Separating the Spatial and Environmental Variation of Reef Fish Communities: PCNM and Partitioning Analyses

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ABSTRACT

Modern ecology research has sought to explicitly integrate spatial organization as critical functioning aspects of communities and ecosystems. Objectives of this study were to establish the spatial scales of variation of reef fish communiies and environmental characteristics, and quantify the isolated effect of environmental and spatial variales on fish community composition. By using a spatial survey consisting of 472 line transects on four reef habitat and 12 sites of the Caribbean coast of Mexico we collected fish abundance, environmental characteristics and geographic coordinates data. In order to epitomize the spatial structure of the data we used Principal Coordinates of Neighbor Matrices (PCNM) technique. Partitioning analysis was used to quantify and test the partial effect of environmental and spatial variables on fish community composition. Results showed that significant PCNM´s variables ($p < 0.05$) described mainly fine to intermediate scale variation (< 30 km). Total explained variation on reef fish communities fluctuated between 60 and 71% respect to the surveyed habitat. The highest fraction of variation was environmental (30 - 40%). Spatial variation varied from 10 - 15%, depending on the scale of analysis. These fractions were associated with structural components of the environment, ecological processes, and external causes. Methods and hypotheses proposed were consistent with the existing theory of reef fish communities and provide new evidence about fish-habitat relationships over explicit spatial scales - useful information for the design of MPA and coral reef ecosystem management.

KEY WORDS: Environmental variation, spatial variation, reef-fish communities

Separando la Variación Espacial y Ambiental de las Comunidades de Peces Affecifales: Análisis PCNM y de Partición

La investigación ecológica moderna demanda incluir la organización espacial como un componente crítico en el funcionamiento de sistemas biológicos y de los ecosistemas. Los objetivos de esta investigación fueron: definir las escalas espaciales de variación en la composición de la comunidad de peces y las características del ambiente, y cuantificar el efecto independiente de las variables del ambiente y las espaciales en las comunidades de peces. Sobre un diseño espacial que incluyó 472 transectos lineales en cuatro hábitat arrecifales de 12 sitios de la costa del Mar Caribe en México, se tomaron datos de abundancia de peces, características del hábitat y posiciones geográficas. Para evidenciar la estructura espacial en los datos se utilizó Análisis de Coordenadas Principales de Matrices Cercanas (PCNM). Se empleó análisis de partición para cuantificar y probar el efecto independiente de las variables ambientales y de las espaciales en la composición de la comunidad de peces. Los resultados indicaron que las variables espaciales (PCNM´s) significativas ($p < 0.05$) representaron principalmente variación de los datos a pequeña y mediana escala (< 30 km). La variación total en la composición de la comunidad fue entre 60 y 71% dependiendo del hábitat analizado, la fracción mayor correspondió a variación ambiental (30 - 40%). La variación espacial fluctuó entre 10 - 15%, dependiendo de la escala de análisis. Estas fracciones de variación pudieron asociarse a componentes estructurales del ambiente, procesos ecológicos y causas externas. Los métodos e hipótesis propuestas fueron consistentes con la teoríaa ecológica existente de comunidades de peces y aportaron nueva evidencia sobre las relaciones peces-ambiente a escalas espaciales definidas –información útil en el diseño y manejo integral de ecosistemas arrecifales.

PALABRAS CLAVES: Ecología de comunidades de peces, variación espacio-ambiental, partición de la variación

La Séparation de la Variation Spatiale et de L'environnement de Communautés de Poissons de Récf: PCNM et Analyses de Partition

La recherche moderne écologique a cherché à intégrer explicitement l'organisation spatiale comme un aspect critique du fonctionnement des communautés et des écosystèmes. Les objectifs de cette étude étaient d'établir les échelles spatiales de la variation des communautés de poissons de récif et les caractéristiques environnementales, et de quantifier l'effet isolé des variables environnementales et spatiales sur la composition des communautés de poissons. En utilisant une enquête spatiale composés de 472 transects linéaires sur quatre habitat de récif et 12 sites de la côte caribéenne du Mexique, nous avons recueilli une abondance de poisson, des caractéristiques environnementales et des données coordonnées géographiques. Afin de personnaliser la structure spatiale des données, nous avons utilisé la technique de Principal Coordinates of Neighbour Matrices (PCNM). Une analyse de partition a été utilisée pour quantifier et tester l'effet partielle des variables de l'environnement et du territoire sur la composition des communautés de poissons. Les résultats ont montré que d'importantes variables PCNMs ($p < 0,05$) décrivent principalement des variations de niveau intermédiaire et subtile (<3 0 km). Le total a expliqué une variation sur les communautés de poissons de récifs qui ont fluctué entre 60 et 71%, quant à l'habitat de l'enquête. La plus forte proportion de variation est environnementale (30 - 40%). La variation spatiale a varié de 10 à 15%, selon l'échelle d'analyse. Ces fractions ont été associées à des éléments structurels de l'environnement, des processus écologiques et des causes externes. Les méthodes et hypothèses proposées étaient conformes à la théorie actuelle des communautés de poissons de récif et fournissent de nouvelles preuves concernant les relations poisson-habitat sur des échelles spatiales explicites -informations utiles pour la conception de gestion d'AMP des récifs coralliens et des écosystèmes.

MOTS CLÉS: Communauté de poissons de récif, variation spatiale, variation environnemente, analyse spatiale, habitat

INTRODUCTION

Patterns of variation in reef fish community composition have been recognized to be a result of the effect of habitat structure (Syms and Jones 2000), biotic interactions among species (Hixon 1991), larval recruitment (Doherty 1981), external factors, both natural and anthropogenic (Hawkins *et al*. 2003), the geographic position of the reef along the shoreline (Gust *et al*. 2001), connectivity between reefs (Ault and Johnson 1998), among other origins. According to Jones (1991), generally, the hypotheses concerning coral reef fish community structure fit into one of four basic models: the competition model, the lottery model, the predation model, and the recruitment-limitation model. However, from diverse studies and intuitive knowledge we now know that field observations are more likely the result from a combination of models differing in the spatial scale of expression. Evidence suggests that on a scale of metres, reef-fish species are affected by environmental factors such as depth (Beukers and Jones 1997), topographic complexity (Nuñez-Lara and Arias-González 1998), and the biotic and abiotic components of the reef substratum (Chabanet *et al.* 1998). Recognisable patterns of variation in the community composition at scales from tens of metres to kilometres could be associated with biotic interactions such as predation or competition (Hixon and Beets 1993, Jones and McCormick 2002), while broad scale variation is generally associated with the recruitment process (Doherty 1991) and the effect of biophysical components of the environment, which exhibit a spatial arrangement in the system revealing a classical hierarchical organization (Casseles and Warner 1996).

Given that multiple theories may be appealed about the factors and processes causing variation in reef fish community structure and those depend strictly of the scale of analysis, we intended to cut out multiplicity by using partition examination over a multi-scale design. The study was designed threefold:

i) To quantify the effect of environmental and spatial variables on reef fish community composition at different spatial scales;
ii) To model the fraction of variation, which is not directly explained for the analysed variables, with regard to the ecological theories proposed on reef-fish ecology. We anticipate that the PCNM variable combined with partitioning of variance may lead us to resolve what significant is the fish-habitat interaction according to the scale: fine (10^2 -10^3 m), intermediate (10^4 - 10^5m) or broad (>10^5m), respect to other sources of variation acting on fish species.
iii) Central question to rejoin were: which of the evaluate variables are significant to explain patterns of variation in community composition? At which scale(s) are these variables operating?

METHODS

A fringing reef system in the eastern coast of the Yucatan Peninsula runs roughly continuously parallel to the coast. It extends ca. 400 km and comprises an important part of the Mesoamerican Coral Reef System (Figure 1). This region is spatially divided into three similar-length sectors according to the predominant human activity: tourism (from 20º to 21º N), which includes plentiful hosting and recreational infrastructure with an associated urban development; the Sian Ka'an Biosphere Reserve (from 19º to 20º N), which comprises a protected area covering 5,280 km^2 of coastal ecosystems, including 1,200 of coral reefs; and the fishing sector (from 18º to 19º N), where artisan and self-consumption fishing are the predominant activity (Figure 1).

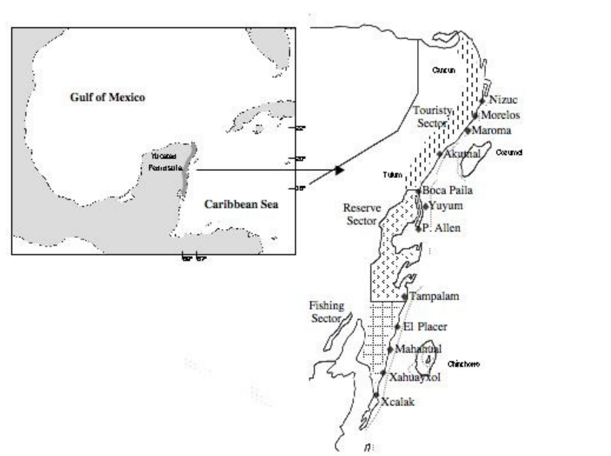


Figure 1. Caribbean sea coast in the eastern Yucatan Peninsula of Mexico

Taking advantage of the particular distinctiveness of the study area in terms of the spatially separate human activities, we surveyed reefs subjected to the three different types of human influence. The main goal was to decompose the total variation of reef fish community composition data into four main components: *environmental*, interpreted as the isolated effect of the environmental variables; *spatial*, variation produce for the spatial variables, which may reflect the effect of biotic processes or another source of variation not strictly associated with the analyzed variables; *environmental spatially structured*, the variation that is explained by the redundant portion of environmental and spatial data sets, which could be understood as the effect of environmental variables, which themselves exhibit a structure in the space at large scale and, *unexplained* variation, which may be attributable to survey error, implicit biological variation or variables omitted from the analysis (Legendre and Legendre 1998).

Given the multi-scalar nature of reef fish communities and of the forces acting on them, we adopted a hierarchical spatially multi-scale design to estimate the components of variance bearing in mind the spatial scales suggested for studies on reef-fish ecology (Sale 1998). The whole region extent represented the largest scale of analysis and the three human sectors the primary sampling division in the hierarchy. Within each sector four nested sites were selected for survey with a distance of 20 to 70 km between each other (Figure 1). Four geomorphologic zones of the reef profile differing significantly in fish community composition (Núñez-Lara *et al*. 2005) and considered as latitudinal continuous habitats, were examined: reef lagoon (1 - 4 m depth, 100 - 500 m from the coastline), reef front (6 - 8 m depth, 500 - 600 m from the coastline), reef inner slope (11 - 14 m depth, 700 - 1000 m from the coastline) and reef outer slope (20 - 25 m depth, 800 - 1200 m from coastline). Twelve transects per habitat were placed at each one of the surveyed sites, representing the sampling units or replicates.

Survey Techniques and Data Collection

Belt transects 50 m long by 2 m wide were placed over the reef formations maintaining a continuous direction and leaving an approximate distance of 50 m between transects. Geographical coordinates were estimated for each transect by a global positioning system (GPS). All fish species observed along transects were identified and the individuals counted by underwater visual census technique. Underwater video of the reef substratum was recorded for another diver at each transect. A continuous video of the 50 m transect resulted in approximately 40 video squares of 1 m^2 each. Data of substratum variables were obtained during laboratory analysis of the videos on a high-resolution screen. The percentages of substratum cover for eleven benthic components were calculated according to the categories proposed by Garza-Perez (2003) for each one of the transects:

i) Spherical and semi-spherical coral (*e. g*. *Diploria*, *Colpophillya*, *Montastrea*),
ii) Branching and finger coral (*e. g*. *Acropora*, *Millepora*, *Porites*),
iii) Leafy and plate coral (*e. g*. *Agaricia*, *Scollimia*, *Mycetophillia*),
iv) Encrusting and sub-massive coral (*e. g*. *Montastrea*, *Siderastrea*, *Porites*),
v) Soft coral (*e. g*. *Gorgonia*, *Plexaura*, *Muricea*),
vi) Calcareous and macro-algae (*e. g*. *Halimeda*, *Dyctiota*, *Padina*),
vii) Sea-grass (*e. g*. *Thalassia*, *Syringodium*),
viii) Rock and rubble,
ix) Calcareous floor, and
x) Sand.

Complementarily, the mean depth and topographical complexity, measured using the chain method, were estimated along each transect ad up to thirteen environmental variables per transect.

Data Processing and Numerical Analysis

Fish species abundance data were subjected to Hellinger transformation, which converts the relative abundance values of the species registered in each transect by taking their square root. This method helps to preserve the Euclidean distances making data suitable for PCA/RDA (Legendre and Gallagher 2001). In order to epitomize the spatial structure of the data over the three different scales included in the survey design, we used Principal Coordinates of Neighbour Matrices (PCNM) technique (Borcard and Legendre 2002). Principal eigenvectors (PCNM variables) were obtained by principal coordinates analysis of a truncated matrix, which in turns came out from a euclidean distance matrix composed for the geographic coordinates of the transects. Results with empirical and real data (including a prior analysis with the present data comparing PCNM and polynomial terms variables) proved that this method conducts to a good reconstruction of spatial structures from small to large scales (Borcard *et al*. 2004).

The thirteen environmental variables and the resulting PCNM variables were submitted to forward selection process (Dray *et al*. 2006) with the purpose to reduce inflation of the explain variation attributable to pure chance. So, three sets of data were involved in the subsequent analyses: matrices **X** and **W** composed with the forward selected independent variables, environmental and spatial, respectively, and the matrix of dependent variables **Y** composed with the Hellinger transformed abundance values of the fish species.

Numerical analyses were carried out using the method proposed by Borcard *et al*. (1992), to fractionate the variation of reef fish community composition data. This approach gives a comprehensive result of the proportional importance of the explanatory variables on the species data. Canonical redundancy analysis was used as ordination base method, presuming a lineal response of the fish species to environmental gradients across the study region. Routines of analyses were made using library “vegan” vrs. 1.15-2 (Oksanen *et al*. 2009), and packages “packfor” vrs 0.0-7 (Dray *et al*. 2009); “PCNM” (Legendre *et al*. 2009); and “varpart” (Legendre 2009), all them for R version 2.9.0 (Development Core Team 2009). Analyses were performed separately for each habitat at three different spatial scales:

i) Small-scale (< 3 km), including separately the data of each one of the twelve surveyed sites,
ii) Intermediate-scale (90-120 km), including the data of the four sites belonging to each one of the sectors, and
iii) Large-scale (ca 400 km), including all together the data of the twelve sites of study area.

For each analysis, the statistical significance of the constraint axes was estimated using ANOVA with 1000 random permutations under the direct model. In addition, environmental variables were tested one by one in order to determine how significant was their effect to explain fish community composition variation. This procedure was run in R project following routines exampled in Legendre (2005). Ordination biplots were produced in order to represent the relationship between the surveyed samples and the environmental variables. We illustrate these relationships intending to identify a trend in the array of the data as a function of the human influence and to offer a more detailed visual interpretation of the fish-habitat relationships.

RESULTS

A gradient in species richness was observed across the four habitats surveyed, with the lowest number of fish species in the reef lagoon (98) close to the shore, and the highest in the reef terrace (140), the most distant habitat. A total of 182 reef-fish species were identified in 480 transects along the approximate 400 km of the fringing coral reef system in the eastern Yucatan Peninsula, most of them rare species restricted in their distribution to one or two contiguous habitats. Among the sectors, the highest number of species per transect was recorded in the fishing sector (14.9) followed by the reserve sector (13.5) and the tourism sector (11.4). Relative abundance showed a similar trend with the highest mean value in the fishing sector (53 individuals/transect), followed by the protected area (49 individuals/transect) and the tourism sector (45 individuals/transect).

Partitioning Variation

A considerable amount of explained variation was observed at all the spatial scales investigated, despite the highly random distribution and abundance of the reef-fish species in the sampled site of the Caribbean reefs. This indicated an accurate selection of variables and the application of a correct spatial and causal approach.

A similar partition of the fish community composition data was observed for each one of the survey sites after averaged the values obtained for the four habitats (Figure 2). The total explained variation fluctuated between 50% and 60% with approximately five sixth parts of this corresponding to the environmental fraction [A]. This pattern indicated an important response of fish species to environmental variables, which reflect an important local influence of the habitat characteristics. Fraction [B] showed a minimal amount of explained variation, attributable to biophysical features and biological processes acting at scale from hundreds of meters to kilometres, principally. Fraction [C], corresponding to spatial variation, represented from 7% to 13% of the total variation of fish community data. This amount is explained by the large-scale processes like recruitment, dispersion, ontogeny and historic events, which should constantly regulate the structure of communities on reefs despite the pressure of other variables.

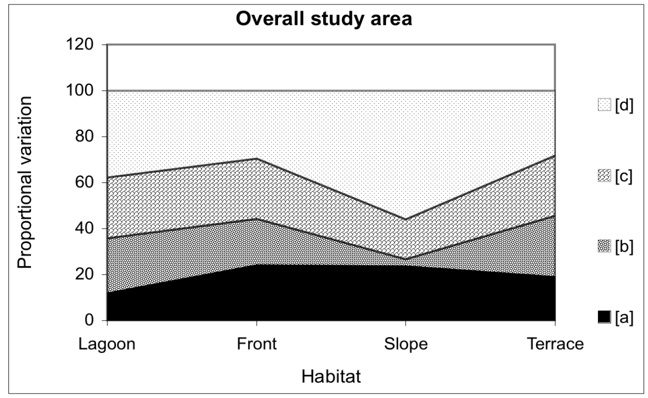


Figure 2. Fractions of variation obtained from partitioning analysis for reef-fish community composition data for the four surveyed habitat of the Mexican Caribbean. [a] Environmental variation, [b] environmental spatially structured variation, [c] spatial variation, [d] undetermined variation.

Table 1 shows the sum of canonical eigenvalues, which express the amount of variation in the species data associated with the matrix of the explanatory variables, its significance (*P*), and corresponding proportions of variation calculated through these values. Although the canonical eigenvalues obtained from the analyses of the step [1] were always considerably inferior with respect to those of the steps [2] and [3], this were also always significant. The total explained variation W in the lagoon fish community varied around 60% from touristic to fishing sectors. At reef front habitat total explained variation fluctuated from 50% in the touristic sector to 70% in the fishing one. The variation explained at reef slope habitat was approximately the same for reserve sector (73%) and fishing sector (71%), for reef terrace the total variation in reef reserve sector was 75% and 55% for fishing sector (Table 1).

The most significant environmental variable on reef lagoon habitat was the branching coral cover of the reef substratum, which indicates that despite its relatively low abundance in this habitat, it could be determinant in the community composition of reef-fishes. Depth in the reserve sector, and sand and seagrass cover on the fishing sector, were also significantly important explaining variation in the fish data (Table 2). The ordination biplot for reef lagoon displayed in Figure 3a shows a clear division between the tourism sites (squares in the left) and

Table 1. Summary of results obtained by partitioning analysis for each combination of habitat and sector and habitats overall of the Mexican Caribbean reef fish communities. The total explained variation (W), as well as four fractions of variation: [A] = environmental, [B] = environmental spatially structured, [C] = spatial and [D] = non-explained are presented. Habitats: L = lagoon, F = front, S = Slope, T = Terrace.

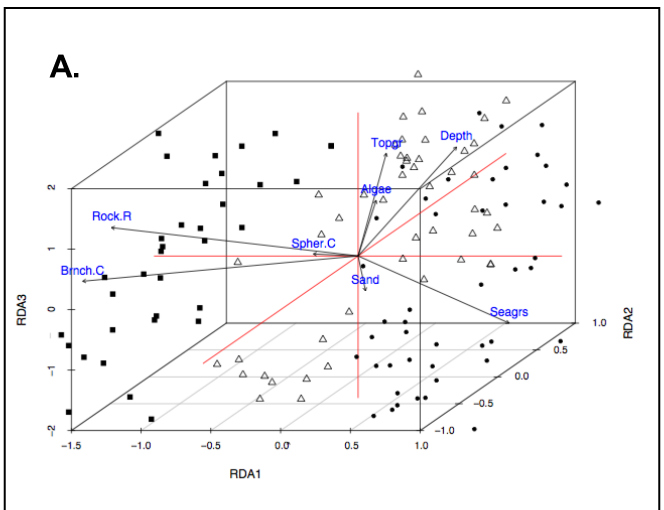
	[0]	[1] (*P*)	[2] (*P*)	[3] (*P*)	W (%)	[A] %	[B] %	[C] %	[D] %
L Tourism	1.326	0.449 (***)	0.692 (***)	0.791 (***)	59.6	7.5	26.3	25.8	40.4
L Reserve	1.934	0.549 (***)	0.737 (***)	1.020 (***)	52.7	14.6	13.7	24.4	47.3
L Fishing	2.100	0.258 (*)	1.167 (***)	1.263 (***)	60.1	4.6	8.2	47.9	39.9
L Overall	10.815	3.881 (***)	5.485 (***)	6.759 (***)	62.3	11.7	24.0	26.6	37.7
F Tourism	1.802	0.612 (***)	0.679 (***)	0.900 (***)	49.9	12.3	21.6	16.0	50.1
F Reserve	1.810	1.055 (***)	0.874 (***)	1.196 (***)	66.0	17.8	40.4	7.8	34.0
F Fishing	1.853	0.551 (***)	1.215 (***)	1.293 (***)	69.7	4.2	25.5	40.0	30.3
F Overall	12.559	5.558 (***)	5.849 (***)	8.843 (***)	70.4	23.9	20.3	26.2	29.6
S Reserve	1.807	1.220 (***)	1.082 (***)	1.324 (***)	73.2	13.4	54.1	5.7	26.8
S Fishing	1.767	1.034 (***)	0.680 (***)	1.265 (***)	71.5	33.1	25.4	13.0	28.5
S Overall	5.873	1.565 (***)	1.212 (***)	2.594 (***)	44.1	23.5	3.1	17.5	55.9
T Reserve	1.867	1.216 (***)	1.205 (***)	1.417 (***)	75.8	11.3	53.8	10.7	24.2
T Fishing	1.776	0.458 (***)	0.700 (***)	0.988 (***)	55.6	16.2	9.4	29.9	44.4
T Overall	5.867	2.680 (***)	3.101 (***)	4.218 (***)	71.8	19.0	26.6	26.2	28.2

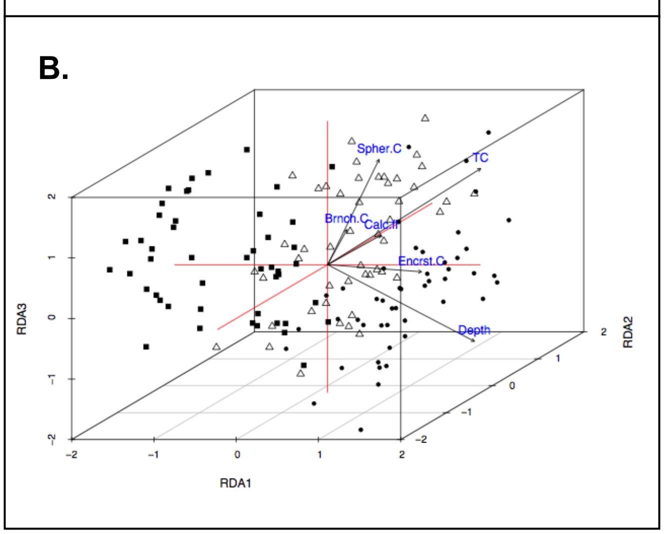
Table 2. Results of significance tests of the environmental variables involved on RDA analyses after forward selection. The effect of the environmental variables was tested for reef fish communities of the four habitats in general: reef lagoon (L), reef front (F), reef slope (S) and reef terrace (T) and for the three sectors: t = tourism, r = reserve and f = fishing. *P* values were obtained using 1000 permutations: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1.

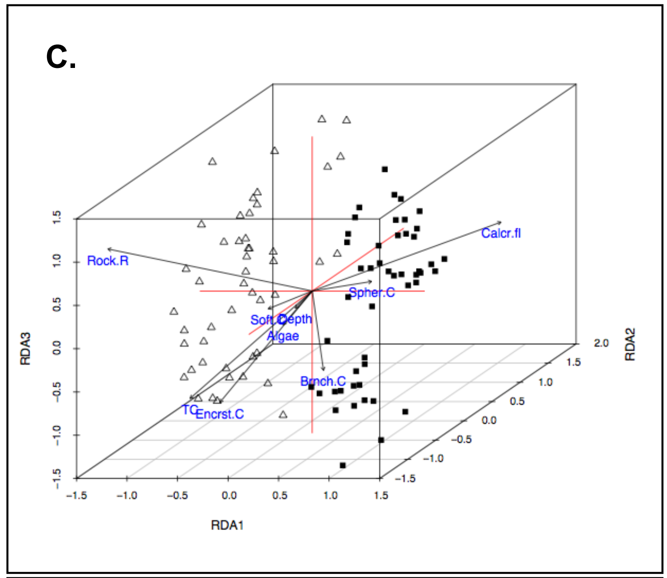
	L	L/t	L/r	L/f	F	F/t	F/r	F/f	S	S/r	S/f	T	T/r	T/f
Depth	.	.		n.s	***	*		***	n.s	n.s		n.s	n.s	
T.Complexity		n.s			***		n.s			n.s		*		**
Algae				**	***		n.s	n.s	n.s		**	*	n.s	*
Soft C	***		*		n.s				***	***	***	n.s	*	n.s
Spheric C			n.s							n.s		n.s	*	
Branching C	**	***		n.s		*	n.s	***	n.s		.		n.s	
Leafy C											.	.	.	
Encrusting C					*	*			n.s	*	*	n.s	n.s	
Calcareous floor							**		n.s	n.s	.	n.s	n.s	
Rock & rubbles	***					.	*	n.s		***	***	**	n.s	n.s
Sand	**		n.s					n.s						
Seagrass	*	n.s												

the reserve and fishing sites (triangles and points in the right), principally as a function of the branching coral, and the rock and rubble cover. A secondary division could be established in relation to depth, separating the sites of the reserve and fishing sectors in narrow (upper section of the diagram) and deep (lower section).

Amongst the most important environmental variables in the reef front of the tourism sector were depth and soft coral cover of the substratum. In the reserve sector the coral cover of encrusting shapes and the percentage of calcareous floor were the most significant, and depth and branching coral cover in the fishing sector. Although the topographical complexity of the reef substratum was not particularly significant in each one of the sectors it was highly significant considering the complete region (Table 2). In a visual inspection of the 3D biplots it was observed a separation of most of the sites of the tourism sector in the left hand side of the diagram respect to those of the protected and fishing sectors in the right, corresponding principally with differences in topographical complexity and depth (Figure 3).







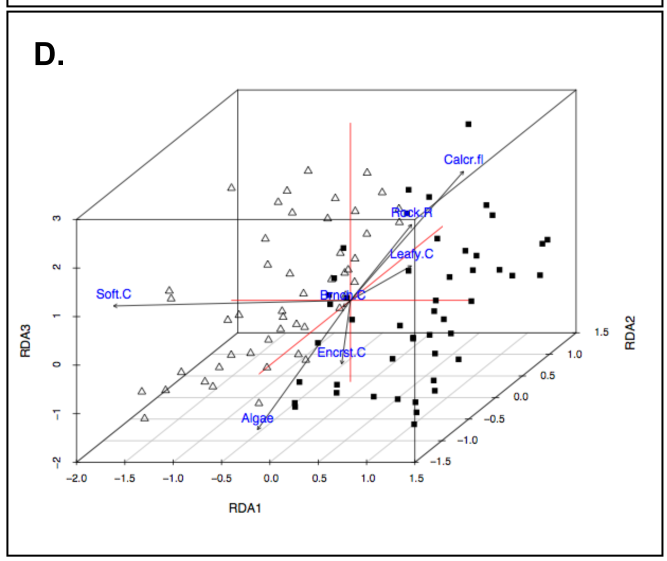


Figure 3. 3D ordination biplots showing the distribution of the surveyed sites by each habitat as correlated with the environmental variables. Variables displayed were those better fitted for each particular model according to the forward selection method. Squares = tourism sector sites; empty triangles = reserve sector sites; points = fishing sector sites. a) reef lagoon, b) reef front, c) reef inner slope, d) reef outer slope.

DISCUSSION

Theories on reef fish ecology are not necessarily mutually exclusive, exclusivity or "inclusivity" depends of the scale of examination. The analysis of multivariate variability in fish assemblages at different spatial scales revealed that the greatest variation occurred from small to intermediate spatial scales. The variation at broad spatial scale spatial might represent not only permanent process regulating the structure of the biological systems but the influence of external factors as well. This aspect is important when we presume an influence, maybe anthropic, on communities or their habitats. A great compromise will be to generate a proportional equilibrium index. A numerical value calculated through well-delimitated proportions of variation of the community composition. This index will reflect a particular dynamic and structural functioning of the community and further than the condition of the coral reef. We stated that an index based on ranges of variation explained by the different types of variables is more complete and informative than an analysis of single variables.

Chittaro (2004) found that habitat variables explained 31 – 81% (at scales of 1 – 200 m^2) of the variation in the number of individuals and species. Similar analyses were also performed on the abundances of the nine most common species, and whether their specific habitat associations were independent of scale. Results indicated that habitat variables explained 19 – 73% (at scales of 1–200 m^2) of the variation in abundances of each species. Unique fish-habitat relationships were observed for each species, and most such relationships were consistent across spatial scales. No generalization can made across large areas, although there is an intrinsic liaison of the pattern of community structure across spatial scales, it does not necessarily imply that those patterns observed at local or small scale can be extrapolated to larger or regional scales. If we had been studying the importance of the habitat variables on reef fish species on each one of the sectors of the Caribbean by using only the data of one site in that sector the results had showed a high proportion of variation in composition of the community explained for environmental variables, which was not true in the multi-scale inspection. From our point of view, for a comprehensive full description of a multi-scale ecological systems, a multi-scale approaches should be preferred. In a similar study Bounchon-Navaro, *et al.* (2005) found through partitioning analysis that a significant proportion of variation was explained by habitat classes (15%), geographic gradients described by the Caribbean arch, latitude (8.4%) and depth (3.9%) for reef-fish species of the Caribbean West Islands. We anticipated that separation would occur according to the type of habitat. We therefore, focused on the variation explained by environmental variables *per se*, and spatial variables that could be hypothetically reflecting an ecological process like competition or predation generating patterns in space, detectable for the analysis. Given that reef-fishes express relatively short ranges of motion on the reef there is a temptation to think that they are mostly sedentary and depend strictly on the substratum characteristics of the neighborhood. According to Munday (2002) habitat availability measured at tens of meters explained 47-65% of the variation in the abundance of habitat-specialist reef fish species among locations spanning over 2,000 km. Therefore, local-scale patterns of habitat use appear to determine much larger-scale patterns of abundance. Either geographic variation in local-scale processes that was not measured, or additional processes acting at very large spatial scales influence species. Intermediate scale variation can be only hypothethise caused by processes like predation, recruitment and competition because there were not time scales implied in the study (Jones and McCormick 2002), so clear conclusions can not be achieved.

Large-scale statistical patterns are helpful in predicting some properties of local assemblages. Relative certainty and simplicity of large-scale patterns is balanced by the uncertainty and complexity of their explanations. The greatest achievement of macroecology is the recognition of the influence of the large-scale constraints on small-scale patterns and processes, whereas its greatest challenge is to understand how these large-scale regularities emerge, and moreover, how they are connected to each other (Storch and Gaston 2003). The relationship between local and regional species richness appear to indicate that local processes (predation, competition and habitat selection) are relatively unimportant in comparison to the role of the regional species pool (Caley and Schluter 1997); however, Leps (2001) has shown evidence that the reverse effect could be possible. The spatial dependence model implies that the response variable is spatially structured because it depends upon explanatory (*e.g*. physical) variables that are themselves spatially structured by their own generating processes (Legendre *et al.* 2002). This is an extension of the environmental control model developed by Wittaker (1956), Hutchinson (1957), and Bray and Curtis (1957). The spatial autocorrelation model implies that the response variable results from some dynamic process within the variable itself. Spatial autocorrelation actually refers to the lack of independence among the error components of field data, as a function of the geographic distances among sites.

Despite that comparatively clear separation of the coast in the Mexican eastern Yucatan Peninsula in terms of the human activities, a quantitative reciprocity is not such as clear. Results indicated that intermediate scale spatial patterns could be associated with natural causes like heterogeneity composition of the reef. What is clear is that without an understanding of the quantitative aspects of the patterns found we will not be able to resolve different theories concerning the causes (Storch and Gaston 2003). The approach employed was useful to separate the variation in reef fish community composition data into different components. Numerical methods as that proposed by Borcard *et al.* (1992) to separate the variation into different components facilitates the analysis of complex data and the understanding of the functioning of multi-species systems. "It is evident that identifying and understanding scale-dependent changes in pattern and process must be a prerequisite for predicting the consequences of changes in ecological systems induced by natural disturbances and human alterations of the environment" (Avois-Jacket 2008).

Although nowadays a number of papers adduce the use and virtues of a spatially multi-scale approach in the understanding of scale-dependent ecological processes the number of studies that have been applied this and obtained conclusive results is not comparative. After an exhaustive data collection over an explicitly spatial sampling design we analyzed the data according to the contemporary numerical methods attaining categorical outcomes. Accomplishment results for the present investigation may be used in further studies aimed to design marine protected areas on coral reefs from an explicitly spatial perspective, and to model community dynamics, discriminating essential from non-suitable habitat.

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