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Spatial patterns of Yucatan reef fish communities: Testing models using a multi-scale survey design

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Abstract

Using a hierarchical multi-scale survey design, we examined the spatial patterns of reef fish communities and tested ecological models concerning the relative importance of reef geomorphology and anthropogenic pressure possibly driving community structure. Canonical redundancy analysis was used as a form of multivariate analysis of variance (MANOVA) to assess differences in reef fish community composition at two spatial scales: broad (10^5 m) and intermediate (10^4 m). Surveys were conducted on the east coast of the Yucatan Peninsula (Mexican Caribbean fringing reef), including regions and reefs which differed in geomorphologic structure and human use. Seven hundred and fourteen line transects were distributed among 13 reef localities belonging to different regions established a priori. Transects covered four types of reef habitat: lagoon, front, slope, and terrace. Tests of significance were based on permutation procedures. Significant differences among regions were found for the lagoon, slope, and terrace fish communities, consistent with the geomorphologic model, but it is only in the reef lagoon that they were consistent with the anthropogenic model, which may indicate an effect of coastal human activities. Significant differences among reefs within regions were observed, which could be associated with local environmental gradients. Canonical nested MANOVA was an appropriate method for testing ecological hypotheses about the functioning of complex biological systems. The use of a surveying strategy that explicitly incorporated the spatial structure represents an important contribution of this paper to coral reef fish ecology.

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Keywords: Anthropogenic disturbance; Canonical analysis; Nested survey design; Reef-fish community; Reef geomorphology; Spatial analysis; Yucatan Peninsula

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1. Introduction

Awareness of the importance of the spatial structure of complex ecosystems like coral reefs, and the

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communities which inhabit them, is growing. Ecologists know that the spatial organization of the elements of an ecosystem is important for functioning (Legendre, 1993), although it is rarely integrated in the survey methodology and analysis of the results. This is an important reason why many ecological surveys across space do not lead to clear conclusions. Fortunately, the state of knowledge, research procedures, statistical methods, and technology now make it possible to understand spatially-structured data.

1.1. Theoretical framework

According to hierarchy theory, complex stable systems are often hierarchical (Allen and Starr, 1982). Physical forces acting at broad spatial scale can generate identifiable structures at finer scales. Taking this theory into account, we can picture the reef environment as being structured by broad-scale physical mechanisms, like geomorphology or current dynamics, generating broad and relatively homogeneous zones; inside these, finer-scale biotic processes dominate in spatially structuring the environment (Legendre, 1993). Understanding how information is transferred across scales is a fundamental problem in ecology (Levin, 1992). The patterns and processes we discover will depend strictly on the extent at which we examine the system (Sale, 1998).

Some studies have analysed spatial variation of reef fish community structure over broad extents or across a variety of extents (Fowler et al., 1992; Adjeroud et al., 1998; Eagle et al., 2001; Gust et al., 2001; Bellwood et al., 2002). Many others have analysed particular processes of reef fishes on small areas like coral heads and patch reefs (e.g. Clarke, 1988; Doherty and Fowler, 1994; Sale et al., 1994). According to Ault and Johnson (1998), assemblages of species inhabiting small, isolated patch reefs represent a special case in the general ecology and spatial dynamics of reef fishes.

Spatial patterns may result from deterministic processes, or from processes inherent to the community causing spatial autocorrelation, or both (Legendre et al., 2002). Field observations often present a combination of spatial dependence on environmental factors, which provides for the broad-scale spatial structures, and spatial autocorrelation, which produce the finer-scale structures. Although different ecological processes are capable of generating similar patterns, the quan-

tification of spatial patterns may provide clues as to the identity of these processes (Borcard and Legendre, 1994; Leibold and Gurevitch, 2002).

Testing ecological hypotheses on reef fish communities has been an objective of scientists for many years: “Scientifically, the understanding of the relationships of reef fishes to each other and to their environment has grown by leaps, and the reef fish system promises to become a standard system for testing ideas in ecology” (Ehrlich, 1975 in Sale, 1991). Different theories and models have been proposed to explain ecological structures of reef fish communities, primarily focused on processes such as recruitment (Doherty, 1991) and predation (Hixon, 1991), and the effect of habitat structure (Jones and Syms, 1998; Syms and Jones, 2000). Scientists now generally agree that many different factors and processes are important in governing reef fish communities (Waltho and Kolasa, 1996; Caley et al., 1996). Some of these factors are more important in the early life stages of fishes (from larval to pre-settlement) and are often operating at broad scale; others are acting during subsequent life stages (from settlement to adult) and are operating at smaller scale (Casselle and Warner, 1996; Doherty, 2002; Lecchini and Galzin, 2003).

Several natural factors, geomorphologic, historical, ecological, and biological have been hypothesized to explain the spatial variation in reef fish community structure (Harmelin-Vivien, 1989). Alternatively, positive anthropogenic effects, like human interventions to protect coral reef fauna by the creation of marine reserves, or negative, through habitat disturbance by activities like fishing and tourism, have been suggested as causes of spatial variation on fish species assemblages (Russ, 2002). Human activities could have a direct effect on fish species by removal of individuals, or indirect effects resulting from damage to the coral reef habitat (Russ, 1991). New ideas have led ecologists to pay attention to spatial scaling; one of them is the role of disturbances as modifiers of community patterns and dynamics (Schneider, 1994).

1.2. Explanatory models

At the onset of this study, two complementary explanatory models were considered to describe the distribution patterns found in the species composition

and abundance of reef fish over a range of spatial scales. A natural differentiation of Yucatan reefs in the Mexican Caribbean Sea due to geomorphologic configuration provided an excellent opportunity for testing hypotheses concerning the relative importance of this factor on fish community composition. There also exists a clear division of the Caribbean coastal zone in terms of use by humans; we took advantage of it to compare the influences of tourism, fishing, and protection policies.

The first model states that the geomorphologic structural characteristics of the reefs (past history) are responsible for the spatial variation observed among reefs. Structural physical forces (-10^2 to -10^3 years) generated a recognizable spatial organization of the reef, which has been a determinant of the establishment and persistence of fish species. This model results in patterns of distribution of fish species detectable at fine to broad scales. The second model suggests that anthropogenic effects determine the spatial patterns found in reef fish communities. Human activities on coral reefs and adjacent coastal zones (present events: -10^3 years) can directly affect fish species and modify the reef habitat. These effects can be better detected through the variation observed in fish community composition at broad scale, through the comparison of regions subjected to different types of human influence.

The objective of this study was to find support for the following multiple-cause model: (i) differences in physical structural characteristics (reef geomorphology) significantly contribute to explaining the spatial variation of reef fish community structure; and/or, (ii) anthropogenic effects explain this variation. A latitude gradient along the study area alone could modify the patterns generated by the proposed models. Differences in fish species composition and abundances as a function of latitude have been identified (Harmelin-Vivien, 2002; Bouchon-Navaro et al., 2005). The precise questions that we attempted to answer were the following: (1) Are the spatial patterns detected in reef fish community composition a consequence of variation in geomorphologic structure? (2) Are those patterns a consequence of anthropogenic disturbances? (3) What other factors and processes may be responsible for the spatial patterns detected? And (4) at which scale(s) do these factors and processes operate?

2. Methods

2.1. Study area and survey design

The Mexican Caribbean fringing reef system is located along the eastern coast of the Yucatan Peninsula, running close and parallel to the coast for about 400 km, from $18^{\circ}00'$ to $21^{\circ}00'N$ (Fig. 1). Reefs are distributed in a semi-continuous barrier along the coast, with intermediate flat karstified floor between reef formations. From the central area towards the Belize border, reef structures show what is commonly called a “spur and groove” system. According to geomorphologic criteria (Weidie, 1985), the reef presents three major zones in profile from the littoral to the open seawater: a reef lagoon (back reef), a crest, and a reef front (fore reef); these main zones can be subdivided into sub-zones (Gutiérrez-Carbonell et al., 1993). Núñez-Lara and Arias-González (1998) classified the reef fish communities of the southern Mexican Caribbean Sea into three main habitats: lagoon (l), front (f), and slope (s); we sampled these three types of habitat and added a fourth habitat, the reef terrace (t) at 20–25 m depth (Fig. 1d). In the central section of the Caribbean coast is found the Sian Ka'an Biosphere Reserve ($20^{\circ}06'$ to $19^{\circ}05'N$), a protected area of 528,000 ha of coastal ecosystem, including two bays (Fig. 1b), as well as 37,000 ha consisting mostly of reefs, which were added to the Reserve 12 years after it was created by Presidential decree in 1986.

Based on previous descriptive works (Milliman, 1973; Gutiérrez-Carbonell et al., 1993; Arias-González, 1998; Núñez-Lara and Arias-González, 1998) and our knowledge of its structural characteristics, the study area was divided into four regions (Fig. 1c). (1) Northern region (NT): from Punta Nizuc to Punta Maroma ($21^{\circ}01'$ – $20^{\circ}42'N$); sites N, P, R. Reef formations are not continuous along the coast; they are often separated by extents of calcareous floor and sandy substratum. The architectural structures are neither extensive nor high above the sea floor; they drop off after reaching the 6–8 m depth. (2) North Sian Ka'an (NS): from Boca Paila to Punta Allen ($20^{\circ}06'$ – $19^{\circ}49'N$); sites B, Y, A. Spur and groove reef structures are typical. Coral structures show very high development in terms of extent and height. Spurs may reach more than 50 m in width and 10 m in height. The substratum is highly complex,

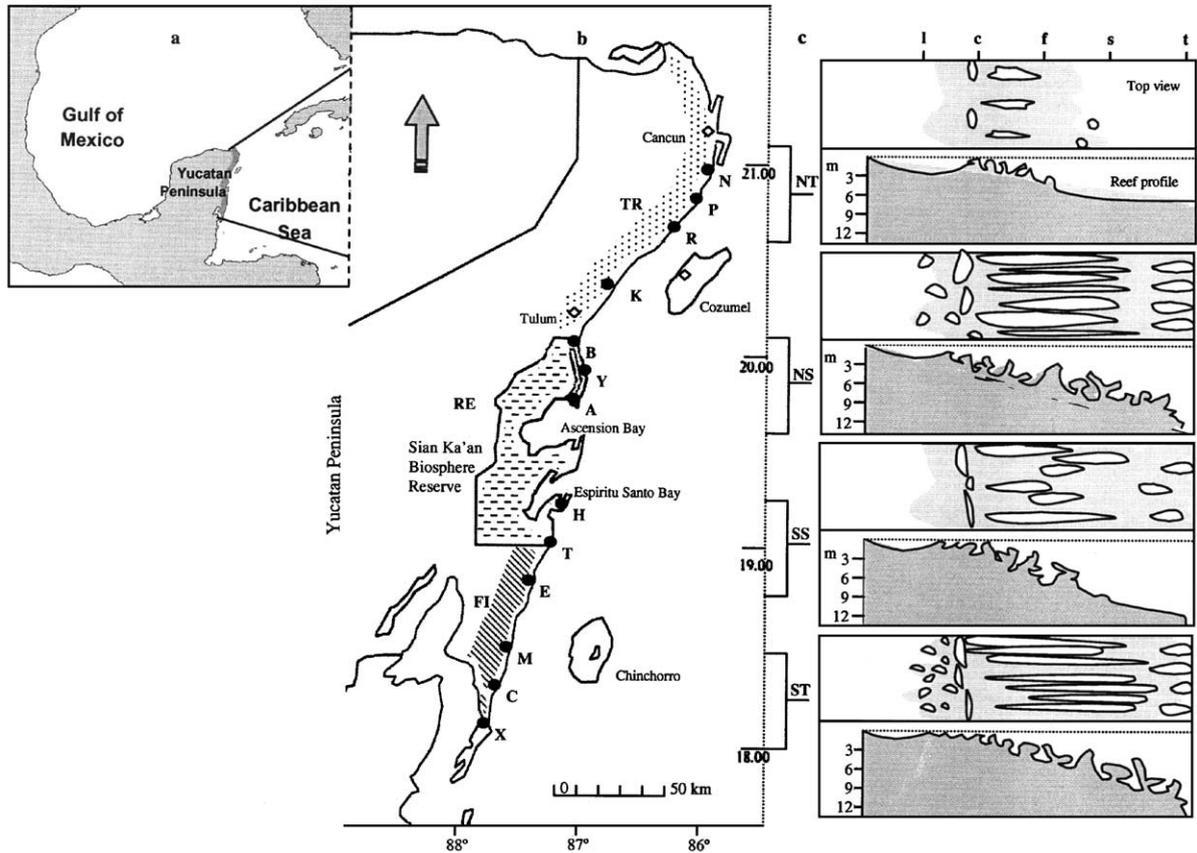


Fig. 1. Study area. (a) Yucatan Peninsula. (b) Mexican Caribbean coast, with three regions representing the types of human uses: tourism (TR), reserve (RE) and fishing (FI). Thirteen reef sites along the coast were selected for the survey: Punta Nizuc (N), Puerto Morelos (P), Punta Maroma (R), Akumal (K), Boca Paila (B), Yuyum-Xamach (Y), Punta Allen (A), Punta Herrero (H), Tampalam (T), El Placer (E), Mahahual (M), Xahuayxol (C) and Xcalak (X). (c) Suggested division of the Mexican Caribbean reefs according to geomorphology: Northern region (NT), North Sian Ka'an (NS), South Sian Ka'an (SS) and Southern region (ST). Typical habitats of reef geomorphology in the fringing reef system are illustrated: lagoon (l), crest (c), front (f), slope (s) and terrace (t). Depths in metres.

especially from the reef crest to the reef slope. Various characteristics distinguish this region from the other three: its submerged crest, its proximity to a bay and coastal lagoons, and the open reef lagoon to the sea. The lagoon is in general deeper having a greater coverage of seagrass, coral and algal patches (Arias-González, 1998). (3) South Sian Ka'an (SS): from Punta Herrero to El Placer ($19^{\circ}18' - 18^{\circ}55'N$); sites H, T, E. Although the El Placer reef (site E) is located outside the Sian Ka'an Reserve, it presents similar geomorphology to the other two. For comparative reasons and to insure the balance of the design, it was included in this region. Although the reef formation consists of spurs and grooves, it is uncharacteristic. Spur elevation is less than 4 m and

the grooves do not ever run in perpendicular direction to the coast, as is typical of grooves. The reef lagoon is similar to the Northern and Southern regions. It is very shallow and includes reef patches and seagrass beds. (4) Southern region (ST); from Mahahual to Xcalak ($18^{\circ}41' - 18^{\circ}17'N$); sites M, C, X. The reef formations are typical spurs and grooves. Spurs can reach a large extent and height. The reef structures are almost continuous in the north-south direction. Reefs include substratum with a complex architecture.

In terms of uses by humans, the east coast of the Yucatan Peninsula can be divided into three regions (Fig. 1b). (1) Tourism region (TR) ($20^{\circ}25' - 21^{\circ}01'N$); sites N, P, R, K. The reefs surveyed are in the touristy

Cancun-Tulum corridor. The coastal zone in this section is almost exclusively used for tourist activities and related infrastructures. Many urban settlements are present in the area. (2) Reserve region (RE) (19°20'–20°06'N); sites B, Y, A, H. The reefs surveyed are included in the Sian Ka'an Biosphere Reserve, and are more than 40 km from the focal human population centres. Fishing practices are restricted and can be considered at low intensity; there were, however, no detailed fishing reports before the Reserve was created. Punta Allen (A) and Punta Herrero (H) are small fishing communities (<300 inhabitants) dedicated mainly to spiny lobster and artisanal fishing. (3) Fishing region (FI) (18°17'–18°55'N); sites E, M, C, X. From the southern limit of the Sian Ka'an Bio-

sphere Reserve to the Belize Border. Conch and lobster are the preferred fishing catches. Some fish families (Lutjanidae, Serranidae, Haemulidae, Sphyrnaenidae) are also seasonally exploited. Fishing is not selective; the use of nets, lines, and traps is not formally regulated.

In the present study, surveys were hierarchically organized at four spatial scales in order to estimate the spatial variation in fish community composition. The survey units (transects) were distributed across the four types of habitat (l, f, s, t). Surveying took place at the 13 reef sites shown in Fig. 1b, which have been selected to characterize different degrees of geomorphologic development and types of use by humans, as described in the previous paragraphs (Figs. 1 and 2).

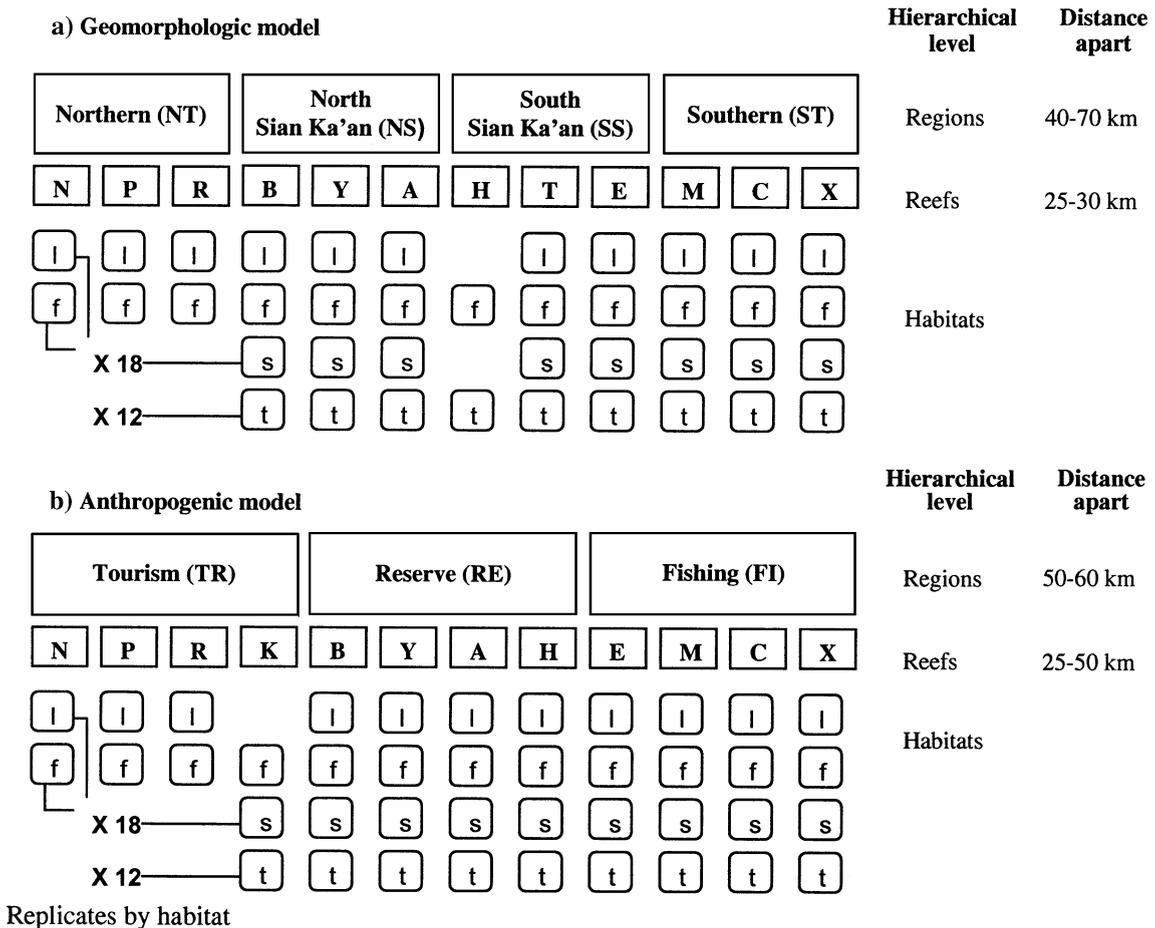


Fig. 2. Survey design. Two different schematic arrangements are presented corresponding to the two explanatory models: (a) geomorphologic and (b) anthropogenic. Codes as in Fig. 1.

Field observations under the hierarchical model are viewed as the result of the nested contributions of various levels corresponding to the spatial organization of the community components (Dutilleul, 1993; Bellehumeur and Legendre, 1998). Since some reefs could be atypical of the region into which they are included, we sampled more than two reefs per region, as recommended by Sale (1998). Reefs were nested into a priori established regions; there were three reefs per region for the geomorphologic model and four for the anthropogenic one (Fig. 2).

2.2. Data collection

Using the differences between regions and the characteristics of the reef biota, our survey was structured as a mensurative experiment (sensu Hurlbert, 1984). Eighteen replicate transects, 50 m long by 2 m wide, were set parallel to the coast in each of the first three types of habitat: reef lagoon (1–3 m depth), reef front (6–8 m depth) and reef slope (11–14 m). Twelve transects were used on the reef terrace (20–25 m) (Fig. 2a,b). The distance between transects was approximately 50 m and the distance between adjacent habitats was variable: 100–200 m. A plastic tape was placed as visual reference along the full length of each transect. GPS positions were taken at every four or six transects. Depth was noted at each transect. Surveys were conducted between June 1999 and September 2000, and only during the summer rainy season to control for seasonal variability. In order to reduce variability between years, the survey focused on two habitats per year: the reef lagoon and slope in 1999, and the reef front and terrace in 2000. Underwater visual census was used to identify the fish species. All censuses were conducted between 09:00 and 17:00 h by the same person (the senior author). Fish crossing the transect line were included in the visual census, underestimating in a constant manner the nocturnal species and the species with cryptic behaviour.

2.3. Numerical analyses

In order to avoid violations of the assumptions of classical statistics, we used a non-standard method to test for differences in relative community composition of reef fishes. Since ANOVA is an expression of the

general linear model, we carried out multivariate analysis of variance (MANOVA) by canonical analysis. Parametric MANOVA, the method that should logically have been used for analysis, requires multivariate normality and homogeneity of the covariance matrices; these are stringent assumptions, which were unlikely to be met by our data. Tests of the factors in the nested design were carried through the use of the NES-ANOVA computer program (Legendre, 2002). The analyses were based upon transformed species abundances and statistical significance was assessed using permutation tests, which do not rely on distributional assumptions.

Our survey was structured in such a way that the factor reef was hierarchically nested in the factor region. The main factor, region, was fixed, while the nested factor, reef, was random. The underwater transects were the replicates. The relative community composition data (Hellinger-transformed species abundances) were analysed for each habitat separately. Fish community sub-tables were also prepared to test for differences between pairs of regions (a posteriori pairwise comparisons).

Nested MANOVA involved the following steps: (1) Hellinger transformation of the fish species abundance data, as implemented in the NES_ANOVA program; Legendre and Gallagher (2001) have shown that this transformation makes species abundance data amenable to analyses like RDA or PCA. (2) The construction of matrices \mathbf{X} containing dummy variables corresponding to the factors to be included in the analysis, i.e., matrix \mathbf{X}_1 for the main factor region and \mathbf{X}_2 for the nested factor reef, and (3) a permutation tests of the factors included in the analysis by canonical RDA. Two permutation methods were used in the NES_ANOVA program: (a) permutation of the raw data to test the significance of the main factor and (b) permutation of residuals (Freedman and Lane, 1983) to test the significance of the nested factor. Legendre (2002) reports the results of numerical simulations showing that unrestricted permutations produce valid tests in NES_ANOVA, except under the most extreme error conditions (cubed exponential random deviates).

We tested the relationship of the relative reef fish community composition to latitude using multivariate linear regression (Finn, 1974). The analyses were performed using the DISTLM computer program

(Anderson, 2002) based on Hellinger distances of the fish abundance data. Tests of significance involved 999 permutations of the raw data. Since latitude can be influenced by the fish-habitat association (Stevens, 1989), separate analyses were computed for the different habitats. Total species richness and total fish density were related to latitude by simple linear regression.

When the geomorphologic and anthropogenic models both significantly explained the variation in fish communities, data were reorganized to quantify the relative importance of each model in the presence of the other. Hypothesis H_{0a} was: given the effect of geomorphology, there is no significant variation in reef fish community composition among regions subjected to differential human uses. H_{0b} was: given the anthropogenic effect, there is no significant variation in community composition among regions due to geomorphology. In the CANOCO program (ter Braak and Smilauer, 1998), the partial effect of geomorphology can be tested by partial redundancy analysis (Borcard et al., 1992) by treating each region of the anthropogenic model as a block described by a

dummy variable in the matrix of covariables; conversely, the partial anthropogenic effect can be tested by partial RDA controlling for the effect of the geomorphologic regions, by using the geomorphologic regions as a permutational block.

3. Results

3.1. Reef fish community composition

Fish communities of the Yucatan Peninsula contained many rare species, but were generally dominated in terms of abundance by families typical of the Caribbean reefs: Labridae, Scaridae, Pomacentridae and Acanthuridae. We found a mean of 14 species and 50 individuals per surveyed transect. Over the 714 transects, 183 reef fish species were identified. The mean number of species was higher in the southern (ST) region of the geomorphologic model and in the fishing (FI) region of the anthropogenic model. The mean density did not vary markedly among regions. The highest values were observed in the southern (ST)

Table 1
Mean species richness and mean density (\pm standard error) of reef fish communities in the eastern Yucatan Peninsula

Region	Northern	North Sian Ka'an	South Sian Ka'an	Southern	Tourism	Reserve	Fishing
Richness (Spp/transect)	10.8 (5.09)	14.0 (7.49)	12.5 (5.98)	15.3 (7.99)	11.5 (4.97)	13.6 (6.97)	15.0 (7.66)
Density (Ind/m ²)	0.45 (0.33)	0.49 (0.35)	0.46 (0.48)	0.54 (0.39)	0.45 (0.31)	0.49 (0.43)	0.53 (0.39)
Transects	118	198	162	198	166	228	264
Reef	Punta Nizuc	Puerto Morelos	Punta Maroma	Akumal	Boca Paila	Yuyum-Xamach	Punta Allen
Richness (Spp/transect)	11.4 (4.08)	6.97 (3.71)	14.1 (4.64)	13.5 (4.13)	13.9 (7.34)	15.3 (7.34)	12.9 (7.62)
Density (Ind/m ²)	0.54 (0.34)	0.27 (0.20)	0.52 (0.36)	0.45 (0.26)	0.55 (0.41)	0.55 (0.32)	0.39 (0.30)
Transects	36	36	36	48	66	66	66
	Punta Herrero	Tampalam	El Placer	Mahahual	Xahuayxol	Xcalak	
Richness (Spp/transect)	11.2 (2.57)	12.2 (6.52)	14.0 (6.47)	15.4 (8.27)	16.3 (7.25)	14.1 (8.26)	
Density (Ind/m ²)	0.35 (0.14)	0.49 (0.64)	0.54 (0.37)	0.58 (0.45)	0.52 (0.33)	0.51 (0.39)	
Transects	30	66	66	66	66	66	
Habitat	Lagoon	Front	Slope	Terrace			
Richness (Spp/transect)	7.29 (5.53)	13.4 (5.05)	19.3 (5.34)	16.5 (5.64)			
Density (Ind/m ²)	0.27 (0.29)	0.48 (0.40)	0.65 (0.31)	0.67 (0.42)			
Transects	198	234	162	120			

The number of transects varied according to the number of habitats surveyed within each reef and the number of replicates surveyed per habitat (Fig. 2).

Table 2
Nested MANOVA for reef-fish communities in the reef lagoon habitat

Source of variation	F	p
<i>(A) Geomorphologic model</i>		
Among regions (NT, NS, SS, ST)	1.87	0.005**
Among reefs	1.79	0.002**
Among regions (NT, NS)	1.41	0.186
Among reefs	1.99	0.003**
Among regions (NT, SS)	1.95	0.025*
Among reefs	2.21	0.002**
Among regions (NT, ST)	1.17	0.282
Among reefs	2.22	0.001***
Among regions (NS, SS)	2.06	0.026*
Among reefs	1.45	0.052*
Among regions (NS, ST)	1.93	0.042**
Among reefs	1.57	0.025*
Among regions (SS, ST)	2.94	0.004**
Among reefs	1.76	0.006**
<i>(B) Anthropogenic model</i>		
Among regions (TR, RE, FI)	1.84	0.003**
Among reefs	1.81	0.001***
Among regions (TR, RE)	1.85	0.027*
Among reefs	2.02	0.001***
Among regions (TR, FI)	2.00	0.015*
Among reefs	1.89	0.002**
Among regions (RE, FI)	1.65	0.056*
Among reefs	1.55	0.003**

The test for: (A) geomorphologic and (B) anthropogenic model included all regions, followed by all possible combinations of pairs of regions (a posteriori contrasts). For codes see Fig. 1. All tests involved 999 random permutations.

* $p \leq 0.05$.

** $p \leq 0.01$.

*** $p \leq 0.001$.

and fishing (FI) regions, whereas the lowest were found in the northern (NT) and tourist (TR) regions (Table 1).

3.2. Spatial variability

The results of the nested multivariate analysis of variance revealed that relative reef-fish community composition data from the lagoon habitat varied significantly among regions and among reefs within regions. These differences were consistent under the two explanatory models (Table 2). Under the geomorphologic model (Table 2A), significant variation was observed among regions. The strongest pair-wise differences ($p \leq 0.01$) were detected between the north Sian Ka'an (SS) and the southern regions (ST) and between the south Sian Ka'an (NS) and the southern regions (ST). Significant variation was also revealed under the anthropogenic model among the tourist (TR), reserve (RE), and fishing (FI) regions (Table 2B). Further tests contrasting the effects of the geomorphologic and anthropogenic models by partial canonical analysis revealed that, although both models were highly significant ($p < 0.005$), the geomorphologic model explained slightly more of the variation in the reef lagoon communities than the anthropogenic model (Fig. 3). Fraction [a] in the diagram corresponds to the proportion of variation explained exclusively by the anthropogenic model when controlling for the effect of the geomorphologic model. The proportion explained by the geomorphologic model when controlling for the effect of the anthropogenic model is fraction [c] and the variation of the community structure explained by both models taken together is $[a + b + c]$. Fraction [d], which is 92.8%, corresponds to the variation of the reef lagoon fish communities unexplained by the two models.

The relative community composition on the reef front differed only among reefs within regions, not at

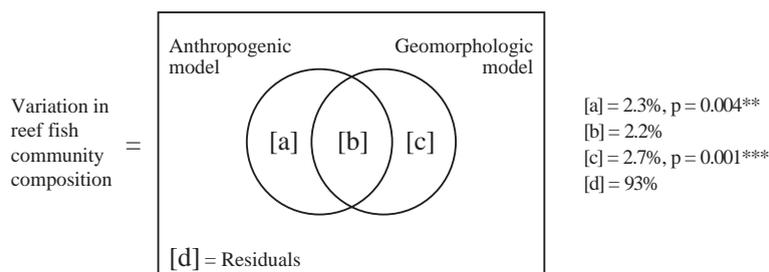


Fig. 3. Partitioning of the variation in reef fish community composition between the anthropogenic $[a + b]$ and geomorphologic $[b + c]$ models. Fraction [b] corresponds to the variation shared by the two models. Fraction [d] is the unexplained variation. Circle areas are not proportional to the values of the components of variation.

Table 3
Nested MANOVA for reef-fish communities in the reef front habitat

Source of variation	<i>F</i>	<i>p</i>
<i>(A) Geomorphologic model</i>		
Among regions (NT, NS, SS, ST)	0.96	0.561
Among reefs	3.73	0.001***
<i>(B) Anthropogenic model</i>		
Among regions (TR, RE, FI)	0.95	0.581
Among reefs	3.60	0.001***

The tests for: (A) geomorphologic and (B) anthropogenic model included all regions. All the a posteriori pairwise contrasts resulted in non-significant differences. For codes see Fig. 1. * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. All tests involved 999 random permutations.

the regional scale (Table 3). Since no significant differences were found among regions, a posteriori tests between particular regions are not presented. On the reef slope, significant differences were found among the geomorphologic regions (Table 4A), except between the north Sian Ka'an (NS) and south Sian Ka'an regions (SS). No significant difference was found between the reserve (RE) and fishing regions (FI) under the anthropogenic model (Table 4B). Again, under both models, significant variation ($p \leq 0.01$) was found among reefs within regions. A similar pattern was observed in the reef terrace habitat. Community composition varied significantly among geomorphologic regions, but not among the

Table 4
Nested MANOVA for reef-fish communities on the reef slope

Source of variation	<i>F</i>	<i>p</i>
<i>(A) Geomorphologic model</i>		
Among regions (NS, SS, ST)	1.77	0.010**
Among reefs	1.86	0.001***
Among regions (NS, ST)	2.08	0.009**
Among reefs	1.50	0.012*
Among regions (NS, SS)	1.31	0.177
Among reefs	1.65	0.004**
Among regions (SS, ST)	2.28	0.005**
Among reefs	1.60	0.003**
<i>(B) Anthropogenic model</i>		
Among regions (RE, FI)	0.95	0.542
Among reefs	2.89	0.001***

The tests for: (A) geomorphologic and (B) anthropogenic model included all regions, followed by all possible combinations of pairs of regions (a posteriori contrasts). * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. All tests involved 999 random permutations.

Table 5
Nested MANOVA for reef-fish communities on the reef terrace

Source of variation	<i>F</i>	<i>P</i>
<i>(A) Geomorphologic model</i>		
Among regions (NS, SS, ST)	2.72	0.001***
Among reefs	2.43	0.001***
Among regions (NS, ST)	1.42	0.151
Among reefs	1.99	0.001***
Among regions (NS, SS)	2.78	0.005**
Among reefs	2.49	0.001***
Among regions (SS, ST)	3.51	0.001***
Among reefs	2.78	0.001***
<i>(B) Anthropogenic model</i>		
Among regions (RE, FI)	1.51	0.710
Among reefs	2.56	0.001***

The tests for: (A) geomorphologic and (B) anthropogenic model included all regions, followed by all possible combinations of pairs of regions (a posteriori contrasts). * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. All tests involved 999 random permutations.

regions defined by human use (Table 5), whereas differences among reefs were significant under both models.

Multivariate linear regression analysis showed a statistically significant relationship ($p \leq 0.001$) between the relative reef fish community composition and latitude. This result was consistently observed for the fish communities in the four habitats. It reveals a broad-scale spatial pattern across the study area, although the proportion of variation explained by latitude was small (Table 6). Univariate linear regressions evidenced a significant positive relationship between total species richness and latitude for the reef lagoon communities ($r^2 = 0.253$, $p \leq 0.01$, $SE = 5.385$) and a negative significant relationship for the reef front communities ($r^2 = -0.285$, $p \leq 0.001$, $SE = 4.935$). There was no significant relationship for the fish commu-

Table 6
Multivariate linear regression between Hellinger distances of reef-fish community composition data and the latitude positions of the surveyed transects

Habitat	Pseudo- <i>F</i>	Permutation <i>p</i>	Variance explained
Lagoon	2.841	0.001	0.0143
Front	4.114	0.001	0.0174
Slope	2.395	0.001	0.0147
Terrace	2.457	0.001	0.0204

Tests involved 999 random permutations.

nities of the deeper habitats, reef slope and terrace. A significant positive relationship was found between latitude and total fish density in the reef lagoon habitat ($r^2=0.319$, $p\leq 0.001$, $SE=0.282$) and a significant negative relationship in the reef slope ($r^2=-0.185$, $p\leq 0.05$, $SE=0.300$). All statistically significant relationships exhibited low values of r^2 , which indicated a light broad-scale latitude pattern in total number of species and relative fish densities.

4. Discussion

Fish communities of the Yucatan Peninsula exhibited significant differences among geomorphologic regions in all habitats except the reef front, and among anthropogenic regions only in the reef lagoon (Table 7).

Although the geomorphologic model explained more than the anthropogenic of the spatial variation in fish community composition in the reef lagoon, the difference between the two models in terms of the variation explained was small. The influence of the nearby terrestrial environment, which clearly delimits zones in the relatively continuous reef along the east coast of the Yucatan Peninsula, appears to play an important role to differentiate fish communities. Fresh and mixed water discharges, coastal lagoons, and mangroves influence coral reefs, especially in the reef lagoon zone. These adjacent environments can modify the habitat composition and consequently the fish community structure (Parrish, 1989; Letouneur et al., 1998). These effects may also explain the differences observed among reefs, which are 20–30 km apart.

Differences in the lagoon between the tourism region and the protected area of the Sian Ka'an bio-

sphere reserve, and between the fishing and reserve regions, suggest a positive effect of the protection policies on the reserved area (Polunin and Roberts, 1993; Bohnsack, 1998; Hastings and Botsford, 1999). Some studies mention that human effects on fish species are mostly indirect through damage to the habitat, rather than direct impacts of fishing catches (e.g. Russ, 1991; Jennings and Polunin, 1996; McClanahan and Arthur, 2001). We also believe that indirect human effects on fish communities of the Mexican Caribbean are greater than direct effects, basically because there are more and more widely distributed activities disturbing the habitat than simply fish catches.

There were significant differences in community composition between adjacent geomorphologic regions and between reefs (<30 km apart), which suggests that despite the apparent broad-scale interconnection of the reefs along the eastern Yucatan Peninsula, the physical connectivity is low, restricting fish migrations in response to habitat preferences (Galzin and Harmelin-Vivien, 2002). Physical connectivity, which is intimately associated to the migration process and has been used as a predictor of spatial variation in reef fish species (Ault and Johnson, 1998), was not directly measured in this study. Available information indicates that multiple barriers between reefs along the coast (e.g. karstified flats or sandy areas) are shaped by the influence of effluents from the terrestrial environment, in addition to the natural patchiness of the reef. This indicates that fish communities of fringing reef systems are well described by the meta-population model (Hanski, 1997; Sale, 2002; Hixon and Webster, 2002; Forrester et al., 2002). Although juveniles and adults are restricted in their latitudinal distribution, interchange of gametes and larvae between the reef and open marine waters is always possible.

The geomorphologic model also explained spatial variation at the region scale in the reef slope and terrace habitats (Tables 4 and 5). The variety of biotic and abiotic structural components in these habitats, which themselves are highly variable spatially, appears to generate consistent responses in the composition of fish communities ranging from fine to broad scale (Jones and Syms, 1998). However, fish communities on the reef front exhibited significant spatial variation only at the reef scale, not at the

Table 7
Summary of the differences among regions (probabilities of the tests of significance) identified in Tables 2–5

Reef habitat	Geomorphologic regions	Anthropogenic regions
Lagoon	$p=0.004$	$p=0.003$
Front	N.S.	N.S.
Slope	$p=0.003$	N.S.
Terrace	$p=0.001$	N.S.

N.S.: not significant.

region scale. We interpret this as indicating the natural response of fish species to the structural heterogeneity of the reef front habitat. Such effects could be detected from small to intermediate scales but are unperceived at broad extent. In the reef front zone, large sections of latitudinally continuous habitat were occupied by reef species, whereas in the reef slope and reef terrace the species were spatially restricted to smaller reef areas due to the presence of numerous gaps of unsuitable habitat. The broader-scale expression of the fish species in the reef front indicates a relatively homogeneous community inhabiting a well-connected reef mosaic.

There were no significant differences in fish communities among anthropogenic regions on the reef front, slope and terrace habitats. This means, on the one hand, that tourist and fishing activities have greater impact on the lagoon, which is closer to shore, than on the fore reef habitats; and, on the other hand, that fishing practices in the reefs located in the southern region of the east coast of the Yucatan Peninsula are so similar that they do not generate recognizable differences in fish community structure among anthropogenic regions.

Although the present study revealed statistically significant variation in reef fish communities at spatial scales from tens to hundreds of kilometres, the proportion of variation explained by the broad-scale factors (regions, latitude) was low. A high proportion of the variance in fish surveys is expressed at small scale. Reef fish survey data are acquired directly by divers through visual techniques or using fishing gears (trawls, nets, etc.). In both cases, the variance among survey units is high for several reasons. Two well-known reasons generating high variance among survey units are: the survey units are very small compared to the surveyed area, and fish are gregarious and often mobile. So it is no surprise that the portion of variance explained by the factors of the sampling design or the environmental variables was small. The best we can hope for is to find factors or variables that explain a significant, albeit small, portion of the variation.

Our survey design and methods of numerical analysis were sufficiently robust to identify that the geomorphologic and anthropogenic factors indeed influenced reef fish community composition. This work is evidence of the advantages of a multi-scale

survey design in examining multi-species systems in a highly heterogeneous environment (Sale, 1998; Bellehumeur and Legendre, 1998; Legendre et al., 2002). We incorporated spatial concepts into our ecological models, and used a spatially explicit survey design as well as numerical methods developed to quantify spatial variation at multiple nested scales. The close distance of the Mexican Caribbean fringing reef to the coast and the well-delineated breaks between reefs in the latitudinal direction indicated that a nested design was appropriate. Correct estimates of coral reef patchiness at local and meso-scale will be necessary in the future to construct a physical model that will help clarify not only the spatial patterns in adult fish populations, but also the processes of larval dispersion–retention (Mora and Sale, 2002).

5. Conclusion

Since the beginning of this study, we used an explicitly hierarchical survey design to test hypotheses concerning the effect of the reef geomorphology and anthropogenic disturbances on the reef fish communities in different habitats. Evidence presented in this paper supports the notion that, in the Yucatan Peninsula, spatial variation in reef fish community composition is influenced by the geomorphology of the fringing reef system. The anthropogenic model was important to explain the spatial variation in reef lagoon fish communities. The close distance of this zone to the coast indicates that human disturbances may be sufficiently intense to affect the relative composition of fish communities. The influence of terrestrial environments in the fringing reef system, drawing frontiers that limit the latitudinal movements of fish, is an alternative factor explaining the spatial patterns detected in the course of this study.

This study has not covered all aspects of the possible spatial influences on community composition. In future research, we will test further hypotheses: the relative importance of particular spatially-structured characteristics of the habitat, the significance of spatial variables like coastal influence, connectivity and current dynamics, which can all help predict community structure, and the effect of different types and intensities of disturbances on reef fish. The information generated is, however, a starting point towards a precise definition of

the spatial scales of variation of reef fish assemblages in Mexican Yucatan reefs, information which is required for a properly designed management strategy.

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