

# Co-occurrence of demersal fishes in a tropical bay in southeastern Brazil: A null model analysis

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## Abstract

Co-occurrence of demersal fishes was assessed in a tropical bay in southeastern Brazil along an environmental gradient (inner, middle, and outer zones), defined according to depth and salinity. The aim was to test whether fish species are distributed randomly and independently of one another in accordance with a null model. The unconstrained null hypothesis for occurrence of a given species by chance in relation to other species was accepted for each zone separately, and rejected for the bay as a whole, for the full year and for each season separately, except summer. Findings of the environmentally constrained null models, which predict species presence or absence as a function of environmental conditions, were not significant, suggesting that the environmental variables we chose are not key factors for these species and that biotic interactions between species are not strong when species–environment relationships are considered. The partition of available resources inside each zone and fish movements along the three zones during summer may have contributed to higher fish species co-occurrence. Habitat segregation in the bay during the remaining seasons could explain the pattern of reduced co-occurrence, indicating the presence of two fish assemblages associated with different environmental characteristics.

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## 1. Introduction

The structure of fish assemblages refers to non-random patterns of local species co-occurrence. With non-experimental data, it is not possible to establish situations of absence of one or several factors to test hypotheses. The hypothesis implicit in numerous community studies that use multivariate methods is the presupposition that species interact with each other or are influenced by environmental conditions, forming structured non-random assemblages with defined species composition (Diamond, 1975). Thus, multivariate methods applied to ecological data can create hypotheses but not test them.

Null models are based on the null hypothesis principle that patterns do not reflect biological interactions but rather represent random variation or sampling effects. In community ecology, the null hypothesis typically would be that species distribution reflects colonization and extinction at random, rather than any biological process. The alternative hypothesis would be that occurrences of species are not independent of one another, reflecting biological interactions. The null model is used to randomize the occurrence of species and to compare the patterns in these randomized communities with those from real data obtained by field sampling. This analysis can be designed in relation to some ecological and/or evolutionary process of interest in an attempt to generate distributions of a given variable of interest, in the absence of a potential causal process, to facilitate the creation of a “control situation”. Some elements of the data are maintained constant, while others are allowed to vary stochastically to create new

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assemblage patterns (Paes and Blinder, 1995; Gotelli and Graves, 1996).

Evidence of non-random patterns in species distribution does not necessarily imply the presence of biotic interaction, but it could relate to other factors such as similarities or differences in dispersal abilities or environmental requirements of the species. Thus, different processes (e.g., competition and environmental suitability) could lead to rejection of the null hypothesis. To distinguish between shaping of fish assemblages by biotic and abiotic patterns, Peres-Neto et al. (2001) incorporated environmental information in null model applications, so that differences in environment are not considered when evaluating patterns of species co-occurrence.

Sepetiba Bay is located in the state of Rio de Janeiro in southeastern Brazil. Its connection with the sea is through a wide area at the west end and a narrow channel at the east, with a sandbank forming the southern limit and the continental margin at the north (Fig. 1). Habitat characteristics shift along the west–east axis, including depth, salinity, transparency, temperature, and influences of human activities. Several marine fish species enter and leave the bay for nursery, reproductive, and feeding purposes (Araújo et al., 2002). Cycles of fish abundance in bays appear to be related to intrinsic biotic processes and can respond to variations in environmental conditions in ways that could confound discerning annual trends, if not properly understood. Because most human activities in the drainage basin of Sepetiba Bay are concentrated in the innermost region, we hypothesized that there would be inner, middle, and outer zones that differ in fish abundance and assemblages; that these differences would be related to environmental variables and anthropogenic

influences; and that biotic interactions could play a role in fish assemblage structure.

On the basis of a null model, the null hypothesis for occurrence of a given species by chance in relation to other species was tested for the fish assemblage in Sepetiba Bay. We expected differences in fish assemblages among the three zones and few changes during the year if biotic interactions predominate as the main driving force structuring fish assemblages. The aim was to assess mechanisms of habitat segregation by fish assemblages associated with different environmental characteristics. We have compared unconstrained and constrained null models to evaluate species association and facilitate the distinction between mutually exclusive processes (biotic vs abiotic) that may be shaping species distribution.

## 2. Methods

### 2.1. Study area and survey design

Sepetiba Bay is a sedimentary embayment ( $22^{\circ} 54' - 23^{\circ} 04' S$ ;  $43^{\circ} 34' - 44^{\circ} 10' W$ ) originated by extensive sand deposition, which formed a barrier beach as its southern boundary (Fig. 1). The bay has a surface area of approximately  $450 \text{ km}^2$ , a mean depth of 8.6 m, a maximum depth of 30 m, and a drainage area of  $2700 \text{ km}^2$ . The tidal range is approximately 1 m. Predominantly northeasterly and southwesterly winds activate thermal currents between the bay and the ocean. The annual rainfall varies between 1000 mm and 2100 mm (Barbière and Kronemberger, 1994) but does not cause great changes in the salinity of the bay because the

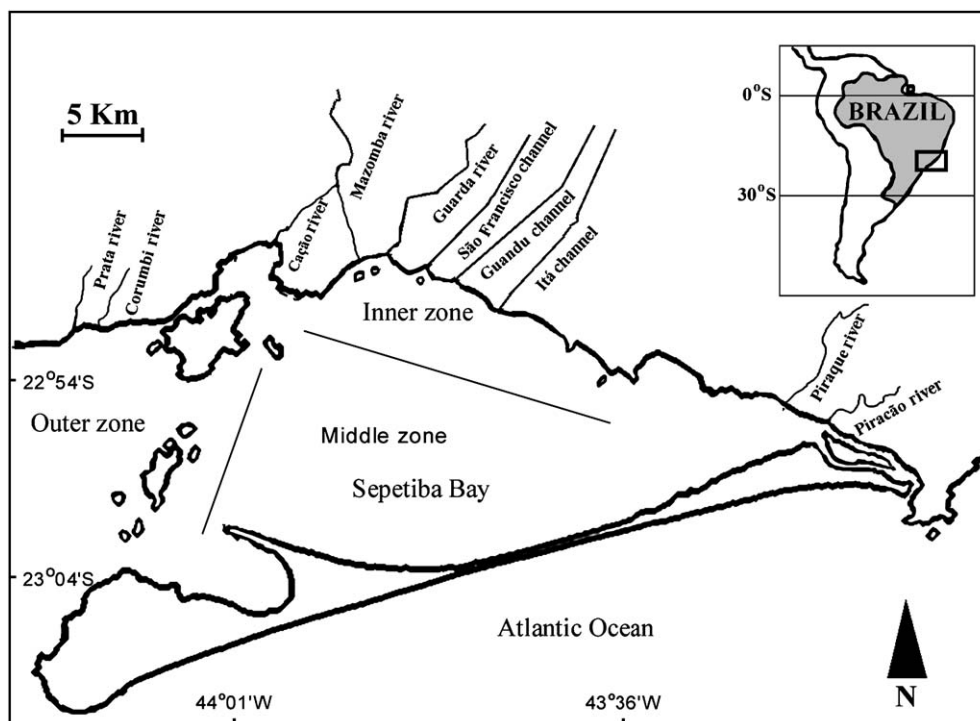


Fig. 1. Map showing the three zones (outer, middle, and inner) of Sepetiba Bay, Brazil.

streams and channels that drain into the bay are small. Most of the substrate in the inner bay is silt and mud.

The bay can be divided into three zones according to environmental characteristics. The inner zone is influenced by discharges from perennial small rivers that contribute to decreased water quality, showing increased turbidity and temperature and decreased salinity. Substrate is mainly muddy, with depth mostly less than 5 m and salinity averaging 28 (Araújo et al., 2002). The outer zone, near the sea, presents the opposite environmental conditions – substrate mainly sandy, comparatively lower temperature, and higher salinity and transparency. Maximum depth in the outer bay is approximately 28 m, and salinity average is 33 (Pessanha and Araújo, 2003). Furthermore, the outer zone is bounded by several islands in the west part of the bay. The central zone presents intermediate environmental conditions between inner and outer zones.

Sampling was conducted by bottom trawl tows during daylight hours between October 1998 and September 1999. A stratified random design was used to permit analysis of effects of habitat characteristics (e.g., depth and salinity gradient). In each zone, three replicate samples were taken at random monthly (Fig. 1). Bottom trawl tows were against the current, had 20-min duration on the bottom, a towing speed of approximately 3 km/h, covering a distance of 1500 m (this defines the unit effort applied to each sample). Following each fish sampling, hydrographic data (including temperature, salinity, and dissolved oxygen) were taken from water near the bottom, collected by a Van Dorn bottle. Transparency was recorded using a Secchi disk, and depth was determined with an echo sounder.

## 2.2. Data analysis

Two jackknife estimators of species richness were used to evaluate the variability of the samples and the adequacy of sample size. In this procedure, the obtainable sample is subsampled to determine the average number of species as a function of size of the subsample. These jackknife estimators produce more accurate and less biased estimates when subsampling a restricted area. The first-order jackknife estimator (Heltsh and Forrester, 1983; Palmer, 1990) is  $Jack1 = S + r_1(n - 1)/n$ , where  $S$  = the observed number of species,  $r_1$  = the number of species occurring in one sample unit, and  $n$  = the number of sample units. The second-order jackknife estimator is  $Jack2 = S + r_1(2n - 3)/n - r_2(n - 2)^2/(n(n - 1))$ , where  $r_2$  = the number of species occurring in exactly two sample units.

We used  $C$  score as a quantitative index of co-occurrence (Stone and Roberts, 1990) for each presence–absence matrix. The  $C$  score calculates the average of the number of “checkerboards units” (CUs) among all possible pairs of species. A CU is a  $2 \times 2$  submatrix of the form 01/10 or 10/01, defined as follows:  $CU = (r_i - S)(r_j - S)$ , where  $S$  is the number of samples with both species, and  $r_i$  and  $r_j$  are the respective total of the rows for species  $i$  and  $j$ . In an assembly structured by competition, the observed  $C$  score will be significantly larger than that expected of a random distribution.

The larger the  $C$  score, the lesser the coexistence between pairs of species. To evaluate the statistical significance of the  $C$  score (conventional level of statistical significance of  $p < 0.05$ ), the number of co-occurring pairs observed in the real data matrix obtained by field sampling would be compared with the distribution of co-occurring pairs for random distribution of simulated data matrices (observed  $\geq$  expected), using randomization tests accomplished with EcoSim software (Gotelli and Entsminger, 2001).

A variety of null model algorithms generate randomizations that can vary from those with almost no constraints to those that are highly constrained by the structure of the real matrix. These constraints of the algorithms are based on maintaining (or not) the same totals of the rows and columns of the real matrix. In a data matrix in which samples are in columns and species are in rows, retaining the column sums preserves the number of species maintained in the samples, while retaining the row sums preserves the occurrence frequency among the species. According to Gotelli (2000), the algorithms that present a lower probability of type I error had the property of preserving the row sums of the real matrix.

In this study, the algorithms differed in how the columns (=sites) were treated. In simulation 1, the observed number of species in a site was maintained, while in simulation 2, the sites were equiprobable: In simulation 1, the sum of rows and columns was fixed as in the real matrix. This model was tested for the whole year and for each season. In simulation 2, the sum of rows was fixed as in the real matrix, and columns were equiprobable. This model was tested for each zone. The chance for a given species to occur randomly in relation to another was maintained in both simulations. Simulation 1 is more appropriate for areas with heterogeneous habitats, and simulation 2 is suited for homogeneous habitats. The aim is to maintain differences among samples, where some species–area effects exist. Additionally, we used an environmentally constrained null model (Peres-Neto et al., 2001) to distinguish co-occurrence patterns as a result of biotic or abiotic forces. A matrix of probability of species occurrence as a function of environmental variables (temperature, salinity, dissolved oxygen, transparency, and depth) was calculated (site-specific probability matrix) using linear discriminant analysis. Then, species presence was reassigned to sites during the generation of “null communities”, following the algorithm Ct-RAI, proposed by Peres-Neto et al. (2001) to calculate  $C$  scores and compare with unconstrained classical null models.

A principal component analysis (PCA) on correlation matrix was used to explore species distribution patterns. These analyses allow identification of groups of species with similar distribution, characterizing associations of species from a multispecies matrix. Component loadings  $>0.5$  were used to define the groups. PCA was applied on log-transformed data ( $\log[x + 1]$ ) of the numerical abundance of fish species to test the validity of results obtained by the null model. Hence, PCA was performed, considering all samples pooled, to obtain a general view of the spatial pattern and for each season separately.

### 3. Results

Ninety-three fish species from 73 genera and 37 families were recorded in the 108 otter trawl samples, corresponding to 20,483 individuals, weighing 653,473.6 g.

The first- and second-order jackknife estimators were well within the expected values for the whole bay, and for each zone and season separately (Table 1). Both estimators showed higher values than the observed values, as expected. Observed and estimated species richness did not change among seasons, but values were slightly higher in the outer zone compared with those in the middle and inner zones. Palmer (1995) warned that these estimators may not be appropriate when sampling large heterogeneous regions because the estimated number of species can never be twice the number of observed species.

The 30 most abundant species were used in the analyses because their abundance in samples seemed more likely to reveal structural patterns in the fish assemblage.

#### 3.1. Null model analysis of species co-occurrence

For the whole year and for each season, we used simulation 1 (Table 2). The observed number of species in each sample was preserved, and the differences among the samples were maintained. The observed *C* scores were significantly higher than that expected by chance for the whole bay, indicating a pattern of lesser co-occurrence among the pairs of species and rejecting the null hypothesis. The same pattern was observed when *C* scores were obtained for the matrix by season (for spring, autumn, and winter), which presented lesser co-occurrence among the pairs of species, and led to a rejection of the null hypothesis. However, for summer, *C* scores were lower than those expected by chance, and the null hypothesis could not be rejected (Table 2). On the other hand, the constrained null model was non-significant for the whole year and for each season separately.

The observed *C* score was lower than that expected by chance for each zone separately, indicating a pattern of high co-occurrence among the pairs of species, and not permitting the rejection of the null hypothesis that the species in the zones were distributed randomly and independently of one another (Table 3). The constrained null model was non-significant for each zone according to *C*-score values.

Table 1  
First- and second-order jackknife estimators of species richness, by season and zone, in Sepetiba Bay, Rio de Janeiro, between October 1998 and September 1999

	Number of observed species	First-order jackknife estimate	Second-order jackknife estimate
All seasons	93	111.8	122.7
Outer zone	74	96.3	113.4
Middle zone	56	65.7	66.9
Inner zone	63	78.6	85.4
Spring	60	75.4	84
Summer	65	84.3	94.8
Autumn	66	84.3	94.8
Winter	66	79.5	83.5

Table 2  
Values of unconstrained and constrained null models of co-occurrence (*C* scores) on 30 most abundant species in Sepetiba Bay, 1998–1999. Significance statistics:  $p < 0.05$  (observed  $\geq$  expected). Significant values in bold-face. Simulation 1 – sum of rows and columns according to real matrix

Matrix	Unconstrained <i>C</i> score		<i>p</i> -Values	Constrained <i>C</i> scores	<i>p</i> -Values
	Observed	Simulated mean			
All seasons pooled	356.95	349.61	<b>0.00</b>	317.48	1.00
Spring	20.41	19.57	<b>0.00</b>	23.67	0.99
Summer	16.37	16.27	0.25	23.58	0.99
Autumn	24.70	23.98	<b>0.00</b>	23.66	0.98
Winter	26.05	25.17	<b>0.00</b>	10.68	0.85

#### 3.2. Principal component analysis

##### 3.2.1. All samples

Two main components were obtained from the ordination of the 30 selected fish species, with eigenvalues exceeding 1.0 and explaining 29.1% of the total variance (Table 4). Component 1 explained 16.4% of the total variance, while component 2 explained 12.7%. The ordination diagram, with samples coded by zone, presented some spatial patterns along component 1, with samples from the inner zone distributed on the left side of the diagram, and samples from the outer zone, on the right side. Samples from the middle zone were distributed widely across the diagram but clustered strongly in an intermediate area (Fig. 2). Species that showed positive correlation with component 1 were abundant and frequent species in the outer bay zone, such as *Ctenosciaena gracilicirrhus*, *Orthopristis ruber*, *Diplectrum radiale*, *Etropus crossotus*, *Synodus foetens* and *Prionotus punctatus*, while *Cetengraulis edentulus*, which showed a negative correlation with component 1, was abundant in the inner zone (Table 4). The species that presented positive correlations with component 2 were *Cathorops spixii* and *Symphurus tessellatus*.

##### 3.2.2. Seasonality

3.2.2.1. Spring. Component 1 explained 20.5% of the total variance, while component 2 explained 12.6%. Species such as *Orthopristis ruber* and *Diplectrum radiale*, which showed

Table 3  
Values of unconstrained and constrained null models of co-occurrence (*C* scores) of 30 most abundant species in three zones of Sepetiba Bay, 1998–1999. Significance statistics:  $p < 0.05$  (observed  $\geq$  expected). Simulation 2 – row sums according to real matrix and columns with the same probability of species occurrence

Matrix	Unconstrained <i>C</i> score		<i>p</i> -Values	Constrained <i>C</i> score	<i>p</i> -Values
	Observed	Simulated mean			
Outer zone	24.26	34.96	1.00	20.72	1.00
Middle zone	26.49	38.44	1.00	22.26	1.00
Inner zone	41.49	50.08	1.00	32.79	1.00



Table 4

Principal component loadings for 30 most abundant fish species in Sepetiba Bay, 1998–1999. Highly significant values in boldface

Species	Component									
	All season		Spring		Summer		Autumn		Winter	
	1	2	1	2	1	2	1	2	1	2
<i>Anchoa tricolor</i> (Agassiz, 1829)	-0.01	0.20	-0.14	0.03	0.21	0.04			0.45	<b>0.66</b>
<i>Archosargus rhomboidalis</i> (Linnaeus, 1758)	-0.07	0.02	0.07	0.49	-0.04	0.14	-0.47	0.17	-0.13	-0.14
<i>Cathorops spixii</i> (Agassiz, 1829)	-0.36	<b>0.55</b>	0.25	<b>0.79</b>	<b>0.80</b>	-0.30	-0.33	<b>0.56</b>	<b>0.53</b>	0.24
<i>Cetengraulis edentulus</i> (Cuvier, 1828)	<b>-0.57</b>	0.42	<b>0.81</b>	0.15	<b>0.59</b>	<b>-0.66</b>	<b>-0.52</b>	0.26	<b>0.70</b>	0.17
<i>Chloroscombrus chrysurus</i> (Linnaeus, 1766)	<b>-0.50</b>	0.45	<b>0.70</b>	-0.04	<b>0.55</b>	-0.28	<b>-0.59</b>	0.41	<b>0.54</b>	0.08
<i>Citharichthys spilopterus</i> Günther, 1862	-0.25	0.34	0.47	0.03	<b>0.68</b>	-0.46	-0.24	0.32	0.32	0.01
<i>Ctenosciaena gracilicirrhus</i> (Metzelaar, 1919)	<b>0.63</b>	0.22	<b>-0.50</b>	0.03	0.29	<b>0.73</b>	<b>0.68</b>	0.14	-0.48	0.21
<i>Cynoscion leiarchus</i> (Cuvier, 1830)	-0.03	0.49	0.36	<b>0.63</b>	<b>0.62</b>	<b>-0.61</b>	<b>0.60</b>	<b>0.52</b>	0.26	<b>0.68</b>
<i>Diapterus rhombeus</i> (Cuvier, 1829)	-0.36	0.27	<b>0.75</b>	0.15	0.40	0.07	-0.35	-0.15	0.48	-0.39
<i>Diplectrum radiale</i> (Quoy & Gaimard, 1824)	<b>0.77</b>	0.29	<b>-0.62</b>	0.28	0.35	<b>0.78</b>	<b>0.75</b>	0.20	<b>-0.79</b>	0.14
<i>Etropus crossotus</i> (Jordan & Gilbert, 1882)	<b>0.55</b>	0.46	-0.38	0.20	<b>0.81</b>	0.27	<b>0.56</b>	0.30	<b>-0.75</b>	0.14
<i>Genidens genidens</i> (Valenciennes, 1839)	-0.36	0.33	0.26	<b>0.60</b>	0.34	-0.01	<b>-0.73</b>	0.33	0.35	0.03
<i>Gerres aprion</i> (Baird & Girard, 1854)	0.08	0.41	0.13	-0.04	<b>0.69</b>	0.43	-0.02	0.13	-0.19	-0.25
<i>Gerres gula</i> (Cuvier, 1830)	-0.36	0.30	<b>0.60</b>	-0.08	0.42	0.11	<b>-0.64</b>	0.09	0.15	-0.38
<i>Haemulon steindachneri</i> (Jordan & Gilbert, 1882)	0.47	0.26	-0.22	-0.13	0.41	<b>0.73</b>	0.41	-0.35	-0.42	0.12
<i>Harengula clupeiola</i> (Cuvier, 1829)	-0.28	0.17	<b>0.51</b>	-0.02	0.33	-0.20	0.03	0.21	<b>0.53</b>	0.06
<i>Menticirrhus americanus</i> (Linnaeus, 1758)	-0.06	0.31	0.21	<b>0.63</b>	0.39	0.38	0.15	-0.33	0.45	0.28
<i>Micropogonias furnieri</i> (Desmarest, 1823)	-0.35	0.44	0.32	0.25	<b>0.77</b>	-0.27	-0.36	0.09	<b>0.58</b>	0.14
<i>Monacanthus ciliatus</i> (Mitchill, 1818)	0.08	0.44	0.29	-0.30	<b>0.66</b>	0.09	0.14	-0.30	-0.01	<b>0.70</b>
<i>Orthopristis ruber</i> (Cuvier, 1830)	<b>0.82</b>	0.26	<b>-0.64</b>	0.12	0.32	<b>0.74</b>	<b>0.87</b>	0.12	<b>-0.85</b>	0.22
<i>Prionotus punctatus</i> (Block, 1797)	<b>0.66</b>	0.35	<b>-0.55</b>	0.42	<b>0.52</b>	0.43	<b>0.62</b>	0.37	<b>-0.80</b>	0.17
<i>Sciadeichthys luniscutis</i> (Valenciennes, 1840)	<b>-0.50</b>	0.41	0.34	<b>0.76</b>	0.33	-0.38	<b>-0.68</b>	0.42	0.46	0.31
<i>Selene setapinnis</i> (Mitchill, 1815)	0.05	0.36	<b>0.51</b>	-0.37	0.47	0.30	0.07	-0.23		
<i>Sphoeroides testudineus</i> (Linnaeus, 1758)	0.06	0.28	<b>0.65</b>	-0.43	<b>0.67</b>	0.25	0.09	<b>-0.68</b>	-0.02	0.09
<i>Sphoeroides tyleri</i> (Shipp, 1974)	0.47	0.04	-0.32	-0.02					<b>-0.74</b>	0.18
<i>Symphurus plagusia</i> (Bloch & Schneider, 1801)	0.04	0.45	-0.23	0.35	<b>0.79</b>	-0.39	0.38	0.14		
<i>Symphurus tessellatus</i> (Quoy & Gaimard, 1824)	0.25	<b>0.56</b>	-0.44	0.25	<b>0.86</b>	-0.10	0.32	<b>0.73</b>	-0.09	<b>0.55</b>
<i>Synodus foetens</i> (Linnaeus, 1766)	<b>0.57</b>	0.17	-0.43	0.19	0.33	0.39	<b>0.62</b>	0.39	<b>-0.65</b>	0.14
<i>Trichiurus lepturus</i> (Linnaeus, 1758)	0.20	0.31	0.09	0.31	0.40	0.30	0.39	0.19	-0.16	<b>0.62</b>
<i>Trinectes paulistanus</i> (Ribeiro, 1915)	-0.30	0.42	0.20	0.45	<b>0.65</b>	-0.46	-0.14	0.22	0.34	0.26
% of explained variance	<b>16.4</b>	<b>12.7</b>	<b>20.5</b>	<b>12.6</b>	<b>29.8</b>	<b>17.4</b>	<b>24.1</b>	<b>12.0</b>	<b>24.7</b>	<b>10.9</b>

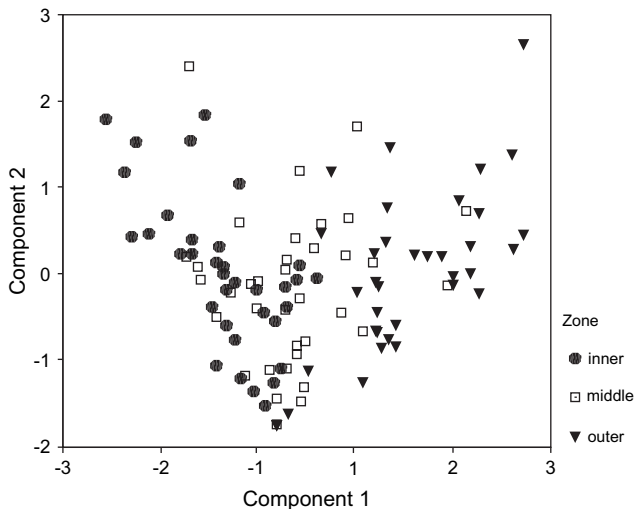


Fig. 2. Diagram for the first two principal components for samples of numerical abundance ( $\log x + 1$ ) of 30 species of fish, coded by zone, in Sepetiba Bay between October 1998 and September 1999. Zones:  $\blacktriangledown$  = outer zone,  $\square$  = middle zone,  $\bullet$  = inner zone.

a negative correlation with component 1, were abundant and frequent in the outer zone. *Cetengraulis edentulus*, *Chloroscombrus chrysurus*, *Citharichthys spilopterus*, *Diapterus rhombeus*, *Gerres gula* and *Harengula clupeiola* showed positive correlation with component 1 and were abundant in the inner zone (Table 4, Fig. 3). The species that showed positive correlations with component 2 were *Cathorops spixii*, *Cynoscion leiarchus*, *Genidens genidens*, and *Menticirrhus americanus*.

**3.2.2.2. Summer.** Component 1 explained 29.8% of the total variance, while component 2 explained 17.4%. The species that showed higher positive correlation with component 1 were *Cathorops spixii*, *Chloroscombrus chrysurus*, *Etropus crossotus*, *Gerres aprion*, *Micropogonias furnieri*, *Monacanthus ciliatus*, and *Prionotus punctatus* (Table 4, Fig. 3). The species that showed positive correlation with component 2 were *Orthopristis ruber* and *Diplectrum radiale*, while *Cetengraulis edentulus* showed negative correlation. No spatial gradient could be shown along component 1. The species that were significantly correlated with component 1 were not associated with any zone, while those associated with component

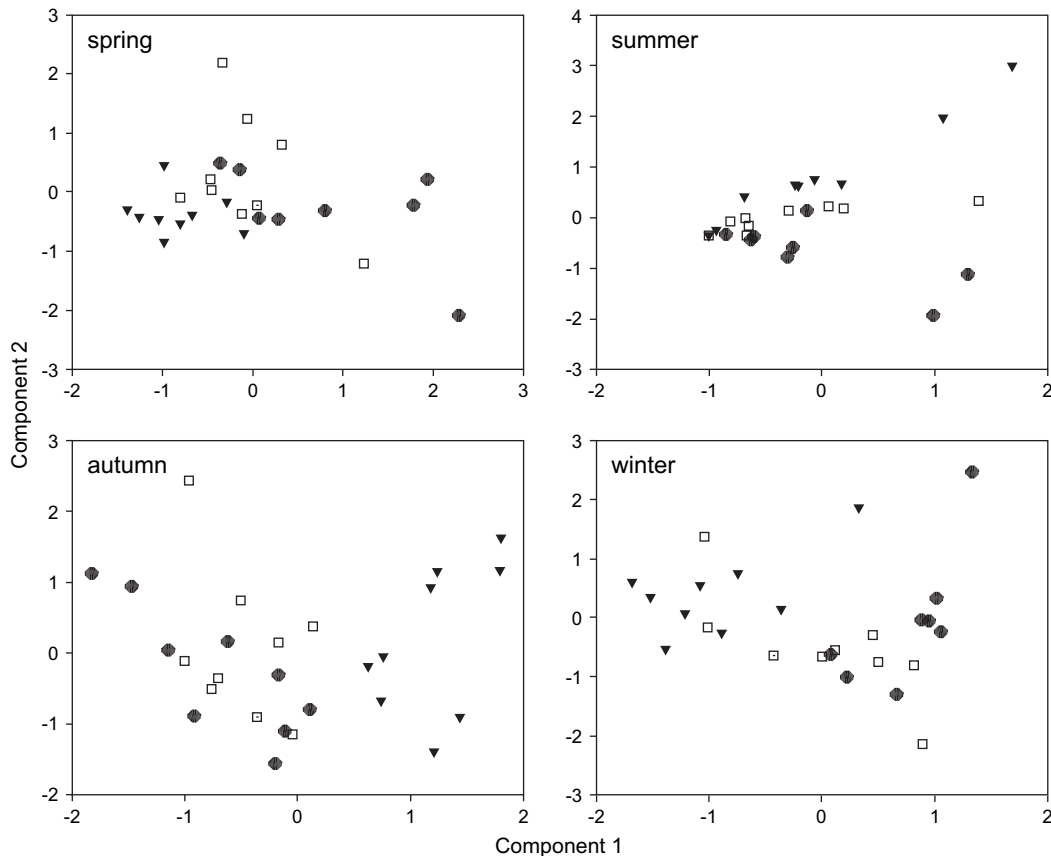


Fig. 3. Ordination diagrams for the first two principal components for samples of numerical abundance ( $\log x + 1$ ) of 30 fish species, by season, in Sepetiba Bay, 1998–1999. Zones:  $\blacktriangledown$  = outer zone,  $\square$  = middle zone,  $\bullet$  = inner zone.

2, such as *O. ruber*, *D. radiale* and *Ctenosciaena gracilicirrhus*, showed a spatial gradient along this component.

**3.2.2.3. Autumn.** Component 1 explained 24.1% of the total variance, while component 2 explained 12.0%. The species that showed positive correlation with component 1 were abundant and frequent in the outer zone (e.g., *Ctenosciaena gracilicirrhus*, *Orthopristis ruber*, *Diplectrum radiale*, and *Prionotus punctatus*). On the other hand, *Cetengraulis edentulus*, *Genidens genidens*, *Gerres gula*, and *Sciadeichthys luniscutis* showed negative correlation with component 1 and were abundant in the inner zone (Table 4, Fig. 3). Component 2 did not show any significant correlation with the fish species. A spatial pattern appeared, with samples of the outer zone distributed on the right side and those of the inner zone, on the left side of the diagram.

**3.2.2.4. Winter.** Component 1 explained 24.7% of the total variance, while component 2 explained 10.9%. A spatial pattern was observed along component 1, in which *Cathorops spixii*, *Chloroscombrus chrysurus*, *Cetengraulis edentulus* and *Micropogonias furnieri* showed a positive correlation with this component and were abundant in the inner zone. On the other hand, *Ctenosciaena gracilicirrhus*, *Orthopristis ruber*, *Diplectrum radiale*, *Etropus crossotus*, *Synodus foetens*, and *Prionotus punctatus* showed a negative correlation with

component 1 and were abundant in the outer zone. Component 2 only showed significant positive correlation with *Anchoa tri-color*, *Cynoscion leiarchus*, *Monacanthus ciliatus*, and *Trichiurus lepturus*.

The distribution of the fish assemblage in coordinate space was clearly different during summer compared with those in other seasons. No pattern of species distribution was shown in summer along component 1; in all other seasons, a clear pattern of species distribution throughout the zones appeared. These findings are consistent with results from the null models (Tables 2 and 3).

#### 4. Discussion

The fish assemblages in Sepetiba Bay seem to be composed of species that have different environmental requirements so that biotic interactions between species are non-existent when species–environment relationships are considered. Although unconstrained null models have suggested that biological forces could structure assemblages, as indicated by species that co-occurred less often than by chance, rejection of the null hypothesis does not identify the cause of the less-than-random associations among species. Furthermore, evidence of non-random patterns in species distribution does not necessarily imply the role of biotic interaction; it could be equally related to other factors such as similarities or differences in dispersal abilities or

environmental requirements of the species (Peres-Neto et al., 2001). The acceptance of the null hypothesis by environmentally constrained null models helped to distinguish among competing hypotheses and ecological requirements of species, by factoring out environmental influences. Thus, two species could have different habitat preferences and colonize different sites independently and not interact, in spite the formation of a perfect CU. This hypothesis may explain the pattern found in Sepetiba Bay, which shows an assemblage associated with the inner zone, and another associated with the outer zone, consistent with the results of Araújo et al. (2002). Gotelli et al. (1997) also suggested that models of low co-occurrence could be reflecting habitat segregation. In relation to the bay as a whole, habitat segregation may explain the co-occurrence pattern found, where the species presented a low overlap in relation to the use of the habitat and, consequently, local co-occurrence was less than that expected by chance.

Habitat segregation seems to be a mechanism that prevails in models of low co-occurrence. However, different processes can produce similar results. For example, allopatric speciation with subsequent interaction can generate effects equivalent to the competition hypothesis because it may lead to a pattern of little or no coexistence among congeners, whether or not there is competition occurring.

Alternatively, the findings of this work can be reflecting current or past competitive interaction because competition can cause modifications in the use of the habitat, through exploration of different resources. According to Wilbur and Travis (1984), different species may have evolved habitat preferences independently, and competition or predation may have driven habitat selection in the past. Ongoing competition or predation may be maintaining habitat segregation in the present. Also, habitat complexity may influence the ability of prey populations to survive predation pressure, and the absence of refuge areas for the prey can lead to local extinction. Thus, predators could affect the choice of habitat by the prey and could have displaced prey species toward other sites with less predation risk (e.g., where predators have access difficulty). This situation could be different from those where predators are not present. Regarding competition, many studies suggest that partition of resources among fish is a more common result of competitive interactions than of competitive exclusion (Ross, 1986; Jackson et al., 2001).

If the hypothesis that two different assemblages exist in the bay were true, with each assemblage associated with only one zone, the same basic patterns should be found when analyzing each of the four seasons separately. These patterns were not found for all seasons analyzed separately (Table 3, Fig. 3). The species assemblage presented a pattern of species co-occurrence different from those occurring purely by chance (null model) during spring, autumn, and winter, and this pattern was not found in summer by the unconstrained null models, although the acceptance of the null hypothesis was shown by environmentally constrained null models for all seasons.

Some speculations can be made about why the null model prevailed in summer in both approaches. The inner and outer assemblages may not have been associated with different abiotic

characteristics, driving the highest co-occurrence among the species. Results from the null model coincide with those from PCA, corroborating that summer presented a different pattern with the species not associated with the zones.

In summer, hydromedusas were abundant and could modify the patterns of co-occurrence of the fish species. Navas-Pereira (1980) also found high densities of hydromedusas in the Sepetiba Bay during summer. Alterations in the co-occurrence patterns can happen with the presence of invasive species as observed by Gotelli and Arnett (2000) in an assembly of ants in the United States. In the presence of an invasive species, the structure of the assemblage converged to random patterns, altering the low co-occurrence observed in the absence of such invasive species.

The most stressful conditions occur in summer, the result of high temperatures and relatively low dissolved oxygen in the waters. This situation can lead eventually to deterioration of water quality, most likely to occur in this season. The greater use of the area for tourism and other anthropogenic pressures can also contribute to the creation of “unstructured” fish assemblages in the various zones, resulting in high co-occurrence patterns by chance during this period of the year.

Movement throughout the study area by some species can also contribute to high co-occurrence of the species in the summer. According to Costa and Araújo (2002), juveniles of *Microponogonias furnieri*, a major abundant species in the bay, recruit in the sandy beach and shallows in the inner bay during the autumn, winter, and spring, then move to deeper areas in the summer, coinciding with highest temperatures. Araújo and Santos (1999) reported movements throughout the bay zones by members of the Gerreidae family, one of the most abundant groups of fish in Sepetiba Bay, also suggesting movement to deeper areas between spring and summer. Gomes et al. (2001) observed that marine catfishes migrate into and out of the bay during their reproductive period, which occurs between October and March. As usual, marine catfishes seek the lower reaches of the rivers and estuarine areas to spawn during spring/early summer (Figueiredo and Menezes, 1978; Moyle and Cech, 1988).

Considering the hypothesis of the existence of two assemblages, one in the outer zone and the other in the inner zone, with the middle zone acting as a transition, when we analyzed the zones separately, we were analyzing different fish assemblages. In this way, differences in habitat influence would not be considered in the results. When both null models (unconstrained and constrained) were applied, the null hypothesis was not rejected, indicating that the species are occurring randomly and independent of one another for each assemblage. The coexistence in high abundance of similar fishes in ecosystems where space or resources are usually limited could occur due to the development of strategies that allow spatial or temporal separation in the use of such environment. Pianka (1982) denominated as sympatric congeners the species that live in the same area and, in general, make use of different habitats or microhabitats or are active at different times. Indications of coexistence strategy were found for several species in Sepetiba Bay, such as marine catfish (Azevedo et al., 1998; Gomes et al., 2001), anchovies (Silva and Araújo, 1999), and mojarras

(Araújo and Santos, 1999). Changes in feeding habits over different stages of the life cycle, including differences in the diet and feeding activity, could reduce overlap in the use of the feeding resource, favoring the coexistence of a guild of fish benthivorous on sandy beaches (Zahorcsak et al., 2000). Castillo-Rivera and Kobelkowsky (2000) suggested that segregation patterns that allowed partition of resources between two species of Clupeidae explained the local coexistence of these species in a coastal lagoon in Mexico.

Overall, the partition of available resources as a coexistence strategy could explain the co-occurrence by chance of the fish inside each zone. Patterns of movement of fish among the three zones of the bay during summer may contribute to higher co-occurrence of the species in this period. The habitat segregation may explain the pattern of no or reduced co-occurrence of the species, evidencing, therefore, the presence of two assemblages of demersal fish having different environmental requirements and being associated with different abiotic characteristics of Sepetiba Bay.

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