The Significance of Adjacent Habitats on Reef Fish Assemblage Structure: Are Relationships Detectable and Quantifiable at a Landscape-Scale?

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ABSTRACT

Shallow tropical marine habitats are being degraded at an alarming rate and new science-based approaches are needed to reverse this trend in order to ensure their long-term conservation. Landscape ecology principles, though rarely tested in marine systems, have proven extremely useful in addressing "real-world" management issues in terrestrial systems. In fact, the successful design and management of many terrestrial reserves is largely dependent on insights gained from the application of landscape-level analyses. Tropical coral reef ecosystems, which exist as a complex mosaic of interacting habitats, e.g., fringing reefs, surrounding seagrass patches and mangrove stands, may be well suited for study using a landscape ecology approach. We explored the utility of two terrestrially proven landscape metrics; a measure of adjacent habitat diversity and measures of the areal coverage of critical adjacent habitats, to predict specific characteristics of reef fish assemblage structure. Adjacent habitat diversity was not a good predictor of total fish abundance or of species richness. However, the areal coverage of specific habitat types, seagrass in particular, was positively related to the abundance of several groups of commonly exploited fishes. Preliminary results suggest that this approach might be used to facilitate the design of marine protected areas, and thus will be of interest to a broad group of marine ecologists and resource managers.

KEY WORDS: Marine Protected Areas, seagrass habitat, coral reef fishes

La Significación del Habitat de Seagrass a las Ensambladuras de los Pescados del Arrecife Coralino: ¿Son los Efectos Perceptibles y Cuantificables en una Escala del Paisaje?

Al decidir a donde localizar las áreas protegidas marinas (MPAs), es esencial que los encargados de recurso entienden cómo su funcionamiento se pudo influenciar por el arreglo de los habitat interior y exterior sus fronteras. Hacia este extremo, un acercamiento de la ecología del paisaje fue probado en St. Juan, islas de la Virgen de los E.E.U.U. para del como los medios de predecir > los hotspots = la abundancia de los pescados del filón y diversidad en una escala apropiada el diseño de MPA y gerencia. Los mapas recientemente desarrollados, digitales usados para cuantificar la distribución espacial del mosaico complejo de los habitat asociados con arrecifes (e.g., arrecife, camas de los seagrass, mangles) eran la fundación para desarrollar un espacial-estratificado y análisis robusto para estudiar estadístico la relación entre los parámetros seleccionados de la ensambladura de los pescados del filón y características del habitat traz de imágenes aéreas. Específicamente, deseamos determinarnos si los habitat adyacentes tales como el área total de los seagrass adyacentes o en proximidad cercana a los arrecifes se puedan utilizar para predecir parámetros de la ensambladura de los pescados del filón. En veinte arrecifes discretos (10 que franjan y el remiendo 10), seleccionados basado en un gradiente del punto bajo al alto grado regional de seagrass, las cuentas visuales al azar-generadas del punto de los pescados del filón fueron conducidas. Los resultados preliminares apoyan nuestras hipótesis generales que la riqueza y la abundancia totales de la especie, tan bien como la estructura de la abundancia, de la diversidad y del tamaño de la especie apuntada, es decir, roncos, groupers y snappers, crecientes con el grado regional (m^2) de seagrass adyacente al filón remiende. La fuerza de esta relación creciente como el grado regional de seagrass en cuatro distancias de los arrecifes del estudio (es decir, 100, 250, 500 y el 1000 m) aumentó. Los resultados finales son probables confirmar la importancia de los acoplamientos del habitat entre los seagrass y las comunidades del filón coralino, proporcionando la justificación científica para la inclusión del habitat de los seagrass en MPAs para proteger la conectividad del habitat requerida para diversas etapas de la historia de la vida de los pescados del filón.

PALABRAS CLAVES: Las áreas protegidas marinas, habitat de los seagrass, el filón coralino pescan.

INTRODUCTION

The management of tropical marine environments calls for radical large-scale approaches that require collaboration beyond traditional fields (Murray et al.1999, Allison et al. 1998, Bell et al. 1997). Landscape ecology is interdisciplinary by nature, with a focus on patterns and ecological processes that occur over broad spatial scales (Forman and Godron 1986). A landscape refers to a heterogeneous area composed of interacting ecosystems (Forman 1995) made up of homogenous units called habitat patches. Habitat patches can differ in their size and structure with consequences on the distribution and abundance of species. The spatial arrangement (i.e. pattern) of habitat patches within the landscape, in turn, influences the function of that landscape, particularly with regard to the flow of energy through interacting ecosystems and among habitat patches. Through the use of georeferenced maps of vegetation, soils and elevation, terrestrial landscapes have been described with a number of metrics that incorporate such attributes as patch size, shape, and/or habitat complexity (Forman 1995, Turner 1989). Landscape metrics quantify large-scale habitat patterns and can be used to more fully understand ecological processes and, in some cases, predict responses such as dispersal success (Gustafson and Gardner 1996, Schumaker 1996), abundance (McGarigal and McComb 1995), distribution (With and Crist 1995), and survival probability (Fahrig 1997) of organisms.

Several landscape metrics have proven to be of value in the design and management of terrestrial reserves (e.g., Simberloff 1986; Diamond 1975; MacArthur and Wilson 1967) and similar metrics might be used to guide the development and implementation of marine protected areas (MPAs) in shallow tropical waters, especially if the responses of reef fishes to varying "seascapes" can be predicted with some degree of confidence. Until recently, we lacked the technology to test landscape ecology principles in marine systems. However, advances in subtidal mapping techniques provide the opportunity to explore the relationship between habitat patterns and species distribution (e.g., Irlandi et al. 1995, Robbins and Bell 1994, Bell and Hicks 1991). Coral reef environments exist as complex mosaics of interacting ecosystems (e.g., patch reefs, seagrass communities, sand, and fringing mangroves), which make them logical candidates for large-scale habitat-based conservation strategies (e.g., MPAs) (Wilkinson 2000, Allison et al. 1998).

Large-scale measures of habitat diversity have been positively correlated with terrestrial species richness and abundance of birds, butterflies, reptiles and amphibians (Ricklefs and Lovette 1999, Rosenzweig 1995, Rafe et al. 1985) and with more complex trophic structures (Rahbek and Graves 2001) in virtually all terrestrial ecosystems (Huston 1979), proving useful in selection of conservation reserves. Spatially and temporally diverse areas are considered superior to homogenous areas (Meffe and Carroll 1997), in part because the species-area relationship is thought to be related to habitat diversity. As size of an area increases, so does the diversity of habitat types (Lack 1976, Williams 1943). Although landscape-scale measures of habitat diversity have yet to be tested in coral reef

ecosystems, fine-scale studies have demonstrated a positive relationship with reef fish diversity and abundance and habitat heterogeneity, measured by parameters such as spatial complexity (Hixon and Beets 1989), living coral (Reese 1981), coral reef zonation (Friedlander and Parrish 1998), and reef surface area (Gladfelter et al. 1980).

This study is one of the first to explore the utility of landscape ecology principles as predictors of species distribution and abundance in coral reef environments. Existing reef fish census data made available through the Virgin Islands National Park, St. John, United States Virgin Islands (USVI), were used to examine the relationship of landscape metrics that describe the spatial distribution of benthic habitats with reef fish assemblage parameters of interest to resource managers. Two questions were addressed:

i)   Is habitat diversity, at the landscape-scale, a good predictor of the abundance or richness of reef-associated fishes? and

ii)   Are landscape-scale metrics of the areal coverage of specific habitat types (e.g., measures of the area of seagrass or hard-bottom) predictors of abundances of reef fishes within trophic guilds and/or specific taxa of reef fishes?

To validate the use of the existing reef fish data, a separate *heterogeneity* study was conducted in 2002 to ensure that our dataset did not violate assumptions inherent to a landscape ecology approach.

METHODS

Existing reef fish monitoring data from St. John, USVI was used to explore the relationship of large-scale measures of habitat diversity and the areal extent of specific habitats with reef fish assemblage structure parameters of interest to resource managers. Of 20 reef fish monitoring sites available, only 11 reefs with similar characteristics, i.e. depth, reef morphology, and dominant live coral (*Montastraea annularis*), were selected for further analysis to reduce variability associated with reef characteristics and to enhance the ability to detect variation associated with landscape features (Figure 1). Reef fish monitoring sites were determined to be sub-sections of larger mapped reef polygons. To account for the possible bias of sampling a section of a larger mapped polygon, reef polygons were modified using ArcView 3.2 to reflect the standardized 25,000-m^2 sub-sections where fish data were collected (ESRI 1996). In addition, a heterogeneity study was conducted in 2002 to determine whether reef fish assemblage structure differed between reef sections and entire polygons. Several precautions helped ensure assumptions inherent to a landscape ecology approach were not violated. First, landscape metrics were calculated with respect to polygon sections where fish data were collected. Second, the areal extent of reef (including adjacent reef) and original reef polygon size were tested as habitat variables. Third, since patch dynamics are predicated on assumptions of similar patch shape, a paired sample T-

test was used to test whether the Perimeter to Area ratio (P: A) of the reef sections differed significantly from the P:A ratio of original polygons (Zar 1984).
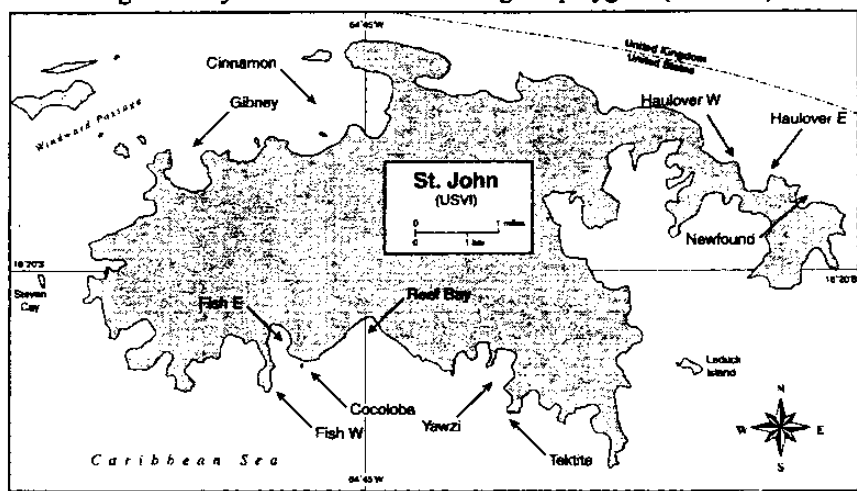

Figure 1. Location of 11 study reefs around the island of St. John, United States Virgin Islands.

Landscape metrics were calculated with ArcView 3.2 software (ESRI 1996) using benthic habitat maps created from aerial photographs acquired in 1999 (Kendall et al. 2001). The original map classification scheme (see Kendall et al. 2001) was condensed from 27 to 9 distinct and non-overlapping habitat classes, i.e. mud, mangrove, sand, reef, hard-bottom, bedrock, seagrass, macroalgae and deep water, to be more broadly applicable for resource managers. Reefs served as focal units, since MPAs are typically designed around individual reefs. A buffer was placed at 100 m (to include the daily range of most reef fishes) from the leading edge of the reef. Buffer shape files and the modified benthic habitat maps were intersected to quantify landscape metrics for each reef (Table 1).

Reef-associated fishes were sampled in 1994 (Beets and Friedlander, unpubl. data) using a modified point count census method (see Bohnsack and Bannerot 1986). The modification involved a reduction in the sample radius from 7.5 m to 5.0 m. In 2002, reef-associated fishes were sampled using the originally described point count method (see Bohnsack and Bannerot 1986). During both data collection efforts, standard lengths of fishes were estimated to the nearest cm. Mean abundance values based on replicate samples at each reef site were calculated and used in subsequent analyses, whether by taxa or trophic guild. Randall (1967) and FishBase (2002) were used as references to classify fishes as either piscivores, herbivores, mobile invertebrate feeders (MIFs), sessile invertebrate feeders (SIFs), planktivores or omnivores. Taxonomic groupings of fishes for commercially and recreationally important species were also examined. Fishes were further subdivided into juvenile and adult categories.

Table 1. Landscape metrics, habitat diversity and areal coverage (ha) of major habitat types, within 100 m of each reef. Areal coverage of mud and mangrove were not included as these habitats were largely absent at the 11 study sites.

	Newfound	Cinn	Cocco	Haul E	Haul W	Gibney	Tektite	Yawzl	Reef W	Fish E	Fish W
Reef size	9.33	7.86	6.92	9.33	7.48	0.54	5.57	4.06	6.92	15.74	10.95
Habitat diversity (H')	0.48	0.41	0.54	0.44	0.67	0.23	0.59	0.43	0.56	0.61	0.47
Reef	10.38	12.0	5.2	8.58	3.67	0.82	3.16	3.20	3.09	4.41	3.69
Seagrass	0.97	0	4.37	0	1.02	5.46	3.16	7.81	1.78	0.31	0
Hard-bottom	9.87	9.24	8.29	12.14	4.98	1.07	5.59	5.34	8.89	7.98	6.52
Bedrock	0.16	0	1.75	0	0.75	0	2.53	1.07	0	3.56	2.83
Sand	0	0	0	0	3.98	0	0	0	6.03	2.22	4.54
Macro-algae	< 0.01	3.42	0	0	0	0	0	0	0	1.48	< 0.01
Deep-water	2.02	0	0	3.91	1.98	0	1.92	0	0	0	0

Habitat Diversity

To test the hypothesis that landscape-scale habitat diversity (H') is a positive predictor of entire assemblage parameters, a modified Shannon-Weiner index (Krebs 1989) was employed using the following equation:

$$H' = -\Sigma p_i \log p_i \text{ (eq. 1)}$$

where the proportion of area of each habitat type i within 100 m of the focal reef is summed for all habitat types. For each 25,000 m² reef section, at least 16 modified point counts per replicate reef were located haphazardly in July 1994, using the same five observers. Simple linear regression was conducted using the reef fish parameter of interest as the dependent variable (e.g., species richness, total abundance) and habitat diversity (H') within 100 m as the independent variable.

Adjacent Habitats

To test hypotheses that landscape metrics that quantify the areal coverage of a specific habitat are positive predictors of abundances of reef-associated fishes by taxa or within trophic guilds, stepwise multiple regression analyses was conducted. The areal coverage of the seven major habitat types within 100 m of each reef was used as independent variables for each of the dependent reef fish variables. P-values for accepting a variable into the model was set at p < 0.15 to reduce Type II error. Results of stepwise multiple regression analyses were used to test simple linear regression relationships between habitat types and reef fish assemblage parameters accepted into the stepwise regression model.

Heterogeneity Study

To ascertain the validity of using the existing 1994 dataset, random reef fish samples were conducted in 2002 at the two largest monitoring reef sites, i.e. Newfound Reef (93,300 m²) and Coccoloba Reef (69,200 m²). Each polygon contained two monitoring sites (e.g., Newfound polygon is comprised of Newfound and Haulover East, Coccoloba polygon has Coccoloba Reef and Reef Bay). Each polygon was redigitized in ArcView and divided into three sections at Coccoloba Reef and four sections for Newfound Reef, of approximately equal sizes to determine whether there were significant differences in reef fish abundances between different, but approximately equal-sized sections of a single mapped reef polygon. Differences in reef fish parameters between reef sections and entire polygons were tested using a Poisson Chi-square statistic with a 0.05 level of significance.

RESULTS

Habitat Diversity (H')

Simple linear regression analyses revealed no detectable relationship between H' and entire assemblage level parameters (e.g., species richness and total

reef fish abundance) (Table 2, Figure 2). H' values ranged from 0.23 to 0.67 for the 11 reefs, but this intermediate range in variability of H' may have constrained a more robust analysis (Figure 2). There was a negative relationship between H' and mean abundance of juvenile herbivores and SIFs (Table 2, Figure 3).   There was a statistically significant, negative relationship between H' and juvenile serranids, juvenile haemulids and juvenile scarids (Table 2, Figure 4).   There was no statistically significant positive relationship for any reef fish assemblage level parameter of interest (e.g., entire assemblage level parameters, trophic guilds or commercially and recreationally important taxa, except a weak positive relationship with mean abundance of juvenile piscivores) with landscape-scale measures of H' at this scale (Table 2).

Table 2. Results of linear regression analyses indicating the relationship between habitat diversity and reef fish assemblage parameters.   Parameter estimates for statistically significant (p < 0.15) regressions are given.

Fish parameter	R^2	p-value	Parameter estimate
Total abundance	<0.01	NS	
Species richness	0.03	NS	
J SIF	0.57	<0.01	-4.96
A SIF	0.10	NS	
J herbivores	0.35	0.06	-43.53
A herbivores	0.04	NS	
J MIF	<0.01	NS	
A MIF	0.009	NS	
J piscivores	0.29	0.08	18.71
A piscivores	<0.01	NS	
J serranids	0.37	0.04	-2.95
A serranids	0.00	NS	
J haemulids	0.44	0.03	-55.24
A haemulids	<0.01	NS	
J lutjanids	0.01	NS	
A lutjanids	0.04	NS	
J scarids	0.26	0.11	-53.25
A scarids	0.04	NS	
J acanthurids	0.06	NS	
A acanthurids	0.09	NS	

NS = Not Significant; SIF = Sessile Invertebrate Feeders; MIF = Mobile Invertebrate Feeders; J = Juvenile; A = Adult

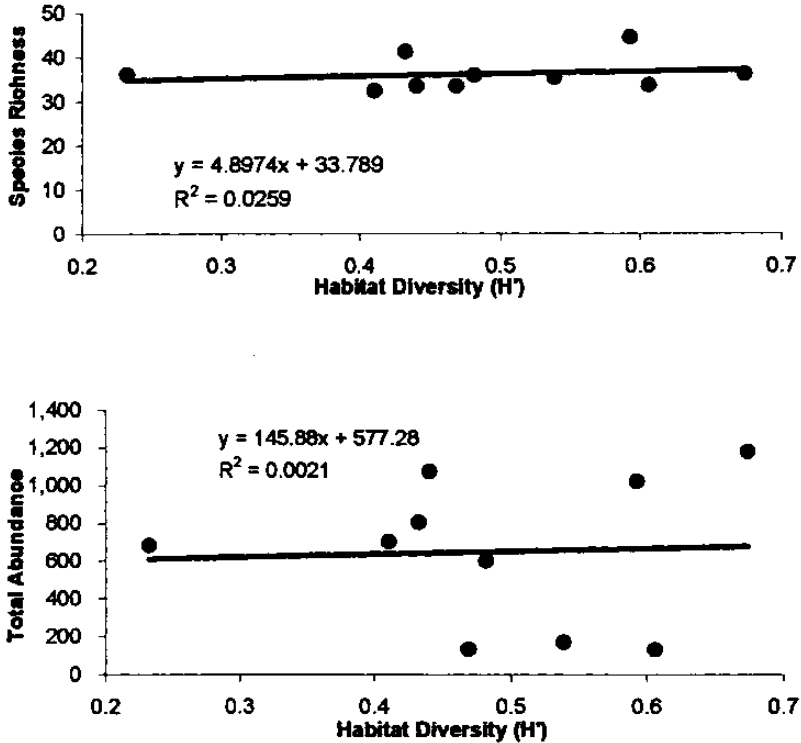y = 4.8974x + 33.789
R² = 0.0259

y = 145.88x + 577.28
R² = 0.0021

Figure 2. Relationship of habitat diversity (H') within 100 m of study reefs (n=10) and species richness and total fish abundance at St. John, United States Virgin Islands.

Juvenile Herbivores

$y = -43.413x + 78.356$
$R^2 = 0.3471$

Juvenile Piscivores

$y = 18.232x - 5.3964$
$R^2 = 0.2791$

Mobile Invert Feeders (juvenile and adult)
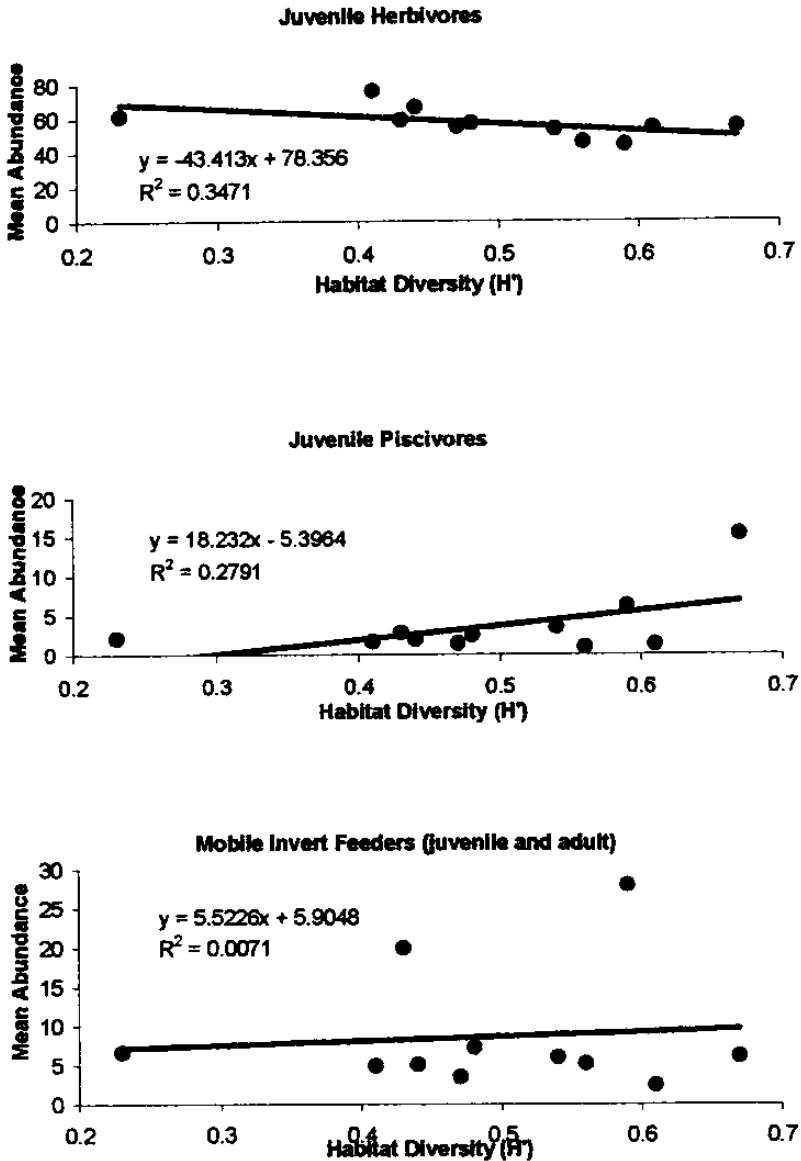

$y = 5.5226x + 5.9048$
$R^2 = 0.0071$

Figure 3. Simple linear regression results of habitat diversity (H') within 100 m and mean abundance within trophic guilds, divided into juvenile and adult components, sampled on 11 reefs around St. John, United States Virgin Islands.
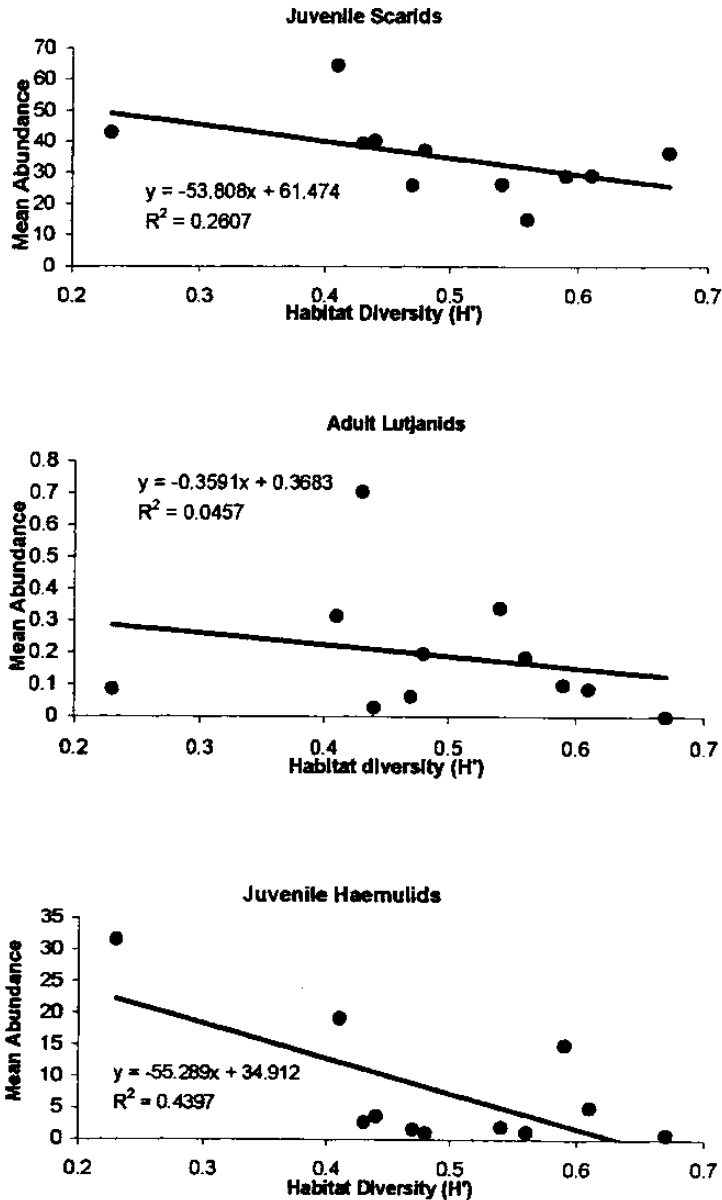
Juvenile Scarids

$$y = -53.808x + 61.474$$
$$R^2 = 0.2607$$

Adult Lutjanids

$$y = -0.3591x + 0.3683$$
$$R^2 = 0.0457$$

Juvenile Haemulids

$$y = -55.289x + 34.912$$
$$R^2 = 0.4397$$

Figure 4. Simple linear regression results of habitat diversity (H') within 100 m and mean abundance within taxonomic groupings, divided into juvenile and adult components sampled on 11 reefs around St. John, United States Virgin Islands.

Adjacent Habitats

Stepwise multiple regressions revealed positive relationships between reef fish assemblage parameters (e.g., total abundance and species richness) with landscape-scale measures of the areal coverage of surrounding habitats (Table 3, Figure 5). Entire assemblage parameters were positively correlated with the total areal coverage of seagrass within 100 m (Table 3). Adult MIFs were positively correlated with the areal coverage of seagrass (Table 3). In addition, some taxonomic groups that we predicted based on their life history to be associated with seagrass habitat, were positively correlated with areal coverage of seagrass, including adult serranids, adult haemulids, and adult lutjanids (Table 3, Figures 5 and 6). Juvenile lutjanids were positively correlated with areal coverage of seagrass and deep-water habitats and juvenile serranids were positively correlated with areal coverage of reef habitat (Table 3). To check for spurious correlations, we verified that there were no relationships between specific taxa and habitats for which a relationship was not expected (e.g., SIFs and seagrass). For statistically significant multiple regression parameters, linear regressions illustrate relationships (Figures 5 and 6).

Heterogeneity Study

There were no statistically significant differences for entire assemblage level or trophic level measures when comparisons were made between entire reef polygons and reef sections (i.e. the historic monitoring sites). However, at Newfound Reef, there were significant differences in mean abundance of lutjanids, haemulids, scarids and labrids between reef sections (W and/or E) and the entire reef polygon (A); there were no statistically significant differences for other reef sections (Table 4). At Coccoloba Reef, only haemulids were found to differ in abundance between reef sections (Table 5). Reef shape, as reflected by the P:A ratio, was not significantly modified as a consequence of standardizing reef area (t = 4.23, df = 10, p = 0.77).

DISCUSSION

Habitat Diversity

A strong experimental approach to reef fish ecology has historically resulted in studies at a small spatial scale (e.g., meter plots), leading reef ecologists to conclude that habitat diversity (defined by various measures of benthic community structure, complexity and reef rugosity) is a predictor of reef fish assemblage structure (Sale 2002, Hixon and Beets 1989, Reese 1981). Our empirical results suggest that, contrary to predictions, habitat diversity as a predictor of reef fish assemblage structure may not scale up at the landscape level (i.e. 100's of meters scale). Therefore, landscape-scale measures of habitat diversity may not prove useful in discerning the value of individual reefs as candidates for protection. In fact, there was frequently a negative relationship between habitat diversity within 100 m and abundances of specific trophic guilds and taxa. We note, however, that at an even larger spatial scale (e.g., at the scale of tens of kilometers), NOAA's Biogeography

Team has demonstrated a positive relationship between reef fish diversity and abundance and habitat diversity (J. Christensen, NOAA, pers. comm.). This larger scale measure of habitat diversity, however, appears to be useful in that it predicts the location of reef habitat (where reef habitat exists is typically the highest abundance and diversity of reef-associated fishes).

Table 3. Results of stepwise multiple regression analyses. Input variables consist of each of the habitat types: hard-bottom, reef, bedrock, seagrass, macroalgae, sand, deep-water and mud, which occur within 100 m of each reef. Parameter estimates for statistically significant (p > 0.15) regressions are given. All parameter estimates are positive except where indicated by a negative sign in parentheses.

Fish parameter	R²	p -value	Habitat estimate
Total abundance	0.16	0.02	Seagrass
Species richness	0.42	<0.01	Seagrass
J SIF	0.79	<0.01	Bedrock (-) Hard-bottom
A SIF	0.88	<0.01	Reef Hard-bottom (-)
J herbivores	0.56	0.04	Hard-bottom Reef
A herbivores	—	—	
J MIF	—	—	
A MIF	0.31	0.07	Seagrass
J piscivores	—	—	
A piscivores	—	—	
J planktivores	0.65	0.05	Reef Bedrock Deep-water
A planktivores	0.55	<0.01	Deep-water
J serranids	0.42	0.03	Reef
A serranids	0.34	0.06	Seagrass
J haemulids	0.47	0.08	Reef Hard-bottom
A haemulids	0.44	0.02	Seagrass
J lutjanids	0.95	<0.01	Seagrass Deep-water Bedrock (-)
A lutjanids	0.69	<0.01	Seagrass
J scarids	0.77	<0.01	Hard-bottom Reef
A scarids	—	—	—

SIF = Sessile Invertebrate Feeders; MIF = Mobile Invertebrate Feeders; J = Juvenile; A = Adult

Table 4.   Results from Newfound Reef to determine whether there was a statistically significant difference in the mean abundance of target taxa between the entire reef polygon (A, n = 33) with the subsections (West, n = 14 or East, n = 14) of the reef used in subsequent analyses. Deviations from a Poisson distribution were tested. Mean abundance and standard deviations, given in parentheses, are presented for each polygon. For labrids, only two species were included for analyses, the numerically dominant species *Thalassoma bifasciatum* and *Halichoeres bivittatus*

Taxa of Interest	Entire Polygon	Mean Abundance	Sub-section	Mean Abundance	SE	Pr. Chi-Square
lutjanids	A	1.77 (3.13)	E	0.71 (1.93)	0.3040	0.0029
	A	1.77 (3.13)	W	2.93 (4.34)	0.1830	0.0075
serranids	A	0.82 (0.98)	E	0.53 (0.72)	0.4300	0.2343
	A	0.82 (0.98)	W	0.71 (0.91)	0.3458	0.6561
haemulids	A	6.19 (25.86)	E	1.24 (2.66)	0.2241	0.0001
	A	6.19 (25.86)	W	16.00 (53.44)	0.0841	0.0001
scarids	A	19.05 (9.53)	E	22.29 (12.68)	0.0590	0.0001
	A	19.05 (9.53)	W	16.21 (7.44)	0.0725	0.1481
labrids	A	6.08 (5.67)	E	4.76 (6.21)	0.1225	0.0712
	A	6.08 (5.67)	W	8.50 (6.59)	0.1051	0.0008

Several factors may have affected our ability to detect relationships between landscape-scale measures of habitat diversity and reef fish assemblage structure parameters as defined in this study. The range in habitat diversity values, for example, may have been too restricted and not representative of the relationships across a broader range of values. In addition, fish censuses were conducted only within reef habitat. As a consequence, we only tested the influence of adjacent habitat diversity on a select assemblage of fishes, i.e. only those fishes directly associated with reef habitat during the day. It is possible that fine-scale measures of microhabitat heterogeneity (e.g., topographic complexity, benthic community composition such as the percent cover of specific algal and coral taxa, and reef morphology) within the reef habitat may be the more appropriate scale for describing and/or predicting measures such as total abundance and total species richness of benthic reef-associated fishes (see: Williams 1991). It is possible also, that our specific definition of landscape habitat diversity may not be the appropriate descriptor of the surrounding seascape, and may not capture elements such as the patchiness of discrete habitat patches, the types of different habitats or the spatial arrangement of those patches with respect to the focal reef. Finally, although a single index such as H' is appealing, it does not distinguish the functional benefits

of different habitat types (e.g., additional reef habitat versus sand which may be important foraging areas for goatfishes or grunts).
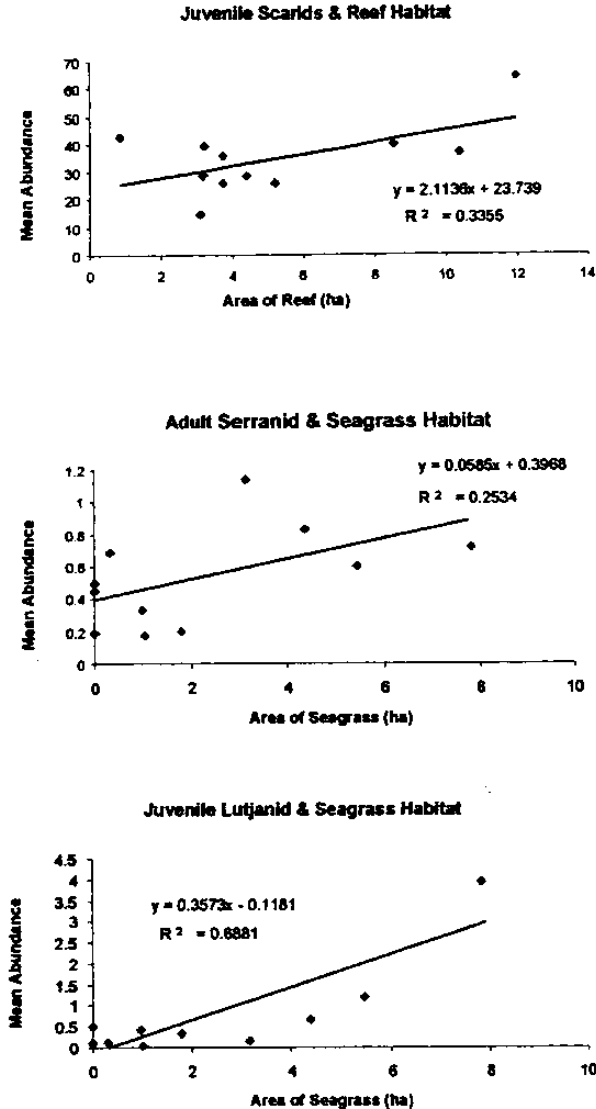
Juvenile Scarids & Reef Habitat

$y = 2.1136x + 23.739$

$R^2 = 0.3355$

Adult Serranid & Seagrass Habitat

$y = 0.0585x + 0.3968$

$R^2 = 0.2534$

Juvenile Lutjanid & Seagrass Habitat

$y = 0.3573x - 0.1181$

$R^2 = 0.6881$

Figure 5. Linear regression results of reef fish parameters that that were statistically significant in stepwise multiple regression analysis with areal coverage of specific habitat types sampled on 11 reefs around St. John, United States Virgin Islands.

Planktivores & Deepwater Habitat

$y = 0.0056x + 0.3351$

$R^2 = 0.632$

Mean Abundance

Area of Deepwater (ha)

Adult Lutjanids & Seagrass Habitat

$y = 0.1365x + 1.0002$

$R^2 = 0.428$

Mean Abundance

Area of Seagrass (ha)

Adult Haemulids & Seagrass Habitat

$y = 0.9942x + 1.024$

$R^2 = 0.4412$

Mean Abundance

Area of Seagrass (ha)

Figure 6.   Linear regression results of reef fish parameters that that were statistically significant in stepwise multiple regression analysis with areal coverage of specific habitat types sampled on 11 reefs around St. John, United States Virgin Islands.

Table 5. Results from Coccoloba Reef to determine whether there was a statistically significant difference in the mean abundance of target taxa between the entire reef polygon (A; n=33) with the subsections (West; n=14 or East; n=14)of the reef used in subsequent analyses. Deviations from a Poisson distribution were tested. Mean abundance and standard deviations, given in parentheses, are presented for each polygon. For labrids, only two species were included in analyses, the numerically dominant species *Thalasssoma bifasciatum* and *Halichoeres bivittatus.*

Taxa of Interest	Entire polygon	Mean Abundance	Sub-section	Mean Abundance	Standard Error	Pr Chi-Square
lutjanids	A	2.15 (3.51)	E	2.86 (4.04)	0.1977	0.1634
	A	2.15 (3.51)	W	2.21 (3.42)	0.2153	0.8716
serranids	A	0.55 (0.75)	E	0.50 (0.76)	0.4454	0.8451
	A	0.55 (0.75)	W	0.29 (0.47)	0.5528	0.2421
haemulids	A	5.36 (18.86)	E	11.79 (28.25)	0.1082	0.0001
	A	5.36 (18.86)	W	0.57 (0.76)	0.3615	0.0001
scarids	A	9.36 (5.04)	E	10.36 (4.73)	0.1007	0.2028
	A	9.36 (5.04)	W	8.5 (4.45)	0.1079	0.3045
labrids	A	28.21 (18.17)	E	23.86 (15.71)	0.0638	0.1499
	A	28.21 (18.17)	W	24.57 (8.17)	0.0631	0.5972

The negative relationship with H' for many taxa, however, suggests that single habitat types (e.g., essential habitats) may be better predictors of abundances of taxa associated with a particular habitat during some portion of their life histories. For instance, proximity of deep-water habitat may enhance the abundance of larvae recruiting to a reef. The amount of hard-bottom habitat adjacent to a particular reef may provide foraging habitat for schools of roving scarids, thereby allowing a reef to support higher abundances of these fishes. Bellwood and Wainwright (2002), for example, have suggested that non-reef areas are important for many fishes, both evolutionarily and ecologically. In this landscape-scale study, the amount and proximity of different non-reef habitat types (deep-water, seagrass communities, hard-bottom) to study reefs was frequently correlated with abundances of taxa associated with specific habitat types.

Adjacent Habitats

Historically, the context of a reef within the surrounding seascape has been largely ignored. Moreover, the relative importance and functional contribution of habitats adjacent to reef structures has been little studied (Sale 2002). Specific

habitat types (e.g., seagrass) are preferred by reef fishes for off-reef foraging or as settlement habitat. Moreover, these habitat preferences may change with ontogeny (Ogden 1998, Shulman and Ogden 1987). Though H' was not a consistent predictor of reef fish assemblage structure at these particular reefs, specific taxa were frequently correlated with those habitats for which an association was expected; particularly seagrass with adult haemulids, lutjanids and serranids. Tropical seagrass beds are important nursery and feeding grounds for coral reef fishes (Shulman and Ogden 1987, Ogden and Zieman 1977), critical habitats for larval settlement (Shulman and Ogden 1987, Ogden and Zieman 1977) and a source of food (e.g., benthic invertebrates) for some species of coral reef fishes (Randall 1963). The proximity of deep-water habitat was also positively associated with juvenile abundances of several taxa, which may suggest the importance of having a larval supply proximal to reef habitat. The total abundance of planktivores was also correlated with the areal coverage of deep-water habitat, perhaps due to the availability of plankton in the water column. Previous studies have demonstrated the relationship between planktivorous fishes and deep-water, although never before at this scale. Allen (1975) found that plankton feeding species of the damselfish genus *Chromis* were largely restricted to outer reef slopes, while Goldman and Talbot (1976) demonstrated that the proportion of plankton feeders was 2-4 times that of benthic invertivores on outer slopes of reef and suggested that this may be related to the greater availability of food due to strong currents. In our study, the areal coverage of hard-bottom and reef habitat was positively associated with sessile invertebrate feeders, such as pomacanthids, which forage on sessile invertebrates associated with hard-bottom habitat such as sponges and herbivores, which forage on algal species that colonize hard-bottom habitat. Our results are suggestive of the potential ecological importance of specific habitats at a landscape-scale. However, the relationships between individual habitat types and the abundances of taxa and life history stages suspected to be associated with these habitat types need to be more fully explored.

If critical habitats can be identified and quantified at a landscape-scale, then fisheries resource managers may use this information to help define characteristics of successful MPAs. Simberloff (1986) warned that the unwarranted focus on the supposed lessons of island biogeography theory detracted scientists away from the focal task of refuge planning, determining the critical habitats for the species of interest to resource managers and determining how to maintain them. Results from this research suggest the potential utility of landscape-scale measures of habitat to predict assemblage level parameters of interest to resource managers. Further experiments are needed to understand the functional linkages between specific habitats and their associated taxa. Understanding the effects of specific habitats and the arrangement of these habitats on abundance, movement, and growth of specific taxa is essential as we strive to manage these complex ecosystems.

Heterogeneity Study

Island biogeography theory assumes patches (or islands) are internally homogeneous and of equal size and quality, and that patches are either equally accessible to dispersing individuals or dispersal is restricted to adjacent patches (MacArthur and Wilson 1967). Analyses of the heterogeneity study reported herein confirm that reef polygons are not internally homogeneous; rather, there is within-patch heterogeneity, which is perceived by some taxa and not by others. For the purposes of this study, however, the 1994 reef fish dataset proved useful to explore the relationship of landscape metrics to reef fish assemblage structure. Future investigators that might employ a landscape approach are advised to representatively sample entire polygons to alleviate concerns or issues of within patch heterogeneity.

CONCLUSIONS

Habitat diversity, defined at a spatial scale on the order of 100's of meters, does not appear to be a positive predictor of entire assemblage level parameters of reef fishes in St. John, US Virgin Islands. The influence of specific and possibly essential habitat types on reef-associated fishes, however, may be detectable and quantifiable at a landscape-scale. The areal coverage of seagrass, hard-bottom, reef and deep-water habitats were positively correlated with the trophic guilds and taxa for which an association would be expected. The utility of landscape-scale habitat measures require further testing to determine whether they can predict abundances of trophic guilds and different life history stages of taxa, where prior ecological knowledge predicts an association with a particular habitat. The challenge will lie in testing the generalities of these initial findings with empirical datasets across systems..

The processes that structure reef fish communities occur across multiple spatial scales, and are influenced by both stochastic and density-dependent factors. Ecologists are increasingly looking at data from larger spatial and temporal scales to provide a framework for interpreting local patterns and small-scale experimental results (Bellwood and Wainwright 2002). This shift in scale is, in part, a response to the current degradation of coral reef communities, which calls for management-oriented research at spatial scales appropriate for resource managers (Sale 2002). The recent development of benthic habitat mapping technologies has provided an opportunity to study coral reef processes at large spatial scales. It is important, however, to determine whether state of the art mapping products are useful for decision making, specifically for designing and managing MPAs. If the benefits of essential fish habitats are both detectable and quantifiable at a landscape-scale, then benthic habitat mapping products may be used to delineate the boundaries of new MPAs or to better understand how an existing MPA functions. Our research contributes to the development of an emerging discipline, which will help understand both the benefits and the limitations of our state of the art mapping products and help resource managers apply this technology more appropriately.

ACKNOWLEDGEMENTS

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