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CROSS-SHELF HABITAT UTILIZATION PATTERNS OF REEF FISHES IN SOUTHWESTERN PUERTO RICO

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ABSTRACT In June 2000, the National Ocean Service and University of Puerto Rico initiated a long-term reef-fish-monitoring program in La Parguera, Puerto Rico. Objectives of this ongoing work are to: 1) develop spatially-explicit estimates of reef fish habitat utilization patterns to aid in defining essential habitats, and 2) provide a quantitative and ecologically sound foundation to delineate marine reserve boundaries. Central to this effort are recently completed digital and georeferenced benthic habitat maps for the near-shore waters of Puerto Rico. The GIS-based map served as a framework for development of a spatially stratified reef-fish-monitoring program across the shelf. Simultaneous collections of fish size and abundance data, and micro-scale habitat distribution and quality data were taken along a 25 x 4 m transect for each monitoring station. Sampling included coral reef, mangrove, and seagrass habitats within three cross-shelf zones unique to the insular shelf of La Parguera (inner lagoon, outer lagoon, and bank-shelf). A total of 106 stations were surveyed during the first year of sampling. Over 50,000 fishes, representing 123 species and 36 families were counted. Analyses showed clear patterns of habitat utilization across the seascape, and ontogenetic shifts in habitat selection within some species. Results also indicated that habitat type was more important than cross-shelf location in determining spatial patterns among reef fishes in the study area. Mesoscale spatially-explicit logistic models were developed to estimate distribution and expected density of some species among habitats.

Introduction

Successful management of coral reef fisheries is a challenging and complex balance between resource protection and exploitation. Habitat degradation due to coastal development and other human activities, combined with overfishing, has resulted in severe declines of both targeted and non-targeted fish populations (Roberts and Polunin 1991, Roberts 1995, Lauck et al. 1998). Marine reserves are often advocated as a management option to compensate for these effects because they protect both fishery stocks and the habitats upon which they depend (Plan Development Team 1990, Roberts and Polunin 1991, Bohnsack 1993, Roberts 1995, Sluka et al. 1997, Guennette et al. 1998, Appeldoorn 2001). Marine reserves can provide many fishery benefits such as the protection of vulnerable spawning stock aggregations, enhancement of stock abundance in adjacent areas due to "spill-over" effects, and the preservation of ecosystem components critical to fish growth and survival (Sluka et al. 1997, Appeldoorn 2001). By maintaining undisturbed habitats, marine reserves can potentially provide benefits that disproportionately exceed their physical dimensions. For example, field studies in the Exuma Keys Land and Sea Park have estimated that 20% closure supplies 60% of local egg production of *Epinephelus striatus* (Nassau grouper) (Sluka et al. 1997) and 70% of larval *Strombus gigas* (queen conch) production (Stoner and Ray 1996, Appeldoorn 2001). Many of these benefits; however, have yet to be empirically demonstrated because most marine reserves lack adequate pre-closure data to test post implementation efficacy. This lack of information, coupled with a limited understanding of species habitat associations, may result in the placement of biologically ineffective marine reserve boundaries.

Strong linkages that exist between fishes and their habitats imply that successful implementation of marine reserves requires a knowledge of the location, distribution, and extent of habitats necessary for successful recruitment, growth, feeding, and reproduction (Parrish 1989, Friedlander and Parrish 1998). The distribution of these habitats varies highly across spatial and, to a lesser extent, temporal scales. In addition, there is increasing evidence that many reef fishes are dependent on systems that comprise a mosaic of habitats, including not only reef structure, but also a mixture of seagrasses, mangroves, and unconsolidated sand flats as well. Each of these habitats contains unique biotic communities that vary differently depending on the scale at which individual or community-level processes are observed (Williams 1991, Sale 1998).

The National Oceanic and Atmospheric Administration's (NOAA) Center for Coastal Monitor-

ing and Assessment (CCMA) and the University of Puerto Rico are collaborating on a long-term study to monitor the distribution of reef fishes among benthic habitats off La Parguera, Puerto Rico. An essential component of this work is the recently completed digital georeferenced benthic habitat maps for the near-shore waters of the region (Kendall et al. 2001). These GIS-based maps were the foundation for developing a spatially stratified strategy for sampling reef fish and benthic habitats. The objectives of this ongoing activity are to provide data necessary to develop spatially-explicit quantitative estimates of habitat utilization by fishes, to aid in defining essential fish habitats, and to define potential marine-reserve boundaries. This study examines the distribution and abundance of fishes among habitats, ontogenetic habitat selection by Haemulidae (grunts) and Lutjanidae (snappers), and differences in fish community structure among benthic habitats along a cross-shelf gradient.

MATERIALS AND METHODS

SCUBA divers surveyed fish communities in a variety of habitats across the insular shelf three times annually for two weeks off La Parguera in southwestern Puerto Rico (Figure 1). Results presented here are from the first full year of sampling, which included two-week sampling periods conducted during August 2000 and January and May 2001.

Benthic habitat mapping

Survey locations within specific habitat types were determined from benthic maps of the southwestern shore of Puerto Rico (Kendall et al. 2001, US National Oceanic and Atmospheric Administration (NOAA) 2001, Kendall et al. In press). In 1999, NOAA acquired and visually interpreted orthorectified aerial photography for the near-shore waters to 25 meters depth of Puerto Rico and the US Virgin Islands. Features visible in the aerial photographs were mapped directly into a geographic information system (GIS). Visual interpretation of the photographs was guided by a hierarchical classification scheme that defined benthic types based on insular-shelf zones and structures of the benthic community. Zone describes the insular-shelf location relative to barrier islands or emergent reefs (inner lagoon, outer lagoon, bank-shelf), whereas structure includes the cover type (reef, mangrove, submerged vegetation, and unconsolidated sediments) of the benthic community (Kendall et al. 2001).

Experimental Design

The digital habitat map was used to stratify the study area into eight distinct zone-structure combinations (hereafter "strata") based on three structures and three zones (Figure 1). Only eight strata were possible because mangroves do not occur in the bank-shelf zone. The entire digital seascape (about 200 km^2) was partitioned into individual 40x40 m sample units (SUs), four of which were randomly selected within each stratum as replicate survey locations. SU's were selected only if their entire extent was of monotypic zone and structure. SUs that contained multiple structures, or that straddled zone boundaries were excluded from the pool of potential samples so as not to confound the analyses. The geoposition for each SU was calculated in the GIS, exported and uploaded into a hand-held differentially corrected Global Positioning System unit, and used to navigate to stations in the field. One station per stratum has been designated as a permanent site that will be sampled during each mission to monitor changes in benthic condition and faunal community composition. Two divers estimated fish abundance, and size at each sample location, while a third diver measured benthic habitat variables, such as percent cover of abiotic and biotic substrates, density of holes smaller or larger than 15 cm, maximum gorgonian canopy height, depth, and rugosity.

Visual fish census

The abundance and size of fishes were visually estimated within each pre-selected SU along a 25 X 4-meter belt transect (Brock 1954 and Brock 1982). Transect divers swam 25m on a random compass heading for 15 minutes at a constant speed. While swimming, the diver identified to the lowest possible taxon, counted, and estimated the size (fork length [FL]) of all fishes observed within 2m on either side of a centerline (100 m^2 transect area).

Fish community metrics and statistical analyses

Data were entered into a database and analyzed with JMP statistical software (Version 4.0, SAS Institute 2000). Mean species density, sighting frequency, richness, and diversity were calculated for each zone, structure, and stratum (zone-structure combination). Sighting frequency is the percentage of all survey dives in which the particular species was observed. Species richness is the absolute number of species observed at a site. A Shannon-Weaver (Shannon and Weaver 1949) index of species diversity was calculated for each dive as follows:

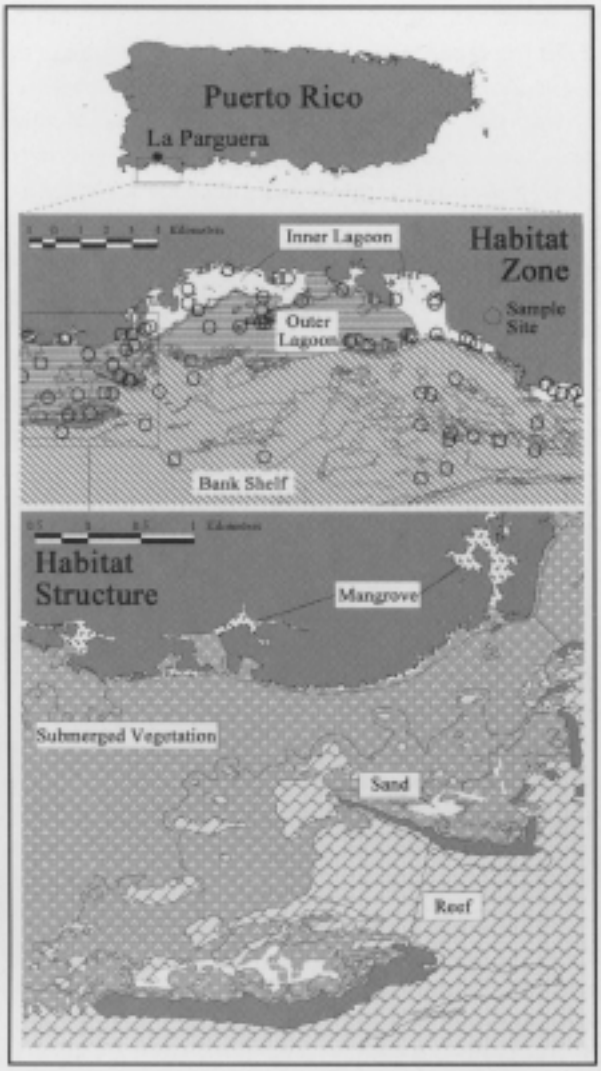

Figure 1. Map of the study area in southwestern Puerto Rico. The top inset depicts sample sites (open circles) superimposed over the cross-shelf zones. The bottom inset is an enlargement of the western-most region in the study area, showing detail of the various habitats sampled.

$$H' = -(\sum_{i=1}^{S} n_i / N \ln n_i / N)$$

where S is the number of species; n_i is the abundance of the ith species and N is the total abundance of all species. Raw data and estimated variables were checked for normality using Dunnet's Test (Sokal and Rohlf 1995), and when necessary, transformed using the Box-Cox procedure (Sokal and Rohlf 1995) for parametric statistical analyses. Data that remained heteroscedastic after transformation were analyzed using non-parametric procedures.

Hierarchical clustering of species presence was used to determine the structure and magnitude of similarity in fish assemblages among habitat strata. Hierarchical clustering was based on Ward's minimum variance method, where the distance between two clusters is the sum of squares added up over all variables (SAS Institute 2000). This technique minimized the within-cluster variance for all variables at each subsequent level of the hierarchy so that sites with similar fish-assemblage variables clustered together. For species presence clustering, a binary contingency table was constructed such that 0–0 and 1–1 were considered a match, and 0–1 was considered a mismatch for all possible species pairs. No weights were given to differentiate 0–0 and 1–1 matches.

Patterns in the distribution of families among strata were determined using correspondence analysis. Correspondence analysis is a graphical ordination that shows the similarity between rows (fish family) and columns (strata) of a frequency table (SAS Institute 2000). The plot axes measure the variation accounted for in each canonical dimension (c_n) and a single point represents each row or column, with the squared distances between points being approximately proportional to the chi-square distances that test the homogeneity between row or column pairs. Points of rows or columns with similar frequencies appear close together, and the strength of the relationship between rows and columns is indicated by the direction of the points from the plot's origin (SAS Institute 2000). A 95% confidence interval (CI) ellipsoid was determined from a bivariate plot of the x-y coordinates of row and column points in the correspondence analysis plot to identify family-strata group membership.

Where appropriate, a series of ANOVA, non-parametric ANOVA, and pair-wise comparisons were used to determine if mean species density, and richness, varied significantly by zone, structure, or strata. Fish density estimates were normalized using the Box-Cox transformation (Sokal and Rohlf 1995). Differences in overall mean density of fishes among strata were determined with a one-way ANOVA. Where significance was detected, *a posteriori* Tukey-Kramer pairwise comparison tests were performed to identify the source of variation (Sokal and Rohlf 1995). Differences in mean species richness among strata were determined with Kruskall-Wallis ANOVA and modified Tukey-Kramer tests (Zar 1999).

Cross-shelf ontogenetic habitat utilization patterns of grunts and snappers were determined with non-parametric tests of independence and correspondence analysis. Differences in mean density of grunts and snappers among strata were determined using the

Kruskall-Wallis procedure and modified Tukey-Kramer tests (Zar 1999). Correspondence analysis and Chi-squared tests were used to determine if the size-class distribution of grunts and snappers was independent of habitat. These taxa were selected for this analysis because they are representative of commercially important fishes in the region.

Logistic regression models also were developed to estimate the probability of occurrence for all snappers (pooled), *Ocyurus chrysurus* (yellowtail snapper), as well as for the distribution of *O. chrysurus* size-classes among strata to determine if distribution patterns differed by taxonomic level (e.g., family, species) and during ontogeny. Logistic regression was used to fit a model to a binary response (Y = 1 if present or 0 if not present) to the independent variable (X = strata), such that for each stratum, there was a probability p of being present or $1-p$ of not being present (SAS Institute 2000). The resulting probabilities were classified into three quantile classes (0–33, 34–66, 67–100th percentile) and imported into Arc View GIS to produce spatially explicit maps of occurrence within the study area.

RESULTS

Species composition and assemblage structure

Appendix 1 shows taxa observed by zones, structures, and strata during the first year of sampling. A total of 106 sites were surveyed, resulting in the identification of about 50,000 individuals from 123 species belonging to 36 families. Hierarchical clustering of species presence showed several patterns in the composition of fish assemblages among strata (Figure 2). Species richness was greatest among reef sites (41–44 species), followed by mangrove sites (25–30), and submerged vegetation sites (17–19). There was a distinct grouping of sites by structure, showing that species composition was more similar among sites within the same structure than among zones. Additionally, clustering showed that the adjacent bank-shelf and outer lagoon zones were more similar to each other in species composition than to the inner lagoon zone, indicating, to a lesser extent, the presence of a cross-shelf gradient in community structure.

ANOVA and modified Tukey-Kramer pair-wise comparisons showed that variation in mean species richness among structures was significant but cross-shelf variation within structure was not (Figure 3). Species richness at reef sites was significantly higher than submerged vegetation sites but the difference among sites in reef and mangrove structures was not significant. Mean species richness was significantly higher for sites in the inner lagoon mangrove than for sites in the outer lagoon submerged vegetation, but was not different from that of submerged vegetation sites in other zones. Because analysis for richness and diversity were very similar, only results for richness are provided.

Transformed mean density values (Box-Cox procedure, $l = -.07$) exhibited significant differences among strata, although the one-way ANOVA model explained only 51% of the observed variation (Figure 4). Cross-shelf variation in fish density within reef, mangrove, and submerged vegetation structures was not significant. Mean fish densities of the outer lagoon mangrove, inner lagoon reefs, and outer lagoon reefs were similar but significantly higher than the mean fish density of submerged vegetation sites across all zones. Mean fish density was significantly higher in the inner mangrove compared with inner and outer submerged vegetation sites.

Correspondence analysis resulted in three family groups, each of which associated with a specific structure (Figure 5). Five families (Haemulidae, Lutjanidae, Gerreidae [mojarras], Atherinidae [silversides], and Sphyraenidae [barracudas]) ordinated closely with mangrove habitats in the c1 dimension, indicating a strong dependence between group distribution and habitat. Ten families were associated with submerged vegetation, and the rèmaining families associated with reef. Only three families (Mullidae [goatfishes], Scaridae [parrotfishes], and Sparidae [porgies]) were shared between two structures—reef and submerged vegetation. Ophicthidae (snake eels) ordinated most closely with submerged vegetation but occurred outside the 95% CI boundary of family-habitat membership.

Distribution of Haemulidae and Lutjanidae among strata

A Kruskall-Wallis ANOVA detected significant variation in the mean density of Haemulidae among strata, whereas the effect of zone was not significant. Mean density of haemulid species in the inner lagoon mangrove was not significantly different from reef or submerged vegetation sites (Figure 6). The distribution of lutjanid fishes among strata was very similar to that of haemulid fishes. Lutjanid species were significantly more abundant in mangrove sites compared with reef and submerged vegetation sites (Figure 7). Within the same structural type, cross-shelf differences in mean density of Lutjanidae were not significantly different. Beyond the notion of statistical significance, it is interesting to note that densities were extremely low (near zero) at reef and seagrass sites for both taxa.

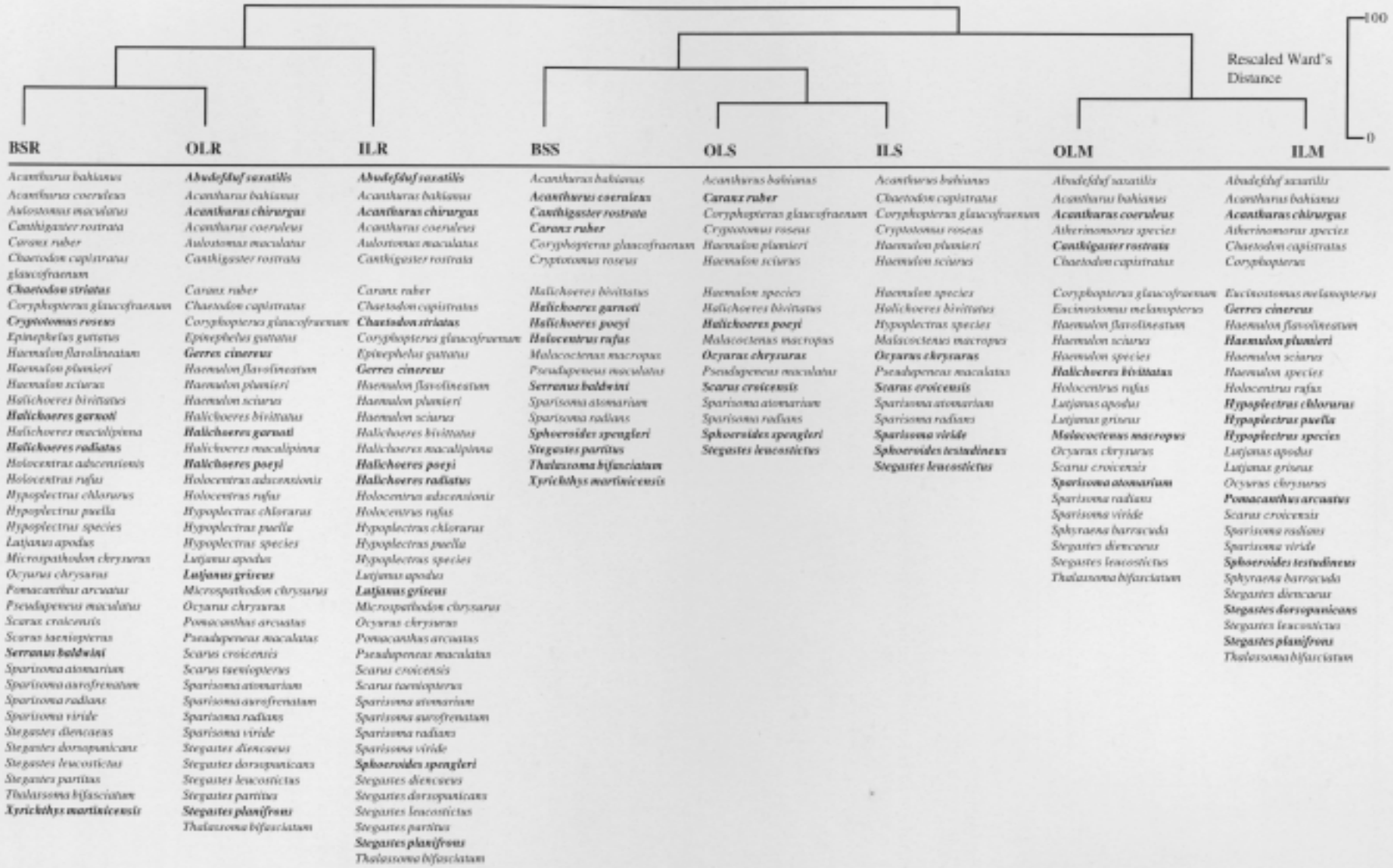

Figure 2. Dendrogram of sample strata clustered by species presence. Habitat strata include bank shelf reef (BSR), bank shelf submerged vegetation (BSS), outer lagoon reef (OLR), outer lagoon submerged vegetation (OLS), outer lagoon mangrove (OLM), inner lagoon reef (ILR), inner lagoon submerged vegetation (ILS), and inner lagoon mangrove (ILM). Only those species with cumulative sighting frequencies greater than 5% were included in the analysis. Species not in bold were common to the groupings within a structure type (i.e. reef, mangrove, and submerged vegetation). Names in bold are species that were unique to one or two, but not all groupings by structure.

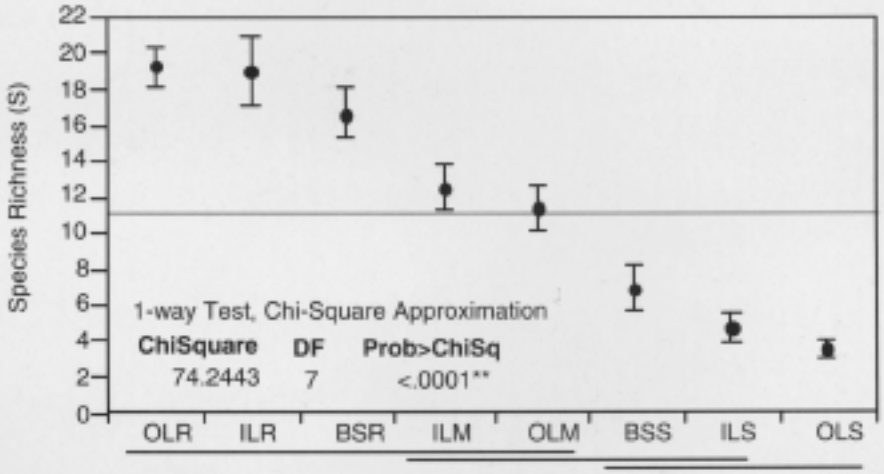

Figure 3. Non-parametric means comparison and modified Tukey-Kramer pairwise comparisons of species richness (S) among sample strata. Strata connected by lines indicate significant groupings (alpha = 0.05) (abbreviations as in Figure 2).

Size-class distribution of Haemulidae and Lutjanidae

Haemulidae showed significant differences in their size-class distribution among structures, zones, and strata. Correspondence analysis revealed significant associations between large haemulid fishes (> 15 cm FL) and reef sites, smaller haemulid fishes (5–10 cm FL) and mangrove, and juveniles (0–5 cm) and submerged vegetation (Figure 8a, Table 1). The proportion of variation explained by the canonical dimensions was 0.48 and 0.11 for c1 and c2 axes, respectively. The distribution of Haemulidae among zones also was significant, but the patterns were less clear (Figure 8b, Table 2). Only 10% and 3% of the variation in haemulid distribution among the zones was attributable to the c1 and c2 axes, respectively. The size-class distribution of haemulid fishes among strata was similar to the pattern observed among structures, with 49%, and 13% of the variation being explained by the c1 and c2 axes, respectively (Figure 8c, Table 1). Large Haemulidae (15–20 cm FL) were significantly associated with reefs in the outer lagoon and on the bank-shelf. Haemulidae in the 10–15 cm FL size-class and those larger than 20 cm FL associated with the inner lagoon reef, whereas those of 5–10 cm FL were more common in the inner and outer lagoon mangrove. Haemulid juveniles (0–5 cm FL) associated most closely with submerged vegetation sites in the inner and outer lagoon.

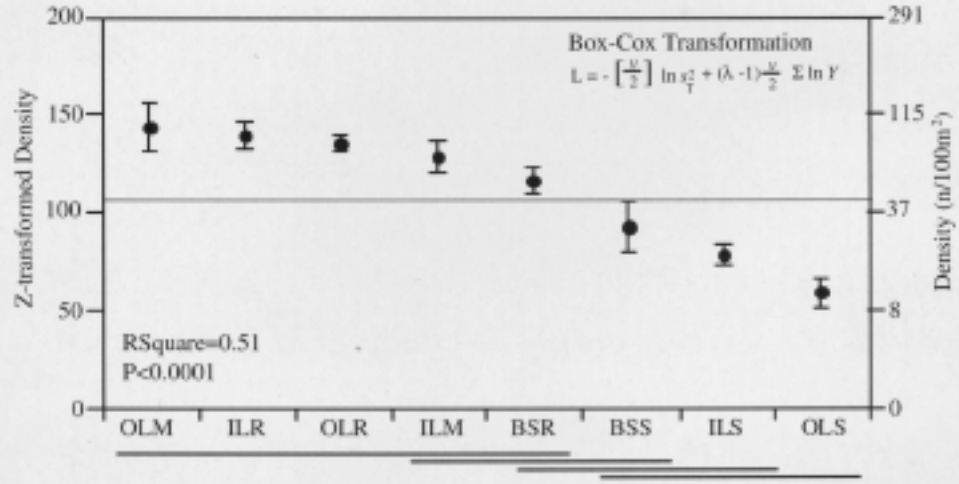

Figure 4. Analysis of Variance and Tukey-Kramer pairwise comparisons of fish density (N/100 m²) among sample strata. Strata connected by lines indicate significant groupings (alpha = 0.05) (abbreviations as in Figure 2).

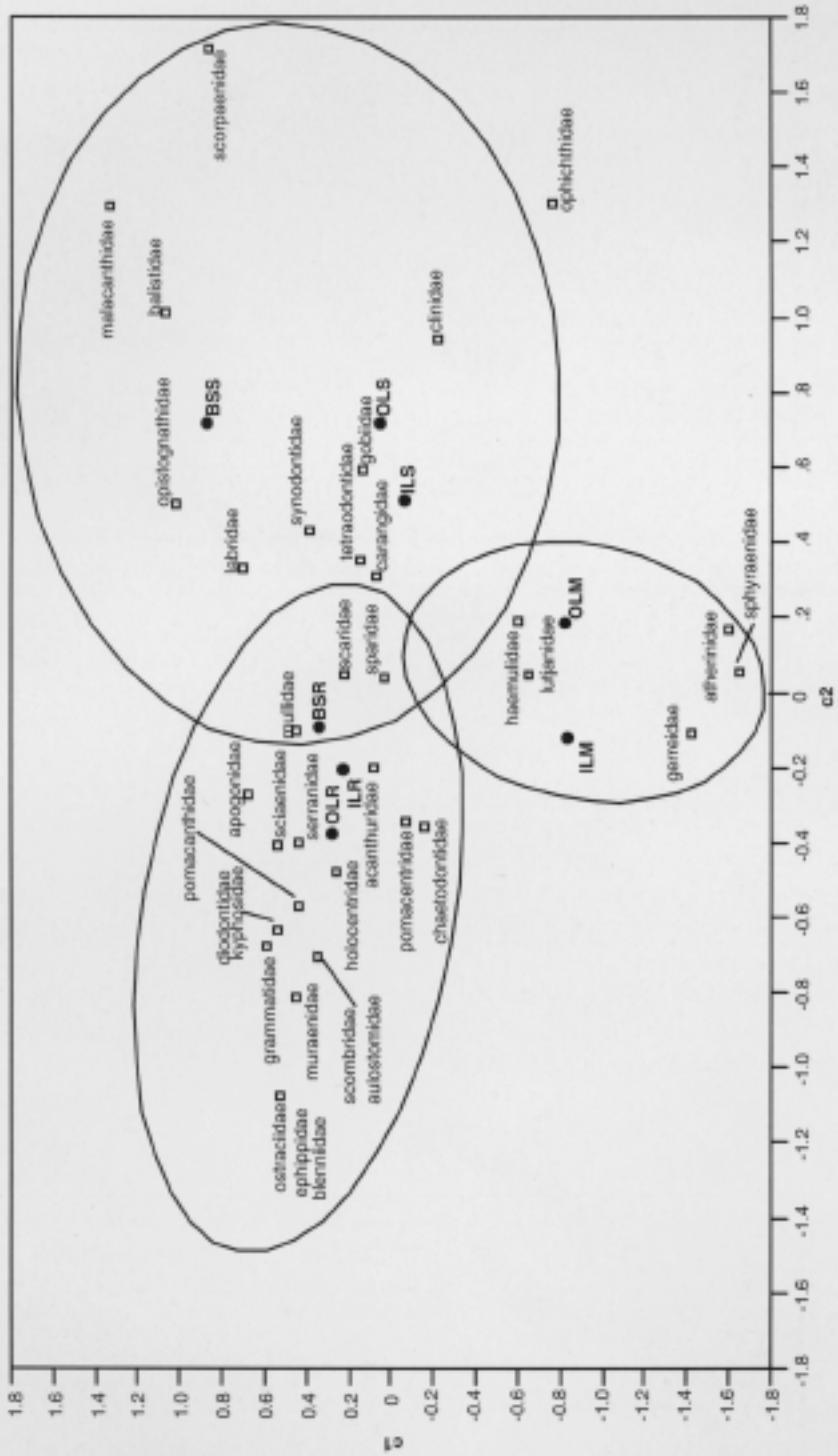

Figure 5. Correspondence plot of fish family and sample strata. Open squares represent family ordinations, while closed circles represent stratum ordinations. Ellipsoids represent 95% confidence boundary for bivariate plots of habitat membership (abbreviations as in Figure 2).

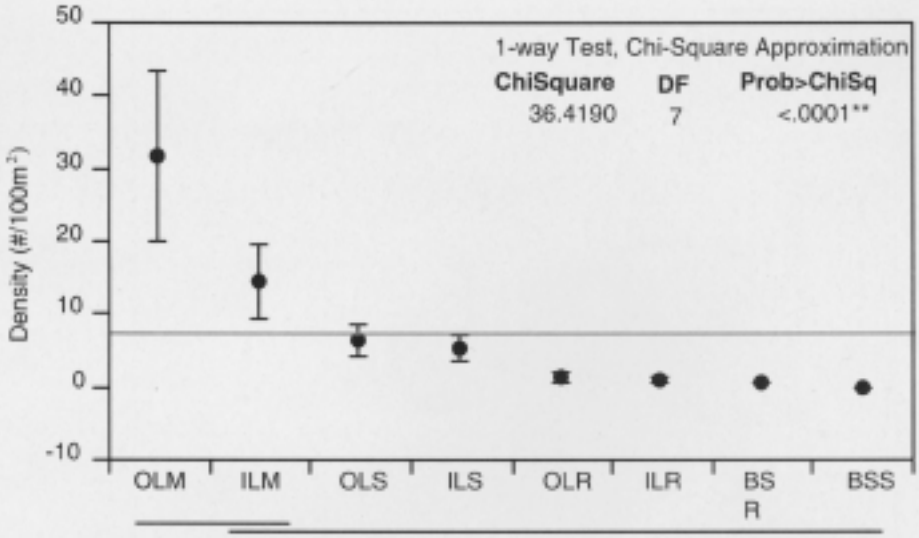

Figure 6. Analysis of Variance and Tukey-Kramer pairwise comparisons of grunt (Haemulidae) density (N/100 m²) among sample strata. Strata connected by lines indicate significant groupings (alpha = 0.05) (abbreviations as in Figure 2).

Like Haemulidae, lutjanid species showed significant differences in their size-class distribution among structures, zones, and strata. Lutjanidae larger than 15 cm FL were observed mainly in reef areas, those of 5–15 cm FL occurred mainly in mangrove areas, and juveniles (0–5 cm FL) dominated the submerged vegetation sites (Figure 9a, Table 1). The c1 and c2 dimensions explained 32% and 14% of the variance in lutjanid size-class distribution. Lutjanidae larger than 15 cm FL dominated the bank-shelf reef zone, whereas those sized 5–15 cm FL occupied the outer lagoon. Lutjanid fishes in the 0–5 cm FL size-class occurred mainly in the inner lagoon; however, the c1 and c2 dimensions explained only 13% and 1.9% of the lutjanid size-class variation, respectively (Figure 9b, Table 1). Among strata, lutjanid species in the 0–5 cm size-class associated with the inner and outer lagoon submerged vegetation strata (Figure 9c, Table 1), whereas those in the 5–10 cm and 10–15 cm FL size-class ordinated toward lagoon and outer lagoon mangrove, respectively. Lutjanid individuals larger than 15 cm FL associated with outer lagoon and bank-shelf reef strata. The c1 and c2 dimensions accounted for 37% and 18% of the size-class variance of Lutjanidae among strata.

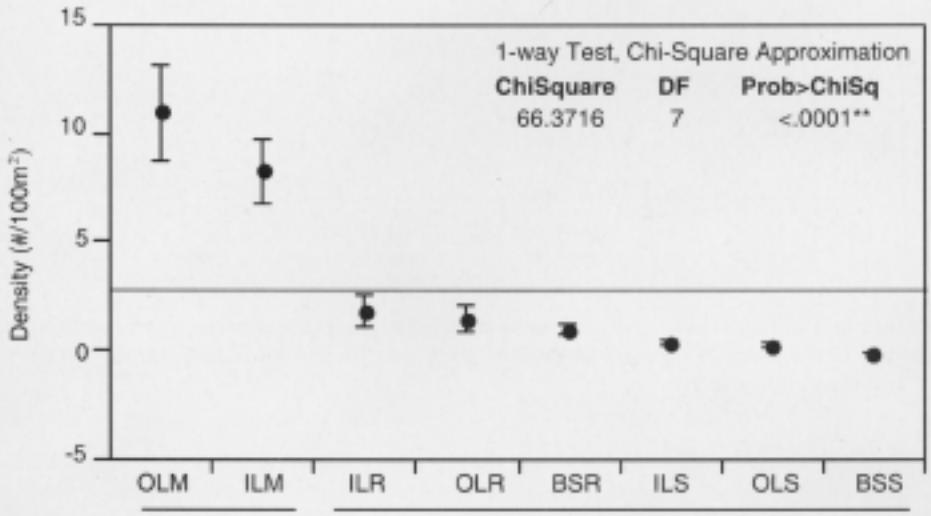

Figure 7. Analysis of Variance and Tukey-Kramer pairwise comparisons of snapper (Lutjanidae) density (N/100m²) among sample strata. Strata connected by lines indicate significant groupings (alpha = 0.05) (abbreviations as in Figure 2).

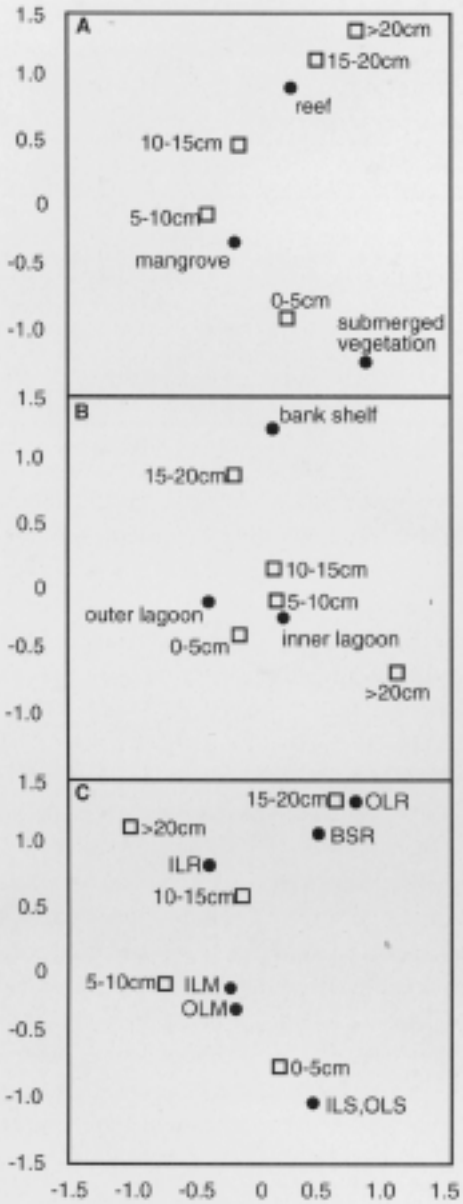

Figure 8. Correspondence plot of grunt (Haemulidae) size class distribution among: a) habitat structures, b) zones, and c) strata. Open squares represent size-class ordinations, while closed circles represent habitat ordinations.

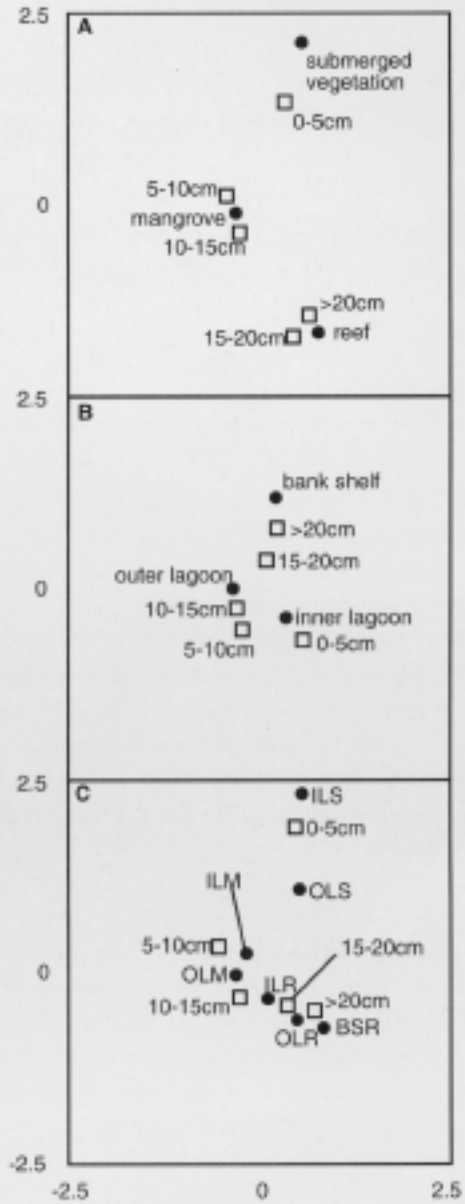

Figure 9. Correspondence plot of snapper (Lutjanidae) size class distribution among: a) habitat structures, b) zones, and c) strata. Open squares represent size-class ordinations, while closed circles represent habitat ordinations.

Spatial distribution of Lutjanidae

Figure 10 and Table 2 show the results of a spatially-explicit logistic regression model to estimate the probability of occurrence for Lutjanidae among strata for a portion of the surveyed area showed in Figure 1. The model was significant, although it explained only 42% of the variation in probability of lutjanid occurrence (Figure 10a). The highest probability of encountering lutjanid species was in mangroves and outer lagoon reefs, whereas the lowest probability was in submerged vegetation sites. Though it seems intuitive, it is interesting to note that the probability of encountering Lutjanidae increased log-linearly with mean density. Therefore, the map indicates where lutjanid species are most likely to occur and where they are most abundant.

To identify species-level patterns of distribution, a spatially explicit model also was developed to predict the probability of occurrence of *O. chrysurus* among strata for a portion of the surveyed area shown in Figure

TABLE 1

Size-class/habitat correspondence analysis statistics for grunts (Haemulidae) and snappers (Lutjanidae). Chi-square, significance (*P*), and inertia values for each cannonical axis are reported.

	Treatment	Figure	ChiSquare	*P*	Inertia C1	Inertia C2
Grunts	Zone	8A	95.5	< 0.001	0.48	0.11
	Structure	8B	19.8	0.011	0.10	0.03
	Stratum	8C	108.5	< 0.001	0.49	0.14
Snappers	Zone	9A	56.6	< 0.001	0.32	0.14
	Structure	9B	25.7	0.001	0.13	0.02
	Stratum	9C	77.8	< 0.001	0.38	0.18

1 (Figure 10b and Table 2). The model was significant but explained much less (18%) of the variation in the response variable than the family-level model. The highest probability of encountering *O. chrysurus* was over the bank-shelf and outer lagoon reef sites. *Ocyurus chrysurus* had the lowest probability of being encountered among the inner lagoon mangroves, outer lagoon submerged vegetation, and bank-shelf submerged vegetation sites. A significant log-linear relationship also existed between mean density and probability of encounter of *O. chrysurus*.

The probability of *O. chrysurus* distribution also was modeled at the ontogenetic level to predict size-specific distributions within the seascape, and to highlight ontogenetic shifts and/or habitat connectivity for the species. Table 2 shows the results of this modeling exercise. As seen with the correspondence analysis, the logistic models indicate that juveniles predominantly select inner lagoon submerged vegetation sites, then move to the outer lagoon mangrove once larger that 5 cm FL. Individuals larger than 15 cm FL then redistribute themselves among the reef structures of the bank shelf. The logistic model for the 0–5 cm size class of *O. chrysurus* was significant ($P = 0.01$); however, it explained only 32% of the observed variance. Likewise, models for the 5–15 cm and > 15 cm size classes also were significant, and explained 25% and 32% of the variance, respectively.

DISCUSSION

The development of a georectified mesoscale benthic habitat map has provided a unique opportunity to approach pertinent community-level and autecological issues that require examination of large regions. The concept of essential fish habitat (EFH) and the principles behind developing marine reserves necessitate examination of greater spatial ranges than those at which typical scientific experiments are conducted. Rather than focusing on a single patch-reef or

TABLE 2

Probability of occurrence for all snappers (Lutjanidae), yellowtail snapper (*Ocyurus chrysurus*), and *O. chrysurus* size-classes (0–5 cm, 5–15 cm, and > 15 cm) among habitat strata as predicted by logistic models. Habitat strata include bank shelf reef (BSR), bank shelf submerged vegetation (BSS), outer lagoon reef (OLR), outer lagoon submerged vegetation (OLS), outer lagoon mangrove (OLM), inner lagoon reef (ILR), inner lagoon submerged vegetation (ILS), and inner lagoon mangrove (ILM). Coefficient of determination (R^2) and model significance (P) are also reported. **Ocyurus chrysururs, Lutjanus analis, Lane, Lutjanus mahogoni, Lutjanus griseus.*

	BSR	OLR	ILR	BSS	OLS	ILS	OLM	ILM	R^2	P
All Snappers*	0.54	0.67	0.46	< 0.01	0.14	0.42	0.99	0.99	0.42	0.0001
Yellowtail Snapper—All Size Classes	0.54	0.50	0.39	< 0.01	0.10	0.42	0.42	0.08	0.18	0.0014
Yellowtail Snapper (0–5 cm)	< 0.01	< 0.01	0.07	< 0.01	0.05	0.42	0.08	< 0.01	0.32	0.01
Yellowtail Snapper (5–15 cm)	< 0.01	0.08	0.23	< 0.01	< 0.01	0.08	0.34	0.08	0.25	0.02
Yellowtail Snapper (> 15 cm)	0.54	0.50	0.23	< 0.01	0.05	< 0.01	0.16	< 0.01	0.32	0.0001

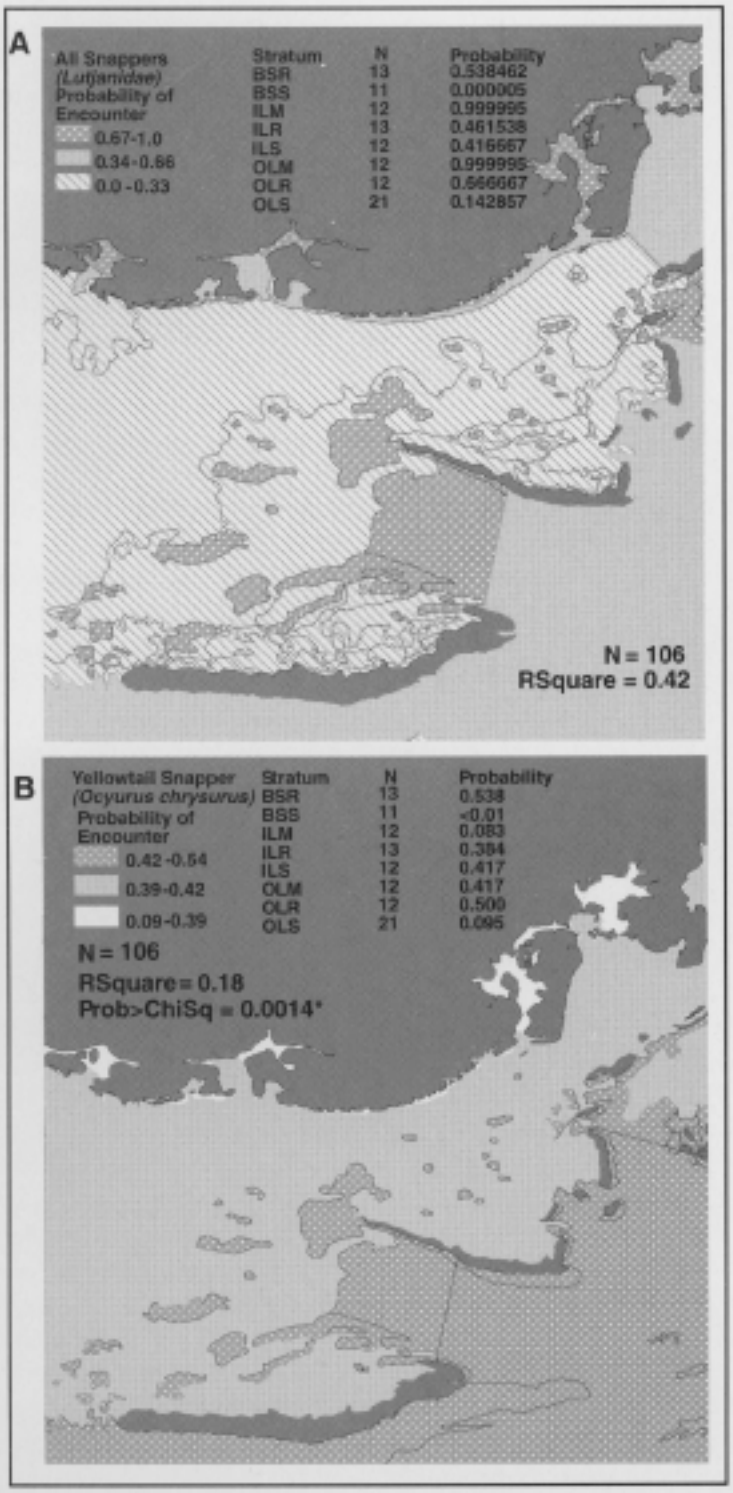

Figure 10. Results of logistic regression. Panel A indicate the probability of encounter of snappers (Lutjanidae) among habitat strata in the seascape, while panel B shows results for yellowtail snapper (*Ocyurus chrysurus*). Refer to Figure 1 for map location.

embayment, we were able to stratify more than 200 km^2 of shelf waters into broad and biologically-significant categories of zone and structure. By using the approach described here, we gained insight into patterns and processes occurring within the integrated seacape. In so doing, we were able to examine large-scale patterns in assemblage structure, and explore very specific questions about particular families of commercially and recreationally important taxa such as Haemulidae and Lutjanidae. Although we lose the detail of a particular patch-reef, we are able to analyze our data and make recommendations at the scale at which management decisions typically are made.

Habitat utilization

Benthic habitats were defined based on two attributes: zones, which refer to the insular shelf location (e.g., lagoon or bank-shelf), and structure or substrate composition (e.g., sand, hard-bottom, or vegetation). The focus of this study was to identify the habitat utilization patterns of reef fishes as determined by habitat zones, structure, or a combination of zone and structure. The results show that structure was more important than cross-shelf location in determining spatial patterns among reef fishes at the family, species, and at the species-life stage level.

Family and species-level analyses

The correspondence analysis (Figure 7) demonstrates the relationship between habitat and reef-fish family occurrence. Only three families out of thirty-six (Sparidae, Mullidae and Scaridae), were found within the 95% confidence ellipsoids of two structural groupings, and only one, Ophichthidae, occurred outside all three ellipsoids. Although, sighting frequency was low for sparid species, we generally found that sparid and mullid juveniles were observed at submerged vegetation sites, whereas larger individuals were more prevalent on reef. Two scarid species, *Scarus croicensis* (striped parrotfish) and *S. taeniopterus* (princess parrotfish), also exhibited this ontogenetic shift in habitat preference. However, scarid species were split between these two strata primarily because of a dichotomy in habitat preference at the species level. *Sparisoma radians* (bucktooth parrotfish) and *S. atomarium* (greenblotch parrotfish) are found predominantly in submerged vegetation throughout their life cycles, whereas, the majority of other scarids are found principally on the reef structure. In the case of the Ophichthidae, an increased sample size may place them within the submerged vegetation grouping.

It is likely that each attribute of habitat (zone and structure), coupled with both stochastic and density-dependent factors, shapes the faunal community structure at any given location within the seascape. One interpretation of the analyses of ichthyofaunal community structure presented here is that the structural component of habitat, rather than cross-shelf location or stochasticity, strongly influences the distribution and structure of communities in the region at the scale of this study. For fishes of southwestern Puerto Rico, this basic premise also is apparent at lower taxonomic levels. For example, the abundance and distribution of single families, species, and even life stages, show strong spatial correlations with, and clear statistical dependence upon habitat type. Snappers and grunts clearly exhibited this relationship at all taxonomic scales (family, species), and even throughout ontogeny. At the family level, an ANOVA indicated that mangrove sites, regardless of cross-shelf location, supported significantly higher densities of snappers and grunts than both reef and seagrass sites. Initially, it may seem logical that preserving mangrove sites in this region is a sound solution to managing these taxa. However, a further deconstruction of the data through correspondence analysis revealed that most of the individuals found in mangrove sites were fishes ranging from 5–15 cm—the most numerically dominant size classes observed. Furthermore, correspondence analysis showed marked ontogenetic shifts in lutjanid and haemulid distributions within the available seascape, with smallest individuals (< 5 cm FL) of these taxa disproportionately selecting for submerged vegetation habitats, while larger individuals (> 15 cm FL) selected for reef habitats. Reduced densities of these two size classes can be explained by factoring in the spatial extent of their preferred structure in relation to that of the mangroves, adult mortality and by recognizing the cryptic nature of juveniles. While mangroves clearly play a role in concentrating 5–15 cm fishes, these additional analyses indicate that preserving a mosaic of habitats (including mangroves) would likely be the best option for managing these taxa. Exclusion of any habitat type would most certainly impose a "bottleneck" at which population maintenance and growth potential might be significantly affected.

The example of using logistic regression to predict habitat utilization further underscores the importance of habitat connectivity intrinsic to the life histories of Lutjanidae, and more specifically *O. chrysurus*. Different habitats along the cross-shelf gradient support specific life-stages of this species, with juveniles more prevalent in seagrass communities of the inner and outer

lagoon, while adults of the species appear to distribute themselves among the structurally complex reef sites of the outer lagoon and bank shelf. The model's result, though significant, only explains a minor portion of the observed variance, and should be interpreted with caution.

Applications to marine reserves delineation

These examples illustrate the value of a deliberate analysis of reef fish distribution among all habitats available in the seascape to develop cogent resource management options. In the past, studies have often focused on one habitat type, typically reef (Friedlander and Parish 1998), because reefs generally support higher biological diversity than seagrass, mangrove, or unconsolidated sediment habitats. Recksiek et al. (2001) and Appeldoorn et al. (2001) first described a modified sampling and analytical protocol to incorporate multiple habitats with the intent of describing EFH in the region. This study builds upon that recommendation, and provides a spatially-explicit cross-shelf habitat matrix of sufficient scale to address the issues of EFH and marine reserves.

Results presented here indicate that most fishes in the region have developed life-history strategies that depend at some point on the range of habitats historically available to them for growth and reproductive success. Additionally, Kendall et al. (In press), using identical protocols as described in this paper, reported similar results for French grunts (*H. flavolineatum*) in the Buck Island Reef National Monument, St. Croix. There, haemulid juveniles were only found at reef sites if soft bottom foraging habitats were within 300 meters of the sample site, and the distance of reefs from foraging habitats was inversely related to the likelihood of juvenile haemulid encounters. These patterns show habitat connectivity and that sampling protocols explicitly including a spatial "effect" are necessary to explore and develop sound strategies for marine reserve delineation. This is true especially of the coral reef and associated habitats, where animal movements are associated closely with specific habitats, particularly where these habitats are distributed heterogeneously (Helfman 1978, Murray et al. 1999).

To test the efficacy of a marine reserve to enhance resource abundance, it is critical to develop a baseline against which future estimates can be compared. Overfishing and habitat degradation have resulted in dramatic stock declines throughout the region, suggesting that management strategies within the US Caribbean must be altered in an effort to preserve and nurture what is left of these fisheries (Olsen and LaPlace 1978, Appeldoorn et al. 1992, Beets and Friedlander 1992, Appeldoorn 1993). This study's findings provide a foundation upon which an ecosystem approach to fisheries management could be developed. Presently, there are no comprehensive maps depicting "essential" benthic habitats adjacent to, and contained within, the existing and proposed marine reserves. Using the high resolution benthic habitat maps as a guide to sample stratification, and subsequently as a spatially-explicit analytical framework, we are poised to quantify mesoscale (<100 km^2) fishery habitat utilization in the area, as well as to suggest cause for the observed patterns by describing species-specific habitat function within the ecosystem.

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APPENDIX 1

Frequency of occurrence for all taxa observed on belt transects. Values are reported for overall frequency and frequency by zone, structure, and stratum.

		TOTAL	ZONE			STRUCTURE			STRATUM							
	Taxon	Cummulative Frequency (N=106)	Bank/Shelf (N=24)	Outer Lagoon (N=45)	Inner Lagoon (N=37)	Reef/Hardbottom (N=38)	Vegetation (N=44)	Mangrove (N=24)	Bank/Shelf Reef (N=13)	Bank/Shelf Vegetation (N=11)	Outer Lagoon Reef (N=12)	Outer Lagoon Vegetation (N=21)	Outer Lagoon Mangrove (N=12)	Inner Lagoon Reef (N=13)	Inner Lagoon Vegetation (N=12)	Inner Lagoon Mangrove (N=12)
Muraenidae	*Gymnothorax funebris*	0.009	.	.	0.03	0.03	.	.	.	.	.	.	.	0.08	.	.
	Gymnothorax miliaris	0.009	.	0.02	.	0.03	.	.	.	.	0.08	.	.	.	.	.
Ophichthidae	*Myrichthys breviceps*	0.019	.	0.04	.	.	0.02	0.04	.	.	.	0.05	0.08	.	.	.
Synodontidae	*Synodus intermedius*	0.047	0.04	0.07	0.03	0.08	0.05	.	0.08	.	0.08	0.10	.	0.08	.	.
Atherinidae	*Atherinomorus species*	0.179	.	0.24	0.22	.	.	0.79	.	.	.	.	0.92	.	.	0.67
Holocentridae	*Holocentrus adscensionis*	0.075	0.17	0.02	0.08	0.21	.	.	0.31	.	0.08	.	.	0.23	.	.
	Holocentrus coruscus	0.009	.	.	0.03	.	.	0.04	.	.	.	.	.	.	.	0.08
	Holocentrus rufus	0.302	0.42	0.22	0.32	0.71	0.02	0.17	0.69	0.09	0.75	.	0.08	0.69	.	0.25
	Myripristis jacobus	0.047	.	0.02	0.11	0.11	.	0.04	.	.	0.08	.	.	0.23	.	0.08
Aulostomidae	*Aulostomus maculatus*	0.057	0.08	0.04	0.05	0.16	.	.	0.15	.	0.17	.	.	0.15	.	.
Scorpaenidae	*Scorpaena plumieri*	0.009	0.04	.	.	.	0.02	.	.	0.09	.	.	.	.	.	.
	Scorpaena species	0.009	.	.	0.03	.	0.02	.	.	.	.	.	.	.	0.08	.
Serranidae	*Epinephelus cruentatus*	0.047	.	0.07	0.05	0.13	.	.	.	.	0.25	.	.	0.15	.	.
	Epinephelus fulvus	0.038	0.04	0.02	0.05	0.11	.	.	0.08	.	0.08	.	.	0.15	.	.
	Epinephelus guttatus	0.057	0.08	0.07	0.03	0.16	.	.	0.15	.	0.25	.	.	0.08	.	.
	Hypoplectrus chlorurus	0.160	0.08	0.18	0.19	0.42	.	0.04	0.15	.	0.67	.	.	0.46	.	0.08
	Hypoplectrus puella	0.132	0.04	0.16	0.16	0.32	.	0.08	0.08	.	0.58	.	.	0.31	.	0.17
	Hypoplectrus species	0.113	0.04	0.04	0.24	0.21	0.07	0.04	0.08	.	0.17	.	.	0.38	0.25	0.08
	Hypoplectrus unicolor	0.019	0.04	0.02	.	0.05	.	.	0.08	.	0.08	.	.	.	.	.
	Mycteroperca bonaci	0.019	.	0.02	0.03	0.05	.	.	.	.	0.08	.	.	0.08	.	.
	Serranus baldwini	0.066	0.29	.	.	0.05	0.11	.	0.15	0.45	.	.	.	.	.	.
	Serranus tabacarius	0.009	0.04	.	.	0.03	.	.	0.08	.	.	.	.	.	.	.
	Serranus tigrinus	0.009	0.04	.	.	0.03	.	.	0.08	.	.	.	.	.	.	.

APPENDIX 1 (Continued)

		TOTAL	ZONE			STRUCTURE			STRATUM							
	Taxon	Cummulative Frequency (N=106)	Bank/Shelf (N=24)	Outer Lagoon (N=45)	Inner Lagoon (N=37)	Reef/Hardbottom (N=38)	Vegetation (N=44)	Mangrove (N=24)	Bank/Shelf Reef (N=13)	Bank/Shelf Vegetation (N=11)	Outer Lagoon Reef (N=12)	Outer Lagoon Vegetation (N=21)	Outer Lagoon Mangrove (N=12)	Inner Lagoon Reef (N=13)	Inner Lagoon Vegetation (N=12)	Inner Lagoon Mangrove (N=12)
Grammatidae	*Gramma loreto*	0.038	0.08	0.04	.	0.11	.	.	0.15	.	0.17	.	.	.	.	.
Apogonidae	*Apogon binotatus*	0.009	0.04	.	.	0.03	.	.	0.08	.	.	.	.	.	.	.
Malacanthidae	*Malacanthus plumieri*	0.028	0.13	.	.	0.03	0.05	.	0.08	0.18	.	.	.	.	.	.
Carangidae	*Caranx bartholomaei*	0.028	.	.	0.08	0.03	0.05	.	.	.	.	.	.	0.08	0.17	.
	Caranx crysos	0.009	.	0.02	.	.	0.02	.	.	.	.	0.05	.	.	.	.
	Caranx latus	0.038	.	0.07	0.03	.	.	0.17	.	.	.	.	0.25	.	.	0.08
	Caranx ruber	0.151	0.13	0.18	0.14	0.29	0.11	.	0.15	0.09	0.33	0.19	.	0.38	.	.
	Selar crumenophthalmus	0.009	0.04	.	.	0.03	.	.	0.08	.	.	.	.	.	.	.
Lutjanidae	*Lutjanus apodus*	0.292	0.04	0.31	0.43	0.18	.	1.00	0.08	.	0.17	.	1.00	0.31	.	1.00
	Lutjanus griseus	0.104	.	0.09	0.19	0.05	.	0.38	.	.	0.08	.	0.25	0.08	.	0.50
	Lutjanus mahogani	0.028	.	0.04	0.03	0.03	.	0.08	.	.	.	.	0.17	0.08	.	.
	Lutjanus synagris	0.047	0.04	0.02	0.08	0.05	0.07	.	0.08	.	.	0.05	..	0.08	0.17	.
	Ocyurus chrysurus	0.292	0.29	0.29	0.30	0.47	0.16	0.25	0.54	.	0.50	0.10	0.42	0.38	0.42	0.08
Gerreidae	*Eucinostomus melanopterus*	0.123	.	0.13	0.19	.	.	0.54	.	.	.	.	0.50	.	.	0.58
	Gerres cinereus	0.075	.	0.02	0.19	0.05	.	0.25	.	.	0.08	.	.	0.08	.	0.50
Haemulidae	*Anisotremus virginicus*	0.038	.	.	0.11	0.03	.	0.13	.	.	.	.	.	0.08	.	0.25
	Haemulon aurolineatum	0.047	0.04	0.04	0.05	0.08	0.02	0.04	0.08	.	0.08	.	0.08	0.08	0.08	.
	Haemulon carbonarium	0.009	.	.	0.03	0.03	.	.	.	.	.	.	.	0.08	.	.
	Haemulon chrysargyreum	0.009	.	.	0.03	0.03	.	.	.	.	.	.	.	0.08	.	.
	Haemulon flavolineatum	0.311	0.21	0.31	0.38	0.34	.	0.83	0.38	.	0.33	.	0.83	0.31	.	0.83
	Haemulon macrostomum	0.028	.	0.04	0.03	0.05	.	0.04	.	.	0.08	.	0.08	0.08	.	.
	Haemulon plumieri	0.104	0.08	0.07	0.16	0.16	0.09	0.04	0.15	.	0.08	0.10	.	0.23	0.17	0.08
	Haemulon sciurus	0.236	0.04	0.18	0.43	0.21	0.07	0.58	0.08	.	0.17	0.05	0.42	0.38	0.17	0.75
	Haemulon species	0.198	.	0.33	0.16	.	0.23	0.46	.	.	.	0.33	0.67	.	0.25	0.25
	Haemulon striatum	0.009	.	0.02	.	.	0.02	.	.	.	.	0.05	.	.	.	.
Sparidae	*Archosargus rhomboidalis*	0.019	.	.	0.05	.	.	0.08	.	.	.	.	.	.	.	0.17
	Calamus pennatula	0.038	0.13	.	0.03	0.08	0.02	.	0.15	0.09	.	.	.	0.08	.	.

APPENDIX 1 (Continued)

		TOTAL	ZONE			STRUCTURE			STRATUM							
	Taxon	Cummulative Frequency (N=106)	Bank/Shelf (N=24)	Outer Lagoon (N=45)	Inner Lagoon (N=37)	Reef/Hardbottom (N=38)	Vegetation (N=44)	Mangrove (N=24)	Bank/Shelf Reef (N=13)	Bank/Shelf Vegetation (N=11)	Outer Lagoon Reef (N=12)	Outer Lagoon Vegetation (N=21)	Outer Lagoon Mangrove (N=12)	Inner Lagoon Reef (N=13)	Inner Lagoon Vegetation (N=12)	Inner Lagoon Mangrove (N=12)
Sciaenidae	*Equetus punctatus*	0.009	0.04	.	.	0.03	.	.	0.08	.	.	.	.	.	.	.
	Odontoscion dentex	0.009	.	.	0.03	0.03	.	.	.	.	.	.	.	0.08	.	.
Mullidae	*Mulloidichthys martinicus*	0.047	.	0.09	0.03	0.05	.	0.13	.	.	0.08	.	0.25	0.08	.	.
	Pseudupeneus maculatus	0.217	0.42	0.11	0.22	0.50	0.09	.	0.62	0.18	0.33	0.05	.	0.54	0.08	.
Kyphosidae	*Kyphosus sectatrix*	0.009	.	.	0.03	0.03	.	.	.	.	.	.	.	0.08	.	.
Ephippidae	*Chaetodipterus faber*	0.009	.	0.02	.	0.03	.	.	.	.	0.08	.	.	.	.	.
Chaetodontidae	*Chaetodon capistratus*	0.462	0.50	0.42	0.49	0.82	0.02	0.71	0.92	.	0.92	.	0.67	0.62	0.08	0.75
	Chaetodon striatus	0.057	0.08	.	0.11	0.16	.	.	0.15	.	.	.	.	0.31	.	.
Pomacanthidae	*Holacanthus ciliaris*	0.047	0.04	0.07	0.03	0.13	.	.	0.08	.	0.25	.	.	0.08	.	.
	Holacanthus tricolor	0.009	0.04	.	.	0.03	.	.	0.08	.	.	.	.	.	.	.
	Pomacanthus arcuatus	0.075	0.04	0.04	0.14	0.18	.	0.04	0.08	.	0.17	.	.	0.31	.	0.08
	Pomacanthus paru	0.009	.	0.02	.	0.03	.	.	.	.	0.08	.	.	.	.	.
Pomacentridae	*Abudefduf saxatilis*	0.179	.	0.18	0.30	0.08	.	0.67	.	.	0.17	.	0.50	0.08	.	0.83
	Abudefduf taurus	0.009	.	.	0.03	.	.	0.04	.	.	.	.	.	.	.	0.08
	Chromis multilineata	0.009	0.04	.	.	0.03	.	.	0.08	.	.	.	.	.	.	.
	Microspathodon chrysurus	0.104	0.17	0.13	0.03	0.29	.	.	0.31	.	0.50	.	.	0.08	.	.
	Stegastes diencaeus	0.085	0.13	0.09	0.05	0.18	.	0.08	0.23	.	0.25	.	0.08	0.08	.	0.08
	Stegastes dorsopunicans	0.160	0.04	0.09	0.32	0.42	.	0.04	0.08	.	0.33	.	.	0.85	.	0.08
	Stegastes leucostictus	0.519	0.17	0.60	0.65	0.63	0.18	0.96	0.31	.	0.83	0.29	0.92	0.77	0.17	1.00
	Stegastes partitus	0.226	0.54	0.13	0.14	0.58	0.05	.	0.85	0.18	0.50	.	.	0.38	.	.
	Stegastes planifrons	0.208	.	0.27	0.27	0.53	.	0.08	.	.	1.00	.	.	0.62	.	0.17
	Stegastes variabilis	0.028	0.04	.	0.05	0.08	.	.	0.08	.	.	.	.	0.15	.	.
Sphyraenidae	*Sphyraena barracuda*	0.160	.	0.16	0.27	.	.	0.71	.	.	.	.	0.58	.	.	0.83
	Sphyraena picudilla	0.009	.	0.02	.	.	.	0.04	.	.	.	.	0.08	.	.	.
Labridae	*Bodianus rufus*	0.009	.	0.02	.	0.03	.	.	.	.	0.08	.	.	.	.	.
	Clepticus parrae	0.009	0.04	.	.	0.03	.	.	0.08	.	.	.	.	.	.	.

APPENDIX 1 (Continued)

		TOTAL	ZONE			STRUCTURE			STRATUM							
	Taxon	Cummulative Frequency (N=106)	Bank/Shelf (N=24)	Outer Lagoon (N=45)	Inner Lagoon (N=37)	Reef/Hardbottom (N=38)	Vegetation (N=44)	Mangrove (N=24)	Bank/Shelf Reef (N=13)	Bank/Shelf Vegetation (N=11)	Outer Lagoon Reef (N=12)	Outer Lagoon Vegetation (N=21)	Outer Lagoon Mangrove (N=12)	Inner Lagoon Reef (N=13)	Inner Lagoon Vegetation (N=12)	Inner Lagoon Mangrove (N=12)
Labridae (cont.)	*Halichoeres bivittatus*	0.255	0.50	0.20	0.16	0.29	0.32	0.08	0.31	0.73	0.17	0.24	0.17	0.38	0.08	.
	Halichoeres garnoti	0.104	0.42	0.02	.	0.26	0.02	.	0.69	0.09	0.08	.	.	.	.	.
	Halichoeres maculipinna	0.066	0.04	0.04	0.11	0.18	.	.	0.08	.	0.17	.	.	0.31	.	.
	Halichoeres poeyi	0.142	0.29	0.11	0.08	0.11	0.25	.	.	0.64	0.08	0.19	.	0.23	.	.
	Halichoeres radiatus	0.057	0.08	.	0.11	0.16	.	.	0.15	.	.	.	.	0.31	.	.
	Lachnolaimus maximus	0.019	.	0.02	0.03	0.05	.	.	.	.	0.08	.	.	0.08	.	.
	Thalassoma bifasciatum	0.292	0.46	0.24	0.24	0.68	0.07	0.08	0.62	0.27	0.83	.	0.08	0.62	.	0.08
	Xyrichthys martinicensis	0.066	0.29	.	.	0.03	0.14	.	0.08	0.55	.	.	.	.	.	.
	Xyrichthys splendens	0.019	0.08	.	.	.	0.05	.	.	0.18	.	.	.	.	.	.
Scaridae	*Cryptotomus roseus*	0.104	0.33	0.04	0.03	0.03	0.23	.	0.08	0.64	.	0.10	.	.	0.08	.
	Scarus croicensis	0.509	0.42	0.44	0.65	0.87	0.18	0.54	0.77	.	1.00	0.14	0.42	0.85	0.42	0.67
	Scarus taeniopterus	0.094	0.21	0.09	0.03	0.26	.	.	0.38	.	0.33	.	.	0.08	.	.
	Sparisoma atomarium	0.160	0.33	0.13	0.08	0.26	0.14	0.04	0.31	0.36	0.33	0.05	0.08	0.15	0.08	.
	Sparisoma aurofrenatum	0.283	0.50	0.27	0.16	0.79	.	.	0.92	.	1.00	.	.	0.46	.	.
	Sparisoma chrysopterum	0.047	.	0.07	0.05	0.08	.	0.08	.	.	0.08	.	0.17	0.15	.	.
	Sparisoma radians	0.406	0.29	0.36	0.54	0.26	0.50	0.46	0.08	0.55	0.17	0.43	0.42	0.54	0.58	0.50
	Sparisoma rubripinne	0.038	.	.	0.11	0.11	.	.	.	.	.	.	.	0.31	.	.
	Sparisoma viride	0.274	0.21	0.27	0.32	0.63	0.02	0.17	0.38	.	0.83	.	0.17	0.69	0.08	0.17
Opistognathidae	*Opistognathus aurifrons*	0.028	0.13	.	.	0.05	0.02	.	0.15	0.09	.	.	.	.	.	.
Clinidae	*Clinid species*	0.019	.	0.04	.	.	0.02	0.04	.	.	.	0.05	0.08	.	.	.
	Malacoctenus macropus	0.075	0.04	0.11	0.05	.	0.14	0.08	.	0.09	.	0.14	0.17	.	0.17	.
	Malacoctenus triangulatus	0.038	0.04	.	0.08	0.08	.	0.04	0.08	.	.	.	.	0.15	.	0.08
Blenniidae	*Ophioblennius atlanticus*	0.009	.	0.02	.	0.03	.	.	.	.	0.08	.	.	.	.	.
Gobiidae	*Coryphopterus glaucofraenum*	0.340	0.13	0.36	0.46	0.34	0.39	0.25	0.15	0.09	0.33	0.33	0.42	0.54	0.75	0.08
	Coryphopterus personatus	0.019	.	0.04	.	0.05	.	.	.	.	0.17	.	.	.	.	.
	Coryphopterus species	0.009	.	.	0.03	.	0.02	.	.	.	.	.	.	.	0.08	.
	Gnatholepis thompsoni	0.038	0.13	0.02	.	0.05	0.05	.	0.15	0.09	.	0.05	.	.	.	.

APPENDIX 1 (Continued)

		TOTAL	ZONE			STRUCTURE			STRATUM							
	Taxon	Cummulative Frequency (N=106)	Bank/Shelf (N=24)	Outer Lagoon (N=45)	Inner Lagoon (N=37)	Reef/Hardbottom (N=38)	Vegetation(N=44)	Mangrove (N=24)	Bank/Shelf Reef (N=13)	Bank/Shelf Vegetation (N=11)	Outer Lagoon Reef (N=12)	Outer Lagoon Vegetation (N=21)	Outer Lagoon Mangrove (N=12)	Inner Lagoon Reef (N=13)	Inner Lagoon Vegetation (N=12)	Inner Lagoon Mangrove (N=12)
Gobiidae (cont.)	*Gobionellus saepepallens*	0.038	0.04	0.07	.	.	0.07	0.04	.	0.09	.	0.10	0.08	.	.	.
	Gobiosoma evelynae	0.038	0.13	0.02	.	0.11	.	.	0.23	.	0.08	.	.	.	.	.
	Gobiosoma genie	0.038	0.04	.	0.08	0.11	.	.	0.08	.	.	.	.	0.23	.	.
	Gobiosoma species	0.009	.	0.02	.	.	.	0.04	.	.	.	.	0.08	.	.	.
	Ioglossus helenae	0.019	0.04	0.02	.	.	0.05	.	.	0.09	.	0.05	.	.	.	.
	Lophogobius cyprinoides	0.009	.	0.02	.	.	.	0.04	.	.	.	.	0.08	.	.	.
	Nes Longus	0.009	.	.	0.03	0.03	.	.	.	.	.	.	.	0.08	.	.
Acanthuridae	*Acanthurus bahianus*	0.472	0.54	0.42	0.49	0.84	0.23	0.33	0.77	0.27	0.92	0.19	0.33	0.85	0.25	0.33
	Acanthurus chirurgus	0.132	.	0.04	0.32	0.26	.	0.17	.	.	0.17	.	.	0.62	.	0.33
	Acanthurus coeruleus	0.236	0.21	0.36	0.11	0.47	0.02	0.25	0.31	0.09	0.83	.	0.50	0.31	.	.
Scombridae	*Scomberomorus regalis*	0.028	0.04	0.02	0.03	0.08	.	.	0.08	.	0.08	.	.	0.08	.	.
Balistidae	*Balistes vetula*	0.028	0.13	.	.	0.05	0.02	.	0.15	0.09	.	.	.	.	.	.
	Cantherhines pullus	0.009	.	0.02	.	0.03	.	.	.	.	0.08	.	.	.	.	.
	Monacanthus ciliatus	0.019	0.04	.	0.03	.	0.05	.	.	0.09	.	.	.	.	0.08	.
	Monacanthus tuckeri	0.019	0.08	.	.	.	0.05	.	.	0.18	.	.	.	.	.	.
Ostraciidae	*Lactophrys triqueter*	0.009	.	0.02	.	0.03	.	.	.	.	0.08	.	.	.	.	.
Tetraodontidae	*Canthigaster rostrata*	0.142	0.25	0.13	0.08	0.29	0.05	0.08	0.31	0.18	0.33	.	0.17	0.23	.	.
	Sphoeroides spengleri	0.066	0.13	0.07	0.03	0.03	0.14	.	.	0.27	.	0.14	.	0.08	.	.
	Sphoeroides testudineus	0.057	.	.	0.16	.	0.02	0.21	.	.	.	.	.	.	0.08	0.42
Diodontidae	*Diodon hystrix*	0.009	.	.	0.03	0.03	.	.	.	.	.	.	.	0.08	.	.