

# Influence of landscape structure on reef fish assemblages

Rikki Grober-Dunsmore · Thomas K. Frazer ·  
James P. Beets · William J. Lindberg ·  
Paul Zwick · Nicholas A. Funicelli

Received: 6 August 2007 / Accepted: 9 August 2007 / Published online: 6 September 2007  
© Springer Science+Business Media B.V. 2007

**Abstract** Management of tropical marine environments calls for interdisciplinary studies and innovative methodologies that consider processes occurring over broad spatial scales. We investigated relationships between landscape structure and reef fish assemblage structure in the US Virgin Islands. Measures of landscape structure were transformed into a reduced set of composite indices using principal component analyses (PCA) to synthesize data on the spatial patterning of the landscape structure of the study reefs. However, composite indices (e.g., habitat diversity) were not particularly

informative for predicting reef fish assemblage structure. Rather, relationships were interpreted more easily when functional groups of fishes were related to individual habitat features. In particular, multiple reef fish parameters were strongly associated with reef context. Fishes responded to benthic habitat structure at multiple spatial scales, with various groups of fishes each correlated to a unique suite of variables. Accordingly, future experiments should be designed to test functional relationships based on the ecology of the organisms of interest. Our study demonstrates that landscape-scale habitat features influence reef fish communities, illustrating promise in applying a landscape ecology approach to better understand factors that structure coral reef ecosystems. Furthermore, our findings may prove useful in design of spatially-based conservation approaches such as marine protected areas (MPAs), because landscape-scale metrics may serve as proxies for areas with high species diversity and abundance within the coral reef landscape.

---

R. Grober-Dunsmore · T. K. Frazer · W. J. Lindberg  
Department of Fisheries and Aquatic Sciences, University  
of Florida, 7922 NW 71st Street, Gainesville, FL 32653,  
USA

R. Grober-Dunsmore · N. A. Funicelli  
US Geological Survey, 7920 NW 71st Street,  
Gainesville, FL 32653, USA

J. P. Beets  
Department of Marine Sciences, University  
of Hawaii-Hilo, 200 W Kawili Street, Hilo,  
HI 96720, USA

P. Zwick  
Department of Urban and Regional Planning, University  
of Florida, Gainesville, FL 32601, USA

R. Grober-Dunsmore (✉)  
National Marine Protected Areas Center, NOAA,  
110 Shaffer Rd., Santa Cruz, CA 95060, USA  
e-mail: rikki.dunsmore@noaa.gov

**Keywords** Coral reefs · Landscape ecology ·  
Context · Marine protected areas ·  
Habitat diversity · Caribbean

## Introduction

The management of tropical marine environments calls for interdisciplinary studies and innovative

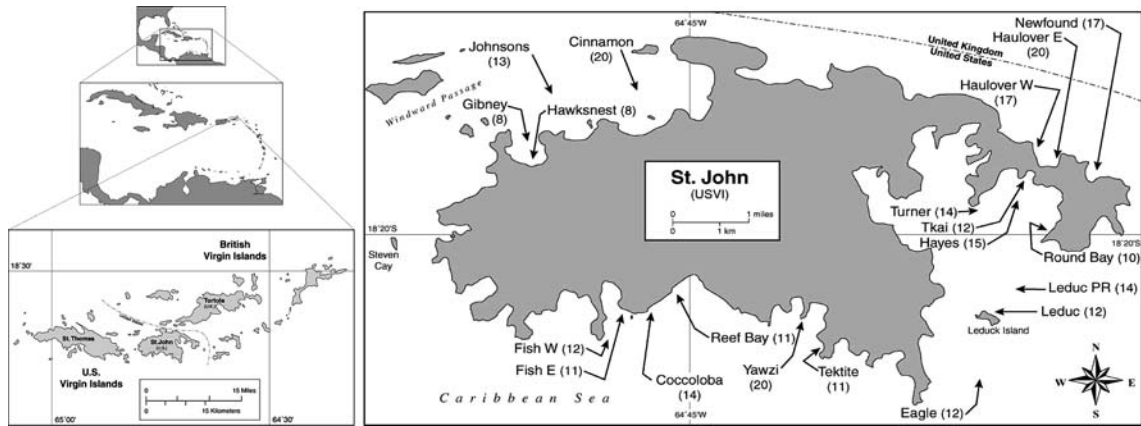
methodologies that consider processes occurring over broad spatial scales (Allison et al. 1998). Landscape ecology has been recognized as a highly interdisciplinary science of heterogeneity (Wu and Hobbs 2002; Wu 2006), with an appropriate focus on broad-scale patterns and ecological processes (Forman and Godron 1986). A landscape generally refers to a heterogeneous area composed of local interacting ecosystems (Forman 1995) made up of homogenous units, called habitat patches. Landscape structure describes the composition and spatial arrangement of the habitat patches (Forman and Godron 1986) that comprise ecosystems, and has been quantified using a number of metrics (O'Neill et al. 1988) including composite indices (e.g., habitat diversity) and measures of configuration (e.g., patch size) and context (size, spatial arrangement and composition of surrounding habitat patches; sensu Forman and Godron 1986) (Turner 1989). The use of such metrics, derived largely from island biogeography theory (MacArthur and Wilson 1967), metapopulation theory (Hanski 1999), and patch dynamics (Pickett and White 1985) has improved our understanding of how landscape features influence terrestrial communities (Turner 1989; Gardner and O'Neill 1991; Wu and Hobbs 2002; Wu 2006). While landscape ecology continues to evolve as a discipline (Wu and Hobbs 2002), the advantages of an ecosystem-based multi-scalar focus has proven extremely valuable in addressing real-world management problems in terrestrial systems (e.g., reserve design, biodiversity conservation) (Noss 1983; Forman 1995; Wu and Hobbs 2002). A landscape ecology approach in coral reefs, however, has received little attention, until recently (e.g., Appeldoorn et al. 2003; Ault and Johnson 1998; Kendall et al. 2003; Kendall 2005; Jeffrey 2004; Nagelkerken et al. 2002), yet may prove invaluable in addressing urgent resource management concerns typical of the new kind of challenges facing those involved with reconciling dynamic interactions between nature and society (Wu 2006) in coral reef ecosystems.

Our understanding of the dynamics of reef fish assemblages has been largely derived from studies conducted at small spatial scales (1-m<sup>2</sup> plots) (Williams 1980; Sale et al. 1994; Forrester et al. 2002). Measures of topographic complexity (Hixon and Beets 1989; Friedlander and Parrish 1998), hole size (Friedlander and Parrish 1998), coral cover (Bell and

Galzin 1984), within-reef zonation (Alevizon et al. 1985) and depth and water motion (McGehee 1994) can be used to predict reef fish assemblage structure. However, larger-scale determinants of reef fish structure are desired by resource managers, as many exploited fishes exhibit patterns of habitat use that extend beyond the scale of isolated reefs (Levin and Grimes 2002; Sale 2002). Although it is unclear whether findings from small-scale studies can be extrapolated to larger-scales, recent studies suggest that large-scale (>100 m) habitat features play important role in structuring stream fish assemblage structure (Roy et al. 2007) and reef fish assemblages (e.g., Ault and Johnson 1998; Christensen et al. 2003; Kendall et al. 2003; Dorenbosch et al. 2004; Pittman et al. 2004). Because coral reef ecosystems exist as a complex mosaic of habitat patches (e.g., reefs, seagrass patches), they are ideally suited for a landscape ecology approach.

A number of landscape metrics (i.e., habitat diversity, measures of context and configuration in addition to fine-scale (<1-m<sup>2</sup>) measures) have helped us understand community structure of terrestrial natural communities. For example, habitat diversity can explain species richness (Ricklefs and Lovette 1999; Sisk et al. 1997). Species abundance and diversity are also frequently associated with measures of habitat configuration (i.e., patch size, shape) (Robinson et al. 1995; Villard et al. 1999); and protected area configuration can influence organisms within and outside their boundaries (Diamond 1975; Sisk et al. 1997; Mazerolle and Villard 1999). In addition, measures of context have proven valuable in conservation planning (Mladendoff et al. 1995; Robinson et al. 1995; Sisk et al. 1997) in terrestrial and riparian systems (Neville et al. 2006; Roy et al. 2007). However, understanding the relative importance of fine and large-scale habitat features is vital to knowing the appropriate spatial scale for management (Mazerolle and Villard 1999).

Our study investigated the utility of landscape metrics (commonly-used in terrestrial systems) for predicting reef fish assemblage structure. A multivariate approach was adopted as a means of exploring the complex coral reef landscape dataset for patterns and relationships, from which hypotheses could then be generated and subsequently tested in controlled experiments. A suite of landscape metrics were calculated and composite indices were developed to



**Fig. 1** Location of St. John, US Virgin Islands, in the Caribbean basin and distribution of the 20 study reefs around the island of St. John, USVI. Below the name of each study reef is the number of reef fish point counts per reef

synthesize data on the spatial patterning of study reefs and surrounding habitats. We then examined the utility of these composite indices to predict which reefs had relatively high species diversity and abundance. The utility of individual habitat features and the importance of a fine-scale habitat measure, i.e., rugosity, were also examined. Terrestrial research led us to expect: (1) composite indices would be positive predictors of reef fish assemblage structure, and (2) individual habitat features would be predictors (both negative and positive) of reef fish assemblage structure. A wealth of literature on reef fishes indicates that fine-scale habitat measures can be important explanatory variables for reef fish assemblage structure (e.g., Bohnsack and Talbot 1980; Hixon and Beets 1989; Friedlander and Parrish 1998). Therefore, we explored the relative significance of rugosity and several landscape metrics in our system.

## Methods

### Study area

Coral reefs around the island of St. John, US Virgin Islands (Fig. 1) were selected for study. Benthic habitat maps were classified by visual interpretation, using 26 discrete and non-overlapping habitat classes, with a minimum mapping unit of 1 acre (Kendall et al. 2001). Sampled reefs were located on the lower fore reef of fringing and patch reefs within a few kilometers from shore. Sampled reefs were all fairly

large (median 2500 m) and dominated by *Montastrea annularis* or mixed corals in water depths between 5 m and 15 m.

About 20 reefs were sampled: 14 in 1994 and six in 2001 (Fig. 1). Reefs were selected from an existing fish database as representative locations that varied with respect to landscape features, yet relatively similar in depth, reef morphology, and coral cover. Analyses were conducted primarily on the 1994 data set to reduce potential temporal variability (due to changes in fishing pressure and storm damage) and a slight modification in methods between years. The 1994 and 2001 data sets were combined for principal component analyses to expand the gradient of several habitat parameters of interest. For all hypothesis-testing, only the 1994 dataset was used to eliminate potential confounding effects, though the strength and nature of most relationships remained consistent when the 2001 was included (R. Grober-Dunsmore, unpubl. data).

### Reef fish sampling

Fish sampling was conducted within reef habitat only. Reef-associated fishes were sampled over a 10-day period in July 1994 (Beets and Friedlander 1994), and over a 5-day period in July 2001. The number of point counts per reef was determined based on reef size following Monte Carlo simulation, and ranged from 8 to 20 per reef (Fig. 1). Samples were stratified equitably in edge and platform portions of each reef.

Reef fishes were censused using a standardized visual point count method (Bohnsack and Bannerot 1986), where all reef fishes were identified within a 5 min sampling period, and enumerated during the following 10 min period within a defined sampling radius. Fork lengths of fishes were estimated to the nearest centimeter, with minimum, maximum and mean recorded. In 1994, a modified Bohnsack and Bannerot (1986) method (sample radius reduced from 7.5 m to 5 m) was used, whereas the original method was used in 2001; comparative analyses between methods revealed few significant differences between most reef fish assemblage parameters (Beets and Friedlander 2003). Mean species richness herein refers to the mean number of species observed for point counts at a replicate reef, whereas cumulative richness refers to the total number of species observed during all point counts at a reef. Abundance refers to the mean number of fishes for point counts at each replicate reef. Two species were eliminated from abundance analyses, since these tended to overwhelm abundance estimates and are difficult to count accurately—*Jenkinsia* spp. (herring) and *Coryphopterus personatus* (masked/glass goby). Randall (1967) and Fish Base (Froese and Pauly 2002) were used to classify all fishes by trophic guild: piscivore, herbivore, mobile invertebrate feeder (MIF), sessile invertebrate feeder (SIF), planktivore, or omnivore (see Grober-Dunsmore 2005). Each adult fish was classified into mobility guilds: resident, mobile or transient, based on their known ecology. Resident species are

sedentary and site-attached, and do not typically move from their primary reef patch. Mobile species are those that exhibit restricted movements and may roam from the primary reef. Transient species are vagile, and can range more widely, often on the scale of kilometers. Taxonomic groups of commercially and ecologically important fishes were analyzed separately (e.g., haemulids, scarids). Fishes were further subdivided into juvenile and adult categories, based on length of maturity where possible (Froese and Pauly 2002), to examine the influence of life-history stage on functional relationships. This resulted in 30 reef fish assemblage parameters (Table 1).

#### Habitat sampling

A single fine-scale measure of rugosity (Luckhurst and Luckhurst 1978) was calculated by running an underwater tape measure over the contour of study reefs. For each reef, 10 rugosity samples were collected along straight line 10-m transects. The resultant mean value was used for statistical analyses.

Landscape-scale habitat measures were calculated from the benthic habitat maps. The original map classification scheme included 26 distinct and non-overlapping habitat classes (Kendall et al. 2001). The habitat classification scheme was simplified for resource management purposes, where 7–10 habitat classes are typically desired (Turner et al. 2001).

**Table 1** Reef fish assemblage parameters ( $n = 30$ ) used as dependent variables in statistical analyses

Entire assemblage level parameters	Trophic guilds	Mobility guilds	Taxonomic groupings
Cumulative species richness	Herbivores (J & A)	Resident	Acanthurids (J & A)
Mean species richness	Mobile invertebrate feeders (J & A)	Mobile	Serranids (J & A)
Total abundance	Omnivores (J & A)	Transient	Haemulids (J & A)
	Piscivores (J & A)		Lutjanids (J & A)
	Planktivores		Pomacanthids
	Sessile invertebrate feeders		Scarids (J & A)
			Holocentrids
			Labrids
			Chaetodontids

#### Statistical analyses

*Note:* Fish groups are not always mutually exclusive. *Hypoplectrus* species were not included in Serranid grouping. For each trophic guild and taxonomic grouping, reef fish parameters were further subdivided into juvenile and adult components, where indicated (J = juvenile, A = adult)

Consequently, the 26 habitat classes were aggregated into nine classes (i.e., mud, mangrove, sand, reef, pavement, bedrock, seagrass, macroalgae, and deep unknown) using a classification similar to other studies (Christensen et al. 2003; Lindeman et al. 1998). Ground-truthing was conducted in every habitat patch (5–10 sample points per patch) within 100 m of each study reef.

Percent cover of benthic invertebrates was estimated using 1-m<sup>2</sup> quadrats (Rogers et al. 1994) within the study reef and in every surrounding habitat patch within 100 m. There were no significant differences in coral cover (mean of 8–30% live coral) between study reefs. High within-patch variability in percent cover of benthic invertebrates in study reefs precluded further analyses.

Fourteen metrics, used to quantify various aspects of the configuration and context of the study reefs (Table 2), were calculated with ArcView 3.2 (ESRI 1996), using spatial analyst and geoprocessing tools. A single value for each (reef) patch metric ( $n = 3$ ) was calculated and each landscape metric was calculated at the 100 m spatial extent (Table 2; Fig. 2). Data were also analysed for the 250 m and 500 m spatial extents and revealed similar yet weaker results compared to the 100 m, therefore the 100 m spatial extent was selected for investigation. These spatial extents were selected to represent a range of potential importance based on the known natural history of reef fishes (Randall 1962; Munro 1983).

## Data analysis

Where necessary, reef fish and habitat data were  $\log_{10}(x + 1)$  transformed to improve normality (Sokal and Rohlf 1995). All statistical analyses were conducted with JMP 8.01 (SAS 2003). Statistical significance was accepted at the  $P \leq 0.05$ .

To reduce landscape metrics into a more parsimonious dataset of composite indices, Pearson product-moment correlations (Ppmc) between each pair of metrics and principal component analysis (PCA) using a correlation matrix were applied. Ppmc was applied sequentially by examining significant pairwise correlations (Sokal and Rohlf 1995) to reduce the number of variables to a 3:1 ratio (observations to variables), which is required for PCA (McGarigal et al. 2000). The choice of an index within a group of

redundant metrics was determined by selecting ecologically meaningful metrics and eliminating redundant variables.

To explore relationships between fish assemblage parameters and landscape structure, stepwise multiple regression analyses were conducted using significant principal components as the independent variables for each of the 30 reef fish parameters. To control family-wise error for multiple correlations, sequential Dunn-Sidak Bonferroni corrections were applied using the number of reef fish parameters ( $n = 30$ ) tested (Sokal and Rohlf 1995) for all subsequent regressions.

To test predictions of individual habitat features, separate stepwise multiple regression analyses were conducted separately for: (1) reef configuration, (2) reef context, and (3) the relative influence of fine- and landscape-scale habitat parameters, using the 1994 reef fish dataset ( $n = 14$ ). Ecologically meaningful variables based on terrestrial studies were selected and those that met assumptions of statistical independence were tested in a given model. Reef configuration variables were: perimeter to area ratio (P:A) of each reef, reef size, and mean patch size. Reef context variables were: surrounding habitat diversity and the areal coverage of reef, bedrock, seagrass and deepwater within 100 m. The fine-scale measure of rugosity was used in simple linear regressions, and then examined with the areal coverage of deepwater, seagrass and reef within 100 m in multiple regression analyses. To optimize model performance and reduce potential effects due to multicollinearity, a series of diagnostic tests were used: (1) Akaike's Information Criterion (Akaike 1974), (2) leverage effects plots, (3) Durbin-Watson statistic, and (4) condition number (Belsley et al. 1980) for every stepwise regression. Sequential Bonferroni adjustments were conducted to ameliorate concerns over multiple statistical testing. Simple linear regressions were created to determine the stability of models using residual plots (Sokal and Rohlf 1995).

## Results

### Landscape structure

Configuration and context of study reefs varied widely. Most metrics had coefficients of variation >50% of the mean, indicating that gradients in many aspects of the landscape were represented (Table 3; Fig. 2).

**Table 2** Patch metrics ( $n = 3$ ) and landscape metrics ( $n = 11$ ) at the 100 m spatial extent used to quantify the landscape structure of the 20 study reefs sampled in 1994 and 2001 in St. John, US Virgin Islands

	Definition	Formula
<i>Patch metric</i>		
Mean patch size	Mean patch size within 100 m	Area (m <sup>2</sup> )
Reef sized	Size of individual sampled reef patch	Area (m <sup>2</sup> )
P:A of a patch	Sum of the patch edge divided by patch area for patch of interest	$\Sigma$ P:A for particular patches
<i>Landscape metric</i>		
Patch diversity	Total abundance and type of different patches ( $p_i$ is the proportion of habitat for every individual patch)	$\Sigma p_i \ln p_i$ ; $p_i$ = proportion of area in (m <sup>2</sup> ) of patch $i$ for all patches
Habitat diversity	Same as patch diversity but boundaries of similar habitat patches (by habitat class) are dissolved so number of patches does not influence index	$\Sigma p_i \ln p_i$ $p_i$ = proportion of area in (m <sup>2</sup> ) of habitat type $i$ for all habitat types
Habitat richness	Number of different habitat types present in an extent	Number of different habitat types
Patch richness	Number of patches of each habitat type in extent of interest	Number of patches
Habitat area	Amount of each habitat type in landscape	Area (m <sup>2</sup> ) in each habitat type
Area of bedrock		
Area of deep		
Area of algal plain		
Area of pavement		
Area of reef		
Area of sand		
Area of seagrass		

PCA revealed four dominant components of variation based on retention of eigenvalues greater than the average, i.e.,  $\lambda > 1$  (Jackson 1993). These components explained approximately 80% of the total variance of the original landscape variables (Table 4). Landscape structure was not adequately represented by a single or even a few gradients. Final communalities indicated that most of the residual indices were well accounted for by these four components, with no notable exceptions.

#### Reef fish assemblage structure

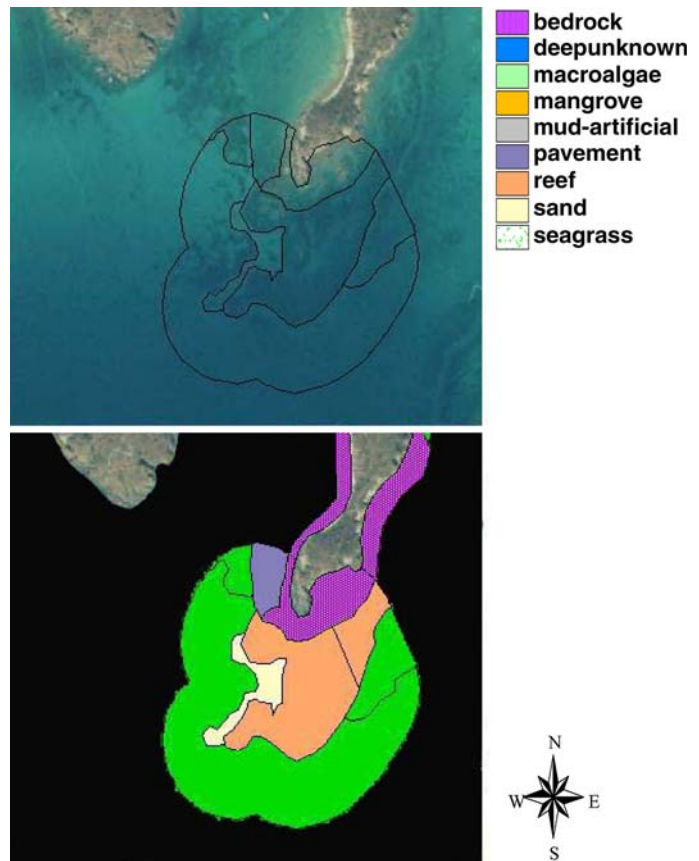
A total of 57,002 fishes representing 171 different species were recorded during 341 censuses at the 20 study reefs.

Principal components explained few reef fish assemblage parameters. Both mean species richness and cumulative species richness were marginally correlated (21% and 26%, respectively) with PC4, a positive seagrass gradient (Table 5).

Configuration was generally a poor predictor of reef fish assemblage structure, though there were a few exceptions. About 74% of the variation in abundance of transient fishes was explained by reef perimeter to area ratio (P:A) and the number of habitat patches (Table 6). Abundances of two other trophic guilds (piscivores and omnivores) and three taxonomic groups were marginally correlated with P:A (Table 6). Examination of regression and residual plots revealed the influence of single points and identified heteroscedascity, which calls into question the stability of these relationships (Sokal and Rohlf 1995). Surprisingly, no reef fish assemblage parameter was correlated with reef size.

Reef context was correlated with 13 of 30 possible reef fish assemblage parameters (Table 7). Species richness was positively correlated with the areal coverage of seagrass (Table 7). Several ecologically relevant relationships between specific habitat types and abundances within trophic and taxonomic groups

**Fig. 2** Study reef landscape within 100 m of Yawzi reef with the area beyond the 100 m blacked out to highlight the area of interest



were also evident. Abundance of adult MIFs was positively correlated with the areal coverage of seagrass ( $R^2 = 0.33$ ) and adult piscivores were positively correlated with the areal coverage of reef habitat within 100 m of focal reefs ( $R^2 = 0.51$ ) (Table 7; Fig. 3). Several taxonomic groups were predicted, based on their life history, to be correlated with a particular habitat type, e.g., adult haemulids and lutjanids with seagrass and adult serranids with reef habitat. About 53% of the observed variation in the mean abundance of adult haemulids, and 68% of the variation in the mean abundance of adult lutjanids was explained by seagrass coverage (Fig. 3). Subsequent examination of residuals plots indicated that most relationships were stable; those that were not were eliminated from reported results.

Counter to expectations, the index of habitat diversity was not positively correlated with any fish parameter; the exception was mobile fishes (Table 7), however, the coefficient of variation for habitat diversity was low (34%). To check for spurious correlations, we verified that there were no

relationships between fishes and habitats for which a relationship was not expected (e.g., pomacentrids and seagrass). There were none.

Also counter to expectations, rugosity was not strongly correlated with many reef fish assemblage parameters. In fact, only five reef fish parameters exhibited a relationship with rugosity (Table 8). In only two cases (juvenile omnivores and piscivores) did rugosity explain more variation than a landscape metric. Furthermore, rugosity was never the single explanatory variable for any final model. Rather, landscape metrics were better predictors of reef fish assemblage structure (Table 8).

## Discussion

Composite indices that quantify the landscape structure of reef environments (principal components and habitat diversity) were generally poor predictors of reef fish assemblage structure, contrary to expectations from terrestrial studies (O'Neill et al. 1988;

**Table 3** Summary statistics of landscape metrics (100 m) and reef fish assemblage parameters for 20 study reefs sampled in 1994 and 2001, St. John, US Virgin Islands

Habitat parameter	Measure	Transform	Min.	Max.	Mean	CV
# of patches	#	$\text{Log}_{10}(x + 1)$	2.00	12.00	7.00	43.32
Size of reef	Ha	None	0.54	15.74	6.59	67.62
P:A reef	Ratio	None	0.03	0.09	0.05	34.33
H' patch diversity	Index	None	1.13	2.45	1.63	20.54
H' diversity	Index	None	0.54	1.57	1.17	24.32
Habitat richness	# habitat types	None	2.00	6.00	4.15	27.39
Patch richness	# patches	$\text{Log}_{10}(x + 1)$	5.00	19.00	8.50	43.09
Reef	Ha	$\text{Log}_{10}(x + 1)$	0.83	17.89	4.18	91.42
Seagrass	Ha	$\text{Log}_{10}(x + 1)$	0.00	7.80	1.32	166.26
Bedrock	Ha	$\text{Log}_{10}(x + 1)$	0.00	3.56	0.80	142.92
Pavement	Ha	$\text{Log}_{10}(x + 1)$	0.00	11.33	2.72	105.72
Deep water	Ha	$\text{Log}_{10}(x + 1)$	0.00	7.30	2.18	120.10
Algal plain	Ha	$\text{Log}_{10}(x + 1)$	0.00	4.02	0.58	222.76
Sand	Ha	$\text{Log}_{10}(x + 1)$	0.00	6.03	1.17	160.39
Rugosity	Index	None	1.38	2.82	2.00	19.48
Reef fish parameter	Units	Transform	Min.	Max.	Mean	SE
Mean spp. richness	Number	$\text{Log}_{10}(x + 1)$	19.67	32.14	23.43	0.67
Cum spp. richness	Number	$\text{Log}_{10}(x + 1)$	51.00	88.00	67.85	2.25
Total abundance	Number	$\text{Log}_{10}(x + 1)$	24.12	88.13	55.23	0.02
A herbivore	Number	$\text{Log}_{10}(x + 1)$	4.89	25.92	10.22	0.04
J herbivore	Number	$\text{Log}_{10}(x + 1)$	14.14	73.13	41.66	0.04
A MIF	Number	$\text{Log}_{10}(x + 1)$	1.04	18.95	4.37	0.05
J MIF	Number	$\text{Log}_{10}(x + 1)$	7.71	32.11	16.38	0.03
A PISCI	Number	$\text{Log}_{10}(x + 1)$	0.05	1.75	0.45	0.02
J PISCI	Number	$\text{Log}_{10}(x + 1)$	0.58	3.27	1.63	0.03
PLANK	Number	$\text{Log}_{10}(x + 1)$	3.17	2950.21	36.15	0.08
A OMNI	Number	$\text{Log}_{10}(x + 1)$	0.00	1.19	0.26	0.02
J OMNI	Number	$\text{Log}_{10}(x + 1)$	1.57	34.48	8.55	0.08
SIF	Number	$\text{Log}_{10}(x + 1)$	1.69	34.48	9.23	0.03
Resident	Number	$\text{Log}_{10}(x + 1)$	32.88	103.7	65.07	0.05
Mobile	Number	$\text{Log}_{10}(x + 1)$	0.48	11.59	1.95	0.03
Transient	Number	$\text{Log}_{10}(x + 1)$	24.12	88.13	55.23	0.04

*Note:* All parameters for mean abundance, except where indicated. All data are backtransformed. CV = coefficient of variation, SE = standard error. A = adult, J = juvenile

Riitters et al. 1995; Robinson et al. 1995). Although the coral reef landscape variables were successfully reduced into four principal components that synthesized a wealth of information on the spatial patterning of the individual coral reef landscapes, these components explained a limited number of reef fish parameters. Most relationships were more easily interpreted using individual habitat features. For

instance, species richness exhibited a marginal association with PC4, a positive gradient of coverage of adjacent reef and seagrass, habitats considered critical for many species (Ogden and Zieman 1977). Several factors may explain the inability of principal components to predict reef fish community structure. First, ecologically meaningful interpretation of the principal components proved difficult, perhaps

**Table 4** Principal component analyses on the correlation matrix of the eight residual landscape-scale habitat variables at the 100 m spatial extent for the 20 study reefs sampled in 1994 and 2001 in St. John, US Virgin Islands

	PC1	PC2	PC3	PC4
Eigenvalue	2.10	1.82	1.49	1.01
Percent	26.33	22.76	18.65	12.61
Cum percent	26.33	49.09	67.74	<b>80.35</b>
# patches	<b>0.488</b>	0.013	-0.149	<b>0.470</b>
Reef size	<b>0.549</b>	0.173	0.033	0.049
Habitat diversity	<b>0.359</b>	0.258	<b>0.493</b>	0.243
Deep	-0.029	<b>-0.422</b>	<b>0.607</b>	0.216
Pavement	0.211	<b>-0.537</b>	-0.163	-0.192
Reef	0.333	-0.227	<b>-0.516</b>	0.084
Sand	0.234	<b>0.490</b>	0.043	<b>-0.570</b>
Seagrass	-0.347	0.381	-0.265	<b>0.550</b>

Note: Loadings in bold represent those that contribute the most to individual components

**Table 5** Stepwise regression results to determine the influence of principal components on reef fish assemblage structure at the 20 study reefs sampled in 1994 and 2001 in St. John, US Virgin Islands at the 100 m spatial extent

Fish parameter	Model	PC1			PC2			PC3			PC4			
		$R^2$ (%)	b1	$R^2$	P	b2	$R^2$	P	b3	$R^2$	P	b4	$R^2$	P
Mean richness	21											1.38	0.21	0.040
Cumulative richness	26											5.17	0.27	0.020
Herbivores	53				0.05	0.22	0.012	-0.06	0.31	0.004				
Omnivores	21							0.14	0.21	0.044				
Haemulids	43	-0.14	0.43	0.002										
Epinephelids	23							-0.05	0.23	0.030				
Acanthurids	35				0.09	0.18	0.073	-0.10	0.17	0.060				
Lutjanids	46	-0.07	0.32	0.006				0.05	0.14	0.080				
Mobile	28				0.05	0.28	0.022							

Note: Each of the 30 reef fish parameters were used as dependent variables. Linear models: log abundance =  $b_0 + b_1$  (PC). Data represented are mean and cumulative species richness values and mean abundances within each guild derived from a minimum of 16 samples per reef. See Table 4 for definitions of individual principal components. The suite of 30 fish parameters were analyzed, however, only those reef fish parameters with statistically significant relationships are reported.  $P$ -values are Sequential Dunn-Sidak Bonferroni-corrected for the total number of comparisons ( $n = 30$ ). All  $P$ -values are presented

because loadings were distributed across many variables. No single component accounted for >26% of the variability of the original dataset. Secondly, these components may contain too much information to be germane to reef fishes, as they may not respond to multiple habitat parameters (see Neville et al. 2006). In fact, our data suggests that specific fish groups respond to specific habitat features (see below). It will be important to identify through exploratory analyses such as this, those metrics that are correlated with reef fish distribution, to provide the basis for

developing specific hypotheses that will be tested in future coral reef studies.

Habitat diversity was also not a good predictor of reef fish diversity and abundance, contrary to our expectations based on terrestrial research (e.g., Rafe et al. 1985; Ricklefs and Lovette 1999). Relationships can depend heavily upon specific definitions of habitat diversity (e.g., elevation) (Rafe et al. 1985; Turner 1989) and it is possible that habitat diversity, as we defined it, is not an appropriate measure. However, Donaldson (2002) and Grober-Dunsmore

**Table 6** Stepwise multiple regression results of the influence of reef configuration on reef fish assemblage structure for 1994 study reefs ( $n = 14$ ) in St. John, US Virgin Islands

Reef fish parameter	Habitat parameter	Model $R^2$	Partial $R^2$	$P$ -value
A piscivores	P:A reef (-)	0.32	0.32	0.050
A omnivores	P:A reef	0.40	0.40	0.010
J haemulids	# patches (-)	0.39	0.39	0.020
A acanthurids	P:A reef	0.33	0.33	0.030
Pomacanthids	P:A reef	0.37	0.37	0.020
J lutjanids	# patches (-)	0.36	0.36	0.030
Transients	P:A	0.74	0.62	<0.001
	# patches		0.12	0.050

*Note:* Independent variables were: P:A of each reef, the number of patches and reef size. Results for 1994 reefs ( $n = 14$ ), with model  $R^2$  and partial regression values for each variable with  $P \leq 0.05$  level.  $P$ -values are Sequential Dunn-Sidak Bonferroni-corrected for the total number of comparisons. Model effects are all positive, except where indicated (-). The suite of 30 fish parameters were analyzed, however, only those reef fish parameters with statistically significant relationships are reported. A = adult, J = juvenile

**Table 7** Stepwise multiple regression results of the influence of reef context on reef fish assemblage structure for the 1994 study reefs ( $n = 14$ ) in St. John, US Virgin Islands

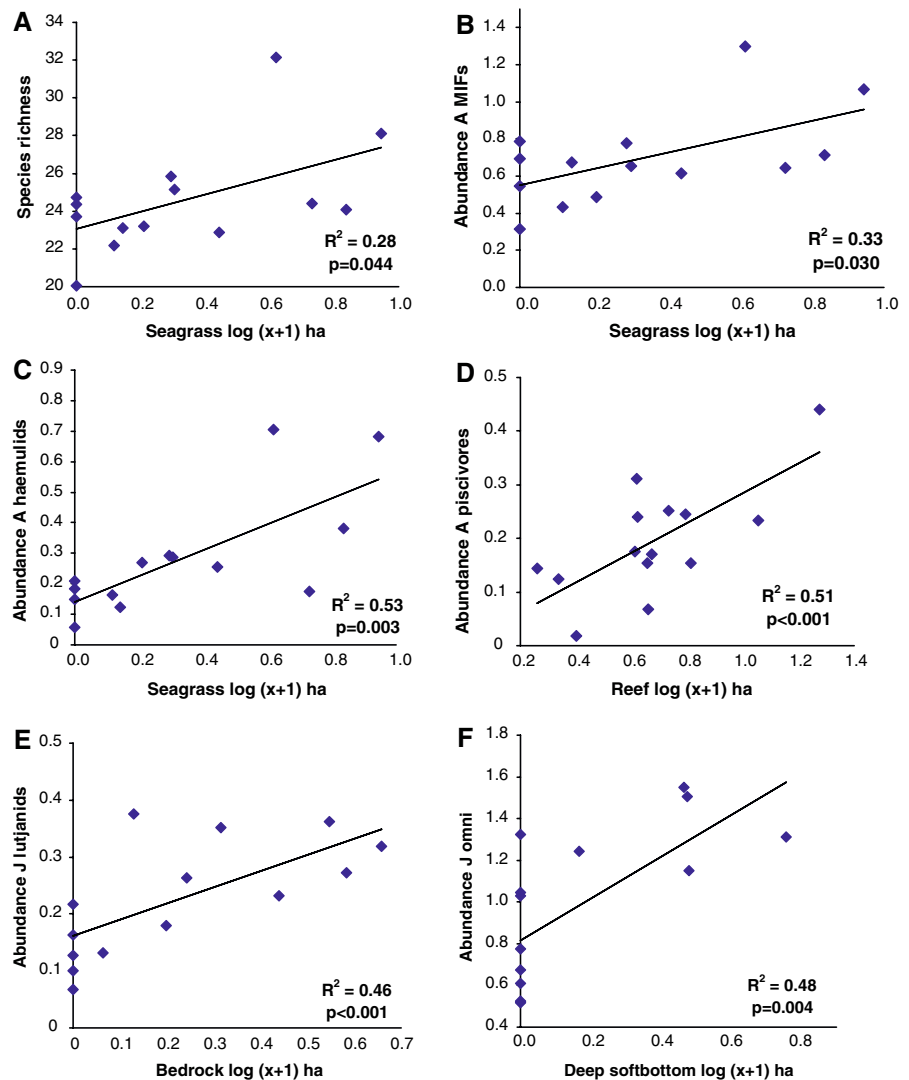
Fish parameter	$R^2$	Partial $R^2$	$P$ -Value	Habitat parameter
Mean species richness	0.28	0.28	0.042	Seagrass
J herbivores	0.30	0.30	0.041	Bedrock
A MIFs	0.33	0.33	0.033	Seagrass
J omnivores	0.48	0.48	<0.001	Deepwater
A piscivores	0.51	0.51	<0.001	Reef
J piscivores	0.47	0.240	0.033	Deepwater
		0.23	0.052	Seagrass
SIFs	0.63	0.39	<0.001	Bedrock (-)
		0.27	<0.001	Deepwater
A haemulids	0.53	0.53	<0.001	Seagrass
A epinephelids	0.52	0.28	<0.001	Reef
		0.24	0.043	Seagrass
J acanthurids	0.67	0.42	<0.001	Deepwater (-)
		0.25	0.011	H' (-)
A lutjanids	0.68	0.50	<0.001	Seagrass
J lutjanids	0.46	0.46	<0.001	Bedrock
Mobile	0.39	0.39	0.022	H'

Independent variables were: H' and areal extent of reef, bedrock, seagrass and deep unknown within 100 m. Model  $R^2$  and partial regression values for each variable with  $P \leq 0.05$  level.  $P$ -values are Sequential Dunn-Sidak Bonferroni-corrected for the total number of comparisons. The suite of 30 fish parameters were analyzed, however, only those reef fish parameters with statistically significant relationships are reported. Model effects are positive except where indicated by (-). A = adult, J = juvenile

et al. (2004) also failed to predict reef fish species diversity using a habitat diversity measure. Jeffrey (2004) found that measures of habitat richness and diversity were correlated (often negatively) with trophic composition and occurrences of several species of fishes. We also found negative associations

of individual reef fish parameters with habitat diversity, which may suggest that specific habitat types are likely to be better predictors of assemblage structure than habitat diversity per se. These findings lead us to concur with those terrestrial studies that challenge the effectiveness of generic landscape

**Fig. 3** Select simple linear regression results of the effects of reef context on mean abundance of particular fish groups for the 1994 ( $N = 14$ ) study reefs in St. John, USVI. **(A)** Mean species richness and areal extent of seagrass 100 m, **(B)** mean abundance of adult MIFs and areal extent of seagrass 100 m, **(C)** mean abundance of adult haemulids and areal extent of seagrass 100 m, **(D)** mean abundance of adult piscivores and areal extent of reef 100 m, **(E)** mean abundance of juvenile lutjanids and areal extent of bedrock 100 m, and **(F)** mean abundance of juvenile omnivores and areal extent of deep unknown 100m. Independent variables are each  $\log_{10}(x + 1)$  in hectares. MIFs refer to mobile invertebrate feeders. A = adult, J = juvenile



indices (i.e., principal components) to design protected areas (Lindenmayer et al. 2003), at the scale of individual reefs. Reef fishes may not all conform to the same landscape pattern, rather each species may respond to specific habitat features at particular spatial scales, a finding consistent with terrestrial studies (Mladenoff et al. 1995; Lindenmayer et al. 2003).

Configuration measures were generally not effective in predicting reef fish assemblage structure, although they have proven useful in some terrestrial systems (Andr n 1994; but see Trzcinski et al. 1999). Our findings corroborate those of Pittman et al. (2004), which revealed that configuration explained less of the variation in the spatial distribution of

fishes than habitat composition. We did find a few potentially, ecologically relevant relationships. For example, the strong, positive association of reef P:A with abundances of transient fishes (e.g., jacks) may reflect their foraging behavior along reef edges (Auster 2005; Sandin and Pacala 2005). Predatory behavior of piscivorous reef fishes can vary with changes in landscape attributes (Auster 2005).

Surprisingly, reef size was not positively correlated with any reef fish parameter. These findings contrast with terrestrial (Diamond 1975), small-scale patch reef (Molles 1978; Bohnsack and Talbot 1980; Sale et al. 1994) and seagrass studies (Irlandi et al. 1999; Hovel and Lipcius 2001), but may be a consequence of scale. Our reefs were larger than most previously studied

**Table 8** Stepwise multiple regression results of the relative influence of landscape and fine-scale habitat measures on reef fish assemblage structure on the 1994 study reefs ( $n = 14$ ) in St. John, US Virgin Islands

Fish parameter	$R^2$	Partial $R^2$	$P$ -value	Habitat parameter
<i>Mean species richness</i>	0.68	0.38	0.004	Seagrass
		0.30	0.001	Rugosity
<i>A MIFs</i>	0.53	0.33	0.010	Seagrass
		0.20	0.050	Rugosity
<i>J omnivores</i>	0.76	0.60	0.009	Rugosity
		0.16	0.020	Reef
<i>A piscivores</i>	0.53	0.53	0.009	Reef
<i>J piscivores</i>	0.71	0.36	0.003	Rugosity
		0.35	0.007	Seagrass
<i>A haemulids</i>	0.71	0.55	0.001	Seagrass
		0.16	0.030	Rugosity

Independent variables are rugosity and the areal coverage of deep unknown, seagrass and reef within 100 m. Results for the 14 reefs sampled in 1994, with model  $R^2$  and partial regression values for each variable significant at the  $P \leq 0.05$  level.  $P$ -values are Sequential Dunn-Sidak Bonferroni-corrected for the total number of comparisons. Relationships in italics are those where rugosity contributed to explanatory power. The 30 fish parameters were analyzed. Only fish parameters with significant relationships are reported. A = adult, J = juvenile

(though see Ault and Johnson 1998). It is possible that beyond a minimum reef size (which our reefs may exceed), the structure of reef fish communities may be mediated by other factors such as reef context, physical disturbance (Syms 1998), larval supply (Sale et al. 1984; Doherty and Fowler 1994), and/or predation (Hixon and Beets 1989).

Reef context appears to be an important determinant of species diversity and richness, corroborating findings in terrestrial (Pearson 1993; McGarigal and McComb 1995; Mazerolle and Villard 1999; Trzcinski et al. 1999), coral reef (Kendall et al. 2003), seagrass (Pittman et al. 2004) and riparian systems (Roy et al. 2007). In particular, the areal coverage of seagrass, an important nursery and larval settlement habitat (Shulman and Ogden 1987; Ogden and Zieman 1977) and foraging area for some fishes (Randall 1967) was strongly associated with entire assemblage parameters (e.g., cumulative species richness). Seagrass habitat may contribute to higher species richness as a result of nutrient transfer and movement of invertebrates and energy from highly productive seagrass to adjacent reef habitat (Duarte 2000). For instance, Tektite and Yawzi reef, structurally complex reefs with the highest mean species richness values, are located within a bay with dense *Thalassia testudinum*. Higher species richness of fishes was also detected in mangroves adjacent to continuous seagrass in Australia (Pittman et al.

2004), and at reefs proximal to nursery habitats in Colombia (Appeldoorn et al. 2003).

Reef context was a strong predictor of fish abundances within specific trophic guilds and taxonomic groupings, and these relationships were remarkably consistent with the ecology of each fish group. For example, the positive relationship of MIF abundances with seagrass is consistent with the foraging behavior of species in this guild (e.g., taxa within mullidae, haemulidae, and lutjanidae). The relationship for haemulids and seagrass was even stronger; haemulids forage off-reef in seagrass nocturnally (Ogden and Quinn 1984). Common piscivorous fishes, which may forage preferentially in reef habitat (e.g., *Aulostomus maculatus*) were more abundant where there were large areas of adjacent reef habitat (e.g., Eagle Shoals). The positive association of juvenile omnivores with deep habitat is consistent with the functional role of deep water as a source of ichthyoplankton. Several species of omnivores (e.g., apogonids, blenniids) are fairly non-mobile as larvae, and are thought to recruit directly to reef substrate from the plankton. A direct test of this hypothesis would be required to determine whether proximity to deep water enhances planktonic larval delivery at the reef scale.

Our findings corroborate those from terrestrial (Turner 1989; Sisk et al. 1997; Ricketts 2001) and marine systems (Pittman and McAlpine 2003;

Pittman et al. 2004), which indicate that specific landscape features are associated with particular groups of organisms. Relationships appear to be functionally relevant and may indicate that local communities are structured by processes operating at much larger spatial scales than previously recognized. Studies in coral reef ecosystems have until recently largely ignored the surrounding reef landscape (dubbed the matrix) yet this study demonstrates, as in terrestrial systems, that the matrix matters (Pearson 1993; McGarigal and McComb 1995; Ricketts 2001) in structuring reef fish assemblages within reef patches. This study was conducted in large, continuous reef patches, therefore we may expect that effects of reef context may actually be greater for small, isolated reef patches, as the processes structuring continuous and isolated reefs can differ (Ault and Johnson 1998).

The fine-scale measure of rugosity was of limited value in predicting reef fish assemblage structure, a finding that is noteworthy. The exception was for highly site-attached fishes, e.g., blenniids, gobiids, and pomacentrids. The inability of rugosity to predict reef fish assemblage structure, though contrary to previous small-scale research (Hixon and Beets 1989), may indicate the ineffectiveness of this measure to characterize topographic complexity within a single habitat at the scale of whole reefs. These results corroborate bird studies that demonstrate landscape influences are greater than within-patch influences when sampling was constrained to forested patches (Pearson 1993). Most previous reef fish studies that detected rugosity relationships were conducted across multiple habitats (Friedlander and Parrish 1998) or used manipulated patch reefs to maximize the gradient of rugosity (Hixon and Beets 1989). When sampling within a single topographically complex habitat type such as reef, landscape parameters may be better predictors of reef fish assemblage structure.

Some reef fishes respond to habitat features at fine spatial scales, while others respond to features at landscape scales. For several fish groups, the combination of fine and landscape-scale features provided the best predictive model, findings that support, in part, small-scale reef (Walsh 1985) and terrestrial research (Pearson 1993). Thus, scale has profound effects on resultant patterns (Wiens 1989) with fine-scale measures often better predictors of

one group of organisms, and landscape measures predictors of others (Pearson 1993; Mazerolle and Villard 1999; Mitchell et al. 2001). This organism-based perspective appears to be true for coral reef fishes (Pittman and McAlpine 2003; Pittman et al. 2004); consequently future studies should acknowledge that fishes respond to habitat structure at multiple scales. Also, species perceive the landscape in different ways, with each species potentially responding to a unique suite of variables. The relevant scale of investigation may depend on life history attributes of individual fish species (Pittman et al. 2004; Neville et al. 2006), or processes under consideration such as foraging behavior (Shulman and Ogden 1987; Sale 1998), and predation (Hixon and Beets 1989).

The correlative nature of our results should be interpreted accordingly. Although a range in the values of different landscape metrics was represented, we had little control on experimental units. These reefs are natural habitat patches, therefore considerable microhabitat variation exists, which was neither measured nor controlled. Reefs also do not represent a perfect gradient in landscape scale features (rather they vary across multiple gradients). Sample units were selected from the naturally available set of reefs. Additionally, while considerable groundtruthing was conducted, the benthic habitat maps were accepted without major modification. Since each decision in the mapping process affects the determination and analyses of spatial structure, it also affects our results. Furthermore, analyses should be conducted across a larger temporal spatial scale to account for year to year variability and across multiple habitat types. Finally, the reef fish populations of the Virgin Islands have been heavily exploited (Rogers and Beets 2001) therefore; future studies should examine reef fish distributions in less fished areas.

Our results have some important implications for applying terrestrial landscape ecology principles to tropical marine environments. First, while composite indices such as habitat diversity can prove valuable in terrestrial systems (Rafe et al. 1985; Ricklefs and Lovette 1999; Opdam et al. 2003), these indices do not appear appropriate for predicting reef fish assemblage structure within single habitat patches. Across a broader marine landscape these indices are likely to perform better. Second, the matrix matters,

which is consistent with terrestrial (Lindenmayer et al. 1999; Ricketts 2001) and riparian (Neville et al. 2006; Roy et al. 2007) studies. The surrounding matrix or context of individual reef patches exerts a strong influence on the assemblage structure of reef fishes, perhaps as much or more than the characteristics within a given patch. Selection of reef patches for MPA design should consider how well a patch relates or links to other patches in the landscape. Third, the same landscape can be perceived quite differently by different species (Lindenmayer et al. 2003; Westphal et al. 2003). Various life history stages and specific trophic and mobility guilds responded to different habitat features. These findings are broadly consistent with those from terrestrial systems, which reveal the importance of the natural history of each organism of interest (e.g., life history stage, mobility, dispersal, habitat generalist or specialist) (Stamps et al. 1987; Sisk et al. 1997; Mitchell et al. 2001). Finally, scale clearly has profound effects on resultant patterns (Wiens 1989) with fine-scale measures often better predictors of one group of organisms, and landscape measures predictors of others (Mitchell et al. 2001; Mazerolle and Villard 1999). This organism-based perspective appears to be true for coral reef fishes (Pittman and McAlpine 2003, Pittman et al. 2004). As a consequence, future studies should acknowledge that species perceive the landscape in different ways.

## Conclusion

A landscape ecology approach provides a powerful means of understanding the influence of coral reef landscape structure on reef fish assemblage structure. Although composite landscape metrics of the spatial arrangement and composition of the coral reef landscapes can be calculated, these composite indices are correlated with few reef fish assemblage parameters. Rather individual habitat features were better measures of the influence of the spatial patterning of the coral reef landscape on reef fish assemblages. Specifically, reef context was associated with reef fish diversity and abundance for many groups of fishes. Strong relationships between specific groups of fishes and reef context were detected, and these relationships were consistent with the life history attributes and habitat

requirements of each group. This finding is noteworthy and is consistent with research in terrestrial systems, suggesting that the landscape context within which habitat patches exist may be as important as the local habitat fragments or patches themselves (Perfecto and Vandermeer 2002, Steffan-Dewenter 2003). If the results detected in this exploratory study are replicable across systems and scales, combining the disciplines of landscape ecology and reef fish ecology offers promise in addressing important management questions relevant to habitat-based conservation of reef fishes. As the design and management of MPAs requires decision-making tools and approaches at a large spatial scale, the identification of landscape-scale metrics that may serve as a proxy for areas with high reef fish diversity and abundance would be a valuable contribution to marine conservation efforts in coral reef ecosystems.

**Acknowledgements** Support provided by the Biological Resources Division of the USGS, the Department of Fisheries and Aquatic Sciences at the University of Florida, the Disney Wildlife Conservation Fund, the Canon Science Scholars program, the American Academy for the Advancement of Science and the National Park Service. Reef fish sampling conducted by Jim Beets, Alan Friedlander, Nicholas Wolff, and RGD. Dr. Caroline Rogers, Rafe Boulon, Jeff Miller and Jim Petterson at the Virgin Islands National Park helped facilitate this research. This manuscript was greatly improved thanks to comments from Victor Bonito, Sky Notestein, Stephanie Keller, and NOAA's Biogeography Team.

## References

- Alevizon W, Richardson R, Pitts P et al (1985) Coral zonation and patterns of community structure in Bahamian reef fishes. *Bull Mar Sci* 36(2):304–318
- Allison GW, Lubchenco J, Carr MH (1998) Marine reserves are necessary but not sufficient for marine conservation. *Ecol Appl Suppl* 8(1):S79–S92
- Akaike H (1974) Factor analysis and AIC. *Psychometrika* 52:317–332
- Andrén H (1994) Effect of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71:355–366
- Appeldoorn RS, Friedlander A, Sladek Nowlis J et al (2003) Habitat connectivity in reef fish communities and marine reserve design in Old Providence-Santa Catalina, Colombia. *Gulf Caribb Res* 14(2):61–77
- Ault TR, Johnson CR (1998) Spatially and temporally predictable fish communities on coral reefs. *Ecol Monogr* 68:25–50

- Auster PJ (2005) Predatory behavior of piscivorous reef fishes varies with changes in landscape attributes and social context: integrating natural history observations in a conceptual model. Diving for science 2005, Proceedings of the American academy of underwater sciences. Connecticut Sea Grant, Groton
- Beets JP, Friedlander AF (1994) Unpublished reef fish monitoring dataset for St. John, USVI monitoring program. National Park Service database, 1300 Cruz Bay Creek. Virgin Islands National Park, US Virgin Islands
- Beets J, Friedlander A (2003) Temporal analysis of monitoring data on reef fish assemblages inside Virgin Islands National Park and around St. John, US Virgin Islands, 1988–2000. USGS Report – Caribbean Field Station
- Bell JD, Galzin R (1984) Influence of live coral cover on coral-reef fish communities. *Mar Ecol Prog Ser* 15: 265–274
- Belsley DA, Kuh E, Welsch RE (1980) Regression diagnostics: identifying influential data and sources of collinearity. Wiley, New York
- Bohnsack JA, Bannerot SP (1986) A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. NOAA Technical Report NMFS 41
- Bohnsack JA, Talbot FH (1980) Species packing by reef fishes on Australian and Caribbean reefs: an experimental approach. *Bull Mar Sci* 30:710–723
- Christensen JD, Jeffrey CFG, Caldwell C et al (2003) Cross-shelf habitat utilization patterns of reef fishes in southwestern Puerto Rico. *Gulf Caribb Res* 14(2):9–27
- Diamond JM (1975) The island dilemma: lessons of modern biogeographic studies for the design of nature reserves. *Biol Conserv* 7:129–146
- Doherty P, Fowler T (1994) An empirical test of recruitment limitation in a coral reef fish. *Science* 263:935–939
- Donaldson TJ (2002) High islands versus low islands: a comparison of fish faunal composition of the Palau Islands. *Environ Biol Fish* 65(2):241–248
- Dorenbosch M, van Riel MC, Nagelkerken I et al (2004) The relationship of reef fish densities to the proximity of mangrove and seagrass nurseries. *Estuar Coast Shelf Sci* 60:37–48
- Duarte CM (2000) Marine biodiversity and ecosystem services: an elusive link. *J Exp Mar Biol Ecol* 250:117–131
- ESRI (Environmental Systems Research Institute) (1996) ArcView spatial analyst. Redlands, CA
- Forman RT (1995) Land mosaics: the ecology of landscapes and regions. Cambridge University Press, New York, NY
- Forman RTT, Godron M (1986) Landscape ecology. Wiley, New York, NY
- Forrester GE, Vance RR, Steele MA (2002) Simulating large-scale population dynamics using small-scale data. In: Sale PF (ed) Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press. San Diego, CA, pp 275–301
- Friedlander AM, Parrish J (1998) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *J Exp Mar Biol Ecol* 224(1):1–30
- Froese R, Pauly D (2002) Fish base world wide web electronic publication. www.fishbase.org December 09, 2002
- Gardner RH, O’Neill RV (1991) Pattern, process and predictability: the use of neutral models for landscape analysis. In: Turner MG, Gardner RH (eds) Quantitative methods in landscape ecology: the analysis and interpretation of landscape heterogeneity. Springer-Verlag, New York, NY, pp 289–308
- Grober-Dunsmore R (2005) Applying terrestrial landscape ecology principles to the design and management of marine protected areas in coral reef ecosystems. Dissertation, University of Florida
- Grober-Dunsmore R, Frazer TK, Beets JP et al (2004) The significance of adjacent habitats on reef fish assemblage structure: are relationships detectable and quantifiable at a landscape-scale? In: Proc 55th Gulf Caribb Fish Inst Conf. Xel Ha, Mexico, November 2002, pp 713–734
- Hanski I (1999) Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. *Oikos* 87(2):209–219
- Hixon MA, Beets JP (1989) Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. *Bull Mar Sci* 44:666–680
- Hovel KA, Lipcius RN (2001) Habitat fragmentation in a seagrass landscape: patch size and complexity control blue crab survival. *Ecology* 82:1814–1829
- Irlandi EA, Orlando BA, Ambrose WG Jr (1999) Influence of seagrass habitat patch size on growth and survival of juvenile bay scallops, *Argopecten irradians concentricus* (Say). *J Exp Mar Biol Ecol* 235:21–43
- Jackson DA (1993) Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. *Ecology* 74(8):2204–2214
- Jeffrey CFG (2004) Benthic habitats, fish assemblages, and resource protection in Caribbean marine sanctuaries. Dissertation University of Georgia, Athens, GA
- Kendall MS (2005) A method for investigating seascape ecology of reef fish. Proc 56th Annu Gulf Caribb Fish Inst 56:355–366
- Kendall MS, Krueger CR, Buja KR et al (2001) NOAA technical memorandum NOS NCCOS CCMA 152 (On-Line) methods used to map the benthic habitats of Puerto Rico and the US Virgin Islands
- Kendall MS, Christensen JD, Hillis-Starr Z (2003) Multi-scale data used to analyze the spatial distribution of French grunts, *Haemulon flavolineatum*, relative to hard and soft bottom in a benthic landscape. *Environ Biol Fish* 66:19–26
- Levin PS, Grimes CB (2002) Reef fish ecology and grouper conservation and management. In: Sale PF (ed) Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press San Diego, CA, pp 377–389
- Lindeman KC, Diaz GA, Serafy JE et al (1998) A spatial framework for assessing cross-shelf habitat use among newly settled grunts and snappers. Proc 50th Gulf Caribb Fish Inst 50:385–416
- Lindenmayer DB, Cunningham RB, Pope ML et al (1999) The response of arboreal marsupials to landscape context: a large-scale fragmentation study. *Ecol Appl* 9(2):594–611
- Lindenmayer DB, McIntyre S, Fischer J (2003) Birds in eucalypt and pine forests: a landscape alteration and its implications for research models of faunal habitat use. *Biol Conserv* 110:45–53
- Luckhurst BE, Luckhurst K (1978) Analysis of influence of substrate variables on coral-reef fish communities. *Mar Biol* 49(4):317–323

- MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton, NJ
- Mazerolle MJ, Villard MA (1999) Patch characteristics and landscape context as predictors of species presence and abundance: a review. *Ecoscience* 6(1):117–124
- McGarigal K, McComb WC (1995) Relationships between landscape structure and breeding birds in the Oregon coast range. *Ecol Monogr* 65:235–260
- McGarigal K, Cushman S, Stafford S (2000) Multivariate statistics for wildlife and ecology research. Springer-Verlag, New York, NY
- McGehee MA (1994) Correspondence between assemblages of coral-reef fishes and gradients of water motion, depth and substrate size off Puerto Rico. *Mar Ecol Prog Ser* 105(3):243–255
- Mitchell MS, Lancia RA, Gerwin JA (2001) Using landscape-level data to predict the distribution of birds on a managed forest: effects of scale. *Ecol Appl* 11:1692–1708
- Mladendoff DJ, Sickley TA, Haight RG et al (1995) A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. *Conserv Biol* 9(2):279–294
- Molles MC (1978) Fish species diversity on model and natural patch reefs: experimental insular biogeography. *Ecol Monogr* 48:289–305
- Munro JL (1983) Caribbean coral reef fishery resources. ICLARM Studies and Reviews 7, International Center for Living Aquatic Resources Management. Manila, Philippines
- Nagelkerken I, Roberts CM, van der Velde G et al (2002) How important are mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale. *Mar Ecol Prog Ser* 244:299–305
- Neville HM, Dunham JB, Peacock MM (2006) Landscape attributes and life history variability shape genetic structure of trout populations in a stream network. *Landscape Ecol* 21:901–916
- Noss RF (1983) A regional landscape approach to maintain diversity. *Bioscience* 33:700–706
- Ogden JC, Quinn TP (1984) Migration in coral reef fishes: ecological significance and orientation mechanisms. In: McCleave JD, Arnold GP, Dodson JJ, Neill WH (eds) Mechanisms of migration in fishes. Plenum Press, New York, NY, pp 293–308
- Ogden JC, Zieman JC (1977) Ecological aspects of coral reef-seagrass bed contacts in the Caribbean. In: Taylor DL (ed) Proceedings of the third international coral reef symposium, vol 1. Rosenstiel School of Marine and Atmospheric Science, Miami, Florida, pp 377–382
- O'Neill RV, Krummel JR, Gardner RH et al (1988) Indices of landscape pattern. *Landscape Ecol* 1(3):153–162
- Opdam P, Verboom J, Pouwels R (2003) Landscape cohesion: an index for the conservation potential of landscapes for biodiversity. *Landscape Ecol* 18(2):113–126
- Pearson SM (1993) The spatial extent and relative influence of landscape-level factors on wintering bird populations. *Landscape Ecol* 8:3–18
- Perfecto I, Vandermeer J (2002) Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. *Conserv Biol* 16:174–182
- Pickett STA, White PS (1985) (eds) The ecology natural disturbance and patch dynamics. Academic Press, New York, NY
- Pittman SJ, McAlpine CA (2003) Movement of marine fish and decapod crustaceans: process, theory and application. *Adv Mar Biol* 44:205–294
- Pittman SJ, McAlpine CA, Pittman KM (2004) Linking fish and prawns to their environment: a hierarchical landscape approach. *Mar Ecol Prog Ser* 283:233–254
- Rafe RW, Usher MB, Jefferson RG (1985) Birds on reserves: the influence of area and habitat on species richness. *J Appl Ecol* 22:327–35
- Randall JC (1962) Tagging reef fishes in the Virgin Islands. *Proc Gulf Caribb Fish Inst* 14:20–24
- Randall JC (1967) Food habits of reef fishes of the West Indies. *Stud Trop Oceanogr (Miami)* 5:665–847
- Ricketts TH (2001) The matrix matters: effective isolation in fragmented landscapes. *Am Nat* 158(1):87–99
- Ricklefs RE, Lovette IJ (1999) The roles of island area per se and habitat diversity in the species–area relationships of four Lesser Antillean faunal groups. *J Anim Ecol* 68(6):1142–1160
- Riitters KH, O'Neill RV, Hunsaker CT et al (1995) A factor analysis of landscape pattern and structure metrics. *Landscape Ecol* 10:23–40
- Robinson SK, Thompson III FR, Donovan TM et al (1995) Regional forest fragmentation and the nesting success of migratory birds. *Science* 267(5206):1987–1990
- Rogers C, Beets J (2001) Degradation of marine ecosystems and decline of fishery resources in marine protected areas in the US Virgin Islands. *Environ Conserv* 28:312–322
- Rogers CS, Garrison G, Grober R et al (1994) Coral reef monitoring manual for the Caribbean and Western Atlantic. National Park Service publication
- Roy AH, Freeman BJ, Freeman MC (2007) Riparian influences on stream fish assemblage structure in urbanizing streams. *Landscape Ecol* 22:385–402
- Sale PF (1998) Appropriate spatial scales for studies of reef-fish ecology. *Aust J Ecol* 23(3):202–208
- Sale P (2002) The science needed for effective management. In: Sale PF (ed) Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, San Diego, CA, pp 359–376
- Sale PF, Doherty PJ, Eckert GJ et al (1984) Large scale spatial and temporal variation in recruitment to fish populations on coral reefs. *Oecologia* 64:191–198
- Sale PF, Guy JA, Steel WJ (1994) Ecological structure of assemblages of coral reef fishes on isolated patch reefs. *Oecologia* 98:83–99
- Sandin SA, Pacala SW (2005) Fish aggregation results in inversely density-dependent predation on continuous coral reefs. *Ecology* 86(6):1520–1530
- SAS Institute (2003) JMP 8.01 software. Cary, NC
- Shulman MJ, Ogden JC (1987) What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. *Mar Ecol Prog Ser* 39:233–242
- Sisk TD, Haddad NM, Ehrlich PR (1997) Bird assemblages in patchy woodlands: modeling the effects of edge and matrix habitats. *Ecol Appl* 7(4):1170–1180

- Sokal RR, Rohlf FJ (1995) *Biometry*, 3rd edn. Freeman, New York, NY
- Stamps JA, Buechner M, Krishnan VV (1987) The effects of edge permeability and habitat geometry on emigration from patches of habitat. *Am Nat* 129(4):533–552
- Steffan-Dewenter I (2003) Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conserv Biol* 17(4):1036–1044
- Syms C (1998) Disturbance and the structure of coral reef fish communities on the reef slope. *J Exp Mar Biol Ecol* 230(2):151–167
- Trzcinski MK, Fahrig L, Merriam G (1999) Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecol Appl* 9(2):586–593
- Turner MG (1989) Landscape ecology: the effect of pattern on process. *Annu Rev Ecol Syst* 20:171–197
- Turner MG, Gardner RH, O'Neill RV (2001) *Landscape ecology in theory and practice: pattern and process*. Springer, New York
- Villard M, Trzcinski MK, Merriam G (1999) Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conserv Biol* 13:774–783
- Walsh WJ (1985) Reef fish community dynamics on small artificial reefs – the influence of isolation, habitat structure and biogeography. *Bull Mar Sci* 36(2):357–376
- Westphal MI, Field SA, Tyre AJ et al (2003) Effects of landscape pattern on bird species distribution in the Mt. Lofty Ranges, South Australia. *Landsc Ecol* 18(4):413–426
- Wiens JA (1989) Spatial scaling in ecology. *Funct Ecol* 3: 385–397
- Williams D McB (1980) Dynamics of the pomacentrid community on small patch reefs on One Tree Lagoon (Great Barrier Reef). *Bull Mar Sci* 30:159–170
- Wu J (2006) Landscape ecology, cross-disciplinarity, and sustainability science. *Landsc Ecol* 21:1–4
- Wu J, Hobbs (2002) Key issues and research priorities in landscape ecology: an idiosyncratic synthesis. *Landsc Ecol* 17:355–365