

Spatiotemporal segregation regulates species richness along biomass gradients in estuarine fish assemblages

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ABSTRACT: The number of fish species in subtropical and tropical estuaries is much greater than in temperate regions and is greater in large estuaries than in small ones. Thus, large estuaries of the tropics are of primary interest for biodiversity conservation, and the processes underpinning the distribution of fish diversity in these ecosystems deserve attention. Factors controlling biodiversity patterns have been the focus of numerous recent investigations and include species interactions, speciation, environmental gradients and heterogeneity, with all of these operating differently at each observation scale. Today, the question is no longer whether particular biodiversity patterns occur, but why they occur and whether they are consistent across scales and organisms under study. In this study we combined the results of 2 classical ecological patterns, namely diversity–biomass relationships and species co-occurrences, into a common framework. Fish sampling was carried out in the coastal Terminos Lagoon (southern Gulf of Mexico) during 2 periods (1980–1981 and 1998–1999) using 408 tows. A total of 22 834 individuals representing 106 fish species were collected. Our study revealed that both diversity–biomass relationships and species co-occurrences show inconsistent patterns across years, seasons and zones. However, taken together, our results show that C-score values, which measure spatiotemporal segregation among species, were closely related to the shape of observed richness–biomass relationships. When fish assemblages showed positive C-score values (species segregation), the relationship between species richness and fish biomass was either hump-shaped or non-significant. Conversely, negative C-score values (species aggregation) were associated with an increase in fish species richness along the total biomass gradient. Our results support the idea that species segregation due to competition or spatiotemporal partitioning can be an important determinant of biodiversity patterns in species-rich tropical fish assemblages, but only during some periods and for some spatial strata.

KEY WORDS: Terminos Lagoon · Co-occurrence · C-score index · Randomization · Species segregation

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INTRODUCTION

The overall goal of coastal management is to sustain the ability of coastal ecosystems to provide goods and services such as fisheries, tourism and aesthetic and cultural values upon which human welfare depends. Reaching this goal has been challenging in the recent decades because coastal ecosystems are facing ever

increasing human pressures through fishing, aquaculture, recreational activities, and demographic increase, which are related to global climatic change (e.g. Harley et al. 2006). These and other human impacts are greatly responsible for an increasing rate of loss in biodiversity and dramatic shifts in the relative abundances of remaining species (Roberts & Hawkins 1999). As a result, these alterations to the diversity and

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structure of marine communities can disrupt the ecological functions performed by the various members of species assemblages (Hughes et al. 2003). Fish biodiversity is obviously critical in this respect as different species have different roles (see Holmlund & Hammer 1999 for a review). The number of fish species in subtropical and tropical estuaries is much greater than in temperate regions and is greater in large estuaries than in small ones. Thus, large tropical estuaries deserve attention, particularly to determine the processes driving fish diversity patterns.

The fundamental idea behind the study of biodiversity patterns is the presumed connection between species richness regulation and the functional ways in which communities are organized. This functional organization refers to how species are related to one another as competitors or members of a web of interactions, and how species are facing similar environmental constraints. Determining what factors influence the number of species in an assemblage and their abundance pattern has always been a central aim in studies of community ecology (Whittaker 1965, Magurran & Henderson 2003) and remains highly controversial (Tilman 2004). Much of the formal theory about community ecology focuses on a single scale, i.e. local assemblages, but local communities are not isolated assemblages in the field. This critical point certainly explains why many investigations aimed at seeking consistent patterns in local community structures have failed (Wilson et al. 1996, but see Magurran & Henderson 2003). Since the pioneering works highlighting the need to include multiscale dynamics to assess abundance patterns, extinction, colonization and species interactions (Holt 1985), it is now generally accepted that community ecology has to be investigated within a metacommunity framework (Hubbell 1997); a metacommunity is defined as a set of local communities that are linked by dispersal of multiple potentially interacting species (Wilson 1992). Thus, the question is no longer whether particular and local community assembly patterns occur, but why they occur and whether they are consistent across several scales and approaches. Our study investigates this key question using fish communities from a tropical coastal lagoon to examine 2 different but complementary components of biodiversity patterns: richness–biomass relationships and species co-occurrence patterns.

One relatively easy way to study biodiversity patterns at a macroecological scale is to investigate the relationship between species richness and productivity. Species richness is often expected to increase and then decrease with productivity to produce a hump-shaped pattern in the relationship (Grime 1973, Huston 1979). The most common rule to explain this hump-shaped curve is that at high levels of productivity and

low levels of disturbance, only the best competitors persist; at low levels of productivity and high levels of disturbance, few specialist or opportunistic species persist; and at intermediate levels, coexistence of species is favoured (Grime 1973, Huston 1979). More precisely, when competitive interactions occur they may lead to exclusion of some species at high productivity levels (or low disturbance levels) and higher species diversity for intermediate levels of productivity can be expected. However, this hypothesis suffers from a lack of empirical support (Mittelbach et al. 2001) and has never been related to co-occurrence patterns and their related null models.

Another way to investigate biodiversity patterns in connected assemblages is to use null models like those recently developed by Gotelli (2000). Based on co-occurrence patterns among local communities, this method allows species interaction hypotheses to be tested. For instance, Sanders et al. (2003) showed that invasive species not only reduce biodiversity, but rapidly disassemble communities, i.e. that invaded communities shifted from a structured to a random community based on species co-occurrences. Basically, 2 nonrandom patterns may be statistically detected: 'species segregation' is inferred when species co-occur less often than expected by chance and similarly 'species aggregation' is indicated when species co-occur more often than expected under random replacement. The first pattern (segregation) may result from either interspecific competition (Simberloff & Connor 1981) or from differential species responses along environmental gradients (Peres-Neto et al. 2001), while in the latter pattern (aggregation) species tend to be positively associated; i.e. they tend to occur or to be absent simultaneously within local assemblages.

Notwithstanding the fact that several studies have produced biodiversity pattern descriptions that give relevant ecological information (e.g. Sanders et al. 2003), richness–biomass relationships and species co-occurrence patterns need further investigation within a common framework (Mouillot et al. 2005). The aim of our study was, therefore, to compare the results given by 2 different approaches related to biodiversity patterns by analyzing fish assemblages of the Terminos Lagoon, a tropical estuarine ecosystem in the southern Gulf of Mexico. During the last 20 yr, the Terminos Lagoon region has faced several types of anthropogenic impacts specifically related to the oil industry and human population growth, wetlands and mangrove forest threats, and shifts in hydrological conditions (Ramos Miranda et al. 2005). This lagoon has several types of habitats and a strong spatiotemporal heterogeneity inherent to coastal lagoon ecosystems for both biotic and abiotic factors (Basset et al. 2006) as

well as species-rich assemblages. For each area and for each season we determined the shape of the relationship between fish species richness and assemblage size (expressed as fish biomass) and identified patterns of fish species co-occurrences. The hypothesis examined was that biodiversity patterns of fish assemblages in the lagoon correspond to linkages between the findings of co-occurrence null models and richness–abundance relationships. Furthermore, this combination of approaches may reveal the existence of general patterns in coastal fish assemblages if any are present.

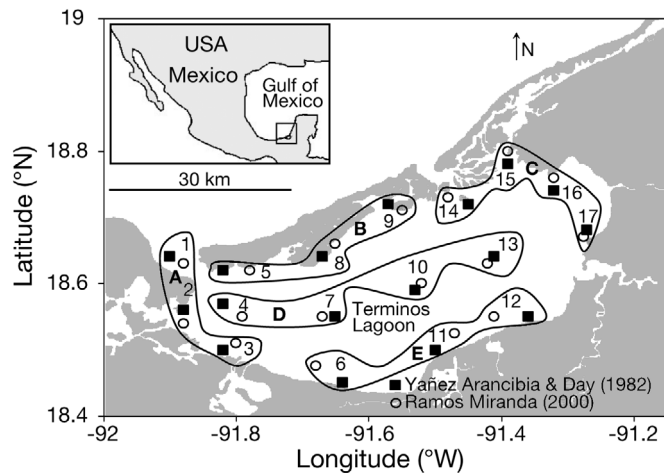


Fig. 1. Study area and sampling sites in the Terminos Lagoon, southern Gulf of Mexico. Zones A to E are the habitats modified from Yañez Arancibia & Day (1982) and Ramos Miranda (2000). Descriptions of the sites are provided in Table 1

MATERIALS AND METHODS

Study area. Terminos Lagoon is located between 18° 25' and 19° 00' N and 90° 00' and 92° 20' W in the southern Gulf of Mexico (Fig. 1). The basin surface area and its average depth are 1661.50 km² and 3.5 m, respectively. The lagoon is connected to the sea by 2 inlets: 'Carmen Inlet' on the western side (4 km long) and 'Puerto Real Inlet' on the eastern side (3.3 km long). These inlets are separated by Carmen Island (30 km long and 2.5 km wide).

Samples were organized spatially in 5 zones and temporally in 3 seasons for each annual period (1980 to 1981 and 1998 to 1999) following 3 criteria: (1) habitat types (Zones A to E; Fig. 1, Table 1); (2) climatic seasons (dry, rainy and windy); and (3) statistical requirements (i.e. homogeneity in sample replication terms). According to Yañez-Arancibia & Day (1982) and Ramos Miranda (2000) frequent afternoon and evening rainfalls occur from June to September (rainy season). From October to January (winter storms or windy season) the climate is characterized by successive wind fronts from the northwest. From February to May dry conditions dominate the region. The ecological conditions that dominate each of the 5 zones (Fig. 1) are described in Table 1 (data sources from Yañez-Arancibia & Day 1982, Ramos Miranda 2000).

Fish collection. Our analysis was based on scientific bottom-trawl surveys conducted at different stations within each zone of the Terminos Lagoon (Fig. 1). These surveys were carried out monthly from February 1980 to April 1981 (Yañez-Arancibia et al. 1988), and

Table 1. Annual mean salinity and transparency values and coefficients of variation (% in parentheses) for the zones comprising sample sites in the Terminos Lagoon during the periods 1980 to 1981 (A to E) and 1998 to 1999 (A' to E')

Zone (see Fig. 1)	Bottom salinity (‰)	Transparency (%)	Approximated observations for 1980 to 1981 from Yañez-Arancibia (1982)
A	20.6 (42.7)	22.4 (40.0)	Ecotone zone at the interface between estuarine and freshwater influences Clay-silt with less than 30% of CaCO ₃
A'	21.0 (54.2)	30.9 (63.9)	Mangrove swamps, macroalgae debris and oyster reefs
B	28.1 (25.0)	49.0 (49.2)	Strong seawater influence Sand and silty-clay with 30 to 70% CaCO ₃
B'	32.5 (17.4)	52.4 (38.2)	Macroalgae, seagrasses and mangrove swamps
C	25.8 (27.5)	42.0 (48.5)	Strong seawater influence Silty-clay with 20 to 30% CaCO ₃
C'	28.0 (22.0)	56.4 (44.4)	Seagrasses, mangrove, swamps and oyster reefs
D	25.6 (27.4)	28.7 (35.0)	Transition zone Muddy with fine sand and clay-silt, 30 to 40% CaCO ₃
D'	30.8 (16.4)	33.4 (53.1)	Macroalgae
E	22.5 (30.85)	32.9 (38.2)	Strong riverine influence Silty-clay with 10 to 30% CaCO ₃
E'	26.6 (22.73)	50.1 (44.6)	Mangrove swamps and oyster reefs

from October 1997 to March 1999 (Ramos Miranda 2000) at 18 and 23 sampling stations, respectively, with 17 stations in common between the 2 studies (Fig. 1). Bottom-trawl tows were grouped by season to get replication within the time period.

During the 1980 to 1981 and 1998 to 1999 surveys, fish were collected using a 5 m long shrimp trawl (mouth opening diameter, 2.5 m; mesh size, 19 mm) with tows of 12 min duration at 4.6 km h⁻¹ (2.5 knots); individual tows covered about 2000 m². To obtain the best representation of the fish lagoon community and reduce sampling bias due to selectivity (i.e. some species being more likely caught than others), an active fishing method (shrimp trawl net) rather than a passive method (e.g. trammel net) seemed more appropriate (e.g. Millar & Fryer 1999). In the laboratory, fish species were then identified with reference to the taxonomic keys of Jordan & Evermann (1886–1900), Hildebrand (1943), Castro-Aguirre (1978), Fischer (1978) and Resendez (1981). All fish were counted and weighed to the nearest 0.1 g.

Richness–biomass relationships. In heterotrophic organisms, productivity is the rate of organic matter accumulation and is often difficult to measure; for this reason, biomass (or standing stock) can be used as a surrogate measure (Poulin et al. 2003).

For the relationship between fish species richness (R , number of species per trawl) and abundance (P , fish biomass per trawl), we first fit quadratic linear regressions to the data based on the formula: $R = \beta_0 + \beta_1(P) + \beta_2(P^2)$. If the 2 coefficients of the regression (β_0 and β_1) were not significantly different from zero, abundance was assumed not to vary with richness. If only the qua-

dratic term (β_2) did not differ from zero the relationship was monotonic linear, and the slope defined the relationship direction. Regressions where the β_2 term explains a significant amount of variance, after fitting the linear term, have a curvilinear shape. In such cases we also tested for a hump-shaped or peaked curve with the Mitchell-Olds test (Mitchell-Olds & Shawn 1987), which is already used in major similar studies because it is more rigorous, though more conservative, than simply looking for a significant quadratic regression (Mittelbach et al. 2001). This method (hereafter referred to as the MOS test) tests whether an unconstrained least-squares model with a particular intermediate maximum provides a significantly better fit to the data than a model with a maximum at either the higher or lower end of the range of values. In other words, it tests whether a hump-shaped pattern exists in the data as opposed to simple monotonic change.

We also performed regression analysis for the relationship between biomass and species richness using ANOVAs. R^2 was also calculated as a measure of the proportion of variance in total biomass explained by species richness.

Co-occurrence patterns. To evaluate the structure of fish communities we calculated and tested by randomization the C-score introduced by Stone & Roberts (1990), an index that quantifies the average number for each unique species pair of 'checkerboard units' (CU) in a matrix of occurrence (fish species \times sampling site), i.e. the number of sub-matrices of the form 01/10 or 10/01 (see Table 2 and Fig. 2 for a theoretical illustration). The number of CU for each species pair is calculated as $CU = (r_i - H)(r_j - H)$, where r_i is the number of

Table 2. C-score indices and relationships between species richness and abundance (g fish biomass per trawl). Symbols for richness–biomass regressions (RB) are: non-significant, –; positive monotonic, /; hump-shaped or peaked, \cap . R^2 : coefficient of determination for the regression models. ^{ns}(non-significant) = $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Zone	Season	1980 to 1981			1998 to 1999		
		RB	R^2	C-score	RB	R^2	C-score
A	Dry	/	0.75***	-0.1324 ^{ns}	/	0.79***	-0.4279 ^{ns}
	Rainy	/	0.6***	-0.9911 ^{ns}	–	0.48 ^{ns}	0.8561 ^{ns}
	Windy	/	0.37*	-1.0360 ^{ns}	–	0.06 ^{ns}	2.6285**
B	Dry	–	0.29 ^{ns}	0.3429 ^{ns}	/	0.33*	-0.7642 ^{ns}
	Rainy	–	0.21 ^{ns}	1.3645 ^{ns}	/	0.83***	-0.8674 ^{ns}
	Windy	/	0.35*	-0.1756 ^{ns}	\cap	0.64**	2.0219**
C	Dry	/	0.39**	-0.7093 ^{ns}	–	0.28 ^{ns}	0.1966 ^{ns}
	Rainy	–	0.04 ^{ns}	1.5682*	\cap	0.57**	1.7240*
	Windy	/	0.31*	-0.4157 ^{ns}	\cap	0.48**	0.7091 ^{ns}
D	Dry	\cap	0.79***	1.1911 ^{ns}	\cap	0.6***	1.4710*
	Rainy	/	0.69***	-0.1714 ^{ns}	/	0.38*	-0.3155 ^{ns}
	Windy	\cap	0.85***	0.8815 ^{ns}	/	0.51**	-0.9376 ^{ns}
E	Dry	–	0.41 ^{ns}	0.6317 ^{ns}	\cap	0.66**	2.1699**
	Rainy	–	0.40 ^{ns}	1.2271 ^{ns}	–	0.24 ^{ns}	0.9773 ^{ns}
	Windy	\cap	0.45*	0.2461 ^{ns}	/	0.51**	0.2366 ^{ns}

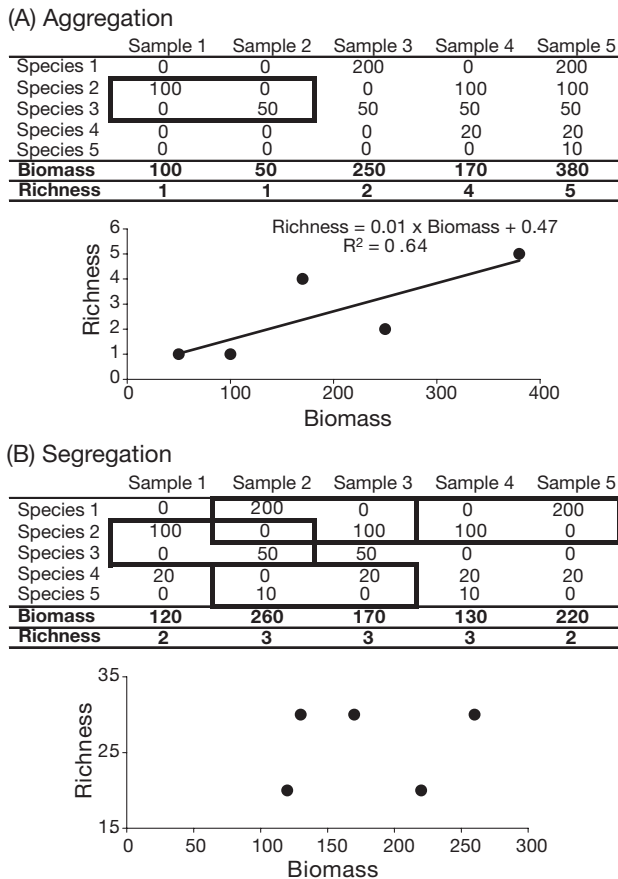


Fig. 2. Theoretical illustration of the link between species co-occurrence patterns and richness–biomass relationships. (A) When species are aggregated, they tend to co-occur in the same samples (5) and be simultaneously absent in the same samples (1 and 2). Consequently under species aggregation we observe a positive richness–biomass relationship. (B) Conversely when species are segregated, they tend to be present in different samples and produce numerous checkerboard units in the co-occurrence matrix (presence/absence alternatively, bold lines encapsulate checkerboard units in each matrix). Under this scenario no significant relationship between total biomass and species richness is expected

occurrences for the species i (over all sampled sites, i.e. the total of the row corresponding to this species in the matrix), r_j is the number of occurrences for the species j , and H is the sampling site number (number of rows). In a competitively structured metacommunity, the C-score tends to be larger than expected by chance with a high number of CU, i.e. with a high segregation of fish species among sampling sites (Case B in Table 2). In contrast, when the C-score is low, relatively few CU are expected, i.e. species are more aggregated and the community is not strongly structured by competition rules (Case A in Table 2).

To assess whether the p-value for the observed C-score is significantly lower or higher than expected by chance it must be compared to a simulated distribution

of C-scores in all tests of null models (Manly 1997). As suggested by Gotelli (2000), we used a ‘fixed-fixed’ algorithm to test the C-score statistic because our samples within a zone and for a season were considered as replicates. By fixing the sums of rows and columns we did not change the structure of assemblages in terms of species richness and we did not modify the number of occurrences of each species. We simply modified associations among species. To accomplish this aim we randomly swapped CU throughout the presence/absence matrix for each zone, season and year to generate 5000 new matrices on which we calculated 5000 simulated C-scores using the Ecosim v.7.0 software. More details about these indices and randomization procedures can be found in Gotelli (2000) and Manly & Sanderson (2002). To observe specific co-occurrence patterns such as segregation between fish species, Pearson’s product–moment correlations were performed on the presence/absence matrices. Only pairs of fish species that showed significant correlations ($p < 0.05$) and that coincided with highly significant C-scores were used in this analysis.

RESULTS

A total of 22 834 individuals representing 106 species from 408 samples (amounting to a total weight of 714.8 kg) were collected monthly during both annual periods. These species were classified into 72 genera, 41 families, 17 suborders, 15 orders and 2 classes. Mean species richness was higher in the lagoon edges than in the central basin. For example, richness observed in sampling Stns 4, 7, 10 and 13 varied from 0 to 19 fish species, while 3 to 23 fish species were caught in sampling Stns 3, 11 and 15 (Fig. 1).

Richness–biomass relationships

Two types of significant relationships ($p < 0.05$) were obtained between fish richness and total fish biomass (positive linear and second order polynomial regressions) as well as non-significant relationships (Table 2). The positive linear or positive monotonic regressions were more frequent during the 1980 to 1981 period. Conversely, hump-shaped or peaked regressions (significant after the MOS test) as well as non-significant relationships were more frequent during the 1998 to 1999 period. These relationships are illustrated for Zone D in Fig. 3. Some significant linear patterns were observed for the rainy season in this zone, although significant peaked relationships were observed between fish richness and total fish biomass especially during the dry season. Both total biomass and fish rich-

ness decreased by 50% between 1980 to 1981 and 1998 to 1999 in Zone D (Fig. 3). The variance explained in fish species richness by total fish biomass varied highly among spatiotemporal strata and ranged from 4 to 85% (Table 2). The highest coefficient of determination for a peaked relationship was observed for the windy season 1980 to 1981 in Zone D (Fig. 3C) although this significant relationship is mainly due to

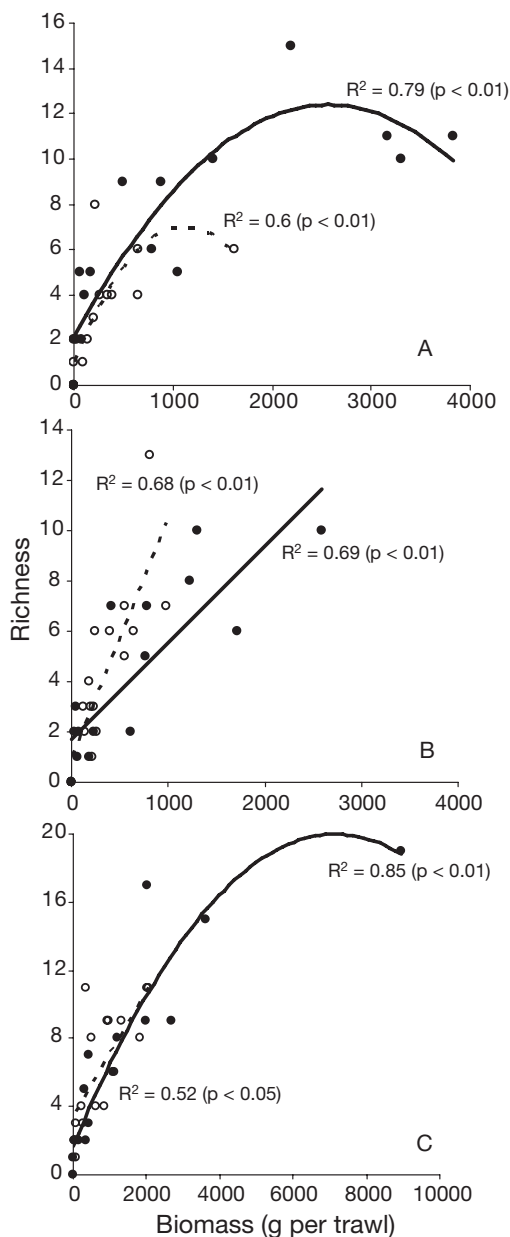


Fig. 3. Relationships between biomass and species richness for Zone D in (A) dry, (B) rainy and (C) windy seasons. ● and ○: relationships for the 1980 to 1981 and 1998 to 1999 periods, respectively. Solid and dashed lines correspond to regression models for the 1980 to 1981 and 1998 to 1999 periods, respectively

one sample in the upper left-hand corner of the graph. In contrast, the highest coefficient of determination for a simple linear relationship was observed for the rainy season for 1998 to 1999 in Zone B.

Co-occurrence patterns

Across zones, seasons and years, fish assemblages had either significantly fewer co-occurrences than expected by chance (larger C-score values, Table 2) or non-significant patterns in species co-occurrences. The C-score index, which measured the mean number of CU in a co-occurrence matrix, was higher than expected by chance under the null model hypothesis only for Zone C during the rainy season of the 1980 to 1981 period. In contrast, fish assemblages across zones and seasons appeared to be more structured during the 1998 to 1999 period when 5 fish assemblages showed significantly higher C-score values than expected by chance, once for each zone (Table 2). The highest positive C-score was observed for Zone A during the windy season of 1998 to 1999. For this extreme case (i.e. the highest C-score), correlations performed on the species presence/absence matrix (Table 3) show highly segregated patterns, i.e. numerous negative correlations between species pairs. Segregation patterns (i.e. significant negative correlations) between pairs of species are illustrated in Figs. 4 & 5. Biomass distribution across months for each sampling site showed high segregation between *Symphurus civitatum* Ginsburg, 1951 and *Diapterus rhombeus* Cuvier, 1829 ($r = -0.63$, $p < 0.05$) as well as between *S. civitatum* and *Micropogonias undulatus* Linnaeus, 1766 ($r = -0.63$, $p < 0.05$) (Fig. 4). The second highest C-score value was observed for Zone E during the dry season of 1998 to 1999, indicating that the presence of many species pairs are highly segregated in space and time (Fig. 5, Table 4).

DISCUSSION

In this study we aimed to compare 2 methods to provide insight into community organization and species coexistence rules at the regional scale, i.e. a set of local assemblages. We used fish data from scientific fishing surveys with a constant protocol to address the key question about community structure: Is there any consistency between richness–biomass relationships and co-occurrence patterns?

After an analysis of the results (Table 2) no consistent pattern appears for either diversity–biomass relationships or for co-occurrence patterns among samples. The 3 types of diversity–biomass relationships (ab-

Table 3. Correlation coefficient matrix for the species presence/absence values for the windy season in Zone A. Significant correlation coefficients ($p < 0.05$) are indicated in **bold** ($n = 12$ [4 mo and 3 sampling stations])

Species	Ca-me	Ba-ma	Ba-ch	Cy-ar	Di-rh	Mi-un	Ol-sa	St-la	Sy-ci	Tr-le
<i>Cathorops melanopus</i> (Ca-me)										
<i>Bagre marinus</i> (Ba-ma)	-0.25									
<i>Bairdiella chrysoura</i> (Ba-ch)	-0.30	0.17								
<i>Cynoscion arenarius</i> (Cy-ar)	0.36	0.31	0.17							
<i>Diapterus rhombeus</i> (Di-rh)	0.67	-0.38	0.00	-0.60						
<i>Micropogon undulatus</i> (Mi-un)	-0.21	-0.24	0.35	-0.60	0.16					
<i>Oligoplites saurus</i> (Ol-sa)	0.17	-0.29	-0.58	-0.29	0.26	0.00				
<i>Stellifer lanceolatus</i> (St-la)	-0.25	0.31	-0.17	0.31	-0.38	-0.60	0.10			
<i>Symphurus civitatum</i> (Sy-ci)	-0.43	0.60	-0.35	0.24	-0.63	-0.63	0.00	0.60		
<i>Trichiurus lepturus</i> (Tr-le)	-0.58	0.49	0.19	0.10	-0.26	0.00	0.11	0.49	0.41	

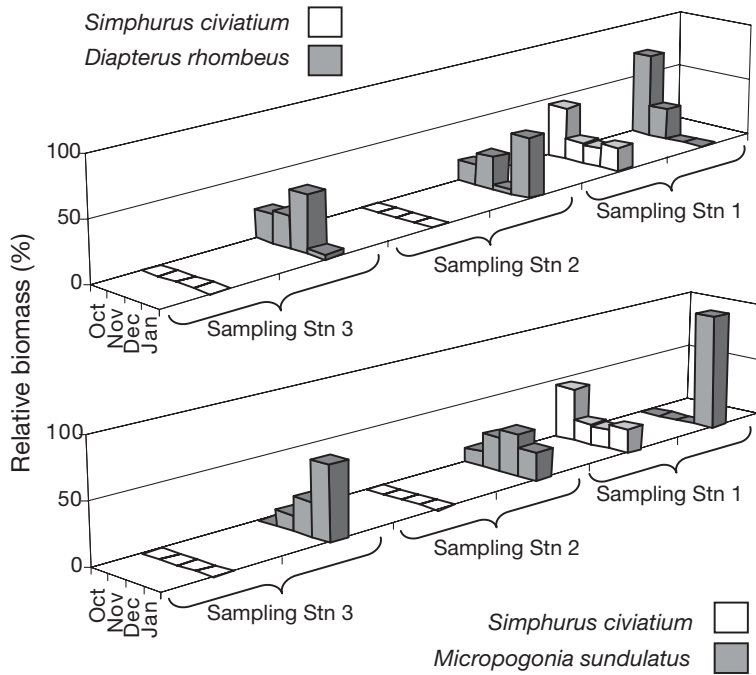


Fig. 4. Two examples of spatiotemporal segregations for species pairs with significant negative relationships between their abundance (see Table 3) during the 1998 to 1999 windy season in Zone A

emerging trend as both positive and negative values were observed for each season and each zone (Table 2).

However, taken together the results reveal very consistent patterns with few exceptions. First, when fish assemblages showed significantly higher C-score values than expected by chance (high segregation leading to high number of CU in the occurrence matrix and negative correlations among species), the relationship between richness and biomass was never a linear increase. Second, C-score values were always positive (fish species tend to be segregated) when hump-shaped or non-significant richness–biomass relationships were observed. Conversely, a positive monotonic relationship between species richness and total biomass was always related to negative C-score values (fish species tend to be aggregated), albeit not significantly different from that expected from a null model. The only exception is for Zone E during the windy season of 1998 to 1999 when a significant linear relationship was observed between richness and biomass

sence of relation, positive linear relation and hump-shaped curve) seem to arise randomly and independently from the period, the season or the zone. This result is in accordance with the main synthesis on the topic (Mittelbach et al. 2001), highlighting the non-consistency of diversity–biomass relationships across space and time and types of organisms. Similarly, the C-score index does not show any

Table 4. Correlation coefficient matrix for the species presence/absence values for the dry season in Zone E. Significant correlation coefficients ($p < 0.05$) are indicated in **bold** ($n = 12$ [4 mo and 3 sampling stations])

Species	Ca-me	Ba-ch	Ce-ed	Sp-te	St-la
<i>Cathorops melanopus</i> (Ca-me)	1.00				
<i>Bairdiella chrysoura</i> (Ba-ch)	-0.24	1.00			
<i>Cetengraulis edentulus</i> (Ce-ed)	0.48	-0.58	1.00		
<i>Sphoeroides testudineus</i> (Sp-te)	0.60	0.13	0.13	1.00	
<i>Stellifer lanceolatus</i> (St-la)	0.84	-0.58	0.63	0.50	1.00

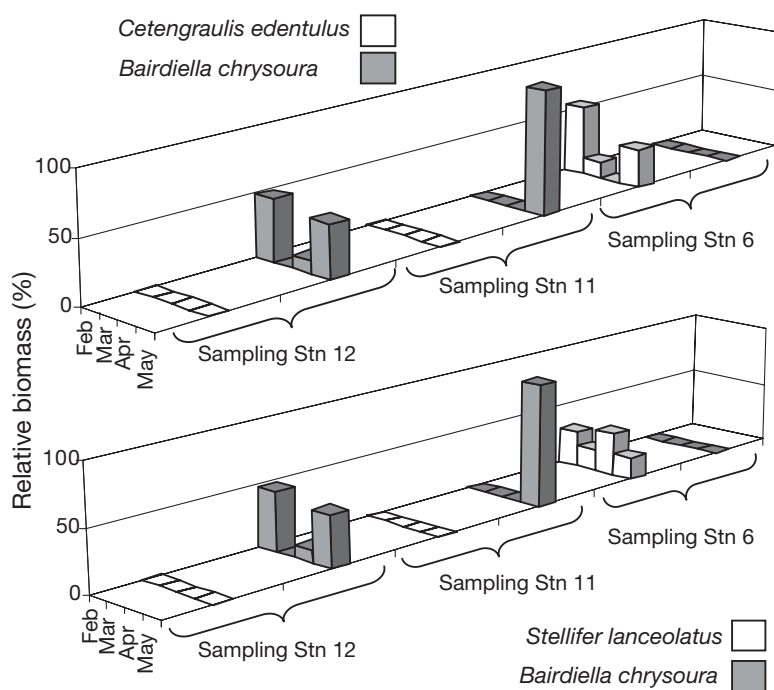


Fig. 5. Two examples of spatiotemporal segregations for species pairs with significant negative relationships between their abundance (see Table 3) during the 1998 to 1999 dry season in Zone E

while the C-score was positive, albeit low (the lowest positive value observed).

The ecological explanation of positive monotonic relationships between productivity and richness is somewhat complex, but can be expected if species are complementary and/or not interactive, i.e. when negative interspecific interactions are not playing a major role (e.g. Loreau & Hector 2001). Thus, fish assemblages that follow this relationship can be considered unstructured. This hypothesis is very consistent with the negative C-score values obtained for these assemblages, suggesting aggregation of species, i.e. fewer CU than expected by chance. Our findings also have implications for another debate in fish ecology: whether fish assemblages are saturated with species (e.g. Angermeier & Winston 1998, Rueda & Defeo 2003). The results of this study provide some support to the view that there is no upper limit to fish species richness set by the size of the assemblage at some spatiotemporal stratum (such as for Zone A over periods and seasons). Indeed, Zone A contains a mixture of freshwater, estuarine and marine taxa as it represents a zone receiving freshwater discharges as well as being close to the adjacent shelf (Fig. 1, Table 1) (Sosa Lopez et al. 2007).

Overall, our results are consistent with ecological hypotheses to explain the shape of the patterns. The significant and positive C-scores were never associ-

ated to linear relationships between richness and biomass, suggesting structured fish communities with some segregation among species. For instance, among the 9 significant coefficients of correlation between pairs of species for the windy season in Zone A (which correspond with the highest C-score value), 6 are negative (Table 3). The negative correlations suggest that a temporal or spatial segregation exists between these pairs of species (they do not co-occur in abundance at the same place at the same time). Among all these pairs of species, 3 benthic species (*Symphurus civitatum*, *Diapterus rhombeus* and *Micropogonias undulatus*) have functional similarities (trophic level between 2.89 and 3.3) and feed mainly on zoobenthos such as benthic crustaceans, worms and mollusks in estuarine, brackish and marine waters (see www.fishbase.org). Thus, these species are potential competitors for space and resources. The temporal and spatial segregation among these 3 species are highlighted in Fig. 4: *S civitatum* was only present at Stn 1 over the 4 mo of the 1998 to 1999 windy season while the 2 other species

(*D. rhombeus* and *M. undulatus*) were present at the 3 sampling stations in Zone A for most months. Moreover, we can observe that the highest abundances of *D. rhombeus* were synchronized with the lowest abundances of *M. undulatus* and vice-versa (Stn 3 in January, Stn 2 in December and Stn 1 in October and January).

In Fig. 2 we propose a theoretical framework linking species co-occurrence patterns and richness–biomass relationships. In Fig. 2A we have few CU because species are aggregated. Then species richness and total biomass tend to be positively correlated with samples having few species and low biomass while others concentrate both species richness and total biomass. Conversely when species are segregated (Fig. 2B) they tend to be present in different samples and produce numerous CU. This species segregation prevents large differences in species richness and biomass among assemblages. When fish species were segregated we never observed a linear increase in the richness–biomass relationship as we had expected to from our theoretical framework.

We are aware that this study does not demonstrate species interactions or competition. This would need appropriate experimental design or knowledge of functional characteristics of fishes to determine pairs of potential competitors (e.g. Dumay et al. 2004). Indeed

our observed spatiotemporal segregation patterns may be due to either competitive exclusion between some species pairs or differences in habitat preferences with a low niche overlap. The former is unlikely for fish assemblages because competitive interactions among fishes usually lead to resource partitioning processes to avoid strong competition rather than to complete competitive exclusion (Jackson et al. 2001). The second case must be discussed in the light of an evolutionary process as segregated patterns among species can arise from past competitive interactions that may lead to adaptive radiations to exploit new habitats and new resources (Day & Young 2004). This pattern can also emerge from highly heterogeneous habitats (Gotelli et al. 1997) and accounting for this environmental heterogeneity may help to identify patterns structured by interspecific competition (Peres-Neto et al. 2001).

In summary, our study does not reject the hypothesis that species interactions can be important determinants of assemblage structure in species-rich tropical regions (Winemiller 1991, Rueda & Defeo 2003), but only for some periods and some spatial strata. Other patterns suggest that coastal fish communities are unstructured assemblages where competition does not play a central role (Mouillot et al. 2007) as this has been demonstrated in previous studies on freshwater ecosystems (Peres-Neto 2004). Our results are in accordance with those of Costa de Azevedo et al. (2006), who found that segregation of fishes among habitats explains co-occurrence patterns observed in Sepetiba Bay, Brazil. The generality of our findings about fish segregation patterns still needs to be demonstrated, at least for estuaries. Finally our study highlights the potential of using a combination of methods to investigate assemblage structures at a regional scale. For instance, richness–biomass relationships and species co-occurrences propose highly congruent patterns that deserve to be studied together in other circumstances.

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