Spatial Patterns in Benthic Composition of Nearshore Seascapes and Implications for Scarid Populations and Fisheries in La Parguera, SW Puerto Rico

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ABSTRACT

Coral reef ecosystems comprise of interconnected habitats including mangrove forests, seagrass beds, unconsolidated sediments, and coral reef and hardbottom substrates, all of which provide shelter and sustenance for fishes that form the basis of important fisheries in the Caribbean. Monitoring of such habitats in Southwestern Puerto Rico from 2001 to 2007 revealed complex spatial patterns in benthic composition that often correlated with the distribution and abundance of fishes. Depth and rugosity of substrates correlated positively with coral cover and taxa richness and influenced the abundance and size-class structure of parrotfishes. Measures of benthic composition were also useful in Maxent predictions of potential occurrence and size-class distribution of scarid assemblages. Benthic characterizations provide the basis for identifying species-habitat relationships, increase our understanding of spatial patterns in the distributions of habitats, and illustrate important and crucial linkages for the successful management of coral reef fisheries and other important marine resources.

KEY WORDS: Coral reefs, coral cover, benthic composition, habitat, parrotfish, seascape, Puerto Rico, Caribbean

Las Pautas Espaciales en la Composición de Denthic de Paisajes Marinos de Nearshore e Implicaciones para el Arrecife Pescan Poblaciones de Scarid y Pesquerías en La Parguera, el SW Puerto Rico

Los ecosistemas del arrecife de coral comprenden de hábitats interconectados inclusive manglares, camas de seagrass, sustratos no consolidados de sedimentos, y arrecifes de coral y hardbottom, todos los cuales proporcionan refugio y sustento para peces que forman la base de pesquerías importantes en el Caribe. La vigilancia de tales hábitats en Puerto Rico del sudoeste de 2001 a 2007 pautas espaciales, complejas y revelados en composición de benthic que a menudo tuvo correlación con la distribución y la abundancia de peces. La profundidad y rugosity de sustratos puso en correlación positivamente con cobertura de coral y riqueza de tasa e influyó la estructura de abundancia y tamaño-clase de parrotfishes. Las medidas de composición de benthic fueron también útiles en predicciones de Maxent de distribución potencial de ocurrencia y tamaño-clase de colecciones de scarid. Las caracterizaciones de benthic proporcionan la base para identificar las relaciones de especie-hábitat, aumentan nuestra comprensión de pautas espaciales en las distribuciones de hábitats, e ilustran uniones importantes y cruciales para la gestión exitosa de pesquerías de arrecife de coral y otros recursos marinos importantes.

PALABRAS CLAVES: Los arrecifes de coral, cobertura de coral, composición de benthic, el hábitat, parrotfish, el paisaje marino, Puerto Rico, Caribe

Tendances Spaciales dans la Composition Benthique des Paysages Marins Côtiers et D'Implications pour les Populations de Poissons de Récif et les Pêcheries

Les écosystèmes des récifs coralliens constituent un système d'habitats connectés, comprenant des mangroves, des algues, des sédiments non consolidés et les récifs coralliens et des substrats de fond dur, qui tous fournissent abri et nourriture aux poissons et aux invertébrés qui forment la base des pêcheries importantes dans les Caraïbes. Une surveillance de ces habitats dans le sud-ouest de Puerto Rico et à Buck Island, îles Vierges américaines de 2001 à 2008 par NOAA Biogeography Banch révèle des tendances spatiales et temporelles complexes dans la composition benthique qui, souvent, établissent une corrélation avec et influencent les tendances spatiales et temporelles dans la distribution des populations de poissons et d'invertébrés. Par exemple, la rugosité du substrat corrélée positivement avec la couverture corallienne et la richesse des taxons ainsi qu'une augmentation de la diversité des poissons et la richesse des espèces de poissons. En outre, le pour cent de couverture de coraux vivants a diminué au fil du temps, ce qui suggère que la qualité des habitats pourrait être en baisse également. Ces caractérisations benthiques fournissent la base pour identifier les relations espèce-habitat, augmentent notre compréhension des tendances spatiales dans la répartition des habitats, et illustrent les liens importants et cruciaux pour la bonne gestion des pêcheries des récifs coralliens et d'autres importantes ressources marines.

MOTS CLÉS: Tendances spaciales, corail, mangroves, algues, poissons de récif

INTRODUCTION

The broad shelf and coastal embayment at La Parguera, Southwest Puerto Rico (Figure 1) is a complex ecosystem of connected mangrove forests, seagrass beds, unconsolidated sediments, and coral reefs and hardbottom substrates. The mosaic of habitats provides shelter and sustenance to marine organisms that provide important goods and services such as fisheries and shoreline protection. Within the past few decades, however, multiple stressors acting at various spatial and temporal scales have changed the ecological structure and function of the La Parguera coral reef ecosystem, and have resulted in severe degradation and a reduction in ecological goods and services provided by the region (Garcia-Sais *et al.* 2005, 2008, Ballantine *et al.* 2008). For example, widespread mortality - caused by disease epidemics, mass bleaching events, and hurricanes - has significantly reduced the occurrence and abundance of acroporid corals in La Parguera (Davis *et al.* 1986, Weil *et al.* 2002, Garcia-Sais *et al.* 2008). Similarly, multiple interacting stressors (*e.g.*, excessive fishing, pollution, and habitat degradation) have decimated fish populations and the fisheries they support (Appeldoorn *et al.* 1992, Matos-Caraballo 2004, Ault *et al.* 2008).

Although major ecological perturbations (*e.g.*, loss of acroporid corals and the demise of several commercial fisheries) have been well documented in the Caribbean, their long-term effects on nearshore ecosystems are still relatively unknown in La Parguera. Understanding how such drastic ecosystem changes affect distribution patterns of marine organisms and their ecological interactions, however, is of foremost concern to resource managers. A major goal of successful coral reef ecosystem management is to ensure the long-term sustainable use and availability of coral reefs and the resources they provide for future generations. Achieving this goal requires first, a knowledge about spatial and temporal patterns of resource availability and second, an understanding of how anthropogenic and environmental factors affect those patterns. Also important is an understanding of the relevant spatial and temporal scales at which natural and anthropogenic processes determine the distribution and abundance of coral reef resources.

This study presents a dataset that quantifies spatial and temporal patterns in benthic composition within habitats that occur in the La Parguera region (Figure 1). The region is the site of a natural reserve; it is managed as a multiple use zone but has no restrictions on fishing. Benthic characterizations based on monitoring data provide the basis for identifying species-habitat relationships (*sensu* Luckhurst and Luckhurst 1978, Friedlander and Parrish 1998, Chitarro 2004), increasing understanding of spatial patterns in the distributions of habitats (Tolimieri 1998, Garcia-Charton and Perez-Ruzafa 1999, Monaco *et al.* 2001), and illustrating important and crucial linkages for the successful management of coral reef fisheries and other important resources (Mumby *et al.* 2008, Dalleau *et al.* 2010). More specifically, this study provides baseline estimates of benthic substrate composition for coral reef and hardbottom, softbottom, and mangrove habitats in La Parguera. First data are presented to characterize the types, distributions and percent cover of benthic flora and fauna within mapped substrates, and second, associations between metrics of benthic composition and parrotfish abundance and occurrence are explored.

METHODS

Study Area

The La Parguera study area is made of a complex mosaic of habitat types that occurred at varying depths (3–30 m). The 146 km^2 area was stratified into 78.7 km^2 of coral reef and hardbottom substrates (hereafter hardbottom), 66.9 km^2 of soft bottom habitats, and 0.6 km^2 of mangroves (Figure 1). Hardbottom habitats consisted of linear reefs, colonized pavement, reef rubble, patch reefs and scattered coral in sand, whereas softbottom substrates were made up of seagrasses, sand and mud. These benthic habitat categories were derived from NOAA's nearshore benthic habitat maps that defined the offshore extent of the study area, which corresponds approximately to the 33 m isobaths (Kendall *et al.* 2001). Hardbottom and softbottom strata occurred throughout the study area within five reef zones: intertidal, lagoon, backreef, forereef, and bank shelf (Figure 1). During the first three years of the study, benthic habitats were categorized for sampling allocation and design according to the habitat types defined and mapped by (Kendall *et al.* 2001). However, between 2004 and 2007, habitats were aggregated into the broader habitat strata – hardbottom, softbottom, and mangroves – for sampling allocation and statistical analysis.

Underwater visual surveys were conducted at La Parguera, Puerto Rico two to three times per year by a team of trained divers. Survey sites were selected using a stratified random sampling design that incorporated hardbottom and softbottom strata. Data on fish assemblage structure and benthic composition of habitats at La Parguera were recorded along 1,167 randomly selected 25 × 4 m (100 m^2) belt transects (Menza *et al.* 2006). These transect surveys were part of a larger project that sampled 3,744 sites (one survey per site) to characterize and monitor benthic habitats and faunal assemblages of coral reef ecosystems in southwestern Puerto Rico and the U.S. Virgin Islands (http://ccma.nos.noaa.gov/ecosystems/coralreef/reef_fish.html).

During each visual survey, the percent areal cover occupied by benthic biota within a 1 m^2 quadrat was estimated to the nearest 1 cm^2 or 0.1%. Visual estimates of cover were made in a two-dimensional plane that was perpendicular to the observer's line of vision. The quadrat was divided into 100 smaller (10 × 10 cm) squares to increase the precision of visual estimates of percent cover.

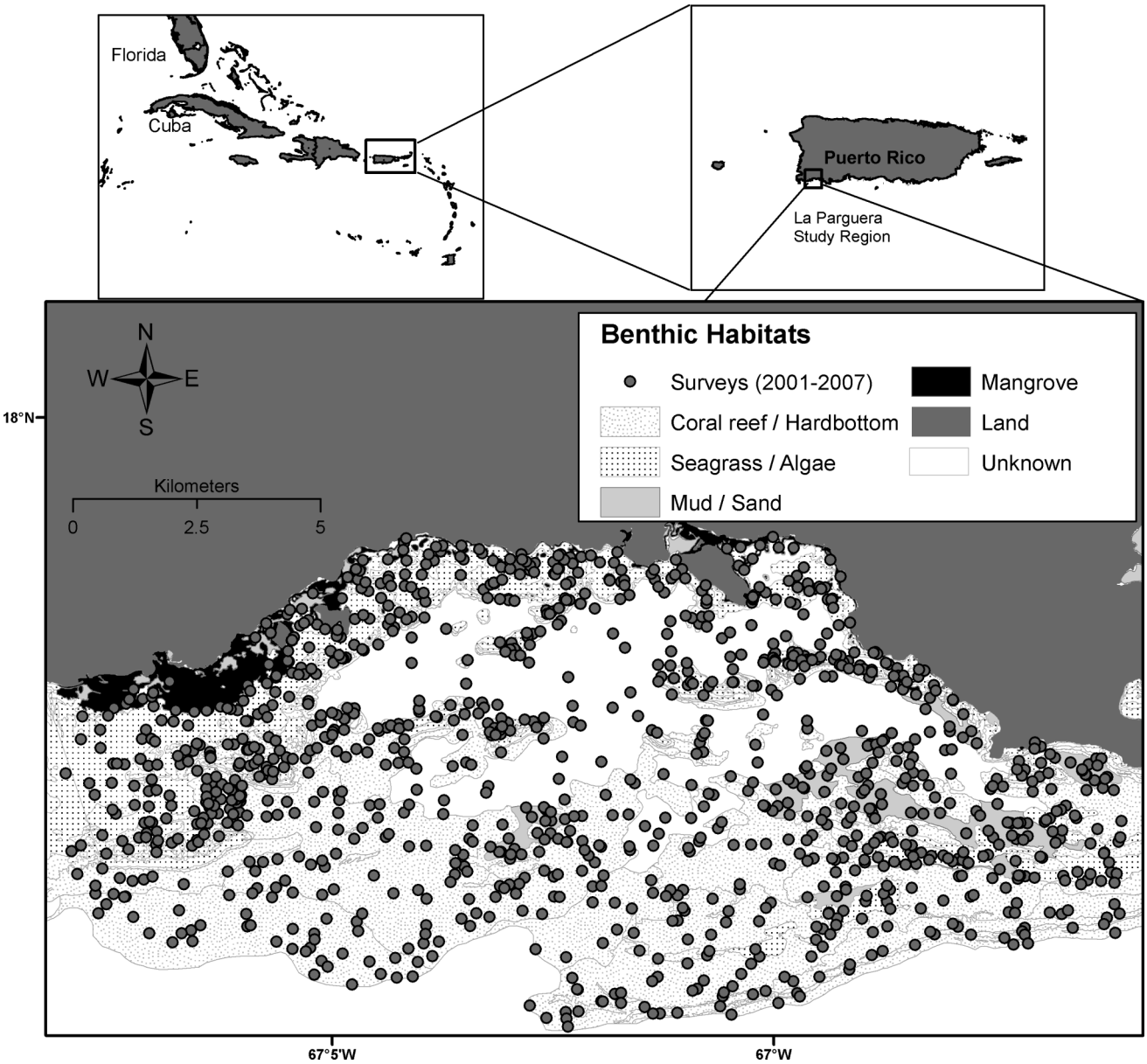

Figure 1. Map of La Parguera, Puerto Rico study region showing the number of visual benthic surveys conducted by Biogeography Branch between 2001 and 2007.

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. Data were collected for many benthic variables, but data analyses reported here focused primarily on describing broad-scale spatial patterns and temporal trends in the areal extent (% cover) of the sessile biotic components indicated in Table 1.

Data on fish presence, absence, and abundance by species and size categories were collected concurrently with data on benthic habitat composition. Each fish survey was conducted along a 100 m^2 belt transect for 15 minutes. The number of individuals per species was recorded in 5-cm size categories up to 35 cm using the visual estimation of fork length. Fish greater than 35 cm in length were rarely encountered; therefore their sizes were estimated to the nearest centimeter. Additional details about the protocols used to sample reef fish assemblages are provided in Menza *et al.* (2006).

Table 1. Abiotic and biotic variables measured to characterize benthic assemblages along fish transects in La Parguera, Puerto Rico. Text in bold indicate variables for which data were analyzed and presented in this study. *Conch with a defined shell lip were categorized as sexually mature; those without a lip were considered immature.

Benthic variable	Cover (%)	Height (cm)	Abundance (#)
Abiotic			
Hardbottom	X	X	
Sand	X		
Rubble	X		
Fine sediment	X		
Rugosity (measured as 1- the ratio of the distance covered by a 6-m long chain draped along the substrate to the total chain length)			
Water depth			
Biotic			
Corals (by species)	**X**		
Macroalgae	**X**	**X**	
Seagrass (by species)	**X**	**X**	
Gorgonians			
Sea rods, whips and plumes	**X**	**X**	**X**
Sea fans	**X**	**X**	**X**
Encrusting forms	**X**		
Sponges			
Barrel, tubes, rope, & vase morphology	**X**	**X**	**X**
Encrusting morphology	**X**		
Other benthic macrofauna			
Anemonies and hydroids	X	X	
Tunicates and zoanthids	X		
Macro-invertebrates			
Queen conch (by sexual maturity)*			X
Spiny lobster			X
Long-spined urchin			X
Mangroves			
Prop roots			X
Prop roots colonized by algae			X
Prop roots colonized by sponges			X
Prop colonized by other organisms			X

Statistical Analyses

Composition of benthic habitat types — In situ data on the cover of benthic biota was summarized from 1,093 of the 1,167 surveys conducted between 2001 and 2007 (Table 2). The additional 74 sites were located in areas mapped as unknown habitat and were excluded from benthic composition analyses because they had no habitat designation or biotic cover. Estimates of percent cover (mean ± standard error [SE]) of selected benthic biota were calculated to describe benthic composition for each site. Sites were used as independent sample units and were considered replicates within survey missions and habitat types. Multiple quadrat measurements (percent cover) for biota within each transect were averaged using the equation: $\Sigma(Q_i - n) / n$ where Q_i = quadrat i, and n is the total number of quadrats. Average site values were then used to calculate means and SE of measured variables per 100 m^2 for each habitat type. Standard errors of means represent variability among sites rather than variability among quadrats within a site. Differences in the cover of benthic biota among habitat types were determined by using a series of One-Way non-parametric Analysis of Variance (ANOVA, Wilcoxon) tests to identify significant differences among habitat types (Zar 1999). When significant differences were found, non-parametric multiple pair-wise comparisons were used to determine the pairs of habitat types that were significantly different (Zar 1999).

Spatial patterns in scleractinian coral cover — Interpolated maps characterizing spatial patterns in live coral cover, species richness, and reef rugosity within the broader seascape of the study region were created using the Geostatistical Analyst tool in ESRI's ArcGIS 9.3. Quadrat data (n = 5 per transect) from hardbottom habitats were averaged to create point layers from which continuous raster surfaces were derived by interpolated inverse distance weighting (IDW). IDW estimated raster cell values by using a linearly weighted combination of sample data points from a predetermined neighborhood of 10 minimum neighbors.

Parrotfish distribution relative to spatial patterns in benthic habitat composition — The influence of benthic composition on the density and occurrence of four parrotfishes (*Scarus iseri, Scarus taeniopterus, Sparisoma*

Table 2. The number of sites and area of mapped benthic habitats surveyed in La Parguera, Puerto Rico from 2001 to 2007. Mapped habitat categories are from Kendall *et al.* (2001).

Mapped habitat types	Mapped area (km^2)	% of mapped area	# sites sur-veyed	Area sur-veyed (km^2)	% of mapped area sampled
Hardbottom	**75,437**	**67.4**	**572**	**57.2**	**0.08**
Colonized bedrock	213	0.2	2	0.2	0.09
Colonized pavement	18,505	16.5	110	11.0	0.06
Colonized pavement with sand channels	32,058	28.6	212	21.2	0.07
Linear reef	11,306	10.1	100	10.0	0.09
Patch reefs (aggregated & individual)	2,738	2.4	53	5.3	0.19
Reef rubble	271	0.4	1	0.1	0.04
Scattered coral / rock in sand	10,345	9.2	94	9.4	0.09
Softbottom (including mangroves)	**36,474**	**32.6**	**521**	**52.1**	**0.23**
Unconsolidated sediments	6,621	5.9	91	9.1	0.14
Macroalgae / seagrass	29,853	26.7	272	27.2	0.09
Mangroves			158	15.8	
Total	***111,911***	***100.0***	***1093***	***93.7***	***0.08***

aurofrenatum, and *Sparisoma viride*) were determined through non parametric correlation analysis and species geographic distribution modeling. First, the strength of associations between parrotfish size-class abundances and seven habitat variables (in situ depth and rugosity; and percent cover of scleractinian corals, gorgonians, macroalgae, turf algae, and crustose coralline algae [CCA]) were estimated using non-parameteric Spearman's ρ (Rho), with higher ρ values indicating stronger associations between habitat and fish variables than lower ρ values. Specific methods used to process LIDAR bathymetry and derive rugosity are available online at http://ccma.nos.noaa.gov/products/biogeography/usvi_nps/data.html.

Second, the suitability of habitats for the two most abundant parrotfishes (*S. iseri* and *S. taeniopterus*) was determined by modeling the geographic distribution of the two species within the study area with maximum entropy modeling (Maxent) software (Phillips *et al.* 2006). Maximum entropy is a statistical approach used to estimate an unknown probability distribution by finding the most uniform distribution (*i.e.*, one with the most spread or uncertainty) from a set of distributions that best describes the data being modeled. For this analysis, the study area was divided into a series of pixels, with each pixel being classified by eight habitat (predictor) variables: mapped habitat type (15 habitat categories); depth and rugosity derived from 4-m resolution hydrographic LiDAR (Light Detection and Ranging, Costa *et al.* 2009) data; and *in situ* measurements of percent cover of live coral, turf algae, macro algae, gorgonians, and CCA. Maxent was used to estimate the probability of occurrence of 5 size classes (0-5, 5 - 10, 10 - 15, 15 - 20, 20 - 25 cm) for each of the two parrotfish species within sampled pixels and to predict the probability of size class occurrence (*i.e.*, habitat suitability) in unsampled pixels based on the geographic distribution of the eight predictor variables. Fish greater in size than 25-cm FL were rarely observed and were excluded from habitat suitability modeling. Maxent outputs reported here include (1) the percent contribution of each predictor variable to model variance to determine habitat variables that were most influential in determining fish size class distributions, and (2) a prediction response value for each pixel within the study area. Prediction response was a continuous variable that ranged from 0 (low suitability) to 100 (highest suitability). Maps of suitability values > 50 were created show differences in habitat preference between the two parrotfish species and to identify areas where they co-occurred.

RESULTS

Composition of Benthic Habitat Types

Surveyed sites were located within four broad thematic habitat types in the study area: colonized coral reef and hardbottom areas (hereafter hardbottom habitats; n = 572), seagrass and algal communities (hereafter sub-aquatic vegetation or SAV; n = 272), unconsolidated sediments (sand and mud habitats; n = 91) and mangroves (n = 158). The number of surveys conducted within hardbottom types varied systematically; relatively low number of sites were allocated to the least abundant habitat types (colonized bedrock and reef rubble) whereas higher numbers of sites were surveyed in more abundant habitats such as colonized pavement and patch reefs (Table 2). Hardbottom habitats comprised a larger proportion (67.4%) of the study region than soft bottom areas. Pavement habitat was the most spatially extensive hardbottom habitat type (45.1% of the study area) and was therefore the most intensively surveyed, followed by seagrass (22.1%) and linear reefs (10.1%; Table 2). The remainder of hardbottom substrates comprised of scattered coral and rock in sand, unconsolidated sediments, macro algae, patch reefs, reef rubble, and bedrock (Table 2). Overall, mean benthic cover on

hardbottom habitats was 60.5 ± 1.3%. Generally, hardbottom habitat types were dominated by algae (27.0 ± 1.0% turf algae, 14.0 ± 0.7% macroalgae, and 1.3 ± 0.3% CCA (Figure 2A). The next most abundant benthic group was the gorgonians (soft corals), which had an average percent cover of 7.4 ± 0.4%. Mean live scleractinian coral cover averaged 5.3 ± 0.3% across the study area. Cyanobacteria and filamentous algae were grouped as a single component and had a mean cover of 1.4 ± 0.2%. Other benthic organisms observed on hardbottom habitats included sponges (2.3 ± 0.1%), seagrasses (1.7 ± 0.3%) and hydroids such as fire coral (0.3 ± 0.1%).

Softbottom habitats (including mangrove areas) comprised approximately 32.6% of the study area, with SAV substrates making up 26.7% of the mapped study area (Table 2). The benthic organisms observed in SAV habitats had total cover of 48.4 ± 2%. Seagrasses had the highest mean cover (28.1 ± 1.8%) in habitats classified as SAV followed by macroalgae (12.4 ± 0.9%, Figure 2A). Four seagrass species were observed, of which *Thalassia testudinum* (turtle grass) had the most cover (21.2 ± 1.7%). Some turf algae (4.2 ± 0.8% cover) was observed in SAV habitat, most likely colonizing fragments of hard substrates that are commonly observed in seagrass beds. Cyanobacteria and unidentified filamentous algae (2.3 ± 0.6%) were also observed colonizing seagrasses, macroalgae, and patches of hardbottom substrates encountered in SAV habitats. Other organisms found inhabiting SAV habitats included sponges, gorgonians, corals, CCA, and hydroids such as fire corals. These organisms were rare with mean estimates of cover less than 0.4 ± 0.1%.

Unconsolidated sediments (sand and mud substrates) comprised 5.9% of the mapped study area (Table 2). Overall, the total benthic cover on unconsolidated sediments was low (18.5 ± 2.6%). Most of the cover observed on this habitat type was turf algae (6 ± 1.6%), followed by seagrass (5.7 ± 1.4%), and macroalgae (4.6 ± 0.7%, Figure 2A). Sceleractinian and hydroid corals, gorgonians, sponges, CCA, cyanobacteria and filamentous algae were also observed, but their mean cover was less than 0.7 ± 0.3%. These organisms were often encountered on small patches of hard substrate that often occurred within unconsolidated sediment habitats. Unlike seagrass habitats in which *T. testudinum* dominated, *Syringodium filiforme* (manatee grass) was the most dominant of the seagrass species in unconsolidated sediments habitats, with a mean cover of 3.1 ± 1.0%.

Benthic substrates within mangrove habitats were fairly well colonized by benthic organisms and had an overall mean benthic cover of 54.9 ± 2.7%. At many sites, mangrove prop roots provided a major benthic substrate for colonization by epiphytic organisms. Macroalgae had the highest benthic cover (14.5 ± 1.5%) and was the most dominant sub-aquatic benthic organism identified on mangrove prop roots and abiotic benthic substrates. Turf algae, seagrasses, cyanobacteria and filamentous algae were also very prevalent and had similar levels of mean cover that ranged from 9.5 ± 1.7% to 8.5 ± 1.4%. Other organisms found colonizing mangrove habitats included sponges, hard and soft corals, CCA and hydroids such as fire corals. One commonly encountered feature of benthic substrates in mangrove habitats was a thick layer of detritus, which had a mean cover of 7.8 ± 1.2%.

Benthic composition was variable among the hardbottom habitat types surveyed (Figure 2B). Turf algae had the most cover on all types of hardbottom habitat. The mean percent cover of live scleractinian coral was highest on linear reef (6.8 ± 0.7%, n = 100), followed by colonized pavement (6.1 ± 0.4%), patch reef (4.8 ± 0.7%), but was lowest on reef rubble (1.2 ± 0%, n = 1; Figure 2B). *Millipora* spp. (fire corals) were the most commonly recorded hydroid species on pavement, linear reef, and patch reef habitat types, with highest percent cover occurring on linear reef habitats (1.1 ± 0.6%). The percent cover of sponges and fire corals were similar among the habitat types surveyed (Figure 2B).

Live scleractinian coral cover included at least 24 coral genera, but only eight had mean cover greater than 0.01%. *Montastraea* spp. and *Porites* spp. had the highest percent cover and were the most frequently observed coral genera in pavement, linear reef, and patch reefs (Figure 3). Three genera (*Agaricia* spp., *Siderastrea* spp., and *Diploria* spp.) also had relatively high cover on hardbottom habitats throughout the study region. The percent cover of *Acropora* spp. was generally low but was highest on linear reef habitat (Figure 3). Several "other" genera observed on hardbottom habitats were rare and included *Cladocora, Dendrogyra, Dichocoenia, Eusmilia, Favia, Helioceris, Isophyllastrea, Isophyllia, Madracis, Manicina, Mycetophyllia, Oculina, Mussa, Scolymia, Solenastrea* and *Stephanocoenia*. For all hardbottom habitat combined, these other genera had a mean live cover of 0.6 ± 0.1%, which ranged from 0 % on bedrock habitat to 0.8 ± 0.2 % on linear reef habitat (Figure 3).

Spatial Patterns in Scleractinian Coral Cover

Interpolations of percent cover of live coral obtained from hardbottom sites revealed distinctive spatial patterns in coral cover (Figure 4A). Although live coral cover on hardbottom averaged 5.3 ± 0.3%, patches of elevated coral cover (hotspots) were scattered throughout the seascape (Figure 4A). Hotspots of live coral (25 - 52%) occurred in the western portion of the study area and also along the bank shelf toward the center of the study area. These areas of high coral cover – especially those along the bank shelf – also were hotspots of coral species richness (10 - 14 species per 100 m^2), diversity (1.4 - 2.5 per 100 m^2), and increased benthic rugosity (Figure 4A).

The observed hotspots of coral cover were dominated by five coral species that accounted for more than 60% of the total coral cover in the study area (Figure 4B). Interestingly, these five corals were also the most frequent-

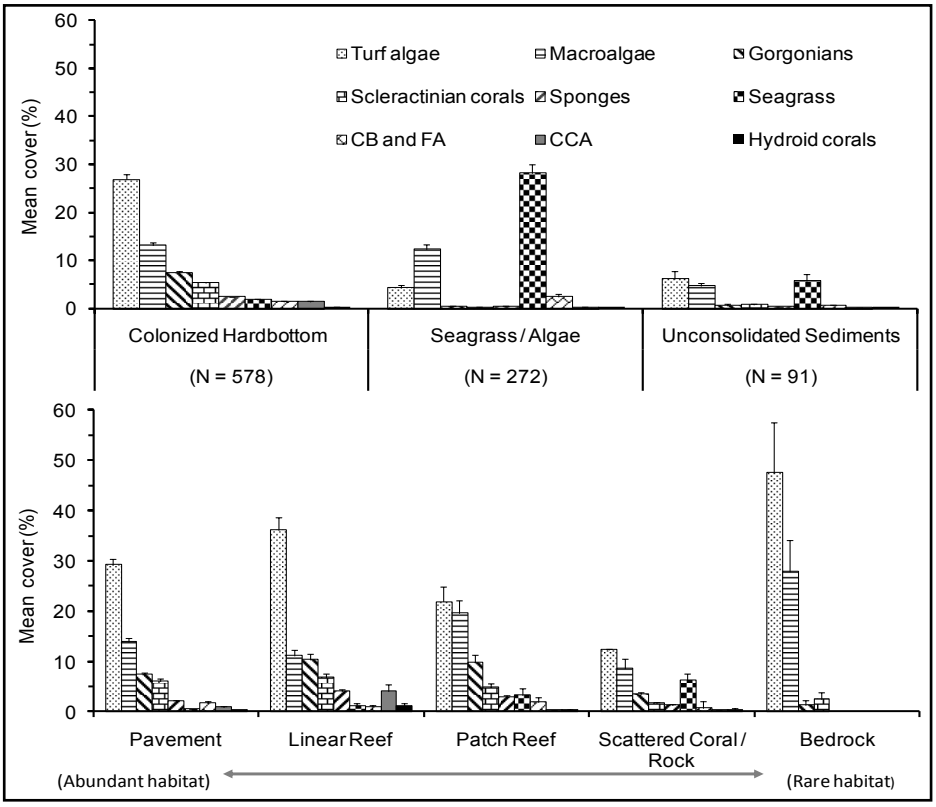

Figure 2. Mean (± SE) percent cover of key benthic components on in la Parguera, Southwest Puerto Rico between 2001 and 2007: (A) all benthic habitat types; (B) hardbottom habitat types only. CCA = crustose coralline algae; CB and FA = Cyanobacteria and filamentous algae.

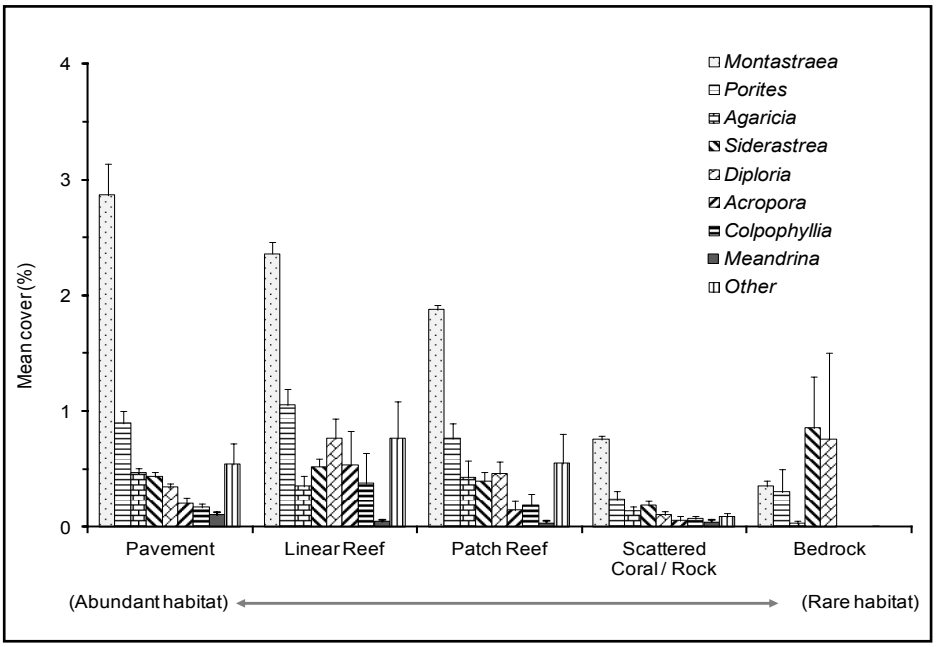

Figure 3. Mean (± SE) percent cover of coral taxa on hardbottom habitat types in la Parguera, Southwest Puerto Rico between 2001 and 2007. Other genera includes: *Cladocora, Dendrogyra, Dichocoenia, Eusmilia, Favia, Heloceris, Isophyllastrea, Isophyllia, Madracis, Manicina, Mycetophyllia, Oculina, Musa, Scolymia, Solenastrea and Stephanocoenia*.

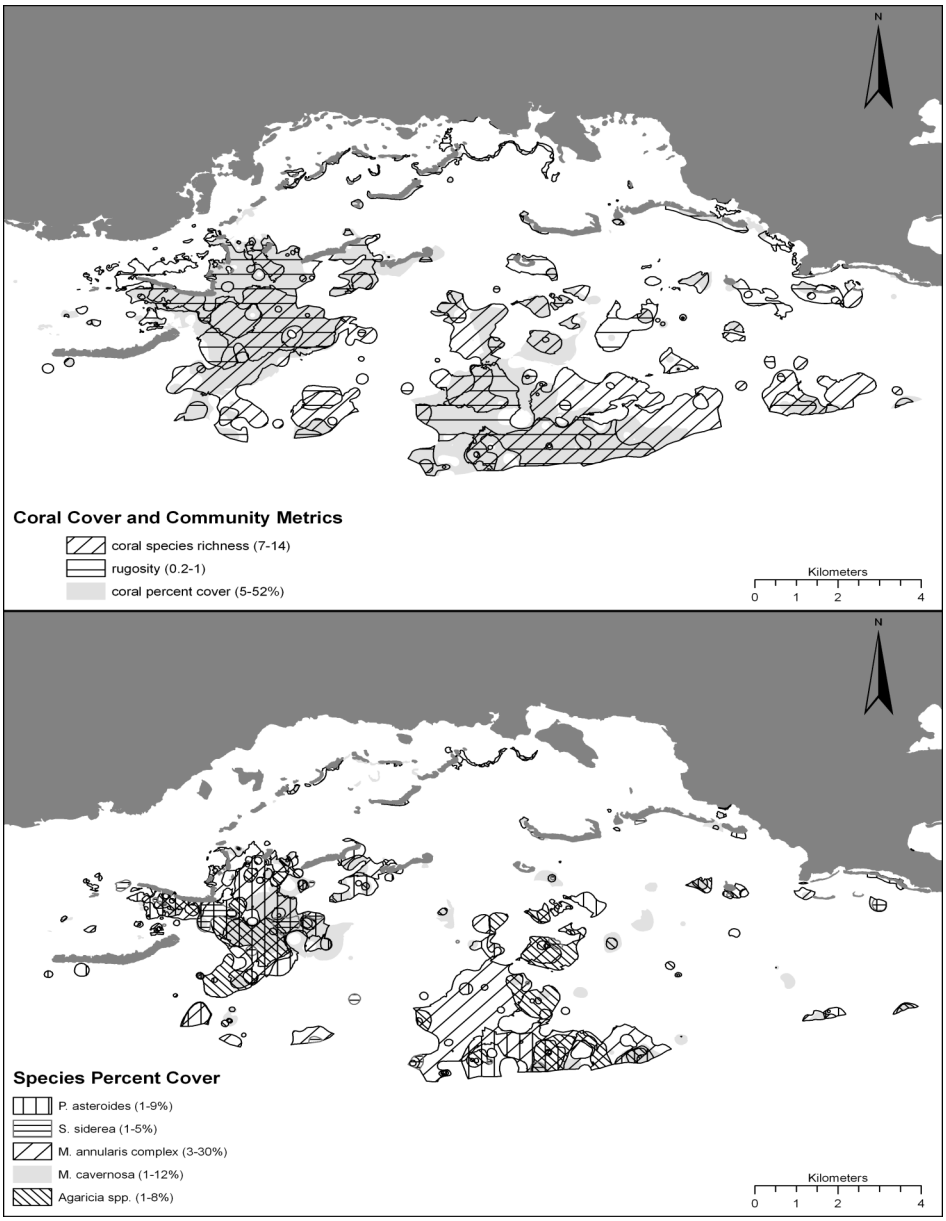

Figure 4. Maps showing spatial distributions of ecological hotspots in La Parguera, southwest Puerto Rico: (A) live coral cover, coral species richness, and rugosity; (B) live coral cover of the five most frequently occurring coral species. Hotspots were derived from interpolations of synoptic point-sample data obtained from visual surveys conducted between 2001 and 2007.

ly observed of all coral taxa in the study area (Table 3). *Porites astreoides* – the most frequently observed coral species - averaged 0.56 ± 0.04% in live cover (Table 3) that ranged from 1 - 9% at sites within the hot spots (Figure 4B). *Montastraea annularis* complex was less frequently observed than *P. astreoides* but had higher cover (mean = 1.89 ± 0.17%) that ranged from 3 - 30% at sites within the hot spots. *Montastraea cavernosa*, *Siderastrea siderea*, and *Agaricia* spp. occurred at 38-47% of sites surveyed, had mean cover ranging from 0.21 ± 0.02% to 0.43% ± 0.04%, and occurred at most of the hotspots for coral cover (Table 3, Figure 4B). In addition, threatened *Acropora* species were rarely observed and occurred at depths <10 m. *Acropora cervicornis* occurred at 11% of surveyed sites with mean cover of 0.18 ± 0.06% whereas *Acropora palmata* was seen at 1% of sites and had mean cover of 0.04 ± 0.02% (Table 3). Both species exhibited highest cover within the large hotspot in the western portion of the study area, with *A. cervicornis* ranging from 9.1 to 27% and *A. palmata* ranging from 4.1 to 10.4% in cover.

Table 3. Estimates of frequency of occurrence and percent cover for scleractinian and hydroid coral species observed on various hardbottom habitat types at La Parguera, Puerto Rico between 2001 and 2007. Taxa are listed in order of decreasing frequency of occurrence (Freq.). SE = standard error of mean. Habitat categories are from Kendall *et al*. (2001). A "+" indicates taxa that accounted for 60% of mean live coral cover (5.3 ± 0.3%) observed in the study area.

	All hardbottom habitats			Colonized pavement			Linear reef			Patch reef			Scattered coral / rock in sand			Colonized bedrock		
	(N = 572)			(N =322)			(N = 100)			(N = 53)			(N = 94)			(N = 3)		
Species	**Freq.**	**Mean cover**	**SE**	**Freq.**	**Mean cover**	**SE**	**Freq.**	**Mean cover**	**SE**	**Freq.**	**Mean cover**	**SE**	**Freq.**	**Mean cover**	**SE**	**Freq.**	**Mean cover**	**SE**
Scleractinian corals																		
Porites astreoides+	0.62	0.56	(0.04)	0.67	0.62	(0.05)	0.77	0.75	(0.08)	0.66	0.56	(0.11)	0.03	0.15	(0.05)	1.00	0.10	(0.00)
Montastraea annularis complex+	0.49	1.89	(0.17)	0.57	2.40	(0.26)	0.49	1.74	(0.38)	0.53	1.54	(0.38)	0.00	0.56	(0.26)	0.50	0.35	(0.35)
Montastraea cavernosa+	0.47	0.43	(0.04)	0.56	0.47	(0.05)	0.45	0.62	(0.15)	0.43	0.33	(0.10)	0.02	0.19	(0.06)			
Siderastrea siderea+	0.43	0.21	(0.02)	0.50	0.25	(0.03)	0.46	0.23	(0.04)	0.38	0.23	(0.07)	0.00	0.07	(0.02)			
Agaricia spp.+	0.38	0.31	(0.03)	0.44	0.37	(0.05)	0.41	0.30	(0.09)	0.32	0.37	(0.15)	0.00	0.11	(0.04)			
Porites porites	0.32	0.20	(0.04)	0.34	0.21	(0.07)	0.34	0.25	(0.08)	0.42	0.20	(0.05)	0.17	0.07	(0.03)	0.50	0.20	(0.20)
Siderastrea radians	0.31	0.16	(0.02)	0.34	0.17	(0.03)	0.40	0.26	(0.06)	0.26	0.14	(0.05)	0.00	0.07	(0.03)	0.50	0.65	(0.65)
Diploria strigosa	0.28	0.18	(0.03)	0.31	0.14	(0.02)	0.39	0.43	(0.15)	0.23	0.17	(0.07)	0.09	0.06	(0.03)			
Meandrina meandrites	0.22	0.08	(0.01)	0.29	0.10	(0.02)	0.18	0.04	(0.01)	0.09	0.03	(0.02)	0.07	0.04	(0.02)			
Dichocoenia stokesii	0.17	0.03	(0.01)	0.21	0.04	(0.01)	0.17	0.04	(0.01)	0.09	0.01	(0.00)	0.03	0.01	(0.00)	0.50	0.05	(0.05)
Stephanocoenia intercepta	0.16	0.03	(0.01)	0.18	0.04	(0.01)	0.20	0.04	(0.01)	0.09	0.02	(0.02)	0.02	0.02	(0.01)	0.50	0.10	(0.10)
Colpophyllia natans	0.16	0.18	(0.05)	0.17	0.16	(0.04)	0.17	0.38	(0.26)	0.15	0.18	(0.11)	0.09	0.06	(0.03)			
Diploria clivosa	0.15	0.12	(0.02)	0.16	0.10	(0.02)	0.18	0.22	(0.07)	0.21	0.19	(0.07)	0.01	0.01	(0.01)	0.50	0.75	(0.75)
Agaricia agaricites	0.13	0.06	(0.01)	0.16	0.07	(0.02)	0.12	0.05	(0.02)	0.15	0.06	(0.03)	0.00	0.03	(0.02)	0.50	0.03	(0.03)
Diploria labyrnithiformis	0.12	0.06	(0.01)	0.13	0.07	(0.02)	0.17	0.06	(0.02)	0.13	0.09	(0.04)	0.02	0.02	(0.01)			
Acropora cervicornis	0.11	0.18	(0.06)	0.14	0.16	(0.04)	0.09	0.42	(0.29)	0.08	0.14	(0.08)	0.00	0.05	(0.04)			
Siderastrea spp.	0.05	0.03	(0.01)	0.05	0.02	(0.01)	0.05	0.03	(0.01)	0.06	0.02	(0.01)	0.00	0.05	(0.03)	0.50	0.20	(0.20)
Favia fragum	0.05	0.01	(0.00)	0.03	0.01	(0.00)	0.08	0.02	(0.01)	0.15	0.04	(0.02)						
Scolymia spp.	0.04	0.01	(0.00)	0.05	0.01	(0.00)	0.02	0.00	(0.00)	0.04	0.00	(0.00)	0.03	0.01	(0.00)			
Madracis spp.	0.04	0.01	(0.00)	0.05	0.01	(0.00)	0.05	0.01	(0.00)				0.02	0.00	(0.00)			
Manicina areolata	0.04	0.01	(0.00)	0.04	0.01	(0.00)	0.06	0.01	(0.01)	0.02	0.00	(0.00)	0.13	0.01	(0.00)			
Mycetophyllia spp.	0.03	0.01	(0.00)	0.04	0.01	(0.00)	0.02	0.01	(0.01)	0.04	0.01	(0.00)						
Madracis decactis	0.03	0.01	(0.00)	0.03	0.01	(0.00)	0.04	0.00	(0.00)				0.02	0.00	(0.00)			
Diploria spp.	0.03	0.03	(0.01)	0.02	0.03	(0.01)	0.05	0.04	(0.02)				0.09	0.00	(0.00)			
Mycetophyllia ferox	0.03	0.01	(0.00)	0.04	0.02	(0.01)	0.02	0.01	(0.00)	0.02	0.03	(0.03)						
Helioceris cucullata	0.02	0.03	(0.01)	0.03	0.05	(0.02)							0.20	0.03	(0.02)			
Eusmilia fastigiata	0.02	0.00	(0.00)	0.02	0.00	(0.00)	0.02	0.00	(0.00)				0.00	0.00	(0.00)			
Dendrogyra cylindricus	0.02	0.02	(0.01)	0.02	0.03	(0.02)	0.01	0.01	(0.01)				0.00	0.01	(0.01)			
Solenastraea spp.	0.02	0.00	(0.00)	0.02	0.00	(0.00)	0.01	0.00	(0.00)	0.02	0.01	(0.01)	0.00	0.00	(0.00)			

Table 3 (cont.)

Species	All hardbottom habitats (N = 572)			Colonized pavement (N =322)			Linear reef (N = 100)			Patch reef (N = 53)			Scattered coral / rock in sand (N = 94)			Colonized bedrock (N = 3)		
	Freq.	Mean cover	SE	Freq.	Mean cover	SE	Freq.	Mean cover	SE	Freq.	Mean cover	SE	Freq.	Mean cover	SE	Freq.	Mean cover	SE
Agaricia lamarcki	0.01	0.01	(0.00)	0.02	0.02	(0.01)	0.01	0.00	(0.00)									
Acropora palmata	0.01	0.04	(0.02)	0.01	0.04	(0.03)	0.04	0.11	(0.07)									
Porites branneri	0.01	0.01	(0.01)	0.01	0.00	(0.00)	0.02	0.04	(0.04)				0.00	0.00	(0.00)			
Mycetophyllia lamarckiana	0.01	0.00	(0.00)	0.01	0.00	(0.00)							0.00	0.01	(0.01)			
Porites spp.	0.01	0.03	(0.03)	0.01	0.05	(0.05)	0.02	0.01	(0.00)									
Porites colonensis	0.01	0.01	(0.00)	0.00	0.01	(0.01)	0.02	0.01	(0.01)				0.24	0.01	(0.01)			
Madracis mirabilis	0.01	0.00	(0.00)	0.01	0.00	(0.00)	0.01	0.00	(0.00)	0.02	0.01	(0.01)						
Isophyllia sinuosus	0.01	0.00	(0.00)	0.01	0.00	(0.00)	0.02	0.00	(0.00)									
Oculina diffusa	0.01	0.01	(0.01)	0.01	0.01	(0.01)							0.14	0.01	(0.01)			
Mussa angulosa	0.01	0.00	(0.00)	0.01	0.00	(0.00)	0.01	0.00	(0.00)									
Isophyllastrea rigida	0.00	0.00	(0.00)	0.00	0.00	(0.00)	0.01	0.01	(0.01)									
Mycetophyllia reesi	0.00	0.00	(0.00)	0.01	0.00	(0.00)												
Agaricia fragilis	0.00	0.00	(0.00)	0.01	0.00	(0.00)												
Mycetophyllia daanana	0.00	0.00	(0.00)	0.00	0.00	(0.00)												
Scolymia cubensis	0.00	0.00	(0.00)							0.02	0.01	(0.01)						
Mycetophyllia aliciae	0.00	0.00	(0.00)	0.00	0.00	(0.00)												
Cladocora arbuscula	0.00	0.00	(0.00)				0.01	0.00	(0.00)									
Hydroid corals																		
Millepora alcicornis	0.25	0.07	(0.01)	0.26	0.05	(0.01)	0.30	0.12	(0.03)	0.30	0.21	(0.12)	0.01	0.02	(0.01)			
Millepora complanata	0.04	0.01	(0.00)	0.03	0.01	(0.00)	0.10	0.03	(0.01)	0.04	0.00	(0.00)	0.00	0.00	(0.00)			
Millepora spp.	0.20	0.22	(0.11)	0.19	0.07	(0.02)	0.35	0.92	(0.60)	0.21	0.16	(0.11)	0.03	0.02	(0.01)			

Parrotfish Distribution Relative to Spatial Patterns in Benthic Habitat Composition

Abundance of four parrotfish species correlated significantly ($p < 0.05$) with five of seven habitat variables (Table 4). *S. iseri* was the most abundant parrotfish species in the study area, and only two size classes showed any significant correlations with depth of sites. The smallest *S. iseri* individuals (0 - 5 cm) were more abundant at shallower sites whereas 10 - 15 cm sized individuals were more abundant at deeper sites. The abundances of *S. iseri* size-classes larger than 10 - 15 cm were not significantly correlated with depth. *S. iseri* abundance within all size classes correlated positively with rugosity, with 5 - 10 cm fish being influenced the most and 20 - 25 cm individuals being influenced the least by that variable. Percent cover of scleractinian corals, gorgonians, and CCA were less influential on *S. iseri* abundance, as indicated by lower ρ values. Percent cover of scleractinian corals was weakly correlated with abundance of individuals in the 5-10 and 15 - 20 size classes. *S. iseri* abundance showed no significant correlations with percent cover of macroalgae or turf algae.

Abundance of *S. taeniopterus* correlated significantly with all seven habitat variables, with some variables being more influential than others (Table 4). Abundance of *S. taeniopterus* within all size classes correlated significantly with depth and rugosity of sites, with 5—10 and 10 - 15 cm sized fish showing the strongest associations with these two habitat variables. All *S. taeniopterus* size categories were significantly more abundant at deeper sites than at shallower sites, and abundances for all size classes were more weakly correlated with rugosity than with depth as evidenced by lower ρ values for rugosity. Percent cover of scleractinian corals and turf algae had weak but opposing effects compared to macroalgae on the abundance of individuals from two size categories (5—10 and 10—15 cm). The cover of gorgonians was weakly influential ($\rho = -0.14$) on the abundance of only one *S. taeniopterus* size class (5 - 10 cm). Crustose coralline algae affected the abundance of the smallest and two largest size classes of *S. taeniopterus* ($\rho < 0.18$, Table 4).

Five of seven habitat variables were correlated significantly with the abundance of *S. aurofrenatum*, with percent cover of gorgonians having the greatest effect on 5-10 cm and 10-15 cm size classes ($0.22 < \rho < 0.31$, Table 4). In contrast to other parrotfishes, the three smallest *S. aurofrenatum* size classes showed a weak positive correlation with depth ($\rho < 0.16$), and only a relatively weak correlation was observed between rugosity and the abundance of 5-10 cm sized individuals (Table 4). Larger *S. aurofrenatum* were more abundant at sites with low cover of algae whereas smaller individuals were more abundant at sites with higher macroalgae cover, but those relationships were fairly weak and resulted in low ρ values (Table 4). Similarly, sites with higher cover of turf algae were weakly correlated with higher abundances of 5 - 10 cm and 20 - 25 cm sized fish.

S. viride — The least abundant of four parrotfish species – also correlated significantly with five habitat variables, such that depth and rugosity of sites had the strongest influence on its abundance (Table 4). Depth correlated negatively with four of five size classes, and rugosity correlated positively with all five size classes of this parrotfish. In addition, *S. viride* was the only parrotfish for which abundances of all size classes were positively and significantly correlated with percent cover of live coral. *S. viride* individuals sized 5 - 10, 10 - 15, and 15 - 20 cm were also significantly more abundant at sites with higher percent cover of gorgonians, but those correlations were weak ($0.1 < \rho < 0.17$). The abundance of the smallest *S. viride* individuals correlated negatively and significantly with percent cover of CCA ($\rho = -0.16$); fewer 0-5 cm sized fish were observed at sites where CCA cover was high than at sites where CCA cover was relatively low (Table 4).

Maxent models of species occurrence also revealed strong associations between parrotfish occurrence and benthic habitat variables. Among all size classes, mapped habitat type and percent cover of live coral were the best predictors of *S. iseri* occurrence and therefore were most influential on spatial distribution of all *S. iseri* size-classes throughout the study area (Figure 5). Of the 15 mapped habitat types, patch reef was the best predictor of all *S. iseri* size classes. The percent cover of turf algae was a better predictor of *S. iseri* occurrence for fish > 5 cm than for fish 0 - 5 cm in size. The importance of depth and rugosity as predictors were more variable among *S.iseri* size-classes; they were more important for individuals < 5 cm and less important for individuals > 5 - 10 cm in size. Percent cover of macroalgae, gorgonians, and CCA generally were least influential on distribution of *S. iseri* size classes throughout the study area.

The predictor variable most influential in determining the spatial distribution of all *S. taeniopterus* size classes was the percent cover of live coral (Figure 5). Coral cover was the strongest predictor of occurrence for *S. taeniopterus*, with almost 50% contribution to model prediction for individuals sized 5 - 10 and 10 - 15 cm. The contribution of mapped habitat type to model prediction of *S. taeniopterus* occurrence was best for individuals 10 - 15 cm and 20 - 25 cm but seemed negligible for other size classes. Of the 15 mapped habitat types, patch reef habitat was the best predictor of *S. taeniopterus* occurrence for 0-5 cm and 20 - 25 cm size classes. Depth, rugosity, and CCA were relatively poor Maxent predictors and contributed ≤ 10% to estimating potential occurrence of any *S. taeniopterus* size class. Percent cover of turf algae was a better Maxent predictor for the potential occurrence of 0 - 5 cm, 15 - 20 cm, and 20 - 15 cm size classes (turf algae contribution ≥ 23%) than for the two other *S. taeniopterus* size classes (turf algae contribution < 10%).

Maps of the 50 - 100% probability of occurrence values which were estimated from Maxent models show the spatial patterns in the habitat use of four size classes (0-

5 cm, 5 - 10 cm, 10 - 15 cm, and 15 - 20 cm) of *S. iseri* and *S. taeniopterus* (Figure 6). A distinct locale toward the western edge of the study area that is comprised of colonized pavement and linear reef habitats was an area of consistent co-occurrence or overlap for all size classes of both species. However, in general, *S. iseri* had 50% or higher probability of occurrence on hardbottom areas closer toward shore than in deeper areas further offshore (Figure 6). In contrast, *S. taeniopterus* had 50% or higher probability of occurrence on deeper hardbottom areas further offshore than on shallower areas closer to shore (Figure 6).

DISCUSSION

Composition of Benthic Habitats Types

Marine benthic maps of near-shore environments have become an important tool for conservation and management of biological resources, but often their resolutions are unsuitable for capturing the full spectrum of spatial variation in the distribution and composition of benthic resources. For example, maps of softbottom habitats may include unidentified benthic features such as sand halos and patch reefs that are smaller than the minimum mapping unit used to create the maps. Such unidentified features are known to influence the spatial distribution and occurrence of marine fauna at multiple scales (Parrish 1989, Kendall *et al.* 2003, Chittaro 2004, Pittman *et al.* 2007a, b). By quantitatively characterizing sub-meter spatial variation in benthic composition and physical attributes of mapped polygons, this study provided important information for use in elucidating species-habitat relationships and understanding spatial patterns in the distribution of marine fauna.

Although the composition of benthic substrates varied spatially within and among habitat types, some general spatial patterns in occurrence and cover of benthic organisms were observed. For example, turf algae – defined as a multispecific assemblage of small filamentous algae – was the most extensively occurring benthic organism group within all hardbottom habitat types, followed by macroalgae and a low occurrence of CCA. A

Table 4. Estimates of correlation, reported as Spearman's Rho (ρ), among benthic variables and fish species size class of four parrotfish species. Correlation estimates are reported only for significant correlations ($p < 0.05$). Numbers in parentheses are the abundance (# of individuals) of fish species within each size class. Totals are the sum of fish species abundance observed across all size classes.

			Scarus iseri			
	0-5 cm	**5-10 cm**	**10-15 cm**	**15-20 cm**	**20-25 cm**	**Total**
Benthic variables	(1498)	(1696)	(1143)	(453)	(100)	(4890)
Depth	-0.33		0.16			
Rugosity	0.29	0.45	0.29	0.17	0.06	
Scleractinian corals		0.19		0.18		
Gorgonians				0.09		
Crustose coralline algae	-0.13		0.09			
			Scarus taeniopterus			
	(233)	(460)	(783)	(307)	(175)	(1958)
Depth	0.27	0.41	0.41	0.32	0.21	
Rugosity	0.1	0.15	0.12	0.04	-0.09	
Scleractinian corals		-0.1	-0.12			
Gorgonians		-0.14				
Macroalgae	0.13	0.17	0.12			
Turf algae		-0.15	-0.11			
Crustose coralline algae	0.12			0.1	0.18	
			Sparisoma aurofrenatum			
	(1021)	(686)	(876)	(537)	(168)	(3288)
Depth	0.14	0.09	0.16			
Rugosity		0.15				
Gorgonians		0.22	0.31	0.16		
Macroalgae	0.09				-0.11	
Turf algae		0.1			0.17	
			Sparisoma viride			
	(344)	(217)	(207)	(204)	(162)	(1134)
Depth	-0.35	-0.24	-0.22	-0.11		
Rugosity	0.31	0.38	0.35	0.31	0.14	
Scleractinian corals	0.18	0.23	0.18	0.13	0.1	
Gorgonians		0.1	0.17	0.1		
Crustose coralline algae	-0.16					

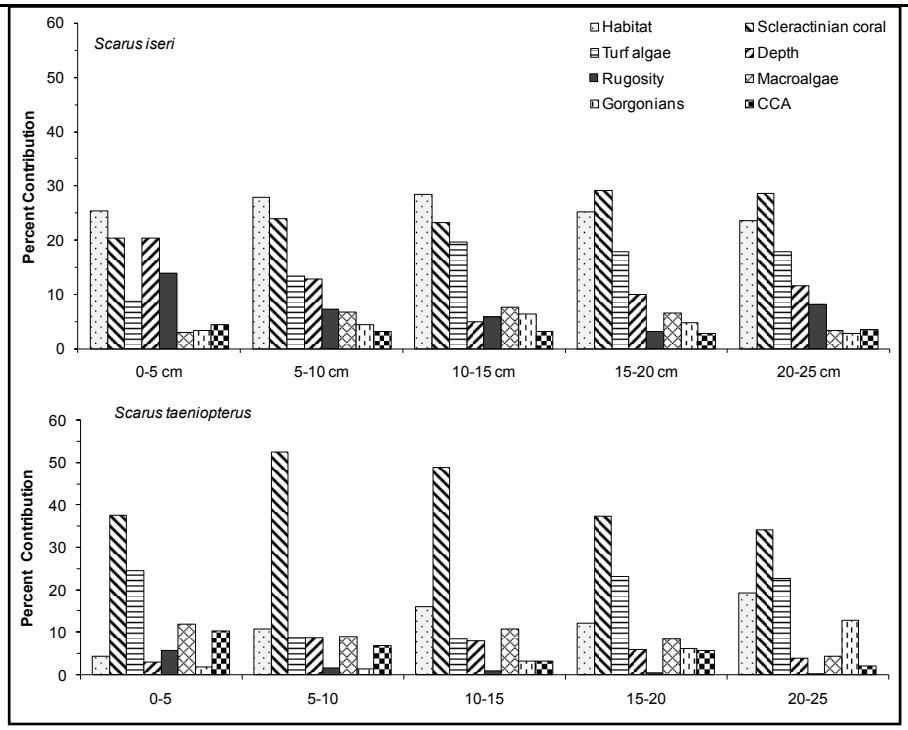

Figure 5. Percent contribution of benthic habitat variables to Maxent models describing spatial patterns in the occurrence and geographic distribution of two parrotfishes (*Scarus iseri* and *S.*

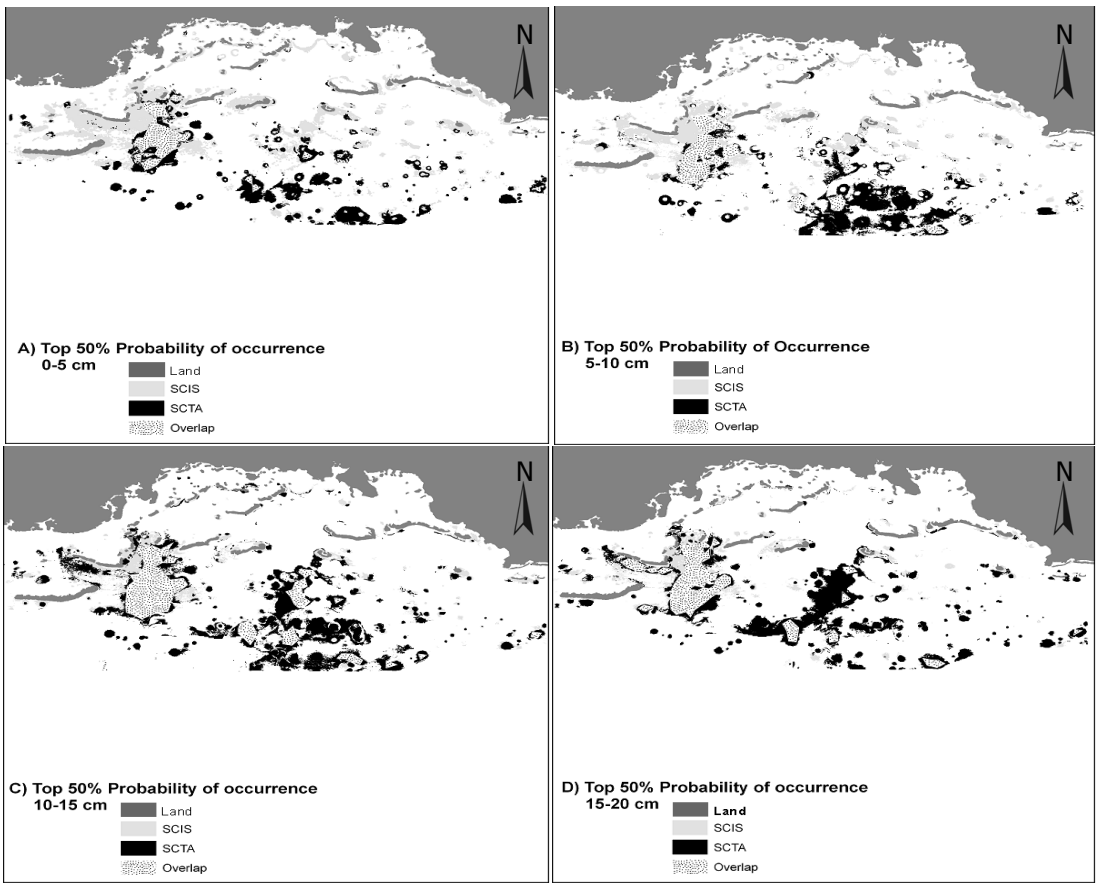

Figure 6. Maps showing the probability of occurrence of four size classes of two parrotfishes (*Scarus iseri* and *S. taeniopterus*) in La Parguera, southwest Puerto Rico between 2001 and 2007.

widely accepted hypothesis is that the abundance of algae on coral reefs typically is controlled by herbivory (Steneck and Dethier 1994). Under high rates of herbivory, coral reefs and hardbottom substrates generally are characterized by low-biomass algal assemblages dominated by turf, with low cover of CCA and macroalgae (Steneck and Dethier 1994). In contrast, under low rates of herbivory, macroalgae forms the dominant algal cover type, followed by turf algae, and few CCA (Steneck and Dethier 1994).

The extensive coverage of turf algae observed during this study suggests that rates of herbivory on reefs and hardbottom areas in la Parguera may be high. This may seem counter-intuitive, given the widely accepted belief that a Caribbean-wide decline in the abundance of the long-spined sea urchin (*Diadema antillarum*) along with serial over-fishing has reduced herbivory and has resulted in a phase-shift from coral-dominated to macroalgal-dominated reefs in the Caribbean (Lessios *et al.* 1984, Hughes 1994, Gardner *et al.* 2003). During this study, the abundance of long-spined sea urchins was relatively low, but small-bodied herbivorous fishes were numerically abundant and dominated fish assemblages across the shelf (Pittman *et al.* 2010). Idjadi *et al*. (2006) implicated structural refugia from long-lived colonies of *M. annularis* complex in a phase-shift reversal from macroalgal-dominated back to coral-dominated reefs in Jamaica. Bechtel *et al*. (2006) also implicated a resurgence of *D. antillarum* and an abundance of other echinoids in an observed decline in macroalgal cover and a corresponding increase in scleractinian coral cover on a reef in Jamaica. Based on our data from La Parguera, it is possible that rates of herbivory from relatively abundant fishes and other observed echinoids may have provided enough herbivory to keep the cover of macroalgae relatively low while turf algae flourished.

The high cover of turf algae on reef and hardbottom areas in La Parguera also may be due to relatively quick growth rates that provide a competitive advantage to this algal group over slower-growing coral and CCA. CCA play a crucial role in coral reef ecology by contributing calcium carbonate to reef structure and by facilitating the settlement and colonization of scleractinian corals (Steneck and Dethier 1994). Turf algae trap and stabilize unconsolidated sediments, but also rapidly overgrow and kill underlying coralline algae and coral colonies through encroachment (Steneck and Dethier 1994). In La Parguera, the coverage of CCA was very low, indicating that overgrowth of CCA and corals may have occurred, and that very little suitable substrates exist for newly settling coral colonies.

Another general pattern in benthic composition observed during this study was the low average cover of live scleractinian coral (about 5%) on reef and hardbottom areas and the virtual absence of *Acropora* spp. thickets on forereefs (0.5 - 6 m depth) in La Parguera. It is possible that the frequency of occurrence and percent cover of acroporid corals may have been underestimated by this study because reef crest habitats, where *A. palmata* is most likely to occur, were under sampled because of logistical reasons. However, low coral cover is now typical of most reefs in the Caribbean, and declines in coral cover have resulted from the synergy of natural and anthropogenic factors operating over the past three decades (Gardener *et al.* 2003). Acroporid populations were formally very abundant on reefs near La Parguera (Weil *et al.* 2002). Since the late 1970s however, successive disease outbreaks, periodic hurricanes, bleaching events, predators, and increased anthropogenic activities have contributed to the demise of acroporid and other coral populations in La Parguera (Weil *et al.* 2002). Following the major outbreak of white band disease, several tropical cyclones decimated shallow-water acroporid populations in La Parguera between 1979 and 1998 and thereby removed a major source of structural complexity from those coral reefs (reviewed in Weil *et al.* 2002, Garcia-Sais *et al.* 2005, 2008). No major hurricane has hit Puerto Rico since 1998, but per this study, reefs at depths less than 18 m in La Parguera remain depauperate of acroporid corals and their associated 3-D structural complexity. Most recently, the major Caribbean-wide bleaching event in 2005 resulted in additional coral mortality, such that coral cover declined by 40-60% (Garcia-Sais *et al.* 2008).

An interesting feature of reef and hardbottom areas in La Parguera, was the preponderance of gorgonians (sea rods, sea whips sea plumes, and sea fans) at sites throughout the shelf. Gorgonians were commonly observed intermingled with other sessile benthic organisms, but often their coverage was much more extensive than other benthic biota on colonized pavement and patch reef habitats. At some colonized pavement sites for example, the canopy created by the high density and cover of gorgonians virtually obscured the sea floor such that other sessile benthic organisms were not visible. Percent cover of soft corals also correlated positively with rugosity, probably through niche partitioning, in which more rugose areas provided a wider variety of benthic substrate for settlement and colonization by soft corals than did less rugose areas (MacArthur and Levins 1964). Although they contribute minimally to calcium carbonate accretion and reef growth, soft corals represent important ecosystem components on the La Parguera shelf in that they provide important habitat for fishes and feeding sea turtles (Gratwicke *et al.* 2006, Blumenthal *et al.* 2009). Additionally, soft corals can affect the spatial distributions of other sessile benthic organisms because they are superior competitors for space, and they are able to secrete allelochemicals that deter growth of other benthic organisms (Fenical 1987, Harvell 1989).

Distinct zonation patterns were observed in the distribution of flora in softbottom habitats. Such zonation patterns result generally from decreasing nearshore-to-offshore gradients of nutrients and light penetration. Softbottom areas in La Parguera exhibited a zonation

pattern typical of Caribbean shallow-water ecosystems; seagrass percent cover was highest near the shore but decreased toward deeper offshore areas. Similarly, the spatial distributions of the two most commonly occurring seagrass species also were zoned. *T. testudinum* dominated near shore areas up to a depth of 16 m, whereas *S. filiforme* dominated deeper areas offshore. Sponges and native coral species (*e.g., Dichocoenia stokesii*) also were observed frequently in seagrass and macro algae habitats. Calcareous macroalgae (*e.g., Halimeda* spp., *Udotea* spp., and *Penicillus* spp.) were commonly encountered on soft bottom habitats, but their percent cover was low relative to those of seagrass and more foliose algae such as *Lobophora*, *Dictyota*, and *Padina* spp. Nevertheless, calcareous algae are ecologically important to coral reef communities because their skeletal remains (*e.g.*, *Halimeda* spp.) are a major component of carbonate sediments occurring within coral reef ecosystems (Hubbard *et al.* 1981, Drew 1983).

Interestingly, benthic organisms typical of coral reefs and hardbottom substrates (*e.g.,* turf algae, CCA, scleractinian corals and gorgonians) occasionally were encountered within areas mapped as softbottom. The atypical occurrence of these reef-associated organisms within softbottom polygons most likely was an artifact of differences between the scale at which map polygons were delineated and the scale at which benthic data were collected. A minimum mapping unit (MMU) of 0.4 ha did not allow delineation of reef and hardbottom patches less than 0.4 ha that were encountered within areas mapped as softbottom. Thus, our fine-scale 1 m^2 quadrat benthic surveys on these hardbottom patches that occurred within softbottom areas provide additional data that may be crucial for understanding observed relationships between faunal species and their mapped habitats.

Several studies have shown that softbottom habitats are ecologically important components of coral reef ecosystems. For example, reef fishes are known to migrate from reef and hard bottom areas, forage on adjacent non coral reef habitats (sand, seagrasses, algal plains), and they represent a trophic pathway of energy transfer among habitats (McFarland *et al.* 1979, Meyer *et al.* 1983, Clark *et al*. In press). Furthermore, several landscape analyses have correlated various seagrass metrics with increased probability of juvenile grunt occurrence on reef and hardbottom areas in St. Croix (Kendall *et al.* 2003), higher sighting frequencies of groupers on hardbottom habitats in the Florida Keys (Jeffrey 2004), and increased fish abundance and species richness in mangrove communities in Puerto Rico (Pittman *et al.* 2007a). Several other studies have demonstrated that both vegetated and non-vegetated softbottom areas are known to provide habitat and food for several coral reef fishery species, endangered and threatened species, and many other marine organisms (Parrish 1989, Nagelkerken *et al.* 2000, Dahlgren and Marr 2004, Adams *et al.* 2006). Fine-scale benthic characterizations, such as those conducted during this study, should provide additional information to further explain these faunal species-habitat relationships.

Another important benthic habitat type that occurs in La Parguera is the mangrove, which forms very distinctive intertidal and near-shore features that are dominated by red mangrove (*Rhizopora mangle*). Extensive mangrove stands occur along the shoreline and form islands in the back reef lagoon areas of the La Parguera coral reef ecosystem, where they support abundant fish populations (Christensen *et al.* 2003, Pittman *et al.* 2007b). The tidal range in La Parguera is less than 0.5 m, thus most prop roots seaward of the mangrove community are continuously submerged. Our benthic characterizations of mangrove habitats found extensive cover of benthic organisms, particularly algae, sponges and hydroids, on both the seafloor and as epiphytes on submerged prop roots. The high mean cover (> 50%) of vegetation observed on benthic substrates indicates that the La Parguera mangroves are highly productive systems which may be providing enough food and nutrients to support resident fish and invertebrate populations. Additionally, many sites had thick deposits of detritus, suggesting that mangroves were performing their function of entrapping sediments. Further research is necessary however to identify additional characteristics of mangrove communities that may vary spatially and may be influencing benthic composition and faunal distributions. For example, mangroves are major producers of detritus that may be contributing to offshore productivity (Odum and Heald 1975). However, rates of productivity and generation of detritus in mangroves will vary based on location, oceanographic properties, composition of submerged vegetation, and frequency of tidal flushing.

Spatial Patterns in Scleractinian Coral Cover

Interpolations of this study's synoptic estimates of live coral cover summed across species revealed areas of relatively high cover that could be considered hot spots of live coral (see Figure 4). These hotspots may be refuge areas where demographic processes have resulted in coral populations that are resilient to multiple synergistic stressors. If so, corals at these locations are more likely to persist longer in the future than corals at other locations. Additionally, the locations of such hotspots corresponded with areas of relatively high rugosity, coral species richness, and diversity (Figure 4). Protection of such hotspots may benefit ecosystem conservation. Interestingly, the five most dominant species in terms of coral cover in La Parguera were two frame building species (*M. cavernosa* and *M. annularis* complex) and three more weedy species (*P. astreoides*, *Agaricia* spp. and *S. siderea*). Frame building corals are important in that they provide structural complexity and are also major contributors to reef growth and persistence, whereas weedy species provide very little complexity and contribute relatively little to reef growth (Hoegh-Guldberg *et al.* 2007). If these

hotspots are to be selected for increased management and protection from anthropogenic stressors, further work is needed to understand the physical and oceanographic properties that correlate with their enhanced ecological features.

Parrotfish Distribution Relative to Spatial Patterns in Benthic Habitat Composition

Significant positive and negative relationships were found between four parrotfishes and the habitat variables measured by this study (Table 4). These relationships supported the broad hypothesis that reef fish assemblages are affected by the composition of the underlying benthic substrate. Interestingly, the abundance of parrotfish size classes was not singularly influenced by any one measure of habitat composition. Instead, abundance generally correlated significantly with five or more variables, suggesting that the four species may associate with and respond to multiple habitat cues throughout their life cycles. Additionally, the strength of associations between fish abundance and habitat metrics were more variable among fish size classes of some species than others, but a few patterns emerged from this study nevertheless. For example, size class abundance of *S. iseri*, *S. taeniopterus*, and *S. viride*, were more correlated with abiotic variables (*i.e.*, depth and rugosity) than with biotic variables (*i.e.*, percent cover of sceleractinian corals, gorgonians, and crustose coralline algae). In contrast, abundance of three *S. sparisoma* size classes were weakly correlated with abiotic variables and one size class was more strongly and positively correlated with the percent cover of gorgonians (Table 4). Another interesting pattern was that smaller size classes (0 - 5 cm) of two parrotfishes (*e.g., S. iseri* and *S. viride*) were negatively associated with depth whereas similar size classes of the two other species were positively correlated with depth.

These opposing associations suggest that spatial partitioning of available habitats could have resulted from interspecific competition among congeners that have similar but competing habitat requirements, as well as from ontogenetic separation among size classes. Indeed, Pittman *et al*. (2007b) observed that *S. taeniopterus* juveniles and adults co-occurred across colonized hardbottom types of the deeper mid and outer shelf zones of La Parguera but were rarely encountered in nearshore and lagoonal areas where *S.iseri* was abundant. Many other studies have observed or alluded to spatial separation among parrotfish and other coral reef fishes (Helfman 1978, Parrish 1989, Nagelkerken *et al*. 2000, Christensen *et al*. 2003, Chitarro 2004, Pittman *et al.* 2007b, Howard *et al.* 2009) but a few studies have also provided ambiguous or conflicting results (Tolimieri 1998, Gust 2002, Kendall and Miller 2010).

Maxent models of parrotfish occurrence also revealed strong associations between fish occurrence and several habitat variables and seemed useful in predicting potential areas of high suitability for *S. iseri* and *S. taeniopterus* (Figure 6). Habitat (reef) type and percent cover of live coral were most influential on size class occurrence and contributed the most to model predictions for *S. iseri* and for *S. taeniopterus*, whereas depth and rugosity had relatively little influence on the occurrence of these two species. These results from Maxent modeling provide an interesting contrast to the results from Spearman correlation analyses reported herein, which suggested that depth and rugosity were stronger environmental correlates of parrotfish size-class abundance than benthic composition. Kendall and Miller (2010) also observed that fish abundance in northeast St. Croix were more correlated with habitat variables such as depth, rugosity, and cross-shelf location than with measures of benthic composition (*e.g.,* live coral cover). It is likely that substrate composition is relatively more important than depth and rugosity in determining the presence of these two species at a site, but once a size-class or species occurs at a locale, variation in its abundance across the seascape is mediated more by differences in depth and rugosity than by differences in benthic composition.

In summary, this study provided a detailed characterization of benthic habitats occurring in La Parguera, identified potential hotspots of high coral cover and taxa richness, and revealed complex spatial patterns in benthic composition that often correlated with the distribution and abundance of fishes. Depth of sites and substrate rugosity correlated positively with coral cover and taxa richness and influenced the abundance and size-class structure of parrotfishes. Additionally, several measures of benthic composition were useful in predicting the potential occurrence and size-class distribution of scarid assemblages. The spatial patterns in benthic composition observed by this study has increased our understanding of broad-scale variation in habitat composition, and the habitat-species associations identified illustrate important and crucial linkages that exist between habitats and fishery resources. The benthic characterizations reported in this study have provided data that can be used as covariates to explain spatial variance in parrotfish abundance and occurrence among hardbottom habitats. This study's findings provide a foundation upon which an ecosystem-based approach to fisheries management could be developed for southwestern Puerto Rico.

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