.46	0.3	0.53	0.49
CCA	0.51	0.49	0.53	0.51	0.5	0.51
Endolithic Chlorophyta	0.7	0.65	0.74	0.66	0.64	0.78
<i>Metapeyssonnelia</i> sp.2	0.7	0.72	0.66	0.72	0.59	0.62
<i>Metapeyssonnelia corallepida</i>	0.64	0.48	0.66	0.5	0.6	0.67
<i>Neogoniolithon accretum</i>	0.18	0.19	0.24	0.21	0.24	0.23
<i>Porolithon pachydermum</i>	0.61	0.55	0.59	0.64	0.48	0.59
Coarse	0.02	-0.08	-0.03	-0.06	0.06	-0.14
Filamentous	0.31	0.32	0.31	0.43	0.41	0.28
Turf	0.31	0.32	0.31	0.43	0.41	0.28
Foliose	0.14	0.08	0.09	0.22	0.13	0.06
<i>Dictyota humifusa</i>	0.09	0.09	0.03	0.22	0.14	-0.08
<i>Dictyota</i> sp.1	0.02	-0.08	0.01	0.11	0.21	0.09
Microalgae	-0.38	-0.32	-0.38	-0.36	0.21	0.45
<i>Schizothrix</i> sp.1	-0.38	-0.32	-0.38	-0.36	0.21	0.45

Metapeyssonnelia corallepida, *Metapeyssonnelia* sp. 2, *Porolithon pachydermum* and endolithic chlorophyta are the algal taxa most responsible for the correlation between the CCA functional group and the biomass of herbivores (Table 3.3, Figures 3.4-3.7). The abundance of CCA is highest at San Cristobal and Enrique reefs, which also have the highest biomass of herbivorous fishes (Figure 2.4). The shallow fore-reef at Las Pelotas also exhibited a distinct algal community with high CCA cover but also with a high abundance of the calcareous green algae *Halimeda opuntia*. The transects on the shallow fore reefs at the other three reefs are dominated by foliose macroalgae (Media Luna), or filamentous algae (Romero and Turrumote), although CCA are also present.

The habitat where the transects were located at the 3 m interval on these latter three reefs has less structural heterogeneity (rugosity), and the herbivorous fish biomass was lower, than the other reefs, although the general trend of high herbivorous fish abundance at shallower depths (when compared to the deeper fore-reef) is still evident (Table 3.1). The scatter plots also reveal that the relationship between CCA cover and herbivore biomass varies by depth and among species (Figures 3.4-3.8). The plots for *Metapeyssonnelia corallepida*, *Metapeyssonnelia* sp. 2, and endolithic chlorophyta reveal similar patterns among depth intervals with higher cover shallow (Figures 3.5-3.7). *Porolithon pachydermum* exhibits a different pattern, where the cover of this species is very low at the 10 and 15 m depth intervals but shows high cover and variability at 3 m (Figure 3.8).

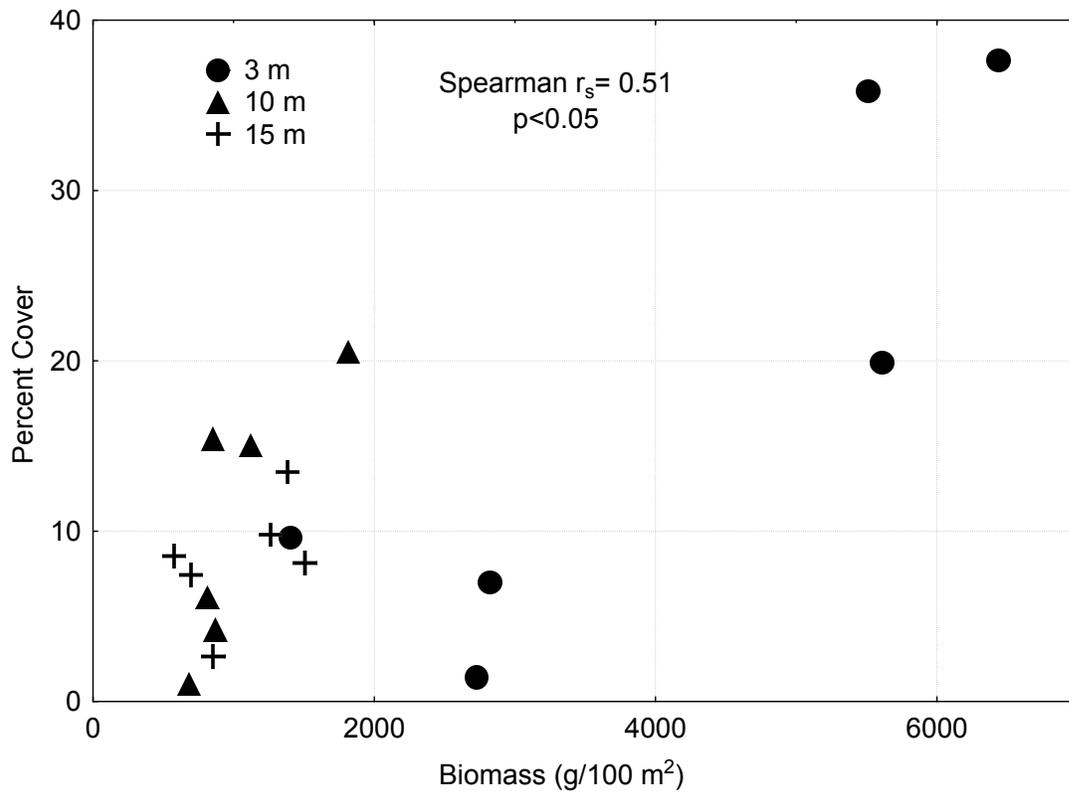


Figure 3.4 Herbivore biomass and the percent cover of CCA for all study reefs and categorized by depth interval. Spearman's correlation coefficient (R_s) was used to examine the strength of relationship and significance level.

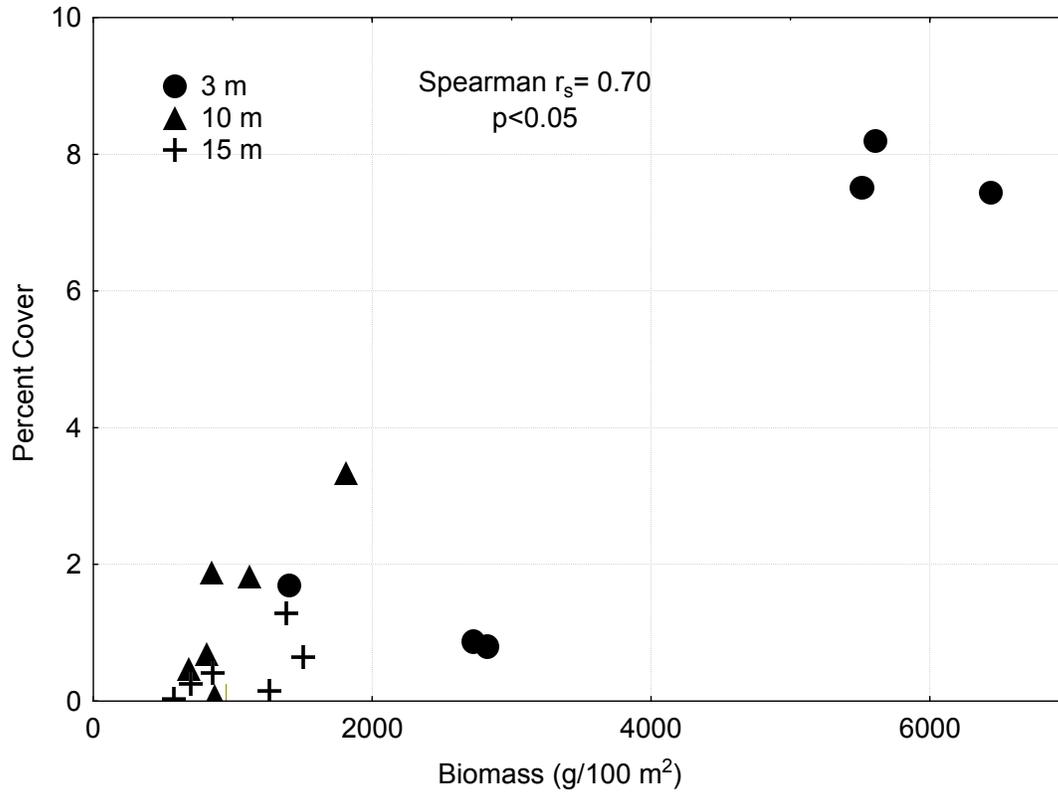


Figure 3.5 Herbivore biomass and the percent cover of endolithic chlorophyta for all study reefs and categorized by depth interval. Spearman's correlation coefficient (R_s) was used to examine the strength of relationship and significance level.

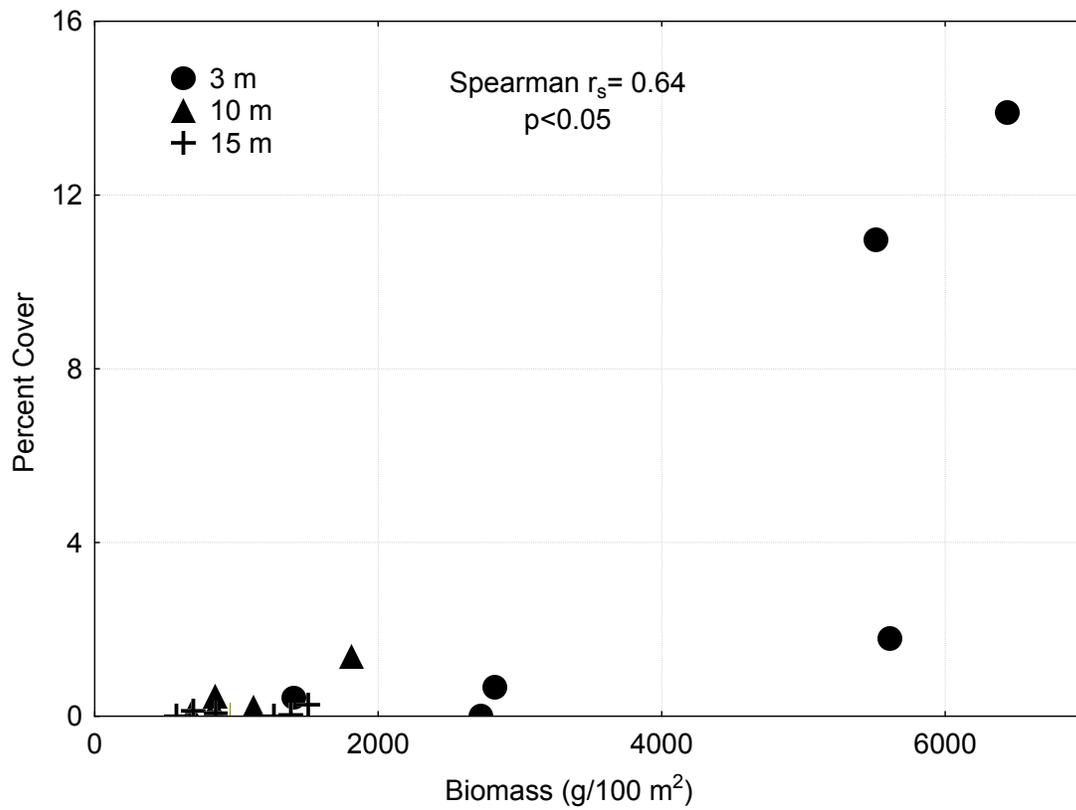


Figure 3.6 Herbivore biomass and the percent cover of *Metapeyssonelia coralliepedia* for all study reefs and categorized by depth interval. Spearman's correlation coefficient (R_s) was used to examine the strength of relationship and significance level.

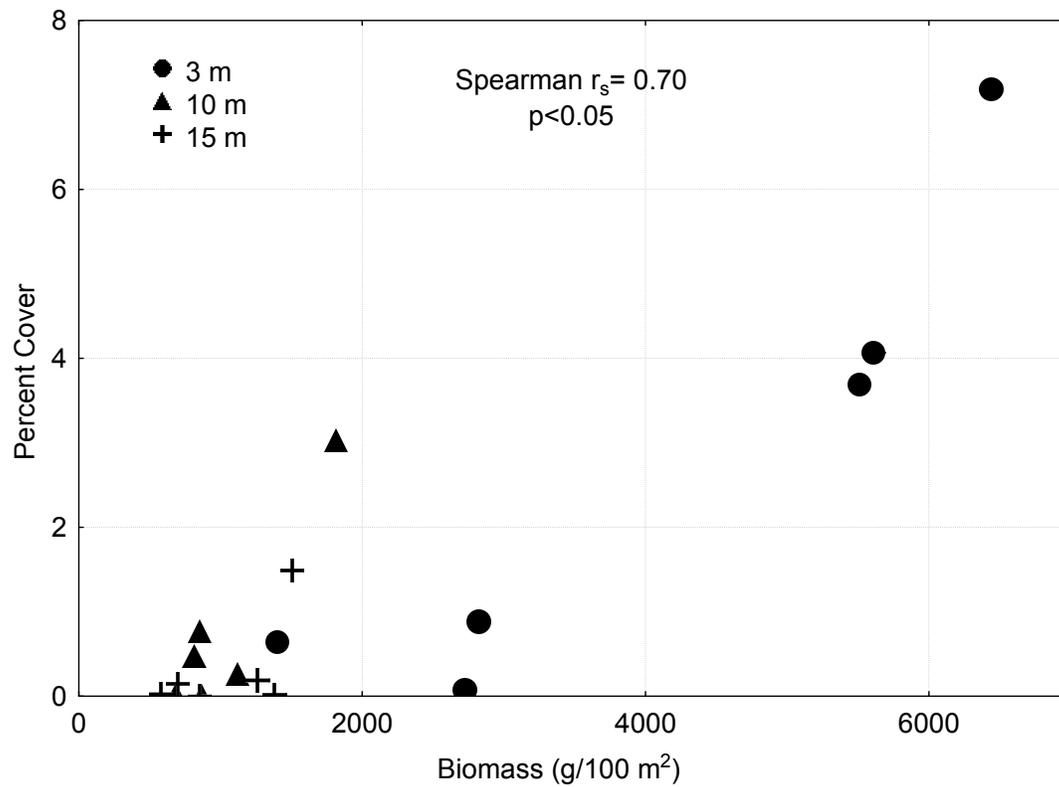


Figure 3.7 Herbivore biomass and the percent cover of *Metapeyssonelia* sp. 2 for all study reefs and categorized by depth interval. Spearman's correlation coefficient (R_s) was used to examine the strength of relationship and significance level.

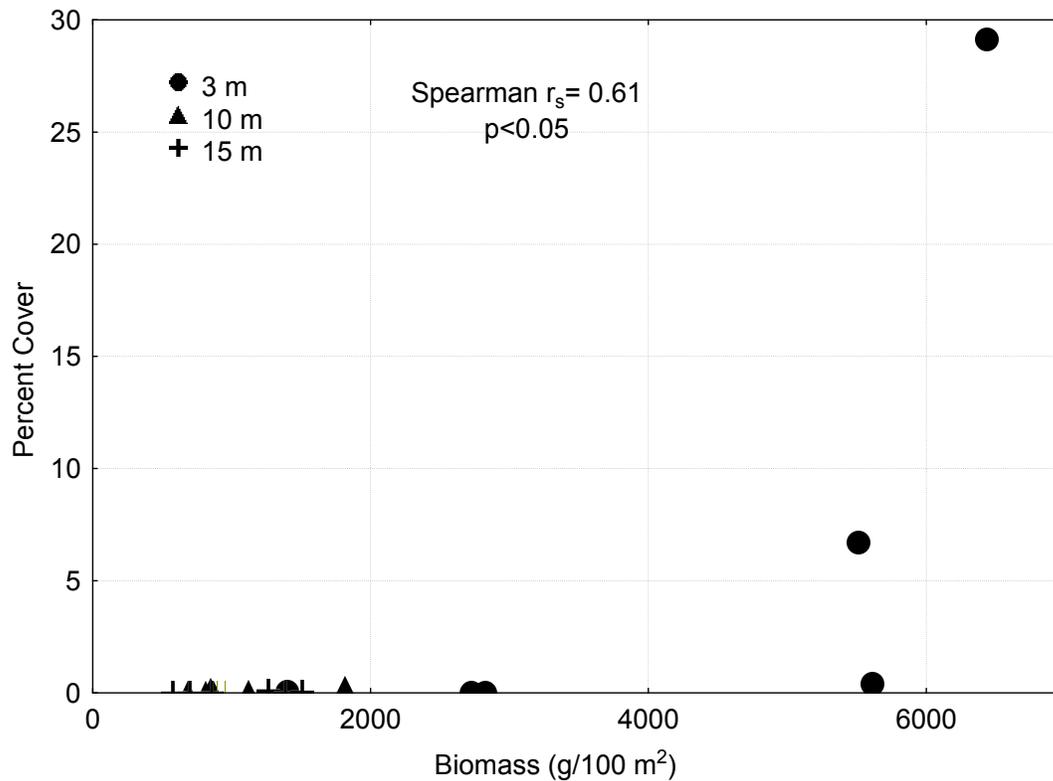


Figure 3.8 Herbivore biomass and the percent cover of *Porolithon pachydermum* for all study reefs and categorized by depth interval. Spearman's correlation coefficient (R_s) was used to examine the strength of relationship and significance level.

The principal component analysis (PCA) plot of water quality parameters reveals that axis one is related to the location of study reefs on the inshore to offshore gradient (Figure 3.9). For the inner-shelf reefs the second PCA represent a longitudinal (east to west) gradient in water quality related to the predominant alongshore currents and land-based inputs from La Parguera and up current from Guánica to the east. The mid-shelf reefs Media Luna and San Cristobal are separate from the inner-shelf reefs of Enrique, Pelotas and Romero. The PCA vectors of the water quality parameters indicate that

turbidity and light extinction coefficient (K_d) were important variables in the location of study reefs along axis 1, which accounts for 51.3% of the variability.

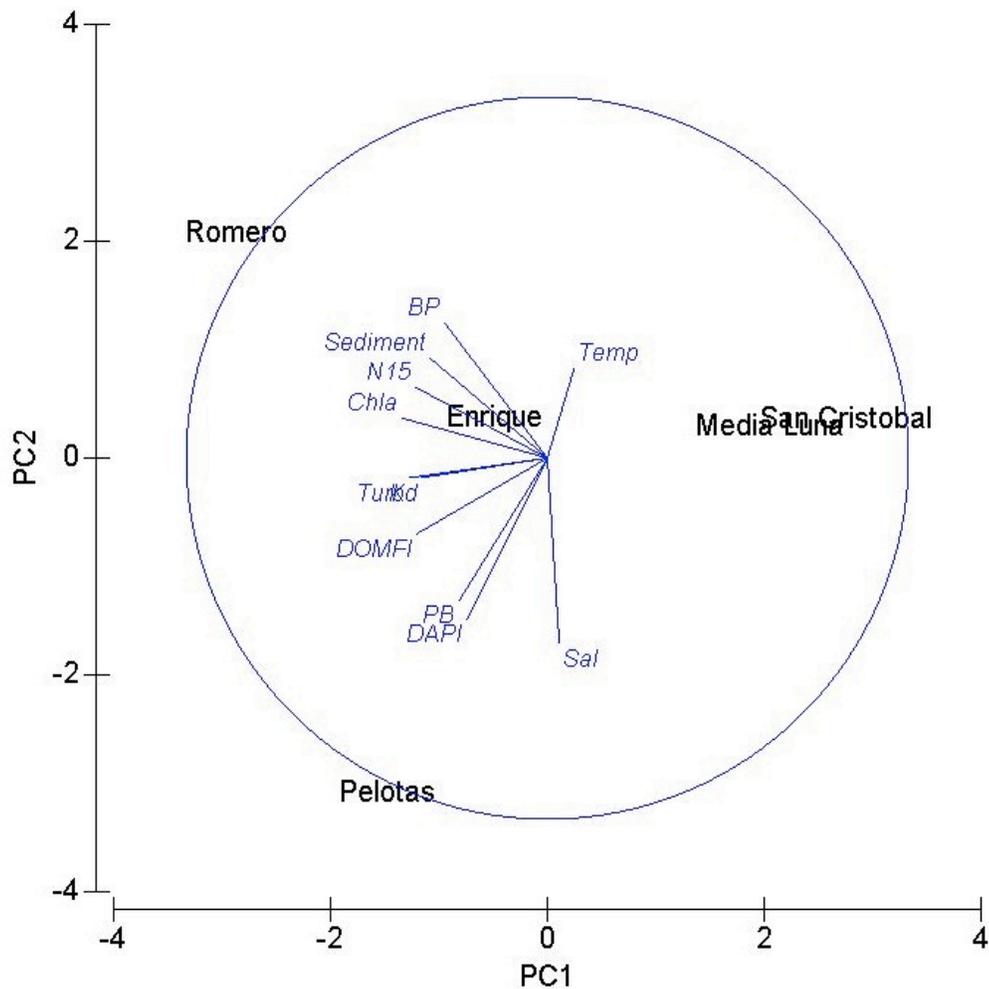


Figure 3.9 Principal Component Analysis (PCA) plot of water quality variables from five of the study reefs. Abbreviations: (BP) bacterial production, (PB) bacteriophytoplankton counts, (Chla) chlorophyll a, (N15) nitrogen stable isotope, (DOMFI) dissolved organic matter, (DAPI) bacterial abundance, (Turb) turbidity, (Sal) salinity, (K_d) light extinction coefficient.

A secondary pattern discerned from the multivariate analysis of the herbivorous fish assemblage data is related to the location of the study reef on either the inner-shelf (Enrique, Pelotas, Romero) or the mid-shelf (Media Luna, San Cristobal, Turrumote)

(Figures 3.1-3.3). For the algal community the CCA functional group, the endolithic chlorophyta taxonomic group, the three CCA species *Metapeyssonnella corallepida*, *Metapeyssonnella* sp. 2, and *Porolithon pachydermum*, and the filamentous algae functional group (turf algae) exhibit different patterns between the inner and mid-shelf reefs (Figures 3.10-3.15). All of these algae generally decline in cover as depth increases. However, the decline is of a greater magnitude on inner-shelf reefs; the mean algal cover at the 10 m depth interval is significantly different between reef position for the above taxa (Mann-Whitney U non-parametric test, $p < 0.05$). A similar pattern is seen at 15 m, but it is not significantly different. The species *M. corallepida* and *P. pachydermum* show a much steeper decline in cover with increasing depth (Figures 3.12, 3.14).

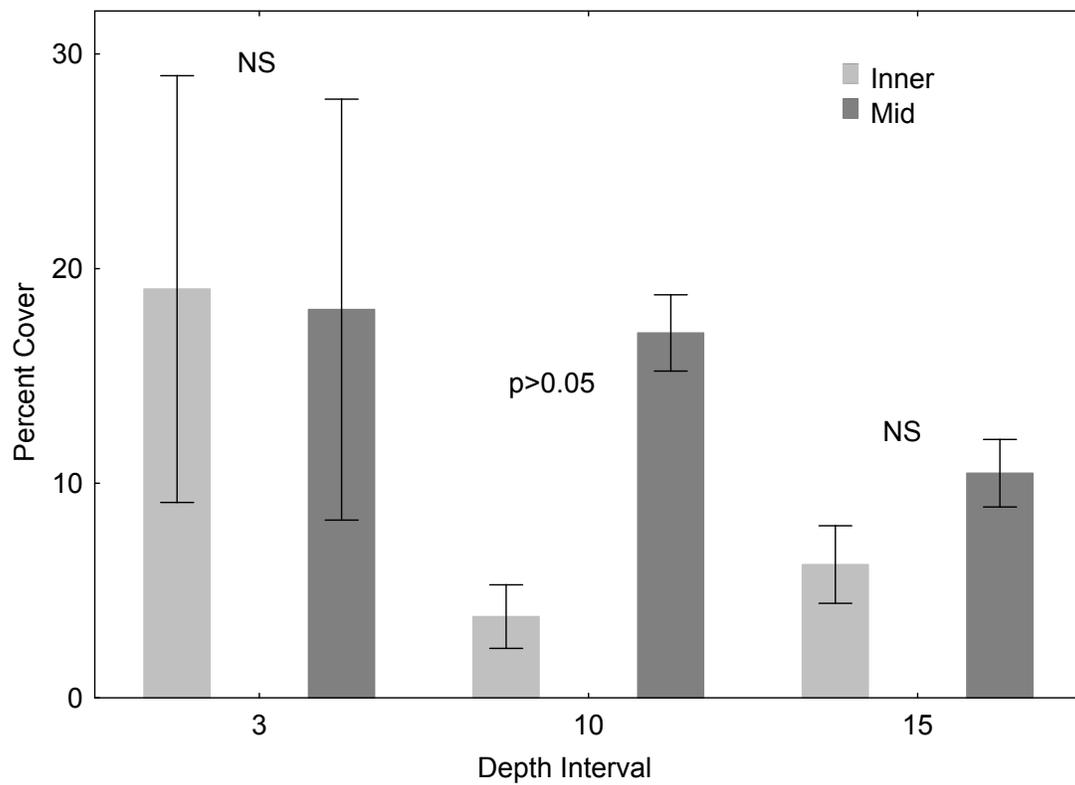


Figure 3.10 Mean percent cover of CCA grouped by inner and mid-shelf reefs and across the three depth intervals. Significant differences between inner and mid-shelf locations were tested with the Mann-Whitney U non-parametric test.

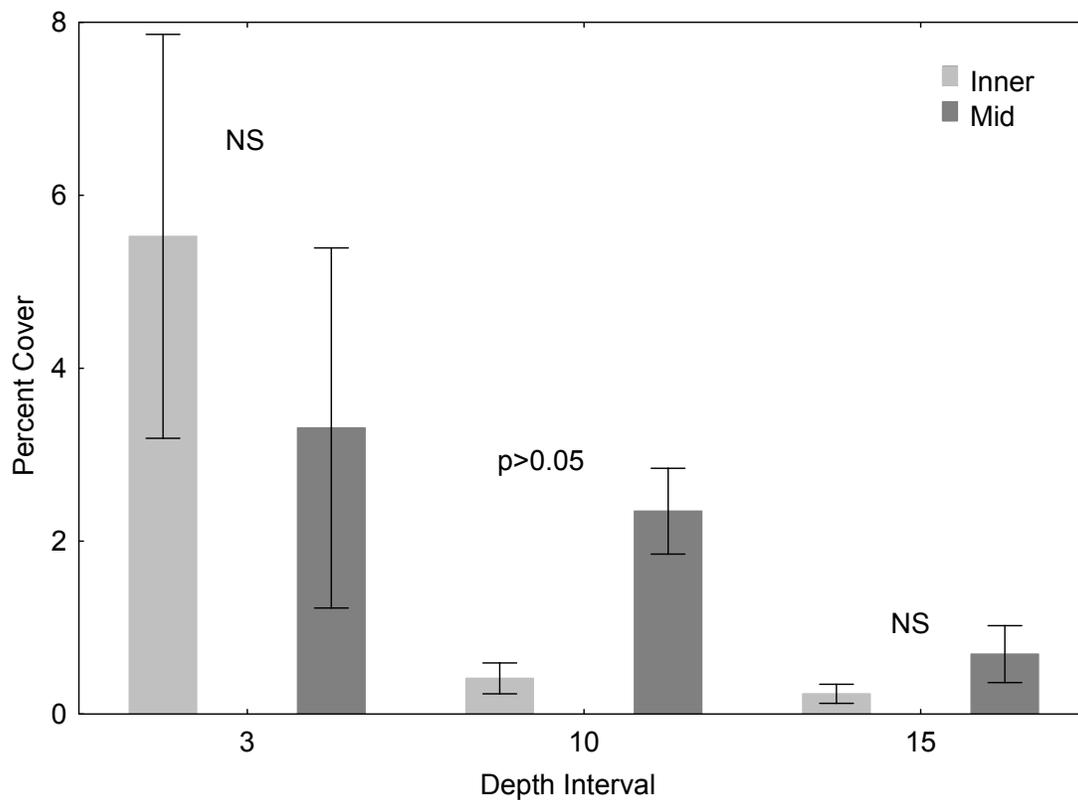


Figure 3.11 The mean percent cover of endolithic chlorophyta grouped by inner and mid-shelf reefs and across the three depth intervals. Significant differences between inner and mid-shelf locations were tested with the Mann-Whitney U non-parametric test.

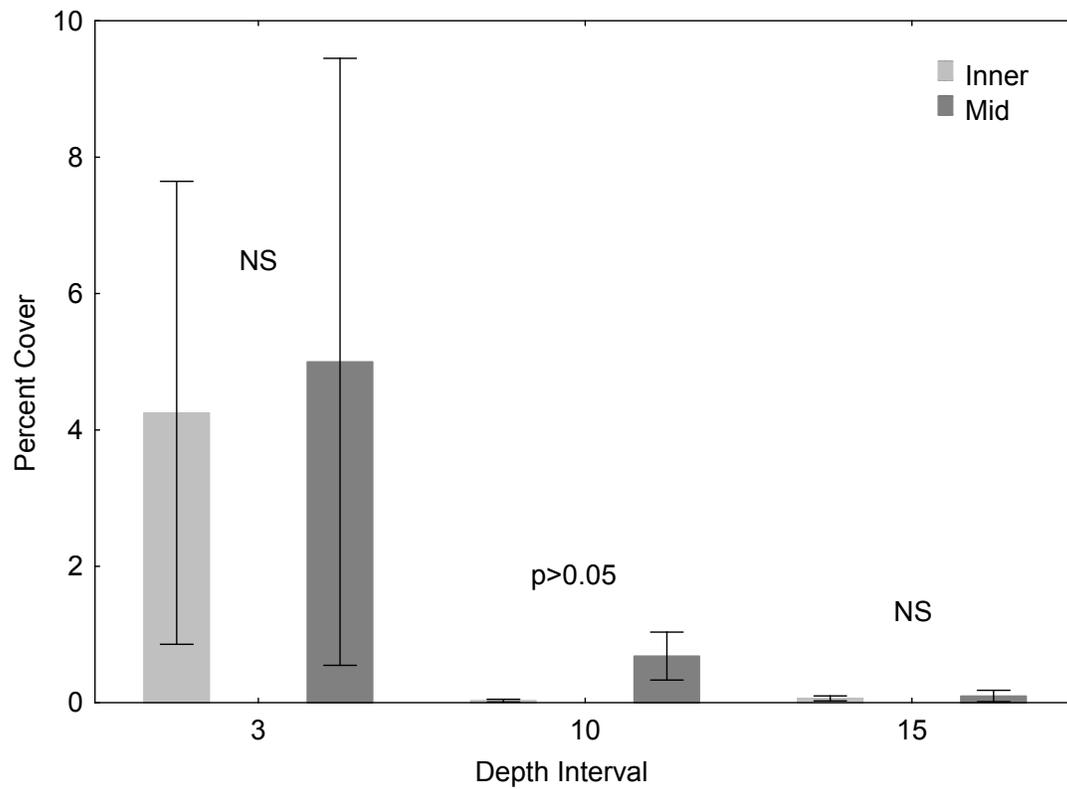


Figure 3.12 The mean percent cover of *M. corallipedia* grouped by inner and mid-shelf reefs and across the three depth intervals. Significant differences between inner and mid-shelf locations were tested with the Mann-Whitney U non-parametric test.

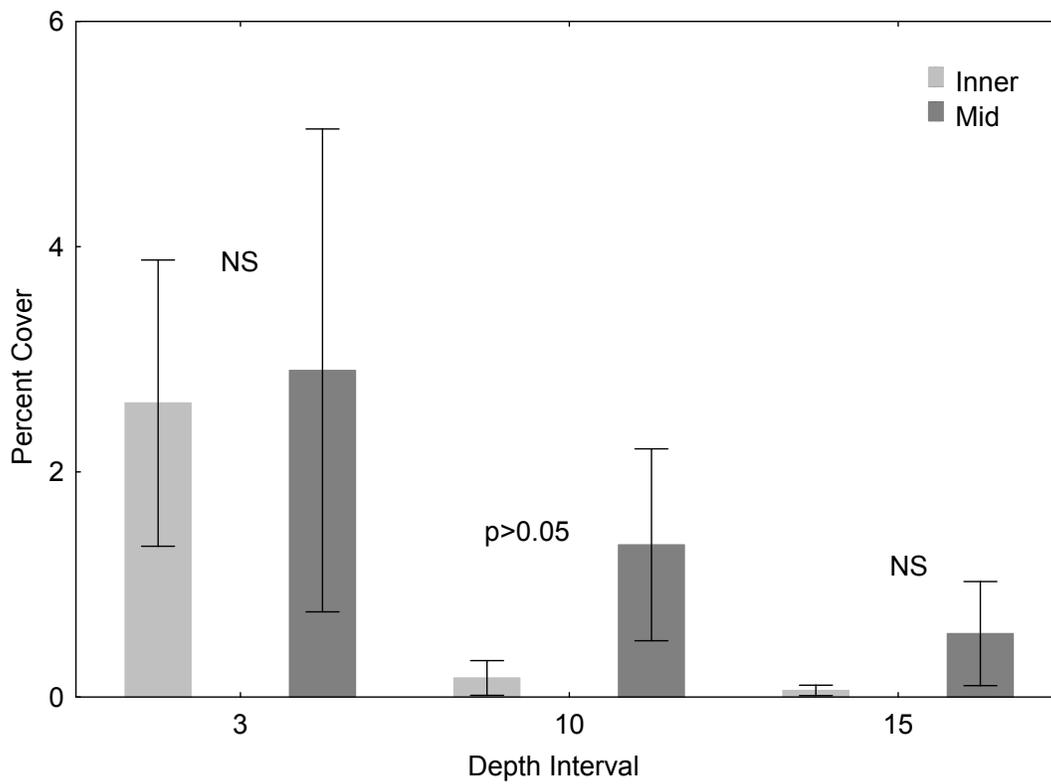


Figure 3.13 The mean percent cover of *Metapeysonnelia* sp. 2 grouped by inner and mid-shelf reefs and across the three depth intervals. Significant differences between inner and mid-shelf locations were tested with the Mann-Whitney U non-parametric test.

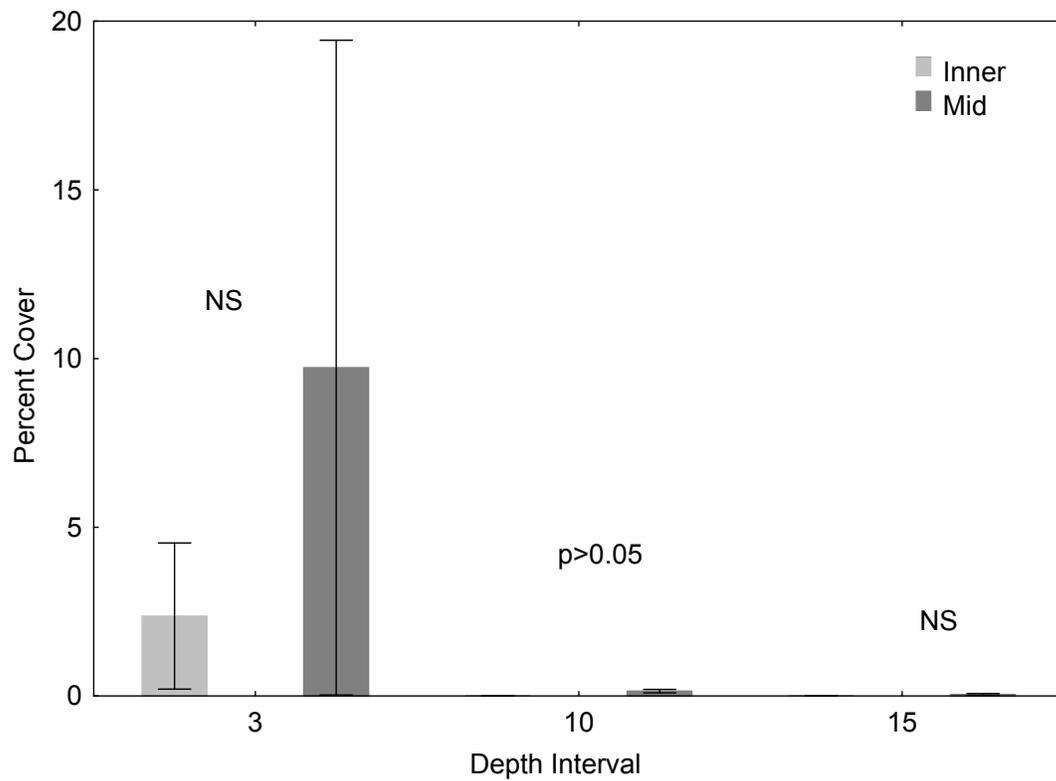


Figure 3.14 The mean percent cover of *P. pachydermum* grouped by inner and mid-shelf reefs and across the three depth intervals. Significant differences between inner and mid-shelf locations were tested with the Mann-Whitney U non-parametric test.

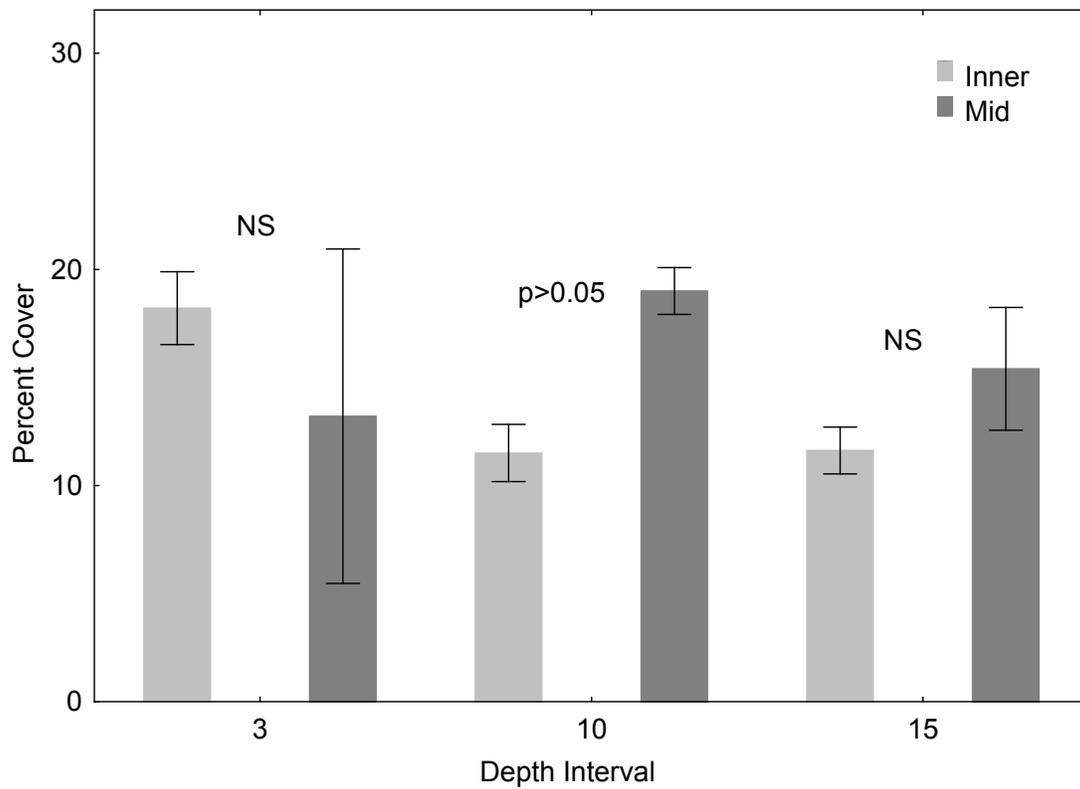


Figure 3.15 The mean percent cover of filamentous algae (turf) grouped by inner and mid-shelf reefs and across the three depth intervals. Significant differences between inner and mid-shelf locations were tested with the Mann-Whitney U non-parametric test.

3.4 Discussion

Ecological research into the interaction between herbivorous reef fish and the algal community has yielded valuable results that help explain the dynamics of benthic reef organisms (Lewis & Wainwright 1985; Littler et al. 2006; Hixon & Brostoff 1996; Williams et al. 2001; Burkepile & Hay 2006; Mumby et al. 2007), as well as the distribution and abundance of roving herbivorous fishes (Russ 2003; Hoey & Bellwood 2010). In the current study patterns in the percent cover of benthic algae and the biomass of roving herbivorous fish were utilized to determine how this relationship varies spatially in relation to a suite of biological, chemical and physical factors; and to describe the key species involved in this relationship. Multivariate analyses revealed that both the algal community and roving herbivorous fish assemblage exhibited a pattern related to depth. A distinct algal community represented by the highest cover of CCA as well as the highest fish abundance occurs on the shallow fore-reef, particularly at locations with high structural heterogeneity.

The structuring of herbivorous fish distributions along a depth gradient has been previously documented in the Caribbean (Lewis & Wainwright 1985; Mumby & Hastings 2008) and the Indo-Pacific regions (Fox & Bellwood 2007). Highest abundances on the shallow fore reef is a common result of these studies, as was quantified in this study. Experimental research indicates that this vertical distribution is driven by the high productivity of algae on the shallow fore-reef and reef crest (Klumpp & Mckinnon 1989; Russ 2003; Hoey & Bellwood 2010). A review of fish grazing studies reveals that the

shallow fore-reef is generally the zone with the strongest correlation between herbivorous fish biomass and a reef substratum dominated by CCA and cropped micro algae (Wismer et al. 2009). This was also the most robust pattern observed in the current study. Undoubtedly other biophysical factors play an important role in this study, as revealed by other sources of variability in the interaction between algae and herbivorous fishes. The existing cross-shelf water quality gradient occurring at the study sites (Otero 2009) and its relationship with variability in the abundance of algal species suggest that water quality modulate the spatial relationship of herbivorous fish and algal interactions.

Collecting detailed algal taxonomic data allowed us to describe what algal species are playing a major role in the trophic processes. The ANOSIM analysis utilized to further examine the spatial patterns showed that the dissimilarity in the algal community was greatest between the 3 and 15 m depth intervals, but the reef and cross-shelf location (inner and mid-shelf) factors did not result in statistically significant results. The SIMPER routine revealed the ten algal taxa that played the most important role in the depth related pattern in this community. The three species of CCA (*Metapeyssonnelia corallepida*, *Metapeyssonnelia* sp. 2, *Porolithon pachydermum*) that drive this pattern have higher average percent cover at the 3 m depth interval and were identified as important contributors to the difference in the algal community between the 3 and 15 m depth intervals. This result is in agreement with the relative dominance model (RDM) for algal communities under variable levels of herbivory (Littler et al. 2006). Since herbivorous fish biomass in this study is highest at 3 m, the model predicts an algal community dominated by CCA and cropped turfs. The cover of CCA and these

three species of algae was positively correlated with the biomass of herbivorous fish (see below). Endolithic chlorophyta also exhibited a similar pattern; although the relationship between endolithic algae and grazing has not been documented previously, it can be an important food source for parrotfish (Bruggeman et al 2004). The group consisting of turf algae, *Halimeda opuntia* and *Dictyota* sp.1 also has a relatively higher percent cover at 3 m, although only the articulated calcareous algae functional group showed a significant correlation with the fish variables. *Neogoniolithon accretum*, *Dictyota humifusa* and *Schizothrix* sp.1 showed an opposite pattern, with a higher percent cover at the 10 and 15 m depth intervals, but none of these species or groups showed a significant correlation with fish biomass. These results suggest that for the study reefs, the most robust relationship between herbivorous fish and algae occurs on the shallow fore-reef where CCA is most abundant and fish biomass is highest.

Correlation analysis between the algal and herbivorous fish variables revealed the significant relationships between these two groups, indicating which algal functional groups and species may be representative of fore-reef locations influenced by relatively higher fish herbivory. The percent cover of CCA, *Metapeyssonnelia corallepida*, *Metapeyssonnelia* sp. 2, *Porolithon pachydermum* and endolithic chlorophyta are all positively correlated with the herbivorous fish variables, in agreement with the RDM (Littler et al. 2006). Although this correlation does not prove causality, caging experiments have shown that high abundance of CCA results from its resistance to fish grazing pressure (Smith et al. 2001; Belliveau & Paul 2002). High herbivory leads to a reef substratum that is dominated by corals and CCA and cropped turfs (Wismer et al. 2009). This interaction is most prevalent on the shallow fore-reef (3 m depth interval,

this study), but it can also be influenced by variability in environmental conditions along an inshore to offshore gradient (Albert et al. 2007, and see below).

This study is one of the few that has examined this relationship at the algal species level, since most previous observational and experimental studies have utilized algal taxonomy at the functional group level (but see Steneck 1988; Littler et al. 2006). We suggest that to describe the interaction between roving herbivorous fishes and algae, both hierarchical levels of taxonomy provide information to understand the underlying ecological processes. The classification of the CCA functional group was useful in this study and others for its correlation to reef locations with high levels of grazing by fishes (Williams & Polunin 2001; Wismer et al. 2009). However, at a greater level of detail, the differences in percent cover in species of CCA among in-shore and mid-shelf reefs suggest there are multiple factors that may structure algal fish interactions. For example, in this study the density of parrotfish feeding scars was observed to be greater on *P. pachydermum* versus *Metapeyssonelia* spp., suggesting that species differences may affect food preference and secondarily the distribution of algal species.

The positive correlations between CCA species and fish biomass were not similar across all depth intervals (see scatterplots), indicating the importance of other factors. Most of the spatial variability in fish biomass and algal cover at the fore-reef scale is present in the 3 m depth interval. This suggests that within a depth interval other factors such as differences in habitat structure or rugosity play a role in structuring the relationship between herbivorous fish and the algal community (Friedlander & Parrish 1998). At the same study sites the density of roving herbivorous fish in La

Parguera was positively correlated to rugosity within, but not equally across, all depths (Nemeth & Appeldoorn 2009).

Spatial variability in water quality has the potential to influence algal community structure, and therefore can play a role in structuring the fish-algae interaction. The water quality dynamics occurring across the La Parguera coral reef system are complex and related to terrestrial inputs of sediment and nutrients, as well as in-situ production of carbonate sediments (Otero 2009; Hernandez et al. 2009). There is a gradient of increasing oligotrophic, clear waters from inshore to offshore with temporal and spatial variability caused by storm events and currents (Bejarano 2006; Hernandez et al. 2009). In general the inner-shelf reefs experience higher turbidity, chlorophyll, nutrient concentrations and terrestrial sedimentation than mid-shelf and outer-shelf reefs. This study examined the influence of this pattern on the interactions between the herbivorous reef fishes and benthic algal communities across the inshore to offshore gradient.

Sediments near-shore are finer and have a greater composition of terrestrial input compared to outer-shelf locations as evidenced by sediment cores (Ryan et al. 2008). However a clear inner through mid-shelf pattern in sediment accumulation and terrigenous input was not found in sediment traps at the study sites (Hernandez et al. 2009). The water quality variables of turbidity and light extinction coefficient (K_d) are the best aligned with the first PCA axis that clearly separates inner and mid-shelf reefs. Since these two variables can be used as indicators of the intensity of light that is available to benthic algae, this gradient likely plays an important role in the depth distribution and primary productivity differences between inner and mid-shelf reefs (Bejarano & Appeldoorn 2013). Other studies have revealed that along a cross-shelf

gradient, inshore algal communities are dominated by algal turf (filamentous and cyanobacteria) whereas offshore sites had a community dominated by CCA and fleshy crustose algae, suggesting an important role of water quality variability in structuring algal communities (Scott & Russ 1987). However, the experimental exclusion of herbivores at offshore reefs has transformed the algal community to a state similar to inshore reefs, particularly with respect to the abundance of CCA, suggesting that herbivory was the primary driver of algal community structure and species composition (Albert et al. 2007). Similarly in this study the biomass of herbivores explained more of the variability at 3 m than water quality and nutrient changes across the gradient.

The multivariate analyses for biological variables did not identify reef position (inner or mid-shelf) as significant factor, but the water quality PCA plot utilizing a suite of parameters shows a division between reef positions along the cross-shelf gradient. In this study a subset of algal species show differences in percent cover between the two shelf positions, with the percent cover of CCA species declining more abruptly with depth on inner-shelf reefs, a result analogous to the herbivorous fish assemblage (Nemeth & Appeldoorn 2009). This suggests that the position of a reef along an inshore to offshore water quality gradient, and its effect on algae is also an important descriptor that can be utilized to explain the distribution of fish herbivory (Scott & Russ 1987). The distribution of algal species identified in this study as being indicators of relatively higher grazing in this reef system is influenced by an interaction between depth, three-dimensional structure and water quality. The CCA species *P. pachydermum* was more abundant on mid-shelf reefs and the two *Metapeyssonnelia* species showed an opposite pattern, having a higher relative cover on inner-shelf reefs. This species level

pattern indicates that algal functional group level taxonomy may oversimplify the ecological processes that play a role in the trophic interaction between algae and fishes on coral reefs. Since turbidity and K_d are important parameters describing the light available to primary producers, they play an important role in how the algal community responds to the cross-shelf water quality gradient. We hypothesize that the productivity of cropped algal turfs co-occurring with CCA may be an important positive driver of roving herbivorous fish distribution, a result which is supported by experimental research (Russ 2003). Parrotfish have been shown to respond strongly to variability in benthic algal productivity in terms of spatial habitat utilization (Bruggemann et al. 1994) and reproductive output (Clifton 1995).

Overfishing and water quality degradation have been implicated in contributing to the decline of coral dominance on reefs (Hughes et al. 2007). In this study we document a potentially important synergistic relationship between variability in reef water quality and its effect on the key ecological process of grazing of benthic algae by herbivorous fishes. Understanding the spatial distribution and interaction between water quality, algal community composition and fish grazing is useful for advancing research and monitoring regarding the factors that influence fish herbivory, an ecological process that has important implications for coral reef management (Mumby et al. 2007). This suggests that water quality degradation from land-based pollution may have effects on important ecological coral reef processes beyond the direct biological impacts to corals.

4 Contrasting seascape factors that influence the distribution of roving herbivorous fishes on coral reefs in La Parguera, Puerto Rico

4.1 Introduction

The distribution of coral reef fishes is influenced by the ecological association between species and their habitat (Appeldoorn et al. 2003; Friedlander and Brown 2007; Schärer-Umpierre 2009), and herbivores from the families Acanthuridae and Scaridae are closely associated with their food source of benthic algae (Bruggemann et al. 1994; Russ 2003). Habitat maps can help describe the distribution and abundance of roving herbivorous fishes, although their usefulness depends on their resolution and how habitats classes are defined (Kendall et al. 2011) and the spatial scale utilized (Pittman and Brown 2011). Advancing the understanding of this relationship can be aided by determining what seascape properties correlate with the spatial pattern in herbivorous fish distribution by utilizing metrics that describe the habitat mosaic. The mosaic of habitat types that occur across the seascape is heterogeneous in terms of three-dimensional physical structure and biotic community. The patterns that can be ascertained are dependent on the scale and resolution of sampling and habitat mapping (Pittman et al. 2011). In coral reef and associated ecosystems the diversity of habitats is high, a condition which complicates the ability to understand fish-habitat interactions (Friedlander and Brown 2007; Pittman et al. 2009).

The way that fish are distributed spatially is influenced by the characteristics of the habitat and properties of the landscape mosaic (Nagelkerken et al. 2002; Appeldoorn et al. 2003; Dorenbosch et al. 2004, 2005; Mumby et al. 2004). For example

recent results reveal that mangrove shorelines across broad spatial scales are not equivalent in their value as fish habitat, and that estimates of 'essential fish habitat' or 'nursery habitat' using a simple total habitat area may misrepresent the habitat used by these fishes (Faunce and Serafy 2008). It is therefore important to understand the biophysical characteristics of the habitats that structure coral reef fish populations at the seascape level and to investigate their relative importance.

A suite of life history processes determines the spatial distribution and abundance of herbivorous coral reef fishes including settlement, post settlement (Tolimieri 1998), ontogenetic migrations (Aguilar-Perera and Appeldoorn 2007), habitat preferences (Pittman et al. 2007a), and feeding ecology (Bruggemann et al. 1994). In broad terms the amount and location of coral reef habitat can describe the distribution of roving herbivorous fishes across the seascape, but important variation in abundance has been found to occur within this habitat type (Lewis and Wainwright 1985; Bellwood 2007; Burkepile and Hay 2009; Hoey and Bellwood 2010). Work to scale-up these patterns to a seascape level has shown important results (Mumby et al. 2006), but research that compares the relative importance of processes that structure roving herbivorous fish assemblages at the seascape level will further improve the ability to monitor and manage these populations and associated ecological functions. In this study we evaluate the relative importance of various factors that influence the distribution and biomass of roving herbivorous fishes from the families Acanthuridae and Scaridae across the seascape. Previous studies have shown the role habitat, depth and ontogenetic migrations in this regard. We include the spatial arrangement of the assumed preferential feeding habitat of high algal productivity (Nemeth and Appeldoorn

2009) as a factor and compare its importance to other factors for which metrics can be extracted from habitat and bathymetric maps. The shallow fore reef and reef crest habitat has been shown to harbor high biomass of herbivorous fishes (Russ 1984a; Nemeth and Appeldoorn 2009; Hoey and Bellwood 2010) which correlates to the high productivity of epilithic algae (Russ 2003). This distribution has important implications for coral reef ecology since fish herbivory can play an important role influencing the competition between algae and coral dominance (Hughes et al. 2007; Mumby et al. 2007).

4.2 Methods

This study was conducted on the coral reefs and associated habitats off of La Parguera, Puerto Rico (N 17° 58.3', W 67° 02.6') (Figure 4.1). This coastal marine ecosystem is composed of a mosaic of coral reefs, seagrass beds, mangrove shorelines and unconsolidated sediments. The insular shelf in the study area varies in width from 4 to 10 km, consisting of emergent bank reefs and patch reefs inshore; grading to deeper submerged reefs, hardbottom and sand offshore. Artisanal scale commercial fisheries occur in the area utilizing nets, fish traps, spears and hook/line; parrotfish and surgeonfish are targeted but considered second-class fish in the fishery.

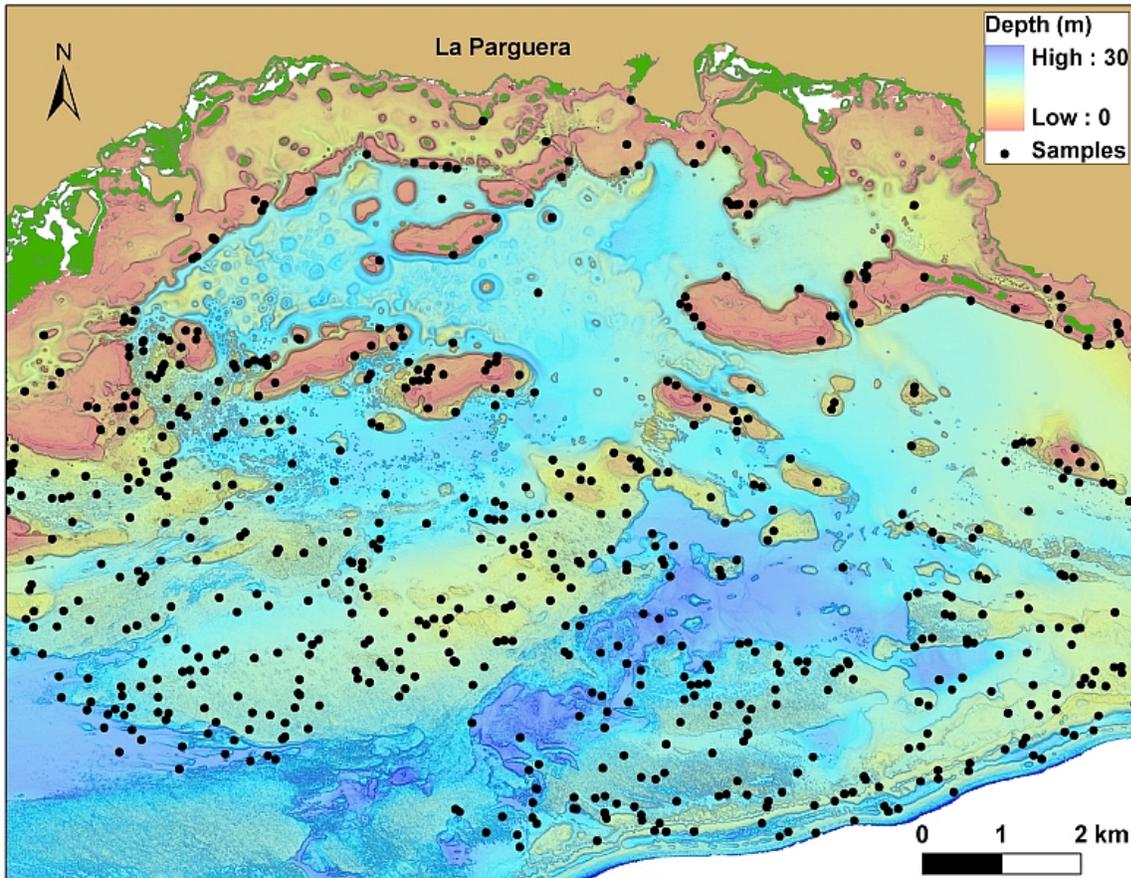


Figure 4.1 Map of study area in La Parguera, Puerto Rico. Depth was derived from a LiDAR bathymetry grid. Black dots show the location of the 810 survey points.

The marine habitats were mapped by NOAA utilizing aerial photographs; and classified at different hierarchical levels including structural habitat, cross-shelf position and geomorphology (Kendall et al. 2001). A bathymetry grid for the area was collected at 4 m resolution utilizing LIDAR (Costa et al. 2009). In addition to depth several derived geomorphic parameters that serve as indexes of topographic complexity of the seafloor were employed to determine which best correlates to fish biomass. The parameters of slope and slope of slope were calculated utilizing the Spatial Analyst routine in ArcMap 9.3 (ESRI 2008) GIS software. Rugosity was obtained from the benthic terrain modeler

(BTM) and slope neutral rugosity was calculated utilizing a dedicated algorithm designed to minimize the confounding effect of slope on rugosity (Tzadik 2009).

Data on the abundance and distribution of roving herbivorous fishes was obtained from a multi-year (2001-2011) dataset of survey points collected utilizing a stratified random design (Pittman et al. 2010). Fish species abundance and size were sampled utilizing 25 X 4 m belt transects and biomass was calculated using published values of the length-weight relationship. The biomass of fishes from the families Acanthuridae and Scaridae were extracted from this dataset for the 810 samples that were conducted on hardbottom and coral reef habitats. Transect depth, variance in depth were taken from five locations along the transect and in-situ rugosity was obtained utilizing a six meter chain at two locations (Jeffrey et al. 2009). The terms transect depth, depth variance and transect rugosity are used herein for these geomorphic parameters associates with the survey transects.

The quadrat was placed at five random locations along a 25-m transect line and resulted in a visual estimate of cover and water depth within every 5 m interval along each transect. Two non-overlapping measurements of rugosity (i.e., complexity of the substrate) were also taken along the transect line at each site with a 6-m long chain carefully draped over the substrate.

The geographical analyses were conducted with utilizing ArcMap 9.3 (ESRI 2008) GIS software, where the data of the 810 survey points, habitat maps, bathymetry grid and its derived geomorphic features were used to extract the values for the seascape level calculations. This provided data on both seascape composition and configuration metrics (Wedding et al. 2008). Since data transformation did not resolve

problems of unequal variances and non-normality within the data, the relationship of fish biomass variables to the seascape metrics from transects (i.e., depth) and the bathymetry derived geomorphology metrics (i.e., rugosity) was examined utilizing the non-parametric Spearman's Correlation Coefficient (R_s). This was used to compare among all composition and configuration seascape metrics to determine which explained most of the variability in herbivorous fish biomass.

Data on seascape composition derived from LIDAR bathymetry was extracted from raster (grid) files generated for depth, slope, and slope of slope utilizing the Spatial Analyst routines from ArcMap. The slope-dependent rugosity raster was calculated utilizing the routine in the Benthic Terrain Modeler tool. Slope neutral rugosity was obtained from an algorithm developed to remove the dominance of slope in other rugosity calculations (Tzadik 2009). The calculations for slope, slope of slope, slope-dependent rugosity and slope neutral rugosity were calculated utilizing the adjacent raster pixels having a 4 m dimension to result in an area of $12 \times 12 = 144 \text{ m}^2$.

Seascape configuration metrics were utilized in ArcMap to calculate the distance of the survey points to four different habitats (Wedding et al. 2011). This provided the nearest distance to land (shoreline), seagrass and mangrove habitats of the fish biomass variables obtained from the transect surveys. Additionally a polygon file was created to represent the preferred feeding habitat of roving herbivorous fishes by combining shallow hardbottom habitat with areas of high rugosity (Nemeth and Appeldoorn 2009).

This was done by creating a raster file utilizing the following equation:

$$[\text{Log}_{10} (1/\text{Depth})] \times \text{Rugosity}$$

Rugosity here refers to that derived from the LIDAR dataset utilizing BTM. The resulting raster was used to obtain both seascape composition and configuration metrics for the correlation analyses.

To determine the importance of the cross-shelf gradient in structuring the roving herbivorous fish assemblage the distance to land was used to select survey points that were located within 2000, 4000, and 6000 m of land; as well as the full set of 810 survey points. By selecting a subset of survey points at different distances the effect of various spatial scales on the relationship between fish and the seascape could be examined. The effect of varying distance of survey points from land was examined utilizing the most relevant metrics of seascape composition and configuration by analyzing their correlation at different spatial scales with fish biomass variables. The limit of 2000 m included all points within that distance in the analysis, the 4000 m limit included all point from that line to land and so forth, The biomass variables of total herbivores, *A. coeruleus* and *S. viride* were selected for their overall applicability to the questions of interest and the species that displayed relatively important correlations with the suite of seascape metrics. These two species were chosen because they showed significant correlations across all transect level variables in order to test the hypothesis that the inverse correlation with depth would be strongest inshore following Nemeth and Appeldoorn (2009).

4.3 Results

4.3.1 Species structure

The roving herbivorous fish assemblage sampled at the 810 surveys on coral reef and hardbottom was composed of three acanthurid species and eight scarid species. The biomass and frequency of *Acanthurus bahianus*, *A. chirurgus* and *A. coeruleus* revealed that the first species is the most abundant from this family (Figures 4.2, 4.3). The parrotfishes *Sparisoma aurofrenatum*, *S. viride* and *Scarus iseri* were the three most abundant species in terms of biomass and frequency (Figures 4.2, 4.3). *Scarus taeniopterus* was also common in the surveys, but this parrotfish predominates offshore on hardbottom habitats where reef depth gradients are minimal (Pittman et al. 2010, Tzadik and Appeldoorn 2013), so this species was not utilized in further analyses.

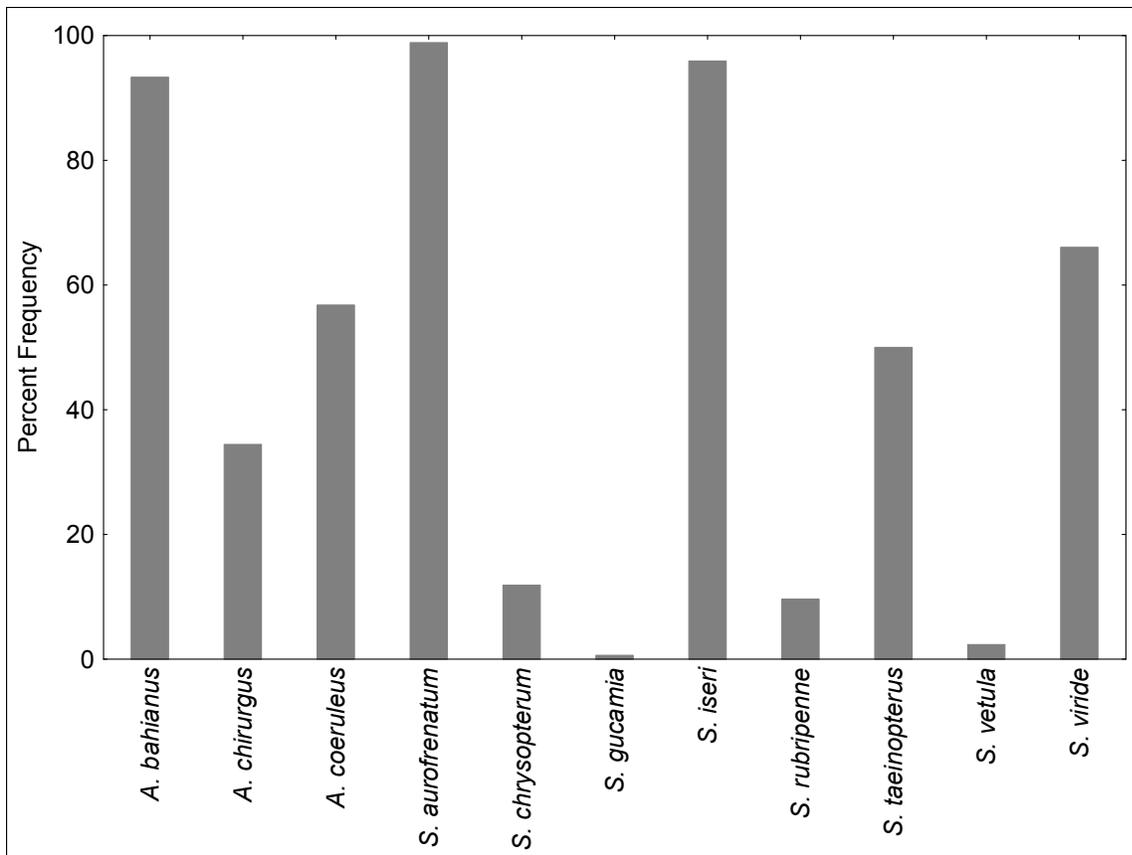


Figure 4.2 The percent frequency of occurrence for roving herbivorous fishes from all of the survey transects (n=810).

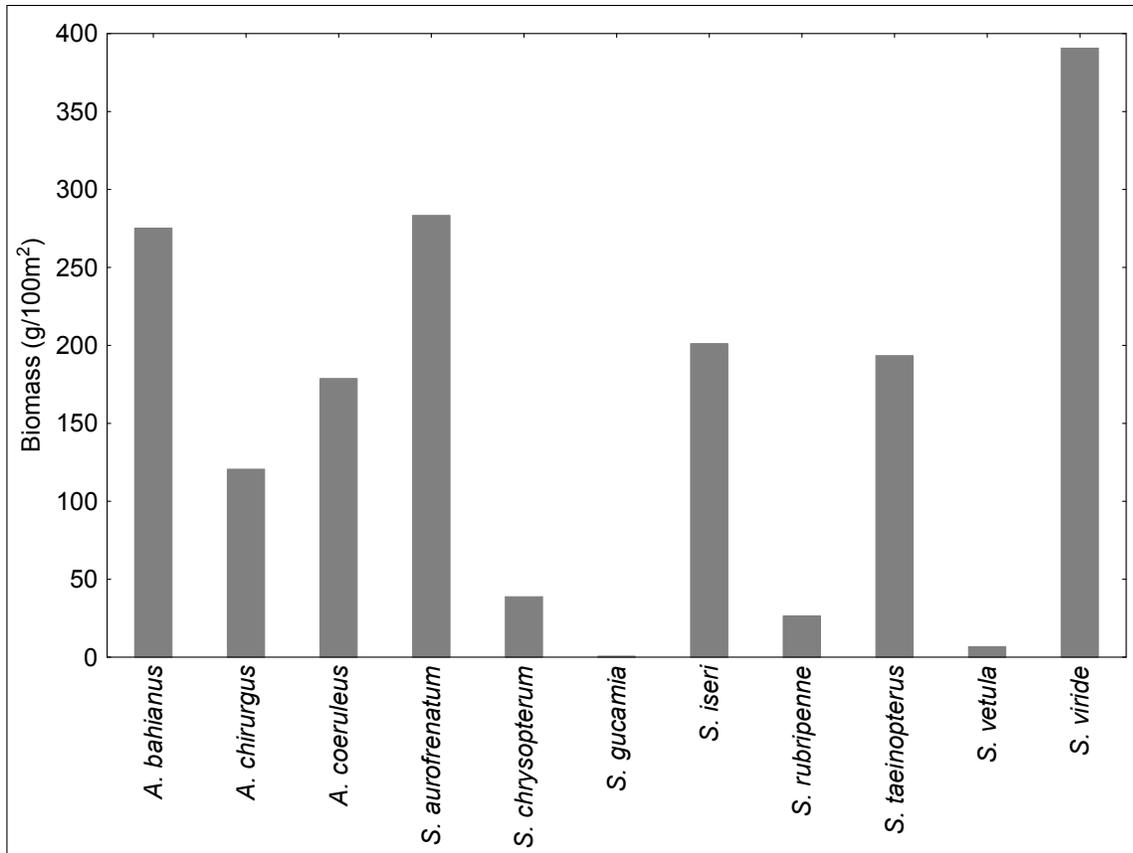


Figure 4.3 The mean biomass of roving herbivorous fishes from all of the survey transects (n=810).

4.3.2 Pattern of biomass by depth interval

The overall pattern of roving herbivorous fish across 5-m depth intervals between 5 and 30 m revealed a decrease in mean biomass with increasing depth (Figure 4.4). The difference in biomass across the depth intervals was significant ($p=0.00004$, Kruskal-Wallis non-parametric ANOVA).

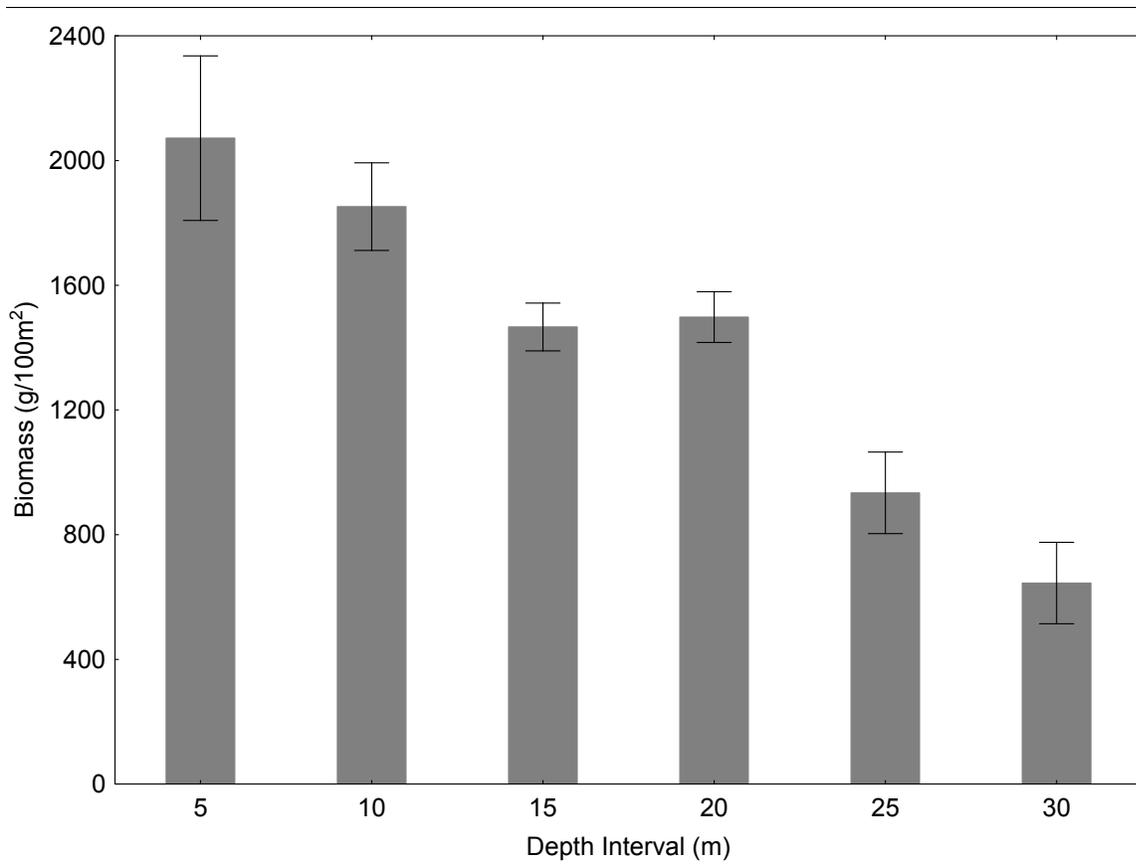


Figure 4.4 The mean biomass (SE) of all roving herbivorous fishes categorized by depth intervals. Interval values represent the maximum depth for each class.

4.3.3 Biomass and transect level metrics

The parrotfish *Sparisoma viride* revealed the highest correlation values with the three habitat composition metrics obtained from the survey transect data (Table 4.1). The three surgeonfishes had better correlation with transect depth, although the relationship was not significant when grouped at the family level. The parrotfishes as a family showed higher correlation values with depth variance and transect rugosity, with differing results for the three species. Among the transect metrics rugosity was best

correlated with the biomass of total herbivores and this was also the case at the family and species level.

Table 4.1 Spearman's Correlation coefficients (R_s) for the herbivorous fish biomass and the habitat composition metrics from the survey transects (n=810). Values in bold are significant at $p < 0.05$.

	Transect Depth	Depth Variance	Transect Rugosity
Herbivores	-0.08	0.22	0.31
Acanthuridae	-0.07	0.12	0.15
Scaridae	-0.04	0.26	0.33
<i>A. bahianus</i>	0.09	-0.00	0.04
<i>A. chirurgus</i>	-0.17	0.07	0.00
<i>A. coeruleus</i>	-0.15	0.18	0.27
<i>S. iseri</i>	-0.04	0.26	0.33
<i>S. aurofrenatum</i>	-0.06	0.13	0.15
<i>S. viride</i>	-0.17	0.36	0.40

4.3.4 Biomass and seascape level metrics

The six habitat composition metrics obtained from the raster grids derived from LiDAR bathymetry data revealed similar results to the transect metrics, with the surgeonfishes having better correlation with depth and the preferred feeding habitat model (a combination of depth and rugosity) than the parrotfishes (Table 4.2). All significant results with depth show negative coefficients indicating an inverse relationship, i.e., higher biomass at shallower depths. The parrotfishes exhibited better correlations with the metrics representing geomorphology and topographic structure, although *A. coeruleus* also showed a similar pattern. *Sparisoma viride* showed the best correlation

with most variables for both families. Across the LiDAR-based habitat variables slope neutral rugosity explained relatively more of the variability in herbivorous fish biomass.

Table 4.2 Spearman's Correlation coefficients (R_s) for the herbivorous fish biomass variables and the habitat composition metrics extracted from the raster data based on LiDAR bathymetry at the survey points (n=810). Values in bold are significant at $p < 0.05$.

	Depth	Slope	Slope of Slope	Neutral Rugosity	Model	Rugosity
Herbivores	-0.10	0.18	0.22	0.25	0.09	0.22
Acanthuridae	-0.09	0.05	0.08	0.10	0.08	0.07
Scaridae	-0.05	0.24	0.27	0.31	0.04	0.29
<i>A. bahianus</i>	0.08	-0.05	-0.02	0.01	-0.07	-0.03
<i>A. chirurgus</i>	-0.19	0.05	0.07	0.02	0.19	0.04
<i>A. coeruleus</i>	-0.16	0.12	0.16	0.20	0.14	0.15
<i>S. iseri</i>	-0.02	0.23	0.24	0.32	0.01	0.28
<i>S. aurofrenatum</i>	-0.08	0.10	0.11	0.14	0.08	0.13
<i>S. viride</i>	-0.19	0.31	0.35	0.38	0.16	0.35

4.3.5 Biomass and distance (configuration) metrics

The most robust patterns of the analysis between fish biomass and distance metrics was displayed at the species level (Table 4.3). The biomass of *A. bahianus* and *S. aurofrenatum* displayed a positive relationship with the distance to the four habitat classifications, with the former having higher coefficient values. *Acanthurus chirurgus*, *A. coeruleus* and *S. viride* revealed the opposite pattern with a negative relationship with the distance to the habitats, and the first species showed the strongest relationship.

Among the distance variables there were no clear trends in differences for the four habitat classifications.

Table 4.3 Spearman's Correlation coefficients (R_s) for the herbivorous fish biomass variables and the configuration metrics of the nearest distance from the survey points (n=810) to four habitats. Values in bold are significant at $p < 0.05$.

	Distance to Seagrass	Distance to Mangroves	Distance to Model	Distance to Land
Herbivores	0.07	0.06	0.03	0.06
Acanthuridae	0.05	0.07	0.09	0.05
Scaridae	0.10	0.07	0.02	0.09
<i>A. bahianus</i>	0.23	0.29	0.29	0.27
<i>A. chirurgus</i>	-0.23	-0.25	-0.21	-0.26
<i>A. coeruleus</i>	-0.10	-0.10	-0.12	-0.11
<i>S. iseri</i>	0.05	-0.04	-0.08	-0.01
<i>S. aurofrenatum</i>	0.11	0.07	0.03	0.08
<i>S. viride</i>	-0.12	-0.16	-0.17	-0.14

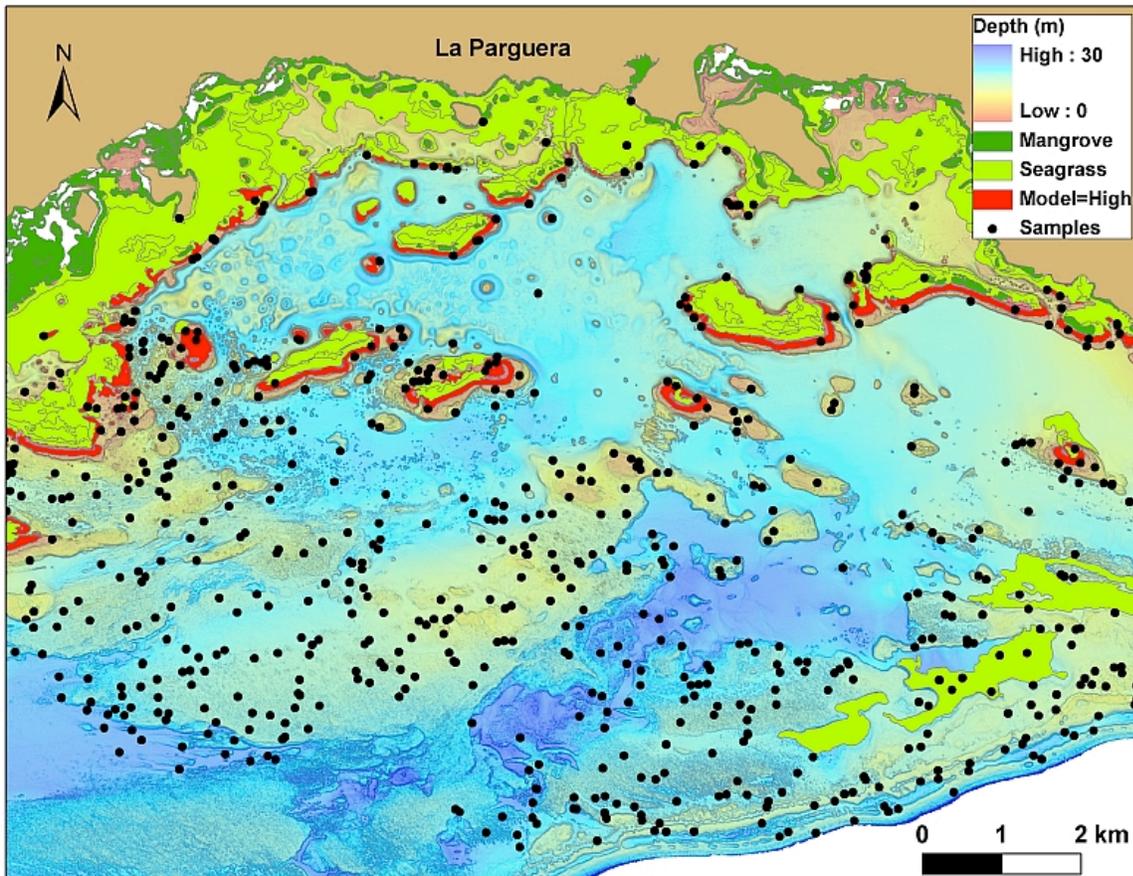


Figure 4.5 Map of the study area showing mangrove, seagrass and model polygons used to calculate the nearest distance from survey points to these habitats.

4.3.6 Varying spatial scales

The analysis of selecting survey points at varying distances to land showed that the number of significant correlations increased from 2000 m to 6000 m and then decreased slightly when all of the samples were included (Table 4.4, Figure 4.6). For the fish biomass variables total herbivores and *A. coeruleus* the relative ranking of the variability explained by the five seascape metrics remained the same in the order: transect rugosity, slope neutral rugosity, depth, model value and lastly distance to the

high model polygons. *Sparisoma viride* differed in that the correlation values for transect rugosity and slope neutral rugosity were very similar at all distances, and these were greater than the other metrics. However for this species the distance to the high model at 4000 and 6000 m from land had higher correlation values than LiDAR depth.

Table 4.4 Spearman's Correlation coefficients (R_s) between the three selected herbivorous fish biomass variables and five seascape metrics for survey points located within four distances from land. Values in bold are significant at $p < 0.05$.

	2000 m	4000 m	6000 m	Overall
Transect Rugosity				
Herbivores	0.30	0.33	0.34	0.31
<i>A. coeruleus</i>	0.18	0.25	0.29	0.27
<i>S. viride</i>	0.26	0.39	0.41	0.40
LiDAR Depth				
Herbivores	0.10	-0.06	-0.12	-0.10
<i>A. coeruleus</i>	-0.06	-0.08	-0.15	-0.16
<i>S. viride</i>	0.04	-0.18	-0.26	-0.19
Neutral Rugosity				
Herbivores	0.21	0.25	0.28	0.25
<i>A. coeruleus</i>	0.13	0.16	0.24	0.20
<i>S. viride</i>	0.29	0.39	0.41	0.38
Model				
Herbivores	-0.14	0.04	0.11	0.09
<i>A. coeruleus</i>	0.03	0.07	0.13	0.14
<i>S. viride</i>	-0.07	0.15	0.23	0.16
Distance to Model				
Herbivores	0.07	-0.01	-0.07	0.03
<i>A. coeruleus</i>	-0.14	-0.05	-0.12	-0.12
<i>S. viride</i>	-0.04	-0.23	-0.30	-0.17

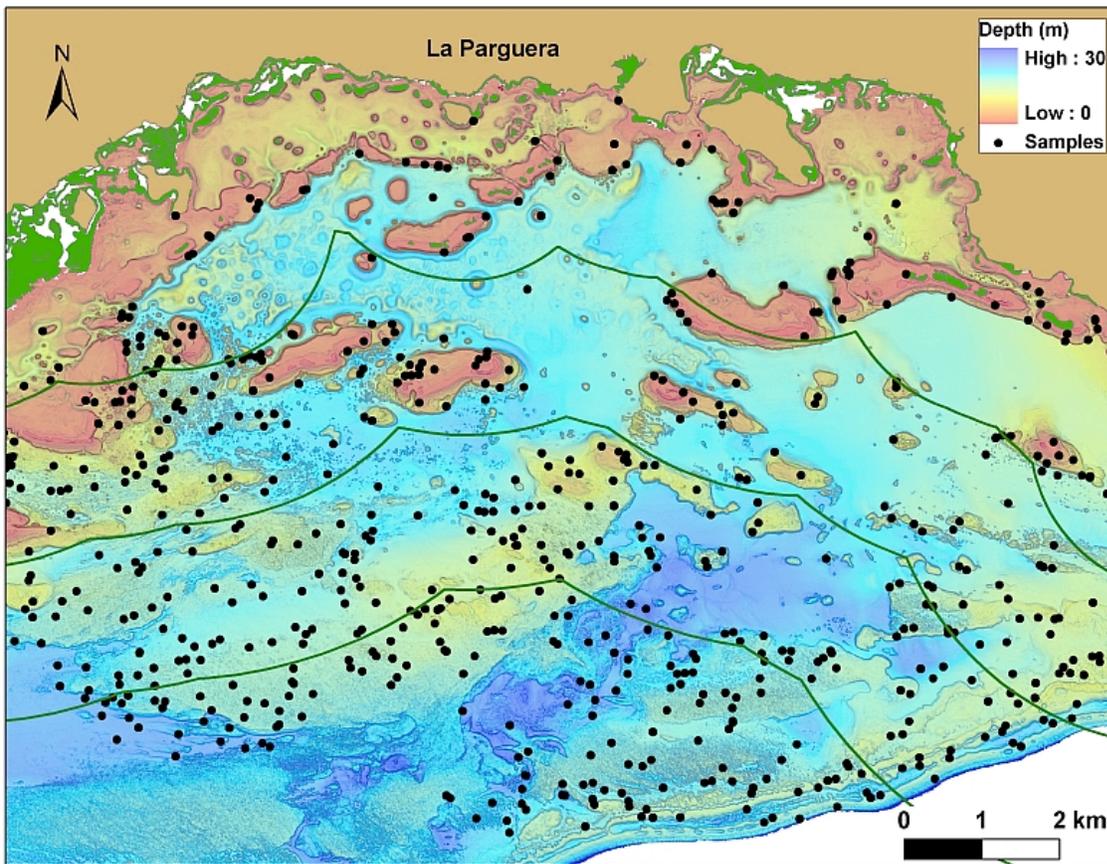


Figure 4.6 Map showing the position of the concentric lines used to select the survey points at 2, 4 and 6 km from land.

4.4 Discussion

4.4.1 Species structure

The pattern of biomass and frequency from the stratified random surveys on hardbottom across the shelf were similar to the results previously obtained by Nemeth and Appeldoorn (2009) looking only at fore-reef locations. However, a notable difference was the increased abundance of *A. bahianus* and *S. taeniopterus* from the 810 surveys from shore to the shelf-edge. These two species, particularly *S. taeniopterus*, show a distinct pattern of being more abundant offshore over the outer shelf whereas its abundance was low on the inshore emergent bank reefs (Pittman et al. 2010). Both studies also documented the low abundance of large bodied parrotfishes particularly *Scarus guacamaia*, *S. coelestinus* and *S. vetula*.

4.4.2 The pattern of biomass by depth interval

The pattern of a decrease in roving herbivorous fish biomass with increasing depth is similar to the fore-reef study but the decline in biomass with depth here (?) was of a lesser magnitude (Nemeth and Appeldoorn 2009). The pattern of higher abundances at shallower depths coincides with studies that have sampled herbivorous fishes across reef zones and depth gradients (Russ 1984b; Bellwood 2007; Fox and Bellwood 2007; Hoey and Bellwood 2010). Since the depth distribution of surgeonfishes and parrotfishes at the fore-reef sites is influenced to some degree by turbidity and light

attenuation (Nemeth and Appeldoorn 2009), the pattern in this study would be expected to show less change across depths since the cross-shelf spatial coverage is greater. Less turbidity and light offshore should decrease the effect of light attenuation, and the biomass across depth intervals will be averaged to result in less change. This is one of the few studies to examine explicitly the depth related pattern along a cross-shelf gradient.

4.4.3 Transect level metrics

The results of the correlation between the fish biomass variables and the habitat composition metrics for the 810 transects revealed patterns at the family and species level, as well as differences among metrics. The biomass of *A. chirurgus* and *A. coeruleus* was weakly and inversely related to transect depth, indicating a slight preference for shallow reef areas. In contrast, the three parrotfish species (principally *S. viride*) positively correlated with transect rugosity and depth variance, which indicates a relatively stronger response to the topographic heterogeneity of the habitat and a weaker relationship with depth. This difference in results between families was also observed at the fore-reef scale on these reefs (Nemeth and Appeldoorn 2009). Overall transect rugosity had the strongest correlations among the habitat composition metrics. The correlations observed at the family level were weaker than at the species level suggesting that species respond differently to the habitat variables.

4.4.4 The correlation from the rasters of geomorphology

The correlation of fish biomass and the metrics extracted from the rasters of geomorphology provided similar results as obtained from the in-situ measurement within the transects; topographic heterogeneity was the most important factor in explaining variability and the species *A. chirurgus*, *A. coeruleus* and *S. viride* were influenced by sample depth. The habitat metrics of slope, slope of slope, rugosity and slope neutral rugosity are calculated from the eight adjoining raster values of the survey point (144 m²), and therefore represent an increase in spatial scale from the transect metrics. Since the results from these two spatial scales coincide, it suggests that similar ecological processes are occurring.

4.4.5 Biomass and distance (configuration) metrics

The role of seascape configuration was examined with the correlations between the herbivore biomass variables and the nearest distance to seagrass, mangroves, the feeding model and land of the geographic location of the 810 survey points. Since the correlation values at the total herbivore and the family level did not show conclusive results, in contrast to the results for individual species, it suggests that at the larger spatial scale of habitat configuration the ecological aspects of individual species play a more important role. Species level differences to habitat characteristics has been documented for other assemblages. Other studies have documented the role of connectivity with seagrass and mangrove nursery habitats to the abundance of

parrotfishes on coral reefs (Dorenbosch et al. 2004; Mumby et al. 2004; Aguilar-perera and Appeldoorn 2007) but these sampled the fish community at smaller spatial scales and did not include the ample variability provided by the stratified random sampling design of the data set utilized in this study (Pittman et al. 2010). *Acanthurus bahianus* and *A. chirurgus* displayed relatively strong results to the habitat distance metrics but in opposite directions, suggesting potential niche partitioning by these two congeners.

4.4.6 Varying spatial scales for subset of metrics

The role of sample location across the in-shore to off-shore gradient was examined by selecting subsets of survey points within distances of 2000, 4000, 6000 m from land; as well as the total set of 810 samples. This permitted analyzing the effect of varying spatial scales or habitat configuration on the relationship between herbivorous fish biomass and the seascape metrics. Overall, most the correlations were more relevant as the distance from shore increased from 2000 to 6000m, and then decreased slightly with the total samples. Distance to shore has been demonstrated to be an important seascape predictor of reef fish abundance in previous studies in La Parguera (Pittman and Brown 2011). Other studies examined the role of spatial scale as the habitat configuration within a radius of samples where the spatial scale of maximum relationship has been in the order of 100's of meters (Appeldoorn et al. 2003; Kendall et al. 2003, 2011; Grober-Dunsmore et al. 2007). One focal question in this study was the role of the water quality along cross-shelf gradient on the response of fishes to habitat and the proximity to the hypothesized preferred feeding habitat. Therefore the pertinent

spatial scales were an order of magnitude greater than previously studied. That the 6000 m subset provided the strongest correlations may be due to multiple factors that cannot be separated with the available data. One potential explanation is that as distance from land increases, the number of samples increases and the value of R_s tends to increase, suggesting either there is more variability to explain, or that the correlations are tighter. Also the distribution of shallow (<15 m) hard bottom areas occur more commonly inshore, and these may be a prerequisite for biomass samples to correlate with depth related habitat metrics. However, these explanations would result in the analysis with the complete set of samples (no minimum distance to land) to show the strongest correlations; and this was not the case. The total herbivore and species show a consistent pattern for the subset of habitat variables and distance from land, except *S. viride* that shows an increase in the correlation values and then a large increase to a maximum correlation coefficient at 6000m.

Although the correlation values within this study may be considered low, the significant relationships help provide valuable ecological results to the seascape level analyses.

Sparisoma viride showed the highest correlations across all comparison suggesting this species has ecological requirements related to depth and rugosity (Bruggemann et al. 1994). Transect rugosity was the variable that explained most of the habitat related variability in the biomass of the herbivorous reef fish assemblage. The variable representing the survey point distance to the preferred feeding areas (model polygons) represent the combination of shallow reef areas with high topographic relief suggesting that the interaction of these two factors plays a role in structuring some herbivorous fish species. The results from this study that indicate the importance of habitat topographic

heterogeneity (especially slope neutral rugosity) in explaining variability in herbivorous coral reef fish abundance coincides with those of previous studies (Friedlander and Brown 2007, Pittman et al. 2007b). The importance of reef “rugosity” has been established as a factor that must be included in any studies that aim to explain the spatial distribution of reef fishes. The present study attempts to provide other important habitat characteristics that are useful in predicting the distribution and abundance of Caribbean roving herbivorous fishes (Acanthuridae, Scaridae) across the seascape. We examined the role of the assumed preferential feeding habitat in contributing to the understanding of how herbivorous fishes interact with their habitat at seascape spatial scales.

The usefulness of scaling-up the relationship between coral reef fishes and habitat beyond the transect scale has been demonstrated and the information from this study may prove to be valuable to incorporate important ecological processes (i.e. fish grazing) into strategies that adopt the ecosystem-based approach to marine resource management. By highlighting the role of high productivity preferred feeding habitat of roving herbivores and describing the spatial and species level variability, we aim to contribute to efforts to manage and monitor the critical ecological process of fish grazing on coral reefs.

5 Conclusions

The three studies included in this dissertation provide information that advance our understanding of the distribution and abundance of herbivorous coral reef fishes.

Roving herbivorous fishes are an integral part of the biodiversity of coral reefs due to their abundance and their ecological role as grazers of benthic algae (Williams and Polunin 2001). The interaction between algae and fish grazing has been shown to be a determinant factor in maintaining coral dominance on reefs or being part of a shift to algal cover (Mumby et al. 2006). Based on these ecological processes the three studies presented provide information to understand the factors influencing the distribution and abundance of roving herbivorous fishes.

The first study revealed that depth and topographic relief, as well as the complex interaction between these two variables structured herbivorous fish distribution. These findings support the importance of these factors suggested by previous studies (Friedlander and Parrish 1998; Bellwood 2007; Fox and Bellwood 2007; Jeffrey et al. 2009; Pittman et al. 2010; Pittman and Brown 2011), but also provide quantitative data specific to the habitats and dominant herbivorous fish species in the La Parguera Reef system. This study also provides new information regarding the interaction between herbivorous fish distribution and the cross-shelf water quality gradient related to coral reef degradation. Previous studies in La Parguera have documented the effects of turbidity and light penetration to reef fish communities (Bejarano and Appeldoorn 2013), but this study is the first to look at its role in structuring the habitat use by herbivores.

In the second study the interaction between fish and algae utilizing Non-metric multidimensional scaling revealed under what conditions this interaction is most prevalent, as well as the fish and algal species driving the observed pattern. The results showed that sites with high biomass of herbivorous fishes were correlated to a high benthic cover of CCA. Previous studies have also shown the strong correlation between the abundance of herbivorous fishes and the dominance of CCA (Smith et al. 2001; Belliveau and Paul 2002; Littler et al. 2006; Albert et al. 2007; Wismer et al. 2009). However few studies have examined the role of algae at the species level. The taxonomic resolution in this study suggest that there are patterns in algal species composition that may be related to the inshore to offshore water quality gradient where turbidity and light penetration vary. Previous studies have found that algal productivity and preferred feeding sites are correlated (Clifton 1995; Russ 2003). These results have implications in the suitability of feeding habitat for roving herbivorous fishes where water quality gradients exist.

A large scale data set on herbivorous fish biomass available for the La Parguera reef system (Pittman et al. 2010) provided an opportunity to scale-up the spatial analysis to compare with the transect scale data for the third study. A set of habitat composition and configuration variables was extracted from GIS to determine their usefulness in explaining the variability in fish biomass. Previous seascape studies with reef fishes have found topographic relief, depth and distance to land as valuable metrics (Pittman et al. 2007; Wedding et al. 2008; Jeffrey et al. 2009; Pittman and Brown 2011). This study is the first study to model the preferred feeding areas of roving herbivorous fishes as a habitat class to determine its role in the distribution of fishes. The results

revealed that herbivore fish families and individual species exhibited varying responses in the correlation with seascape metrics. The role of sample location along the cross-shelf gradient was evaluated to determine if location on the shelf, and the resulting differences in environmental conditions, affected the strength of correlation with the habitat composition and configuration metrics. The results of maximum correlations at 1000's of meters contrasts with other studies that have found maximum correlations at 100's of meters (Pittman et al. 2009; Kendall et al. 2011; Pittman and Brown 2011). This discrepancy is likely due to the different seascape metrics selected since different questions were being investigated. However the magnitude of correlation values among this and other studies are similar with maximum ranges of 40% of the variability in fish abundance explained by the various seascape metrics.

In conjunction the results suggest that the distribution of roving herbivorous fishes is influenced by habitat characteristics related to preferred feeding sites that can be described by a combination of in-situ and seascape scale metrics. This information can be utilized for the design of research and monitoring of these important herbivorous fishes by improving the thematic resolution of habitat maps. The results related to the response of herbivorous fishes and algae along the cross-shelf water quality gradient have implications for the management and conservation of coral reef resources. Due to the probable degradation of inshore coral reefs from land-based sources of pollution, this study suggests that herbivore populations may be experiencing a combination of disturbance from reduced habitat quality as well as overfishing. Further work is needed to tease apart the interaction of the multiple factors influencing the process of fish

grazing on coral reefs in order to design appropriate management strategies and assess population trends.

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