COMMUNITY ECOLOGY - ORIGINAL PAPER

Effects of habitat heterogeneity at multiple spatial scales on fish community assembly

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Abstract Habitat variability at multiple spatial scales may affect community structure within a given habitat patch, even within seemingly homogenous landscapes. In this context, we tested the importance of habitat variables at two spatial scales (patch and landscape) in driving fish community assembly using experimental artificial reefs constructed across a gradient of seagrass cover in a coastal bay of The Bahamas. We found that species richness and benthic fish abundance increased over time, but eventually reached an asymptote. The correlation between habitat variables and community structure strengthened over time, suggesting deterministic processes were detectable in community assembly. Abundance of benthic fishes, as well as overall community structure, were predicted by both patch- and landscape-scale variables, with the cover of seagrass at the landscape-scale emerging as the most important explanatory variable. Results of this study indicate that landscape features can drive differences in community assembly even within a general habitat type (i.e., within seagrass beds). A primary implication of this finding is that human activities driving changes in seagrass cover may cause significant shifts in faunal community structure well before complete losses of seagrass habitat.

Introduction

The importance of scale is a core tenet of the ecological sciences (Levin 1992; Schneider 2001). Spatial heterogeneity, once ignored by ecologists in order to simplify models or theory, is now recognized as a central driver to many ecological processes (Pickett and Cadenasso 1995). In this context, landscape ecology is often defined as the study of how habitat identity and habitat configurations at larger spatial scales affect particular aspects of community structure and ecosystem function (Turner 1989). The degree of heterogeneity in environmental variables and resource distribution varies depending on the particular scale of study, necessitating a multi-scale approach to describe organism–environment interactions (Sandel and Smith 2009).

Causal mechanisms explaining patterns of organism abundance become more difficult to identify with increasing scale of study (Wu and Hobbs 2002; Ims 2005). The notable lack of mechanistic-driven experiments at a landscape scale is primarily the result of feasibility (Ims 2005), as the broad spatial scales at which many landscape processes occur make manipulation and replication difficult. However, such experimental manipulations of landscapes are needed to mechanistically link ecological processes to landscape structure, as correlative relationships may not provide sufficient background to build appropriate predictive models. For example, experimental manipulation of

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habitat fragmentation in terrestrial systems have failed to consistently support predicted relationships between patch size and species richness from observational studies (Debinski and Holt 2000).

While landscape ecology started out as primarily a terrestrial discipline, it is increasingly applied to explore organism–habitat relationships in aquatic environments (Robbins and Bell 1994; Grober-Dunsmore et al. 2009). For example, the surrounding landscape, or landscape context, has been shown to affect important ecological factors (e.g., growth or predation risk) for macroinvertebrates and fishes in temperate seagrass beds and oyster reefs (Irlandi et al. 1995; Irlandi and Crawford 1997; Grabowski et al. 2005; Hovel and Fonseca 2005). Even variations within habitat types (e.g., patchiness of seagrass cover at large spatial scales) have been correlated with predation risk and foraging efficiency of predators (Irlandi 1994; Irlandi et al. 1995). Initial studies applying landscape approaches to tropical marine systems indicate that landscape structure (cover and pattern of surrounding habitat types) likely play an important role in determining fish community composition, abundance and species richness (Pittman et al. 2004, 2007; Grober-Dunsmore et al. 2008). While such correlative evidence is accumulating, a mechanistic understanding of such processes is fundamentally lacking.

Many nearshore systems are considered to be structure limited (Hixon and Beets 1989), and thus structurally complex habitats (e.g., patch reefs) are critical habitat for many ecologically and economically important species (Nagelkerken et al. 2000b). Further, because many of the species that use structurally complex habitats during the day are known to migrate to adjacent areas at night to feed (Ogden and Ehrlich 1977; Nagelkerken et al. 2000a; Luo et al. 2009), characteristics of preferred foraging grounds (e.g., distance to feeding area, cover of soft-bottom habitats) may be correlated with faunal abundance (Kendall et al. 2003; Pittman et al. 2007). In such cases, it is expected that landscape context would be particularly important in structuring communities.

The objective of this study was to determine how habitat variables at two spatial scales (which we term patch and landscape scale) affect fish community assembly in subtropical nearshore systems. By creating new structures (i.e., artificial reefs), we could model natural patch reef community assembly and control for variation inherent in observational studies of patch reef communities. Also, we were able to manipulate the habitat context of artificial reefs by creating reefs across a gradient of seagrass cover to explore the link between landscape structure and fish colonization. We tested if fish community assembly followed expected patterns of community stabilization through time, and if variation in landscape structure within a single matrix habitat (within seagrass beds) affects fish community structure independent of reef characteristics. Specifically, we tested the following hypotheses:

1. Overall, species richness and fish abundance will increase over time, eventually reaching an asymptote.
2. (a) The composition of the fish community will change over time, and (b) variation in environmental variables will better predict differences in community structure among reefs as time increases, as deterministic processes become more important at higher fish densities.
3. Following community stabilization, landscape context will affect the diversity, abundance, and community structure of fishes on artificial reefs. Specifically, the cover of seagrass at a large spatial scale will positively affect species richness and fish abundance, and body size of fishes will determine the spatial scale at which they respond to their landscape, i.e., small fish abundance will be more closely related to patch-scale habitat variables and larger fish abundance will be more closely related to landscape-scale variables.

Materials and methods

Data collection

The study was conducted in The Bight of Old Robinson, Abaco, Bahamas (ESM, Fig. S1). The Bight of Old Robinson is a semi-enclosed bay with a mosaic of seagrass, sand, and hard-bottom habitats. Artificial reefs were constructed in sand and seagrass habitat in the Bight. Artificial reefs support similar communities to natural patch reefs (Alevizon et al. 1985), and have been used extensively as experimental units for studies of patch reef communities (Shulman 1985; Hixon and Beets 1989; Miller 2002). Artificial reefs were constructed of 40 cinder blocks ($\sim$41 cm $\times$ 20 cm $\times$ 20 cm) in a pyramid shape (Fig. 1). Nine reefs were constructed along a gradient of seagrass cover in March 2009. Reefs were placed at least 125 m apart to minimize among-reef movements of more transient fish species. Previous artificial reef studies support this assumption, e.g., similar artificial reefs placed 50 m apart, have been treated as spatially independent (Hixon and Beets 1989). Additionally, site fidelity by fishes on our artificial reefs was supported with preliminary results of a tagging study on one of the dominant fish species, white grunt (*Haemulon plumierii*), where 100% of fish that were re-captured 6 months after tagging ($n = 6$) were on their original reef of capture (L.A. Yeager, unpublished data). We confirmed that there was no relationship between the locations of the reefs (based on spatial x, y coordinates) and

their landscape composition (i.e., measures of patch- and landscape-scale habitat variables, see below) with linear regression. This supports the assumption that the spatial arrangement of the reefs did not affect landscape context or community assembly.
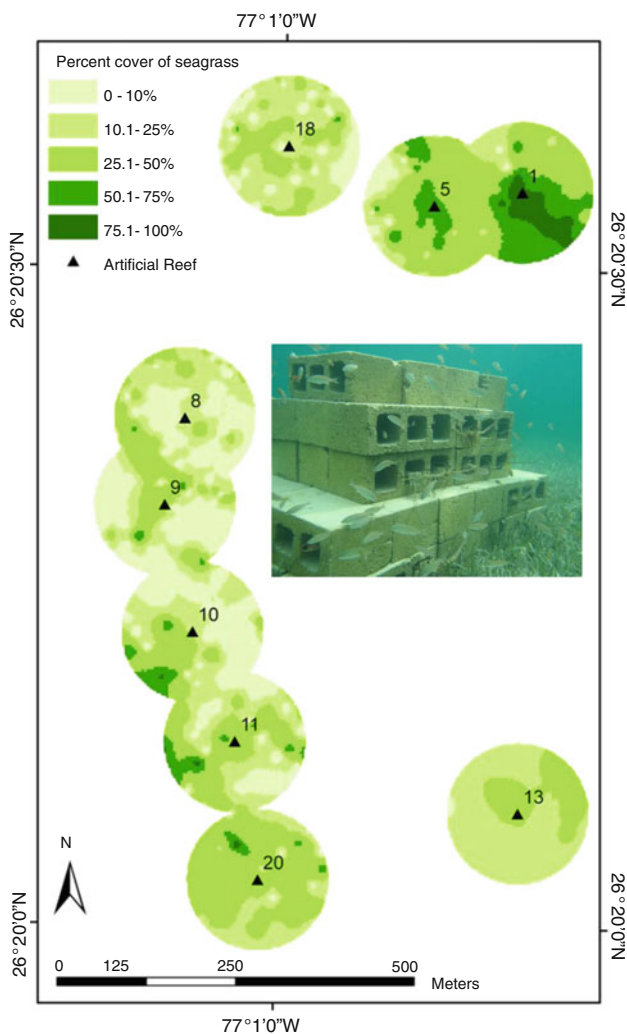
Underwater visual census was employed throughout the study period to estimate fish abundance and recruitment (Layman et al. 2004). All fishes within 4 m of each reef were surveyed until the observer was confident all fishes had been recorded. Fish communities were surveyed on 12 dates (1, 7, 20, 27, 34, 51, 70, 96, 126, 152, 212, 259 days after reef construction). All fishes enumerated were identified to the lowest possible taxonomic level, and size (total length) of each individual was estimated to the nearest cm. Surveys were completed by a snorkeler (LAY or CAL)

Fig. 1 The study site showing locations and seagrass cover surrounding artificial reefs. *Inset* shows an artificial reef 3 months after construction (June 2009). Each reef is identified by a *solid triangle* and *number*. Reefs were located in the Bight of Old Robison, Abaco Island, Bahamas (ESM, Fig S1)

trained in fish identification and underwater fish size estimation.

Habitat variables were measured for each reef and were then grouped at patch and landscape spatial scales (the term "habitat variables" will be used to describe variables measured at either spatial scale; Table 1). Patch scale was used to describe habitat variables measured in close proximity to the reef (extent of measurement = 4 m). Previous studies have reported 100 m to be the scale at which the most abundant species in this study respond to their environment (Kendall et al. 2003; Pittman et al. 2007), and therefore this was chosen as the focal landscape extent. Exploratory data analysis using landscape areas with smaller radii (e.g., 50 m) gave similar results, but with poorer model fit, so 100 m was retained as the focal landscape extent.

Patch-scale variables included depth, mean seagrass shoot density within 4 m of the reef, and mean seagrass shoot height within 4 m of the reef. Tide-corrected depth to the base of each reef was measured to the nearest 0.1 m. In order to quantify the amount of seagrass (*Thalassia testudinum*) around each reef, 18 0.01-m^2 quadrats were placed haphazardly between 2 and 4 m from the base of the reef. Within each quadrat, all seagrass blades were counted and the heights of five haphazardly selected blades were measured to the nearest centimeter. Shoot densities and shoot heights measured in each quadrat were averaged among all 18 quadrats to estimate patch-scale values for each reef. Seagrass shoot density and shoot height within 4 m of the reef were used to assess fine-scale differences in seagrass bed characteristics, as these metrics (as opposed to seagrass percent cover at a scale of 100s of meters) accurately capture seagrass heterogeneity over small spatial scales (Fonseca et al. 2002). While other seagrasses or macroalgae may affect the function and fauna associated with seagrass beds within the study area (Seese et al., unpublished data), seagrass beds surrounding the reefs were dominated by *T. testudinum* and, therefore, we focused only on this species.

Landscape-scale variables included distance to open ocean, distance to structure, mean seagrass cover within 100 m of the reef, habitat diversity within 100 m of the reef, and habitat contrast within 100 m of the reef. Distance to open ocean (mouth of the Bight) was included as a proxy for the larval recruitment source. Alternatively, distance to the nearest structure (natural patch reefs or large artificial structures such as sunken boats) could affect the recruitment rate of sub-adult and adult individuals to reefs. Distance to open ocean and distance to structure were estimated using Google Earth® (Google 2010). To assess seagrass densities at larger spatial scales, estimates of percent cover were used. Quadrats of 1 m^2 were placed at 609 haphazard points throughout the study area and the

Table 1 Description of habitat variables measured with range, mean, and standard deviation among reefs

Habitat variable	Explanation	Spatial scale	Range	Mean ± SD
Depth	Water depth of reef base at mean low water	Patch	1.3–2.5 m	1.8 ± 0.3 m
Mean seagrass shoot density within 4 m	Density of seagrass blades averaged within 4 m of the reef	Patch	6.1–20.2 blades/100 cm^2	15.7 ± 4.3 blades/100 cm^2
Mean seagrass shoot height within 4 m	Height of seagrass blades averaged within 4 m of the reef	Patch	5.5–9.6 cm	6.7 ± 1.6 cm
Distance to open ocean	Distance to larval recruitment source	Landscape	2.1–2.8 km	2.6 ± 0.3 km
Distance to structure	Distance to recruitment source of non-larval fishes	Landscape	170–950 m	550 ± 200 m
Mean seagrass cover within 100 m	Mean percent cover seagrass within 100 m of each reef	Landscape	15.2–49.3% cover	25.7 ± 11.2% cover
Habitat contrast	Index of habitat patchiness; measures variability in percent cover of seagrass between adjacent cells within 100 m of each reef	Landscape	1,130–1,600	1,480 ± 150
Habitat diversity	Index of diversity of seagrass patches; alternate measure of habitat patchiness within 100 m of each reef	Landscape	0.6–1.3	1 ± 0.2

percent cover of seagrass was estimated using the modified Braun–Blanquet method (Fourqurean et al. 2001). The distribution of seagrass in the study area was mapped using the measured percent cover of seagrass at these fixed points and interpolating these coverages to a 31,000-m^2 area (circle with 100 m radius) around each reef with an inverse distance-weighted interpolation (Lirman and Cropper 2003). Seagrass cover mapped within 100 m of each reef (Fig. 1) revealed a gradient in percent cover of seagrass and patchiness. While there may be some seasonality in the cover of seagrass (Fourqurean et al. 2001), seagrass was mapped near the end of the growing season when seagrass cover would be at its maximum (August 2009). The map of seagrass cover around each reef was used to calculate the remaining landscape-scale variables described below.

The mean percent cover of seagrass was estimated within 100 m of each reef using ArcGIS v 9 (ERSI 2008). Patches of varying seagrass cover were defined by grouping seagrass cover in five categories (0–10.0, 10.1–25.0, 25.1–50.0, 50.1–75.0, and 75.1–100%). Habitat diversity around each reef was calculated by the same method as Shannon–Weiner diversity (Pielou 1966) indices for community data, but with the area of patches used instead of species abundance. Habitat diversity within 100 m for each reef was calculated in Fragstats 3.3 (McGarigal et al. 2002). Habitat contrast (a measure of patchiness) was also computed in Fragstats 3.3 by calculating the "difference" in the value of seagrass cover between each 1-m^2 cell and those bordering it, where differences were weighed by the change in percent cover (e.g., a cell with 50.1–75.0% cover was weighted as 0.25 different from one with 75.1–100%

cover). When adjacent cells vary greatly in percent cover of seagrass, the contrast index is higher and the landscape is considered to be patchier.

Data analysis

All fish taxa were assigned to a functional group based on trophic guild (herbivorous, omnivorous, invertivorous, piscivorous) and foraging habitat (benthic, pelagic) following previously reported dietary information (Randall 1967; Layman and Silliman 2002; Cocheret de la Moriniere et al. 2003) and observations from our study system. Forty-five taxa observed on the reefs were classified as benthic feeders. These species (referred to as "benthic") may be most likely to respond to habitat variables because they utilize resources that were dependent on the benthic habitat type. As such, some analyses only focused on this particular functional grouping. Other analyses required consideration of the entire fish community (e.g., diversity metrics) and included 14 additional taxa that were more transient and/or are expected to be primarily pelagic feeders (e.g., tomtates, *Haemulon aurolineatum*, and jacks, Carangidae). These transient taxa often comprised large schools that may have been loosely associated with reefs during a survey event.

Patterns in species richness and benthic fish abundance were evaluated over time (Hypothesis 1). Benthic fish abundance was ln transformed in order to homogenize variance among reefs over time. Next, the mean of species richness and ln(benthic fish abundance) for each survey date was calculated across all reefs. In order to evaluate the

overall trajectory of species richness and fish abundance over time, the relationships between time and both mean species richness and mean ln(benthic fish abundance) were modeled with various linear, polynomial and asymptotic models based on visual inspection of the data. Specifically, we fit linear, second order polynomials, inverse first and second order polynomials, exponential rise to maximum models with two and three parameters, and second order power functions. We evaluated candidate models based on adjusted r^2 values, where the coefficient of determination (r^2) is adjusted for the number of parameters in the model. In this way, the adjusted r^2 value is useful in determining if adding new parameters into the model increases overall model fit (Draper and Smith 1998). For this reason, we used the adjusted r^2 in order to select the most appropriate and parsimonious model that best modeled trends in each of species richness and fish abundance over time. Data met the assumption of normality in both cases ($P = 0.69$ and $P = 0.61$, respectively).

Next, analyses of community structure were performed for all benthic species and evaluated over time. Community data were analyzed using species-by-sample matrices that were square-root transformed to down-weight the influence of dominant taxa (Clarke 1993). The similarity between community structure over time and among reefs was evaluated graphically using non-metric multidimensional scaling (nMDS), where communities that are more similar are closer together in 2-dimensional space (PRIMER© v.6; Clarke 1993; Clarke and Gorley 2006). This nMDS was used to visualize the clustering among surveys through time (Hypothesis 2a).

Additionally, the strength of the correlation between benthic fish community structure and habitat variables was evaluated over time (Hypothesis 2b). First, a BIOENV algorithm was employed, which predicts which habitat variables best explain differences in community structure and reports the correlation between habitat variables and fish community structure in PRIMER© v.6 (Clarke 1993). The BIOENV algorithm maximizes the rank correlation between the Bray–Curtis similarity matrix of square-root transformed abundance data for each taxa and a resemblance matrix of normalized habitat data to select the habitat variables that explain most of the variation in community structure. Similar to the treatment of species richness and abundance data, linear, polynomial and asymptotic regression models were used to test the relationship between time and the variation in fish community structure explained by habitat variables (correlation output from the BIOENV). Data met the assumption of normality ($P = 0.93$).

We selected the last three survey dates (days 152, 212, and 259) for the remaining analyses investigating which habitat variables were most important in driving differences in community structure, fish abundance and species richness among reefs (Hypothesis 3). We selected these dates, as species richness, fish abundance, and community structure remained relatively constant following this time period, and thus we considered the community to be relatively stable. First, we treated communities surveyed on each date separately and used the results of the BIOENV algorithm described above on these dates to identify the most important variables driving differences in community structure. Next, because mean seagrass cover within 100 m was suspected to be one of the most important variables explaining community structure, we a priori grouped sites into "high" (reefs 1, 5, 11, 13, 20; mean seagrass cover within 100 m >20%) and "low" (8, 9, 10, 18; mean seagrass cover within 100 m <20%) seagrass groups. A similarity percentages (SIMPER) analysis was used to determine which fish taxa were most important in driving differences between these two groups for the last three survey dates (PRIMER© v.6, Clarke 1993). This analysis is also based on similarity matrices of fish abundance data and examines which species contribute most to the Bray–Curtis dissimilarity between groups of reefs (high and low seagrass).

Next, we examined the relationship of species richness and fish abundance with habitat variables. For the following analyses, we took the mean of species richness and fish abundance estimates for each reef across the last three survey dates. In order to reduce the number of predictor variables used, all habitat variables were grouped by factor analysis to account for co-linearity. A principal component analysis was used to generate orthogonal axes of habitat variables. Next an equimax rotation of principal component axes was performed to reduce the number of axes and number of variables loading heavily onto these axes (SPSS® v.14.0; SPSS 2005). Separate general linear fodels were used to analyze the relationship between each of the following biotic variables: species richness (all taxa), abundance of all fishes, abundance of benthic fishes, abundance of small fishes (≤5 cm) or abundance of large fishes (>15 cm), with habitat components ($n = 3$ principal component axes) using SAS® software v.9.2 (SAS Institute 2007). We calculated η^2, the proportion of variation in the biotic variable explained by each predictor, as a measure of effect size. Partial regression plots were created to graphically illustrate the relationship between principal component axes and biotic variables. These plots are useful in isolating the effect of a given predictor variable when multiple predictor variables are used, and the slope of the line for each plot is equal to the parameter estimate for a given predictor variable (Velleman and Welsch 1981; Gunst and Mason 1980).

Results

An estimated 13,969 fishes representing 59 different taxa were recorded in surveys on the 12 sampling dates. Of these, 7,344 individuals in 45 taxa were classified as primarily benthic. Over 95% of all benthic fishes observed were from 16 taxonomic groupings: white grunt, post-settlement grunt (*Haemulon* spp.), slippery dick (*Halichoeres bivittatus*), French grunt (*Haemulon flavolineatum*), juvenile parrotfish (*Sparisoma* spp.), reef squirrelfish (*Sargocentron coruscum*), surgeon fish (*Acanthurus* spp.), cottonwick (*Haemulon melanurum*), blue tang (*Acanthurus coeruleus*), squirrelfish (*Holocentrus adscensionis*), spotted goatfish (*Pseudupeneus maculatus*), beaugregory (*Stegastes leucostictus*), blackear wrasse (*Halichoeres poeyi*), drum (*Equetus* spp.), gray snapper (*Lutjanus griseus*), and stoplight parrotfish (*Sparisoma viride*).

Fish community assembly

The relationship between time and species richness was best modeled by a sigmoidal model [$Y = 17.53 (1 + e^{-(x - 68.75)/32.03})$, $df = 2$, $r^2 = 0.95$, $P < 0.0001$; Fig. 2a]. The relationship between time and ln(benthic fish abundance) was best modeled by an exponential, asymptotic model [$Y = 2.08 + 2.87(1 - 0.98^X)$, $df = 2$, $r^2 = 0.91$, $P < 0.0001$; Fig. 2b]. Both models appeared to reach an asymptote by the end of the study period (Fig. 2).

Community structure shifted over time, as communities were relatively similar among the beginning survey dates (days 1 and 7), then became less similar to one another, followed by a period of relatively similarity during the last 3 survey dates (Fig. 3). The relationship between days following reef creation and the correlation between habitat variables and benthic fish community structure was best represented by a quadratic model, although this model was only marginally significant, with time explaining 47% of the variation in the correlation ($Y = 0.18 + 0.0049x + 0.000014x^2$, $df = 2$, $r^2 = 0.47$, $P = 0.055$; Fig. 2c).

Based on results of the previous analyses, we considered the fish community over the last three survey dates to be relatively stable, as species richness and fish abundance had both reached an asymptote, and community structure was changing relatively little among survey dates. On the last three survey dates (days 152–259), the spearman rank correlation between the habitat variables and fish community structure ranged between 0.438 and 0.819 (BIOENV; ESM, Table S1). While multiple habitat variables were important in explaining differences in fish community structure among reefs, mean seagrass cover within 100 m was among the most important on all three dates, and was the only habitat variable included in the best model for all three dates.
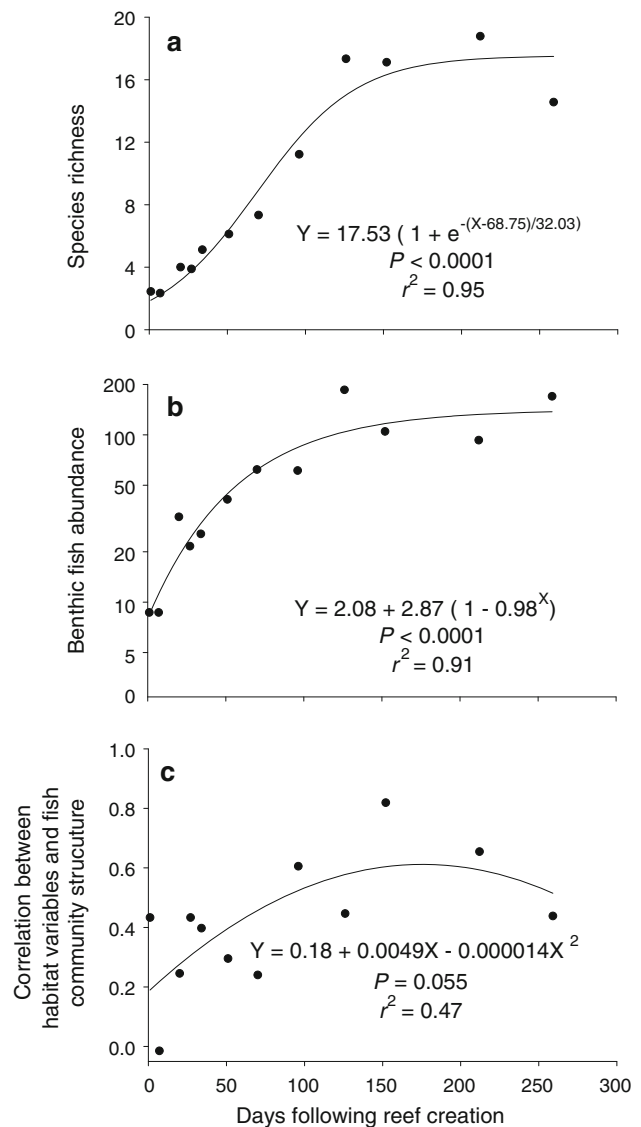
Fig. 2 Trajectory of **a** species richness, **b** benthic fish abundance (mean no. fish/reef), and **c** the correlation between habitat variables and fish community structure through time. Note *y*-axis of **b** is plotted on a natural log scale but *labels* are back-transformed to represent true abundance values

Twenty-four taxa were found to contribute to differences in community structure between reefs with "high" and "low" amounts of seagrass (SIMPER, contributing to 90% of the dissimilarity in communities between groups; ESM, Table S2). The two most important taxa driving differences in community structure both belonged to one family of benthic, invertivorous fishes (grunts, Haemulidae). White grunts were the most important taxa, being more abundant at "high" seagrass reefs (mean abundance ± SE, 80.2 ± 16.4 fish/reef) compared to "low" seagrass reefs (28.4 ± 8.4 fish/reef). The second most important taxa explaining these differences was French grunt, which were
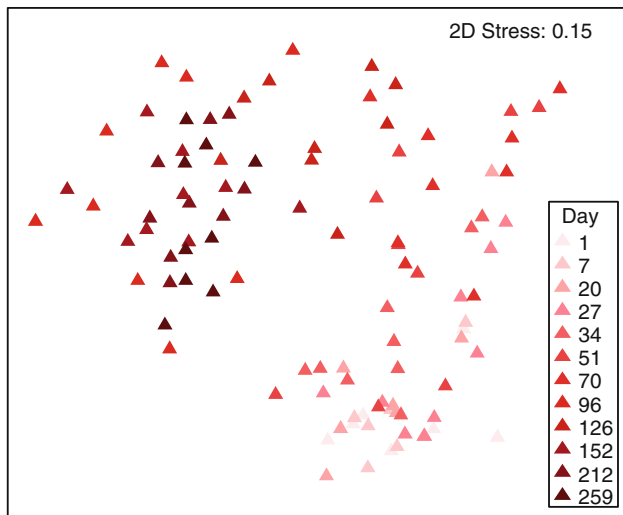
Fig. 3 Non-metric multidimensional scaling plot of community structure on reefs through time. *Triangles* represent an individual survey for each reef (*n* = 9 per day) and are *shaded* according to survey date

more abundant on "low" seagrass reefs ("high" seagrass = 10.3 ± 4.2 vs. "low" seagrass = 19.6 ± 5.9 fish/reef).

Fish abundance and diversity

In the principal component factor analysis, three component axes explained 86.4% of the variation in habitat variables (ESM, Table S3). The distance to open ocean and habitat diversity loaded heavily on the first component axis. Reefs that are positively related to this axis are far from larval recruitment sources in more patchy (diverse) seagrass habitat. Mean seagrass cover within 100 m and depth loaded heavily on the second axis. Reefs that are positively related to this axis are relatively deep with a greater amount of seagrass at the landscape scale. Only mean seagrass shoot density within 4 m loaded heavily on the third component axis; reefs positively related to this axis had a greater amount of seagrass at the patch scale.

Species richness and total fish abundance were not predicted by any of the groupings of habitat variables (Table 2; Fig. 4a–f). In contrast, habitat variables explained 75% of the total variation in benthic fish abundance, although the overall model was only marginally significant (Table 2). Benthic fish abundance was greater on deeper reefs with more seagrass at the landscape scale (Fig. 4h). Although less important in

Table 2 Results of general linear models of species richness and different abundance measures predicted by principal component groupings of habitat variables

| Overall model					Individual predictors					
Source	*df*	MS	*F*	*P*	Source	*df*	MS	*F*	*P*	η^2
Species richness, $R^2 = 0.20$										
Model	3	4.42	0.41	0.75	Component 1	1	11.06	1.04	0.36	0.17
Error	5	10.69			Component 2	1	0.34	0.03	0.87	0.01
					Component 3	1	1.86	0.17	0.69	0.03
Total fish abundance, $R^2 = 0.13$										
Model	3	5,554.13	0.26	0.85	Component 1	1	12,069.73	0.56	0.49	0.10
Error	5	21,534.63			Component 2	1	3,398.56	0.16	0.71	0.03
					Component 3	1	1,194.07	0.06	0.82	0.01
Benthic fish abundance, $R^2 = 0.75$										
Model	3	3,932.07	4.94	0.059	Component 1	1	709.78	0.89	0.39	0.05
Error	5	796.02			Component 2	1	7,418.38	9.32	0.028	0.47
					Component 3	1	3,668.05	4.61	0.085	0.23
Small fish abundance, $R^2 = 0.57$										
Model	3	306.37	2.21	0.21	Component 1	1	2.07	0.01	0.91	<0.01
Error	5	138.80			Component 2	1	719.02	5.18	0.072	0.45
					Component 3	1	198.02	1.43	0.29	0.12
Large fish abundance, $R^2 = 0.82$										
Model	3	110.83	7.42	0.027	Component 1	1	100.39	6.73	0.048	0.25
Error	5	14.93			Component 2	1	222.48	14.91	0.012	0.55
					Component 3	1	9.61	0.64	0.46	0.02

Source source of variation, *df* degrees of freedom, *MS* mean squares, *F* *F* statistic, *P* *P*-value based on *F* test, η^2 proportion of variation in dependent variable explained by each predictor

predicting benthic fish abundance, the amount of seagrass at the patch scale was also positively related to abundance (Fig. 4i). The abundance of small fishes (≤5 cm) was positively related to the amount of seagrass at the landscape scale and reef depth, although this relationship was only marginally significant (Fig. 4k) and the overall model was not significant (Table 2). Abundance of large fishes (≥15 cm) could be predicted by habitat variables (Table 2), and was greater on reefs that were in more patchy landscapes that were farther from the open ocean, as well as those that are deeper with more seagrass at the landscape scale.

Discussion

Our data support the idea that even seemingly homogeneous habitat types can have sufficient degrees of intra-habitat variation to drive significant differences in faunal community structure. Both patch- and landscape-scale variables related to the seagrass beds were important predictors of fish community assembly. The amount of sea-grass at patch and landscape scales, as well as habitat patchiness, all emerged as important drivers for various components of fish community assembly. The amount of seagrass at the landscape scale was the most important

Fig. 4 Partial regression plots derived from general linear models showing the relationship between principal component axes of habitat variables (x-axes) and **a–c** species richness, **d–f** total fish abundance, **g–i** benthic fish abundance, **j–l** small fish (≤5 cm TL) abundance and **m–o** large fish (≥15 cm TL) abundance. The habitat variables loading most heavily on each principal component are listed under the x-axes. P-values are included for each parameter as well as η^2, i.e., the proportion of total variation explained by each component. Trend lines are shown for significant and marginally significant (P < 0.1) relationships
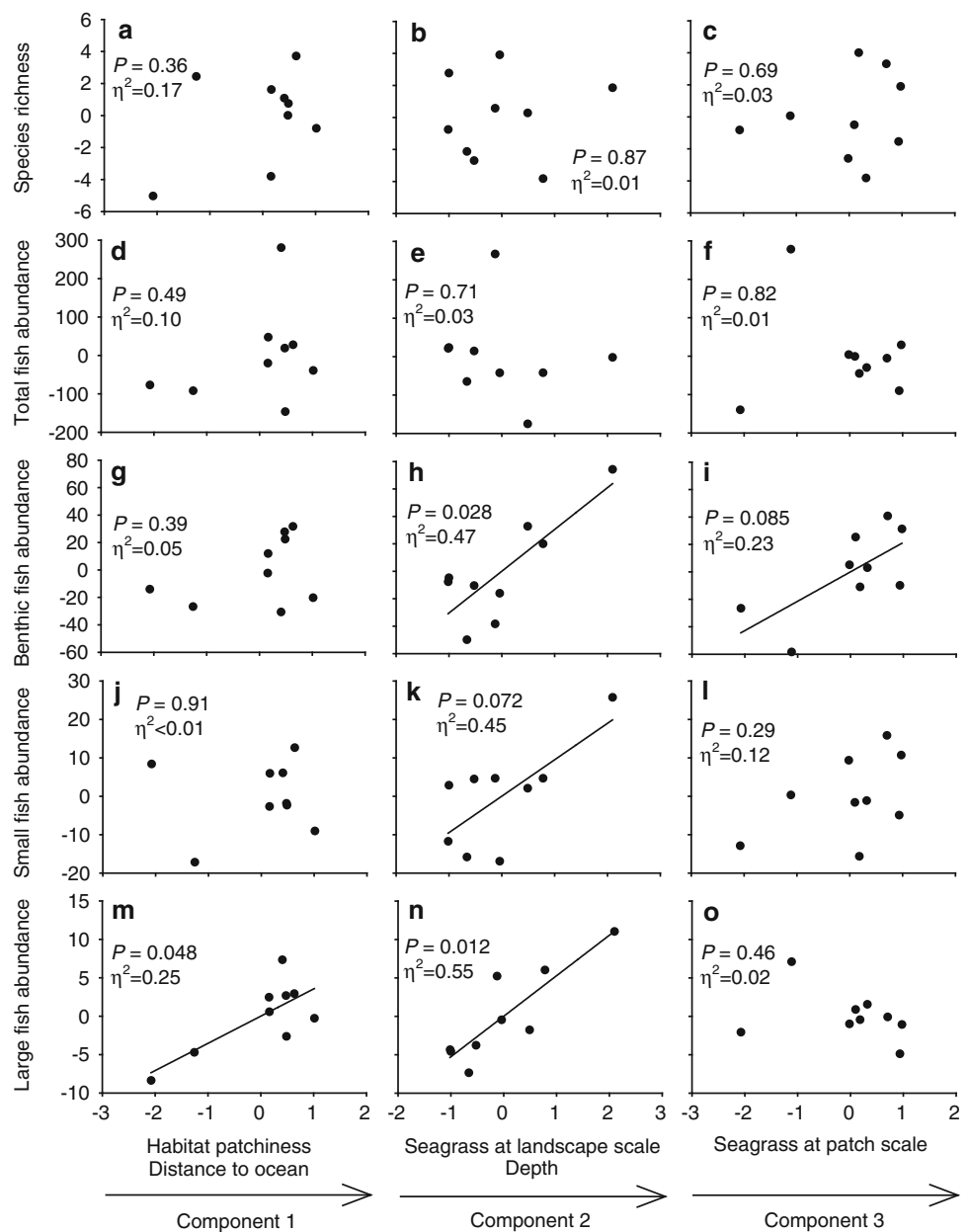
variable driving differences in the abundance of fishes (as well as overall community structure). As such, we provide evidence that links habitat heterogeneity at patch and landscape scales to fish community assembly.

Previous studies of reef fish communities have reported that both stochastic and deterministic processes may be important in determining community assembly. Stochastic processes such as larval supply were at one time thought to be the dominant driver of reef fish community assembly (Sale and Douglas 1984). But deterministic factors have since been found to be important, including mechanisms such as priority effects (Shulman et al. 1983; Almany 2003), post-settlement mortality (Shulman and Ogden 1987), and availability of refugia (Hixon and Beets 1989; Syms and Jones 2000). In this study, the strength of the relationship between fish community structure and habitat variables changed over time, generally increasing (although the last survey point indicates it may have started to decline by the end of the study period, perhaps as a result of seasonal effects associated with the onset colder winter water temperatures). This pattern might be expected if community assembly was at first random, and species interactions and/or habitat associations became stronger over time as fish densities increased (Arrington et al. 2005).

The pattern we found in similarity of fish communities through time supports this notion. Within the first week, communities were fairly similar, as fishes on reefs were mostly represented by individuals common in surrounding seagrass (e.g., slippery dick wrasse). Next, as larval and other fishes began to recruit to the reefs, communities became less similar to one another, and less similar among sampling dates for a given reef, with stochastic processes apparently driving assembly. Finally, near the end of the survey period, fish communities were similar to one another, and more similar over time, and habitat variables explained a larger portion of the variation in fish communities among reefs. While patch reef fish communities are typically dynamic, our results indicate that habitat context can still explain a large proportion of the variability in community assembly once fish densities reach a particular threshold, thereby supporting a model of reef fish community assembly containing both stochastic and deterministic components.

The amount of seagrass at the landscape scale seemed to be the most important driver of community structure and explained most of the variation in fish abundance once communities had stabilized. For analyses assessing effects of habitat variables on species richness and abundance, principal component analysis could not separate variation in depth completely from variation in seagrass cover at the landscape scale, likewise between distance to the open ocean and habitat patchiness. However, in these cases, depth (percent variation = 16.7%) and distance to the

ocean (11.5%) varied less among reefs than variation in the cover (43.6%) or patchiness of seagrass (20.0%). Further, Gladfelter et al. (1980) found environmental context did not seem to drive differences in community structure for patch reefs in St. Croix that varied more in terms of depth, distance to other structures, and oceanic influence than reefs in our study. Therefore, it is reasonable to assume that seagrass variables were more important in driving the observed differences in fish abundance than these other variables.

Seagrass plays two primary functional roles for fishes. First, seagrass habitat is known to harbor greater densities of benthic invertebrates than unvegetated bottom habitat (Ansari et al. 1991; Nakamura and Sano 2005), providing more food for benthic invertivores. Similarly, seagrass and associated epiphytes provide a direct food source for herbivorous fishes (Kirsch et al. 2002). Therefore, greater cover of seagrass likely represents increased food availability for many fish species. Second, seagrass structure may provide shelter from predators (Heck et al. 2003). More generally, the relationship between seagrass cover and predation risk likely depends on the body size and behavior of the focal organism. Since most fishes in our study had a relatively small body size, it is reasonable to suspect that protection provided by seagrass structure contributed to the positive relationship between fish abundance and cover of seagrass across the landscape.

In general, landscape-scale effects emerged as more important in predicting fish community structure and the abundance of fishes than patch-scale effects, regardless of fish body size. This contradicts our original hypothesis, where we predicted that smaller fishes would respond to factors at smaller spatial scales. This could indicate these small fishes are still able to move large distances, and thus select optimal habitat, despite their size. Alternatively, many of the small fishes are juveniles and recruited to these reefs as larvae. This could indicate that larval fish may select settlement habitat based on landscape-scale habitat features that will be important for post-settlement development, possibly based on visual, auditory or chemical cues (Montgomery et al. 2001; Atema et al. 2002; Huijbers et al. 2008). Larger fish were also more abundant on reefs with more seagrass at the landscape scale, possibly associated with increased abundance of prey organisms. Large piscivores may also find it easier to locate prey in patchy seagrass (Hovel and Lipcius 2002), possibly explaining the greater abundance of large piscivores in patchy landscapes.

Greater abundance of benthic species on reefs with more seagrass cover at the landscape scale was primarily driven by abundance of white grunts. Conversely, the congeneric French grunt was more abundant on reefs with less seagrass (more sand) at the landscape scale. Both species are known to feed on benthic invertebrates in soft bottom habitats

(Ogden and Ehrlich 1977; Cocheret de la Moriniere et al. 2003), yet they do not seem to respond to the landscape in the same way. This separation in daytime habitat preference may be an effect of habitat partitioning by these two potential competitors for nighttime foraging grounds. These results are consistent with those from a study in the US Virgin Islands that observed partitioning of nocturnal foraging habitat between these two species, with white grunts feeding primarily in seagrass beds and French grunts feeding primarily over sand flats (Ogden and Ehrlich 1977). These data emphasize the importance of exploring organism–habitat relationships on a species-by-species basis.

We did not see significant differences in species richness among reefs in different landscape contexts. Our study only dealt with differences in α diversity, i.e., differences in diversity among sites within a single habitat type. At 10–100 m spatial scales, structural complexity (which was held constant in this study) has been found to be the most common variable affecting species richness in coral reef ecosystems (Mellin et al. 2009). Similarly, Grober-Dunsmore et al. (2008) found only a weak relationship between species richness and landscape matrices (cover of seagrass) on similar patch reefs. In our study, because the amount of structured habitat was held constant, it is not surprising that we observed no significant difference in diversity measures among reefs.

Recently, ecologists have emphasized the variability within marine habitat types that have long been considered homogenous (Faunce and Layman 2009; Kraan et al. 2009). Heterogeneity at both patch and landscape scales may contribute to these observed differences in structure and function of habitats. In order to truly link various aspects of ecosystem function to the surrounding landscape, manipulation of both focal habitats and the surrounding landscape would be necessary, although logistically prohibitive in most cases. In this study, we take a first step towards an experimental approach by utilizing natural spatial variation in landscapes and manipulating the locations of artificial reefs. Reef location did not affect the characteristics of the surrounding landscape, so it is reasonable to assume the difference in community assembly among reefs was driven by differences in the surrounding landscape. This landscape-scale effect may have critical implications for conservation and management efforts, especially as back-reef habitats are included in marine protected area design (Beck et al. 2001; Mumby 2006). More specific habitat characterizations, i.e., more refined than just "mangrove" or "seagrass', may be critical for optimal reserve design (Mumby 2006; Grober-Dunsmore et al. 2009).

Coastal development and land-use change are among the most serious threats to coastal ecosystems (Lotze et al.

2006). Land-use change has the potential to rapidly alter landscape characteristics in these systems, including widespread habitat loss or alterations in the spatial arrangement of habitat types (e.g., Orth et al. 2006). Specifically, coastal development may result in increased habitat fragmentation (Montefalcone et al. 2010), which is known to cause losses in ecosystem functions and diminished ecosystem services (Bell et al. 2001; Layman et al. 2007). Furthermore, seagrass fragmentation is often concomitant with declines in seagrass cover or decreased spatial coverage (Fonseca and Bell 1998). Our study demonstrates that even subtle changes in landscape characteristics have the potential to alter fish community dynamics in nearshore ecosystems.

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