



Demersal fishes in a tropical bay in southeastern Brazil: Partitioning the spatial, temporal and environmental components of ecological variation

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Abstract

This study analyzed the factors structuring demersal fish community in a tropical bay in southeastern Brazil. The results were used to quantify the partitioning of ecological variation among the environmental, spatial and temporal components molding the fish community. Three bay zones (inner, middle and outer) were defined according to depth and salinity gradient. Monthly samplings were conducted by bottom trawl tows during daylight hours, between October 1998 and September 1999. In each zone, three replicate samples were taken. Ninety-three fish species from 73 genera and 37 families were recorded in the 108 samples. Two demersal fish assemblages were evidenced, one in the inner and the other in the outer zone. These assemblages were characterized by changes in species composition and relative abundance. Depth, followed by transparency and salinity, influenced spatial pattern of fish assemblages. The largest part of the explained variation occurred as a result of the spatial structure of environmental variables, which means that both species and environmental variables presented similar spatial structure. The spatial effect, not the seasonal, explained the highest part of species variations. The amount of unexplained variation was relatively high (76%), even assuming that part of it is due to nondeterministic fluctuation, which could be due to local effects of unmeasured (biotic and abiotic) controlling variables. Knowing the relative importance of these factors can be of decisive importance when applying casual hypotheses in the framework of some precise ecological theory and should facilitate management, planning, and usage of bay resources.

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1. Introduction

Many mechanisms may influence the distribution of fish within coastal marine systems. Several investigators have suggested that biotic processes may be influential in driving

the spatial and temporal patterns of occurrence in fish (Ogburn-Matthews and Allen, 1993; Rueda, 2001; Rueda and Deleo, 2001). In addition, a myriad of abiotic factors have been associated with the structure of these assemblage communities, with well-defined boundaries corresponding to discontinuity in the environment, while the opposite situation corresponds to a continuum along the environmental gradient (Akin et al., 2003; Martino and Able, 2003). In many surveys, it is often not clear what environmental factors and

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interactions were most important in determining patterns of fish distribution and community structure because controlling factors are usually complex, obscuring patterns, scales of variability, and the interpretation of causal effects (Jung and Houde, 2003).

Two classic models explaining the observed patterns in biological communities are found in the literature. In the environmental control model, environmental variables are deemed responsible for the observed variations in the presence or abundance of the species; whereas in the biotic control model, the links among organisms, horizontal (competition) or vertical (predation), are considered to be the primary factors structuring communities (May, 1984). Some authors believe that fish communities seem to be dominated by species that respond primarily to a given mechanism (Grossman et al., 1982; Rahel et al., 1984), although they recognize that it would be simplistic to suggest that assemblages are regulated by a process type only. Others consider it a mistake to model the observed variations in patterns and processes of the communities in terms of one cause only (Jackson et al., 2001). Although these two models of community structure can represent fundamental philosophical differences regarding the nature of their organization, the crucial empiric problem is to relate identifiable causal factors to the number of species or relative abundances in fish assemblage (Wootton, 1991). Recently, it has been recognized that the observed patterns in species occurrence or abundance can be caused by a variety of ecological processes as well as evolutionary and geographical circumstances; this means recognizing connections between local habitat and historical events, and between the present moment and the long history of life on earth (Schluter and Ricklefs, 1993). Multivariate statistical methods used to quantify the spatial structure of abiotic and biotic variables can show patterns only, which can be evidence of those several processes that are being generated, or represent a synthesis of the indirect descriptors that are acting on fish assemblages.

There are several different approaches in the description of fish assemblages and their explanatory factors. Some studies focus on environmental influences on the assemblage structure (Thiel et al., 1995; Lara and González, 1998; Marshall and Elliott, 1998; Araújo et al., 2002); others describe seasonal (Maes et al., 1998) and spatial patterns only (Araújo et al., 1997, 1998) without determining an effective cause. In a more detailed view, some other studies tested the hypotheses of the importance of biotic, abiotic and spatial factors (Jackson et al., 2001; Laegdsgaard and Johnson, 2001), and local, regional and historical influences (Jackson and Harvey, 1989; Oberdorff et al., 1997) structuring fish community. While it is possible to obtain measures of some abiotic descriptors of the sites, biotic interactions such as predation and competition, or historical events such as natural catastrophes or human alterations cannot be directly measured. However, due to the diversity and frequently unknown nature of the causes, it is very difficult to evaluate their relative contributions (Borcard and Legendre, 1994; Méot et al., 1998). Anderson and Gribble (1998) studied the temporally structured variation and its overlap with the environmental and spatial components. Borcard

et al. (1992) proposed a method to partition the variation of species abundance data into independent components: pure spatial, pure environmental, spatial component of environmental influence and undetermined. Some assumed relationships between species occurrence and environmental variables can be spurious, implying a common spatial gradient, while others are real. Identifying explanatory variables that are independent can be very useful for a detailed understanding of more local ecological structures. In this scope, the availability of a set of standardized data on fish collections in Sepetiba Bay is a good opportunity to test such models in a tropical area.

Sepetiba Bay is located in the state of Rio de Janeiro in southeastern Brazil. It is connected to the sea through a wide mouth at its west end and a narrow channel at the east, with a sandbank forming the southern limit and the continental margin at the north. Because most human activities in the drainage basin of the 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 on fish assemblage structure. Several marine fishes enter and leave the bay for nursery, reproductive, and feeding purposes (Araújo et al., 2002). Azevedo et al. (2006) reported that habitat segregation in the Sepetiba Bay during most seasons (except summer) explains the pattern of reduced co-occurrence, indicating the presence of two fish assemblages associated with different environmental characteristics. The objective of this work is to explain further these patterns and to try to separate the effects of the several factors and their different forces, thus allowing us to partition the relative importance of the environmental, spatial and temporal components that shape the demersal fish community in Sepetiba Bay.

We partition the total variance of species data in terms of: (1) nonspatial environmental/temporal variation; (2) spatially structured environmental/temporal data; and (3) spatial species variation that is not shared by the environmental/temporal variables. This would be an alternative concept for understanding ecological patterns in terms of the relative contribution of each factor, because it quantifies more precisely the partitioning of the variation among its spatial, temporal and environmental components.

2. Methods

2.1. Study area and survey program

Sepetiba Bay (Fig. 1) is a sedimentary embayment on the coast of Rio de Janeiro State (22°54'–23°04'S; 43°34'–44°10'W) in southeastern Brazil. It was shaped by an extensive process of sand deposition, which formed a barrier beach at its southern end. It ends in a wide confluence with the Atlantic Ocean at its western boundary. The bay has a surface area of approximately 450 km², a mean depth of 8.6 m, a maximum depth of 30 m, and has a continental drainage area of 2700 km² (Fonseca, 1978). The annual rainfall ranges from

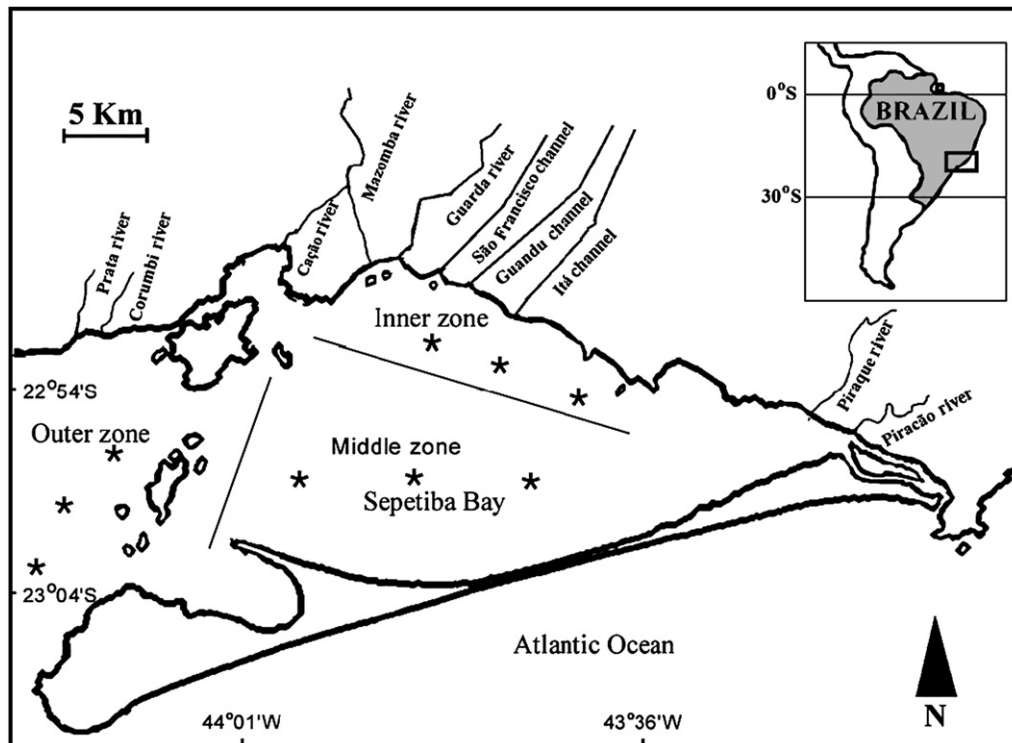


Fig. 1. Map of the study area showing the three zones (outer, middle and inner) and sampling sites (*) in Sepetiba Bay, Brazil.

1000 to 2100 mm (Barbière and Kronemberger, 1994), but this does not influence the bay's salinity much due to the relatively small tributaries. Most of the substrate in the inner bay is silt and mud. The tidal range is approximately 1 m. Predominant northeasterly and southwesterly winds activate thermal currents between the bay and the ocean.

The bay can be divided into three zones (inner, middle and outer) according to environmental characteristics. The inner zone is influenced by discharges from perennial small rivers that contribute to decreased water quality; substrate is mainly muddy, with depths mostly less than 5 m and salinity averaging 28 ppt (Araújo et al., 2002). The outer zone, near to the sea, presents the opposite environmental conditions: substrate mainly sandy, with comparatively lower temperature, and higher salinity and transparency; maximum depth in the outer zone is approximately 28 m, and salinity average is 33 ppt (Pessanha and Araújo, 2003). Furthermore, several islands in the west part of the bay bound the outer zone. The middle zone presents intermediate environmental conditions between the inner and outer zones (Fig. 1).

Monthly samplings were 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. Bottom trawl tows against the current were conducted with 20-min durations at the bottom, at a towing speed of approximately 2.5 knot and a distance of 1500 m; this defines the unit effort. Each trawl followed a given depth contour to minimize the impact of any depth change during a trawl.

The trawl was conducted with an 8-m head line, an 11-m ground rope, a 2.5-cm stretched mesh, and a 1.2-cm mesh cod-end liner. The bottom depth in the trawled areas ranged from 3 to 25 m. Immediately after each haul for fish collection, water near the bottom was collected using a Van Dorn bottle, and hydrographic data, including temperature, salinity and dissolved oxygen, were taken. Transparency was recorded using a Secchi disk, while depth was determined with an echo sounder.

2.2. Data analysis

Average values of the environmental and fish abundance variables were compared among the different zones and seasons using the nonparametric Kruskal–Wallis test at 95% confidence level ($p < 0.05$). This was followed by the Mann–Whitney test to compare each pair of groups every time the null hypothesis was rejected. Canonical correspondence analysis (CCA) was used to visualize and describe the relationship between fish species and environmental variables (CANOCO Software, Version 4.0, 1998). This ordination method is a powerful multivariate technique to assess how multiple species respond simultaneously to environmental factors, and is designed to extract synthetic environmental gradients from ecological data sets (ter Braak, 1991). Following the recommendation of Clifford and Stevenson (1975), only the most commonly occurring species (>0.1% of abundance) were included in the analysis. The CCA constrains the axes in classical correspondence analysis (CA) to become linear functions of environmental factors. The gradients become

the basis for succinctly describing species-differential habitat preference via ordination diagrams (ter Braak and Verdondchot, 1995). Species and sample sites were marked with points representing their mean distribution. A Monte Carlo permutation test (forward selection) was used for selection of the environmental variables, which independently and significantly explain variations in the species data. The explanatory variables were tested by linear correlation coefficient to ascertain whether there was any correlation among them (collinearity) and were represented by vectors pointing towards the maximum change in the value of the associated variable. The length is equal to the multiple correlation of the variable with the displayed ordination axes. Principal component analysis (PCA) was used to explore spatial and seasonal patterns of the environmental data and to describe their relationship. PCA arranges samples along gradients, creating a low-dimensional map (an ordination). Samples that occur in close proximity can be considered to have similar environmental variables. Samples that occur on the same dimension define gradients in the data. The eigenvalues are a measure of the amount of variance explained by each PCA dimension. Environmental and fish data were $\log_{10}(x+1)$ transformed to minimize the differences in the scales of the measured variables and to reduce the weighting of abundant species, respectively.

The total variation of the species data set was partitioned into independent components (purely spatial, purely environmental, spatial component with environmental influence, and uncertain component) following the method of Borcard et al. (1992). The spatial matrix was composed of three binary descriptive variables corresponding to the three zones (outer, middle and inner) that would represent the space component. Value 1 was attributed to the variable “outer zone” when samplings were carried out in that zone, otherwise a zero value was assigned to it. A similar procedure was followed for the middle and the inner zones, with each zone assuming value 1 when samples were taken from it, and a zero value when samples were taken from other zones.

By making canonical ordinations constrained by one of the sets of exploratory variables (environmental and spatial data), we were able to measure the significance of the effects of environmental conditions and spatial structure on species data. After performing this procedure, a measurement of the interaction of the two groups of variables was obtained. Certain species can show common spatial variation though not necessarily a causal relationship or, more precisely, they can have a high co-variation. To evaluate this variation, we used the following partial CCA that excluded the effect of one data matrix: (1) CCA of the species matrix constrained by the environmental matrix; (2) CCA of the species matrix constrained by the spatial matrix; (3) CCA of the species matrix constrained by the environmental matrix but removing the effect of the spatial matrix; and (4) CCA of the species matrix constrained by the spatial matrix but removing the effect of the environmental matrix. With these four constraints of ordination and three data matrices, it was possible to deconstruct the community variation into the following parts:

- A – The nonspatial environmental variation in the species data, which is the fraction of the species variation that can be explained by the environmental descriptors independently of any spatial structure.
- B – The spatial structuring in the species data that is shared by the environmental data (This common variation is partly a consequence of the relations of the species with spatially structured environmental conditions, but a certain amount of it could be noncausal, that is, due to separate relations of both sets of variables with some external space-structuring processes.).
- C – The spatial patterns in the species data that are not shared by the environmental data (In general terms, these patterns may reflect some contingent biological processes like predation, food seeking or competition, that are not dependent on environmental components or, more precisely, without any relation to the environmental variables that were actually included in the analysis.).
- D – The fraction of the species variation explained neither by spatial nor by environmental data, or, the unexplained variations and stochastic fluctuations.

A similar procedure was undertaken to analyze the abundance of the assemblage in relation to seasons. A temporal matrix composed of four binary descriptive variables corresponding to the four seasons (spring, summer, autumn and winter) was used to represent the time. The variable associated with spring assumed value 1 when the samplings were carried out in that season; otherwise, a zero value was assigned to it. A similar procedure was followed for the other seasons, with each variable assuming value 1 when samples were taken during its corresponding season.

Similarly for the environmental \times spatial approach, another series of CCA procedures were performed to analyze the abundance of the assemblage in relation to seasonal (temporal) and spatial variability. Instead of the environmental matrix, a temporal matrix was used.

3. Results

3.1. Environmental variables

Depth and transparency presented highly significant differences ($p < 0.01$) among the zones, but no significant difference was found among seasons (Table 1). The mean depth ranged from 3.05 m in the inner zone to 21.6 m in the outer zone; mean transparency ranged from 1.15 m in the inner zone to 4.08 m in the outer zone. Temperature also differed significantly among zones ($p < 0.05$) and showed highly significant differences among seasons ($p < 0.01$), ranging from 21.7 °C in winter in the outer zone, to 26.9 °C in summer in the inner zone. Dissolved oxygen showed highly significant differences among zones ($p < 0.01$) and significant differences among seasons ($p < 0.05$), ranging from 5.5 mg l⁻¹ in winter in the outer zone, to 3.2 mg l⁻¹ in summer in the inner zone. Salinity showed highly significant differences ($p < 0.01$) among zones and seasons, with averages ranging from 29.1 in

Table 1

Results of the nonparametric Kruskal–Wallis (H) test and a posteriori Mann–Whitney (U) test for comparisons of environmental variables between zones and seasons in Sepetiba Bay, 1998/1999. n.s., Not significant; **highly significant ($p < 0.01$); *significant ($p < 0.05$). Zones: O, outer zone; M, middle zone; I, inner zone. Seasons: SP, spring; SU, summer; AU, autumn; WI, winter

	Zone		Season	
	H	U	H	U
Depth	72.0**	O > M > I	n.s.	–
Transparency	42.2**	O > M > I	n.s.	–
Salinity	35.0**	O > M > I	8.5**	SU > WI
Temperature	8.6*	I > O	37.2**	SU > SP, AU, WI
Dissolved oxygen	13.5**	O > I	7.3*	WI > SP, SU, AU

winter in the inner zone to 34.8 in summer in the outer zone. Thus, a spatial pattern was observed for each one of the examined environmental variables, while only a seasonal pattern was found for temperature, salinity and dissolved oxygen.

The first two components from the ordination of the environmental variables showed eigenvalues exceeding 1.0 and explaining 71.8% of the total variance (Table 2). Component 1 explained 49.8% of the total variance, while Component 2 explained 21.9%. Negative significant correlation was found between Component 1 and depth, transparency and salinity, while Component 2 showed significant positive correlation with temperature and negative correlation with dissolved oxygen.

The ordination diagram of Components 1 and 2, with samples coded by zones (Fig. 2), showed a spatial pattern for Component 1, with samples of the highest depth, transparency and salinity located on the left side, while samples of the opposite situation were shown on the right side of the diagram.

When coded by seasons, no temporal variation was shown for Component 1 (Fig. 3). However, samples from summer were distributed in the upper part of the diagram, while samples from winter were located in the lower part of the diagram, suggesting a temporal variation for Component 2. Temperature and dissolved oxygen were highly correlated to Component 2, with inverse correlation between these two environmental variables (Table 2). Component 1, therefore, can be associated with spatial gradient, while Component 2 with temporal variability.

3.2. Fish assemblages

Ninety-three fish species were recorded in the 108 bottom trawl samples, corresponding to 20,483 individuals, weighing

Table 2

Principal component loadings for environmental variables in Sepetiba Bay, 1998/1999. Values in boldface are highly significant ($p < 0.01$)

	Component I	Component II
Depth	-0.94	0.05
Transparency	-0.89	0.16
Temperature	0.28	0.70
Salinity	-0.79	0.32
Dissolved oxygen	-0.35	-0.69
Eigenvalues	2.5	1.1
Variance (%)	49.9	22.0

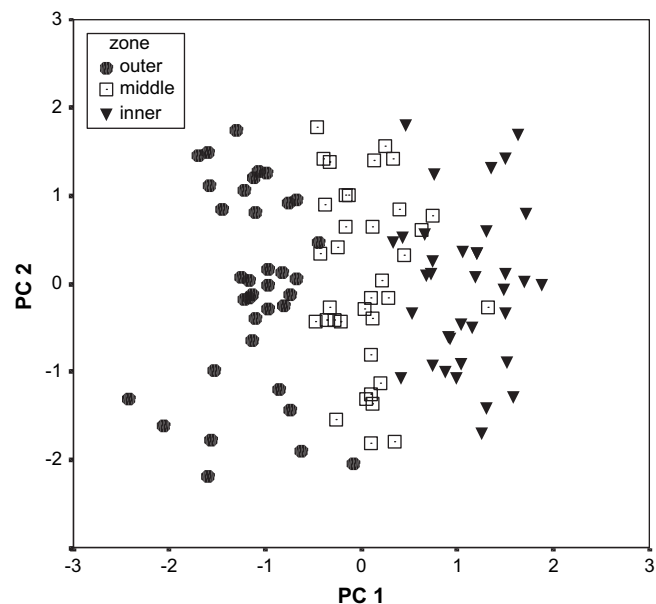


Fig. 2. Ordination diagram of the first two principal component analyses of environmental variables with samples coded by zones in Sepetiba Bay, 1998/1999.

653473.6 g, and comprising 73 genera and 37 families (Table 3). The 30 most numerous species were considered in the analyses, since they were more likely to evince structural pattern in the fish assemblage.

Dominant fish species showed average sizes ranging from 6.48 to 36.94 cm, being predominantly juveniles and subadults (Table 4). Species composition varied spatially, with the most abundant species shifting in rank depending on the zone. *Micropogonias furnieri*, *Cetengraulis edentulus*, *Diapterus*

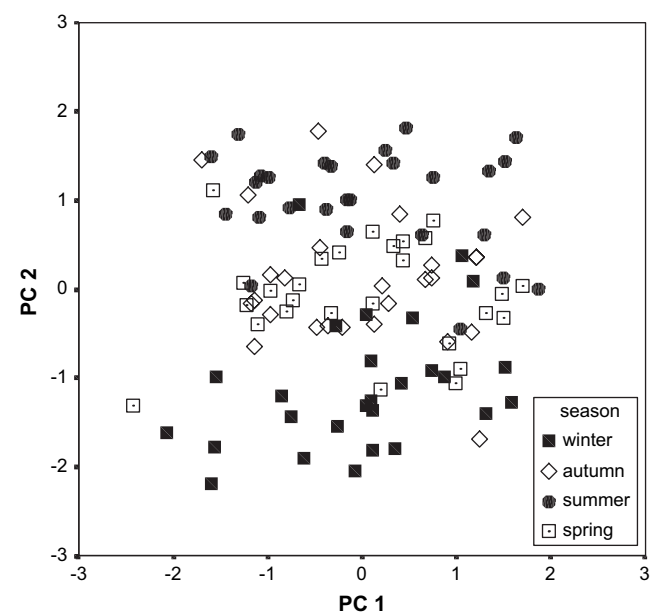


Fig. 3. Ordination diagram of the first two principal component analyses of environmental variables with samples coded by seasons in Sepetiba Bay, 1998/1999.

Table 3
List of the 93 fish species in Sepetiba Bay, 1998/1999. The 30 most abundant species included in the analyses, which contributed to >1% of total fish number data in bold. Families are ordered according to Nelson (1994)

Family	Code	Species
Rhinopteridae	RHIBON	<i>Rhinoptera bonasus</i> (Mitchill, 1815)
Rhinobatidae	RHIPER	<i>Rhinobatos percellens</i> (Walbaum, 1792)
Dasyatidae	DASGUT	<i>Dasyatis guttata</i> (Block and Schneider, 1801)
	DASAME	<i>Dasyatis americana</i> (Hildebrand and Schroeder, 1928)
Gymnuridae	GYMALT	<i>Gymnura altavela</i> (Linnaeus, 1758)
Elopidae	ELOSAU	<i>Elops saurus</i> (Linnaeus, 1766)
Muraenidae	GYMOCE	<i>Gymnothorax ocellatus</i> (Agassiz, 1831)
Clupeidae	HARCLU	<i>Harengula clupeola</i> (Cuvier, 1829)
	SARBRA	<i>Sardinella brasiliensis</i> (Steindachner, 1789)
	OPIOGL	<i>Opisthonema oglinum</i> (Lesueur, 1818)
	CHIBLE	<i>Chirocentodon bleekermanus</i> (Poey, 1867)
	PELHAR	<i>Pellona harroweri</i> (Fowler, 1917)
Engraulidae	CETEDE	<i>Cetengraulis edentulus</i> (Cuvier, 1828)
	ANCTRI	<i>Anchoa tricolor</i> (Agassiz, 1829)
	ANCJAN	<i>Anchoa januaria</i> (Steindachner, 1879)
	ANCLYO	<i>Anchoa lyolepis</i> (Evermann and Marsh, 1902)
	ANCCLU	<i>Anchoa clupeoides</i> (Swainson, 1839)
Ariidae	GENGEN	<i>Genidens genidens</i> (Valenciennes, 1839)
	SCILUN	<i>Sciadeichthys luniscutis</i> (Valenciennes, 1840)
	CATSPI	<i>Cathorops pixii</i> (Agassiz, 1829)
	NETBAR	<i>Netuma barba</i> (Lacépède, 1803)
Synodontidae	SYNFOE	<i>Synodus foetens</i> (Linnaeus, 1766)
Batrachoididae	PORPOR	<i>Porichthys porosissimus</i> (Valenciennes, 1837)
Antennariidae	HISHIS	<i>Histrio histrio</i> (Linnaeus, 1758)
	PHRSCA	<i>Phrynelox scaber</i> (Cuvier, 1817)
Atherinidae	ATHBRA	<i>Atherinella brasiliensis</i> (Quoy and Gaimard, 1824)
Scorpaenidae	SCOIST	<i>Scorpaena isthmensis</i> (Meek and Hildebrand, 1928)
Triglidae	PRIPUN	<i>Prionotus punctatus</i> (Block, 1797)
Dactylopteridae	DACVOL	<i>Dactylopterus volitans</i> (Linnaeus, 1758)
Centropomidae	CETUND	<i>Centropomus undecimalis</i> (Bloch, 1792)
Serranidae	DIPRAD	<i>Diplectrum radiale</i> (Quoy and Gaimard)
	DIPFOR	<i>Diplectrum formosum</i> (Linnaeus, 1766)
	DULAU	<i>Dules auriga</i> (Cuvier, 1829)
Carangidae	SELSET	<i>Selene setapinnis</i> (Mitchill, 1815)
	SELVOM	<i>Selene vomer</i> (Linnaeus, 1758)
	CHLCHR	<i>Chloroscombrus chrysurus</i> (Linnaeus, 1766)
	SELCRU	<i>Selar crumenophthalmus</i> (Bloch, 1793)
	OLIPAL	<i>Oligoplites palometa</i> (Cuvier, 1833)
	OLISAU	<i>Oligoplites saurus</i> (Bloch and Schneider, 1801)
	HEMAMB	<i>Hemicaranx amblyrhynchus</i> (Cuvier, 1833)
	PARSIG	<i>Parona signata</i> (Jenyns, 1842)
	CARHIP	<i>Caranx hippos</i> (Linnaeus, 1766)
	TRALAT	<i>Trachurus lathami</i> (Nichols, 1920)
Gerreidae	GERAPR	<i>Gerres aprion</i> (Baird and Girard, 1854)
	GERGUL	<i>Gerres gula</i> (Cuvier, 1830)
	DIARHO	<i>Diapterus rhombeus</i> (Cuvier, 1829)
	EUGBRA	<i>Eugerres brasiliensis</i> (Cuvier, 1830)
Haemulidae	ORTRUB	<i>Orthopristis ruber</i> (Cuvier, 1830)
	HAESTE	<i>Haemulon steindachneri</i> (Jordan and Gilbert, 1882)
	POMCOR	<i>Pomadasys corvinaeformis</i> (Steindachner, 1868)
	POMCRO	<i>Pomadasys croco</i> (Cuvier, 1830)
Sparidae	ARCRHO	<i>Archosargus rhomboidalis</i> (Linnaeus, 1758)
Sciaenidae	MICFUR	<i>Micropogonias furnieri</i> (Desmarest, 1823)
	CTEGRA	<i>Ctenosciaena gracilicirrus</i> (Metzelaar, 1919)
	MENAME	<i>Menticirrhus americanus</i> (Linnaeus, 1758)
	CYNLEI	<i>Cynoscion leiarchus</i> (Cuvier, 1830)
	CYNJAM	<i>Cynoscion jamaicensis</i> (Vaillant and Bocourt, 1883)
	CYNMIC	<i>Cynoscion microlepidotus</i> (Cuvier, 1830)
	ISOPAR	<i>Isopisthus parvipinnis</i> (Cuvier, 1830)
	BAIRON	<i>Bairdiella ronchus</i> (Cuvier, 1830)
	LARBRE	<i>Larimus breviceps</i> (Cuvier, 1830)
	PARBRA	<i>Paralonchurus brasiliensis</i> (Steindachner, 1875)
	STESTE	<i>Stellifer stellifer</i> (Bloch, 1790)

Table 3 (continued)

Family	Code	Species
Mullidae	UPEPAR	<i>Upeneus parvus</i> (Poey, 1853)
	MULARG	<i>Mullus argentinae</i> (Hubbs and Marini, 1935)
Ephippidae	CHAFAB	<i>Chaetodipterus faber</i> (Broussonet, 1782)
Mugilidae	MUGLIZ	<i>Mugil liza</i> (Valenciennes, 1836)
Sphyraenidae	SPHGUA	<i>Sphyraena guachancho</i> (Cuvier, 1829)
	SPHTOM	<i>Sphyraena tome</i> (Fowler, 1903)
Gobiidae	GOBOCE	<i>Gobionellus oceanicus</i> (Pallas, 1770)
Trichiuridae	TRILEP	<i>Trichiurus lepturus</i> (Linnaeus, 1758)
Stromateidae	PREPAR	<i>Peprilus paru</i> (Linnaeus, 1758)
Bothidae	BOTROB	<i>Bothus robinsi</i> (Topp and Hoff, 1972)
Paralichthyidae	ETRCRO	<i>Etropus crossotus</i> (Jordan and Gilbert, 1882)
	ETRLON	<i>Etropus longimanus</i> (Norman, 1933)
	CITSPI	<i>Citharichthys spilopterus</i> (Günther, 1862)
	CITARE	<i>Citharichthys arenaceus</i> (Evermann and Marsh, 1902)
	CITMAC	<i>Citharichthys macrops</i> (Dresel, 1889)
	SYAPAP	<i>Syacium papillosum</i> (Linnaeus, 1758)
	PARBRA	<i>Paralichthys brasiliensis</i> (Ranzani, 1840)
	PARORB	<i>Paralichthys orbignyanus</i> (Valenciennes, 1839)
	PARPAT	<i>Paralichthys patagonicus</i> (Jordan, 1889)
	Achiridae	ACHLIN
Cynoglossidae	TRIPAU	<i>Trinectes paulistanus</i> (Ribeiro, 1915)
	SYMTES	<i>Symphurus tessellatus</i> (Quoy and Gaimard, 1824)
	SYMPLA	<i>Symphurus plagusia</i> (Bloch and Schneider, 1801)
Monacanthidae	SYMDIO	<i>Symphurus diomedianus</i> (Goode and Bean, 1885)
	MONCIL	<i>Monacanthus ciliatus</i> (Mitchill, 1818)
Tetraodontidae	SPHTYL	<i>Sphoeroides tyleri</i> (Shipp, 1974)
	SPHTES	<i>Sphoeroides testudineus</i> (Linnaeus, 1758)
	SPHGRE	<i>Sphoeroides greeleyi</i> (Gilbert, 1900)
	LAGLAE	<i>Lagocephalus laevigatus</i> (Linnaeus, 1766)
Diodontidae	CYCSPi	<i>Cyclichthys spinosus</i> (Linnaeus, 1758)

rhombeus and *Trinectes paulistanus* were more numerically abundant in the inner zone than in the middle and outer zones, while *Diplectrum radiale*, *Trichiurus lepturus*, *Orthopristis ruber*, *Ctenosciaena gracilicirrhus* and *Haemulon steindachneri* were more abundant in the outer zone than in the middle and inner zones. *Genidens genidens*, *Chloroscombrus chrysurus* and *Cathorops spixii* predominated in the inner and middle zones, *Sphoeroides tyleri* and *Citharichthys spilopterus* predominated in the inner zone only, while *Prionotus punctatus* and *Synodus foetens* predominated in the outer and middle zones and *Etropus crossotus* in the outer zone only. The remaining species did not show significant differences among the three zones (Table 4).

Using the Monte Carlo (forward selection) permutation test, we selected the explanatory variables of depth, temperature and transparency at the significance level of 99% ($p < 0.01$), and of salinity at the significance level of 95% ($p < 0.05$). Dissolved oxygen was close to the level of significance ($p = 0.06$) and thus was included in the analyses.

The correlation coefficients between the environmental variables and the ordination axes (interset correlation) reflect the relative importance of each environmental variable in determining the composition of the fish community. Thus, Axis 1 corresponds to the depth, transparency and salinity gradient, while Axis 2 corresponds to temperature gradient. The species–environment correlation was 0.86 for Axis 1 and 0.70 for Axis 2 (Table 5).

The ordination diagram from the first two axes, with samples coded by zones, showed a clear change in the structure of the fish assemblage from inner to outer zone. Axis 1 explained 63.4% of the species–environment variation (Table 5), coinciding with depth, transparency and salinity gradients (Fig. 4). It separated outer zone samples, characterized by higher depth, transparency and salinity, on the right side, in opposition to inner zone samples, characterized by the lowest values of these variables, on the left side. Samples from the middle zone were located in the central part of the diagram; these samples were characterized by intermediate values of those same environmental variables, although their values were slightly closer to those of the inner zone samples (Fig. 4). Species associated with Axis 1, located on the left side of the diagram, were *Cetengraulis edentulus*, *Trinectes paulistanus*, *Harengula clupeiola*, *Sciadeichthys luniscutis*, *Chloroscombrus chrysurus* and *Gerres gula*; while species associated to Axis 1, located on the right, were *Synodus foetens*, *Trichiurus lepturus*, *Diplectrum radiale*, *Orthopristis ruber*, *Haemulon steindachneri* and *Ctenosciaena gracilicirrhus*.

Axis 2 explained 17.5% of the species–environment variation (Table 5), and was mainly a temporal (temperature) gradient, with samples from summer located on the lower part of the diagram, and samples from winter in the upper part (Fig. 5). The highest temperature values corresponded to the samples from the inner zone, in opposition to samples from the outer zone. Species closely related to Axis 2 associated

Table 4
Mean size (and range) and results of Kruskal–Wallis and a posteriori Mann–Whitney tests for comparisons of average numerical abundance among zones for 30 of the 93 fish species in Sepetiba Bay, Brazil, 1998/1999. $X \pm SE$ = mean and standard error (SE) of catch per unit of effort (CPUE). Zones: O, outer zone; M, middle zone; I, inner zone. Species are coded according to Table 3

Species code	Total length, TL (Min–Max)	Outer zone, $X \pm SE$	Middle zone, $X \pm SE$	Inner zone, $X \pm SE$	Significant differences
MICFUR	14.8 (2.3–43.0)	3.72 ± 0.80	6.89 ± 1.22	45.78 ± 8.77	I > O, M
CETEDE	15.6 (9.3–19.6)	0.03 ± 0.02	0.36 ± 0.10	43.06 ± 11.45	I > O, M
GENGEN	17.2 (4.2–37.5)	2.67 ± 0.68	29.14 ± 7.41	33.67 ± 10.08	I, M > O
CHLCHR	11.7 (3.2–23.5)	1.78 ± 0.44	25.92 ± 6.97	20.08 ± 3.82	I, M > O
DIARHO	12.9 (5.5–22.0)	5.28 ± 1.20	15.03 ± 6.23	16.19 ± 4.65	I > M, O
SPHTES	15.8 (5.8–26.2)	0.36 ± 0.09	0.94 ± 0.14	15.79 ± 0.46	–
GERAPR	11.4 (4.8–20.1)	12.83 ± 2.18	16.03 ± 2.36	11.06 ± 2.36	–
SPHTYL	6.5 (3.8–10.2)	0.28 ± 0.10	0.03 ± 0.02	6.48 ± 0.12	I > O
SCILUN	17.0 (6.1–39.4)	0.61 ± 0.18	6.97 ± 1.92	6.25 ± 1.18	–
TRIPAU	12.6 (8.7–18.7)	0.03 ± 0.02	0.25 ± 0.13	6.14 ± 2.03	I > M, O
ETRCRO	10.9 (4.8–16.8)	16.19 ± 2.04	5.31 ± 0.68	3.75 ± 0.95	O > I
PRIPUN	10.5 (3.3–29.0)	23.78 ± 3.46	15.58 ± 2.87	2.81 ± 0.41	O, M > I
GERGUL	12.1 (7.8–18.2)	0.53 ± 0.14	5.50 ± 1.34	2.53 ± 0.55	M > O
CITSPI	11.9 (6.4–19.5)	1.44 ± 0.49	1.83 ± 0.32	2.44 ± 0.28	I > O
CATSPI	16.8 (3.3–30.2)	0.03 ± 0.02	2.64 ± 1.09	2.39 ± 0.59	I, M > O
ANCTRI	9.9 (0.8–11.6)	2.94 ± 1.18	0.11 ± 0.03	2.03 ± 0.58	–
SYMTEs	15.3 (10.4–20.4)	3.56 ± 0.60	1.69 ± 0.29	2.03 ± 0.29	–
HARCLU	18.7 (13.0–23.5)	0.08 ± 0.05	0.36 ± 0.12	1.61 ± 0.51	–
SELSET	7.8 (3.4–16.0)	68.61 ± 27.43	0.14 ± 0.05	1.33 ± 0.36	–
MENAME	16.4 (8.4–26.3)	1.25 ± 0.22	0.50 ± 0.08	1.31 ± 0.20	–
CYNLEI	13.3 (4.7–30.0)	0.89 ± 0.27	0.31 ± 0.09	1.08 ± 0.26	–
MONCIL	7.8 (3.6–21.2)	0.50 ± 0.08	0.83 ± 0.25	0.86 ± 0.15	–
SYMPLA	17.7 (17.3–18.1)	0.61 ± 0.15	0.56 ± 0.15	0.58 ± 0.19	–
ARCRHO	27.5 (13.0–37.5)	0.14 ± 0.04	0.08 ± 0.04	0.53 ± 0.22	–
DIPRAD	14.4 (5.9–24.0)	9.69 ± 0.74	2.50 ± 0.30	0.53 ± 0.10	O > M, I
TRILEP	36.9 (12.0–105.0)	3.56 ± 1.24	0.28 ± 0.07	0.39 ± 0.09	O > M, I
ORTRUB	19.9 (6.0–29.0)	22.47 ± 2.69	1.44 ± 0.30	0.14 ± 0.03	O > M, I
SYNFOE	17.8 (6.9–27.5)	1.92 ± 0.35	2.64 ± 0.55	0.03 ± 0.02	O, M > I
CTEGRA	8.8 (4.1–14.0)	6.92 ± 1.15	0.25 ± 0.06	0.00 ± 0.00	O > M, I
HAESTE	14.4 (2.5–20.2)	0.94 ± 0.22	0.00 ± 0.00	0.00 ± 0.00	O > M, I

with the highest temperature were *Selene setapinnis*, *Archosargus rhomboidalis* and *Gerres gula*, while those associated with the lowest temperature were *Prionotus punctatus* and *Sphoeroides tyleri*.

3.3. Partitioning the variation

The sum of all eigenvalues in the canonical correspondence analysis of the species matrix was 1.962 (Table 5). From here, we obtained the relative importance of each factor that controls the variation in the composition of species in Sepetiba Bay. Partitioning of the variation was assessed using CCA procedures as follows: (1) environmental *versus* spatial variation and (2) temporal *versus* spatial variation (Table 6).

3.3.1. Environmental versus spatial variation

The environmental variables explained about 19.77% of the variation of the species matrix (Step 1) (Table 7). About 12% out of this variation was related to spatial structure of the environmental variables. Roughly one-fifth of the explained variation (24.36%) was due to the spatial matrix (5%), while the amount of unexplained variation was 76% (Tables 6 and 7).

3.3.2. Temporal versus spatial variation

A great part of the explained variation (24.36%) was due to the spatial matrix (17%). The temporal variables explained about 7% of the variation of the species matrix (Step 1). Only 0.1% out of this variation was a function of the spatial structure of the temporal variables while the amount of unexplained variation was 76.0% (Tables 6 and 7).

Table 5
Results of the main ordination for the canonical correspondence analysis. The boldface values are $p < 0.05$

Axes	1	2	3	4
Interset correlation of environment variables				
Depth	0.84	–0.10	0.03	–0.04
Transparency	0.67	0.20	–0.25	–0.09
Temperature	–0.23	–0.50	–0.29	0.04
Salinity	0.59	–0.01	–0.30	0.10
Summary of the main ordination diagnostics				
Eigenvalues	0.24	0.07	0.04	0.02
Correlation species–environment	0.86	0.70	0.60	0.51
variance accumulative (%)				
Species data	12.5	16	18.2	19.2
Relation species–environmental	63.4	80.9	91.9	97.1
Inertia	1.962			

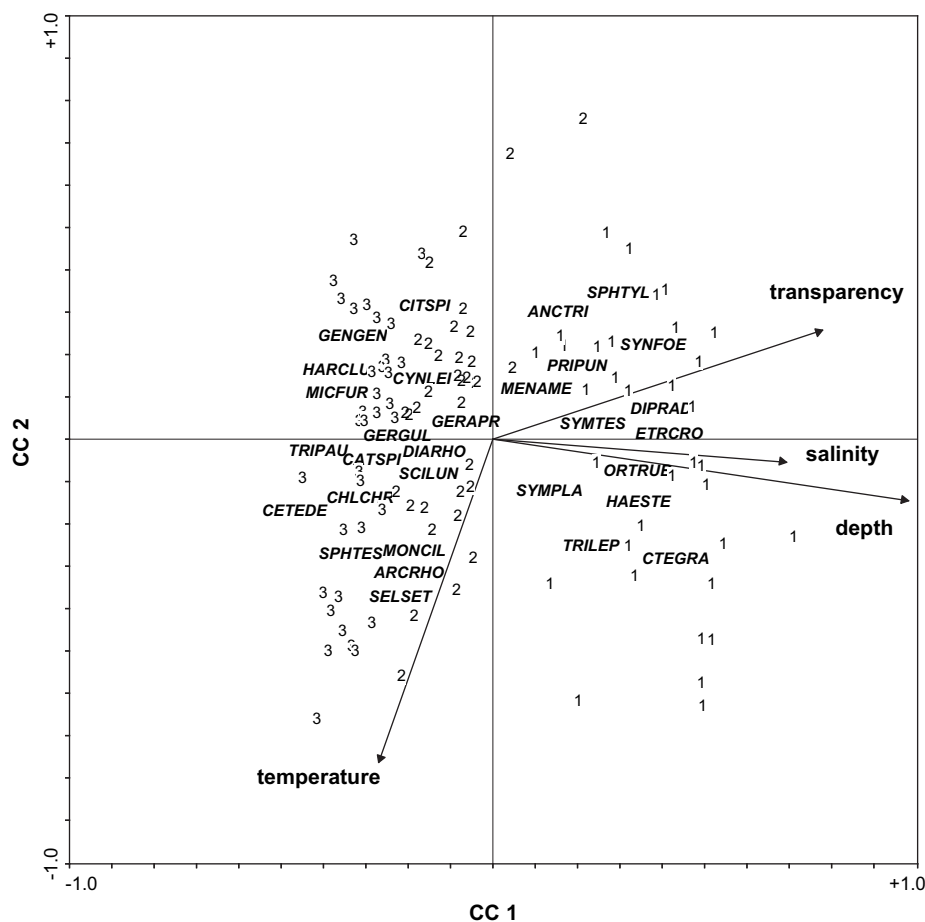


Fig. 4. Ordination diagram from the canonical correspondence analysis in Sepetiba Bay, 1998/1999. Zones: 1, outer; 2, middle; 3, inner. Species are coded according to Table 3.

4. Discussion

Two demersal fish assemblages were defined for Sepetiba Bay along the spatial gradient, one associated with the inner zone and the other associated with the outer zone, which differed in structural characteristics of composition, relative abundance and species occurrence. Consequently, the middle zone can be seen as a transition area connecting the environmental characteristics of the continental drainage area in the inner zone with the more typically oceanic conditions of the outer zone. Differential habitat occupancy occurred for some fish species, such as *Cetengraulis edentulus*, *Trinectes paulistanus*, *Harengula clupeiola*, *Sciadeichthys luniscutis*, *Chloroscombrus chrysurus* and *Gerres gula*, which were associated with the inner zone, and *Synodus foetens*, *Trichiurus lepturus*, *Diplectrum radiale*, *Orthopristis ruber*, *Haemulon steindachneri* and *Ctenosciaena gracilicirrhus*, which were associated with the outer zone.

The relationship between fish assemblage and predominant spatial gradient in Sepetiba Bay was confirmed by the different multivariate techniques. PCA indicated a clear spatial pattern for environmental variables, mainly for depth, salinity and transparency, discriminating between the bay zones. It also showed, to a lesser extent, a temporal variability, associated

with temperature and dissolved oxygen. Water depth was also the primary environmental variable correlated with cross-shelf fish assemblages in the continental shelf of eastern United States (Steves et al., 1999; Walsh et al., 2006). Environmental gradients associated with spatially differentiated fish assemblages were reported in a shallow Mediterranean soft-bottom area by Letourneur et al. (2001) and in the mangrove prop-root habitats of northeastern Florida Bay by Ley et al. (1999). According to Mariani (2001), the structure of the fish assemblages of bays usually reflects the physical, geochemical and hydrological characteristics of the area, and the distribution of the species is consistent with the degree of marine influence in the system.

Some species and environmental variables may share a common spatial or temporal structure. This may be due to the effect of spatially or temporally structured environmental descriptors on the dependent biotic variable(s), or some spurious effect of an extraneous variable, not included in the model, that causes a common spatial/temporal structure to show up in both the independent and the dependent variables of the model. Thus, in these analyses, the amount of variation in the species data that was due to this common spatial/temporal structuring was extracted by both environmental and spatial/temporal sets of explanatory variables.

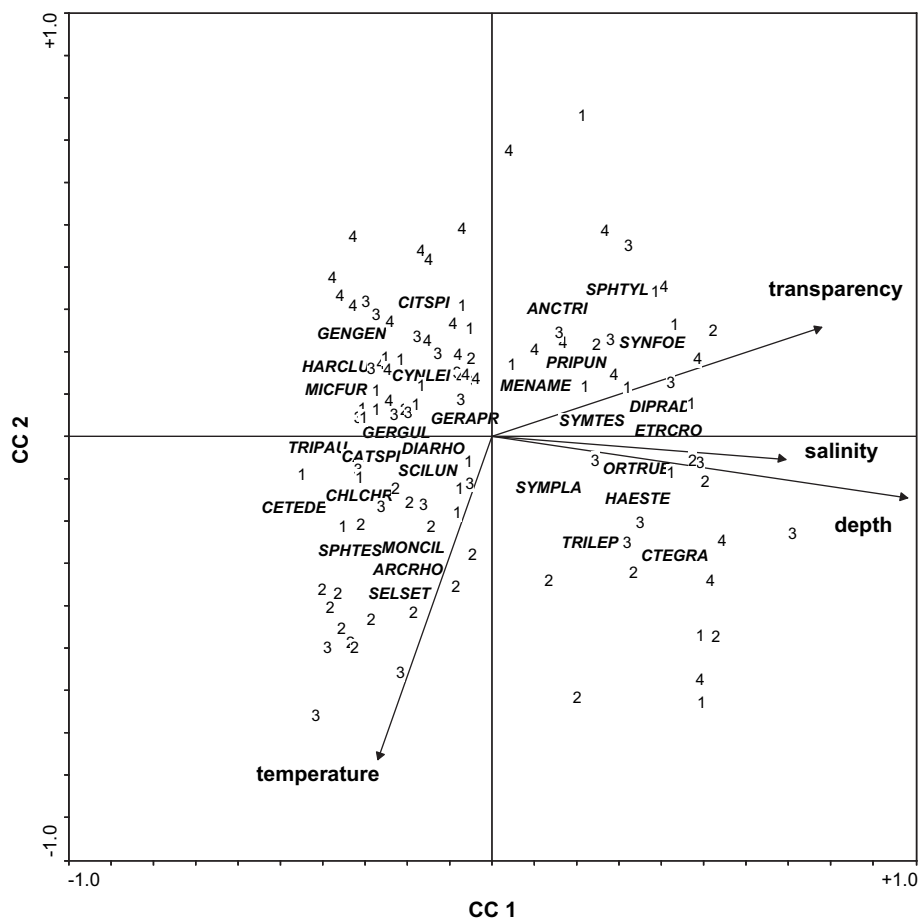


Fig. 5. Ordination diagram of the canonical correspondence analysis in Sepetiba Bay, 1998/1999. Seasons: 1, spring; 2, summer; 3, autumn; 4, winter. Species are coded according to Table 3.

In assessing the relative importance of each factor that controls variation in species composition in Sepetiba Bay, we found that the fish species and the environmental variables showed similar spatial structure. Based on these patterns, we could say that there is a direct relationship between these two data sets, and that species respond directly to changes in environmental variables. The Borcard et al. (1992) model gives a better approach for the interpretation of the interactions between species and their environment. Following the main guidelines of such a model, we concluded that the environmental variables in Sepetiba Bay were spatially structured; therefore, this could be a case of overestimation of the environmental influences dictating fish distribution. The presence of a spatial structure shared by the species and the environmental data sets leads to an overestimation of the interactions between the species and the measured environmental conditions. Sometimes their importance is simply less than could be estimated by means of simple inter-set correlation.

The amount of 'strictly spatial' variation can be of particular importance in ecological investigations. The variation explained by the spatial matrix acts as descriptor of processes that were not measured but were spatially structured, without the influence of the measured environmental variables. Such spatial species variation that is not shared by the environmental

variables is probably linked to factors that generate local effects, such as biological processes related to species life history, or complex interactions among members of the community itself, such as predation and competition, or historical events. A large amount of the variation in Sepetiba Bay involved spatial but not seasonal effects, which means that the seasonality and the spatial structure of the species do not covary. Araújo et al. (1998) did not find a seasonal pattern in the distribution of the fish in Sepetiba Bay, attributing this to the relative stability of the environmental parameters.

In most studies, it is difficult to discriminate between the part that is potentially explained and the part that is real stochasticity (Borcard et al., 1992). Unmeasured factors, such as pollution, environmental disturbances and biological interactions can be acting as underlying causes for this spatial pattern. In our study, the amount of unexplained variation was relatively high (76%), even assuming that part of it was due to nondeterministic fluctuation. Although the underlying process could not be identified from the available data, the analysis gave some information about them: they were (at least partly) independent of the measured environmental variables (which we did not purport to be exhaustive), and their action on the fish community structure could not be totally predicted by the spatial variation. In other words, a fair amount of

Table 6
Results for partitioning variation of the four analyses performed by CCA

Analysis using CCA	Sum of all canonical eigenvalues
Environmental <i>versus</i> spatial variation	
CCA of the species matrix, constrained by the environmental matrix	0.388
CCA of the species matrix, constrained by the spatial matrix	0.323
Like (1), after removing the effect of the spatial matrix	0.155
Like (2), after removing the effect of the environmental matrix	0.09
Temporal <i>versus</i> spatial variation	
CCA of the species matrix, constrained by the temporal matrix	0.136
CCA of the species matrix, constrained by the spatial matrix	0.323
Like (1), after removing the effect of the spatial matrix	0.134
Like (2), after removing the effect of the temporal matrix	0.32

variation was due to local effects of unmeasured (biotic and abiotic) controlling variables.

The distribution of some classes of habitats, determined by type of sediment, local geomorphology or organic input, is very likely to have determined some spatial structures in the fish community, but probably at a very local scale (within a few kilometers). Depth may have acted together with the other factors such as sediment, which tended to be muddy in the inner zone and sandy in the outer zone. Higher habitat complexity in the outer zone, due to the presence of several islands and a more diverse type of sediment, has allowed trophic diversity in the assemblages; on the other hand, the inner zone presented a more homogeneous habitat. *Micropogonias furnieri*, *Genidens genidens*, *Gerres gula*, *Chloroscombrus chrysurus*, *Citharichthys spilopterus*, *Diapterus rhombeus* and *Trinectes paulistanus* are abundant fish species in the inner zone, feeding mostly on soft-bottom benthic macrofauna and detritus. On the other hand, *Ctenosciaena gracilicirrhus*, *Diplectrum radiale*, *Etropus crossotus*, *Orthopristis ruber*, *Priodontus punctatus*, *Sphoeroides tyleri*, *Symphurus tessellatus*, *Synodus foetens* and *Trichiurus lepturus* are more abundant in the outer zone, feeding mostly on benthic macrofauna, fishes and a large variety of other minor items (Figueiredo and Vieira, 1998; Zahorcsak et al., 2000).

Local population abundance is influenced by response to changes in local environmental conditions as well as large-scale seasonal migrations during immature life stages. Kneib (1997) argued that biotic factors, such as reproduction, food limitations, and predation, could be important determinants of recruitment in bays and estuaries. Patterns of abundance of several species at Sepetiba Bay were consistent with those from other studies, which suggested reproductive cycles or migration associated with large-scale environmental variation (e.g., weather fronts, coastal currents, seasons of the year) (Araújo and Santos, 1999; Gomes et al., 1999, 2001; Araújo

Table 7
Percentage of the total variation of the species matrix accounted for by each step of the analysis

Step	Partitioning the variation	%Total variation
Environmental <i>versus</i> spatial variation		
1	Environmental variation	$(0.388 \times 100)/1.962 = 19.77\%$
2	Spatial variation	$(0.323 \times 100)/1.962 = 16.46\%$
3	Nonspatial environmental variation	$(0.155 \times 100)/1.962 = 7.90\%$
4	Nonenvironmental spatial variation	$(0.09 \times 100)/1.962 = 4.58\%$
1 + 4 or 2 + 3	Overall amount of explained variation	24.36%
	Unexplained variation	$100 - 24.36\% = 76\%$
1 – 3 or 2 – 4	Spatially structured environmental variation	11.87%
4	Spatial species variation that is not shared by the environmental variation	5%
Temporal <i>versus</i> spatial variation		
1	Temporal variation	$(0.136 \times 100)/1.962 = 6.93\%$
2	Spatial variation	$(0.323 \times 100)/1.962 = 16.46\%$
3	Nonspatial temporal variation	$(0.134 \times 100)/1.962 = 6.82\%$
4	Nontemporal spatial variation	$(0.32 \times 100)/1.962 = 16.30\%$
1 + 4 or 2 + 3	Overall amount of explained variation	24.36%
	Unexplained variation	$100 - 24.36\% = 76\%$
1 – 3 or 2 – 4	Spatially structured temporal variation	0.10%
4	Spatial species variation that is not shared by the temporal variation	16.3%

and Costa, 2001). For instance, temperature and salinity dictated by coastal currents and rainfall on the regional scale may also have determined changes in relative fish abundance in Sepetiba Bay.

Only 30 of the 93 species recorded in Sepetiba Bay showed numerical contributions higher than 0.1% of the total fish number; these were used in our analyses, which explained only 24.35% of the variance. The amount of unexplained variance did not decrease when we used the entire fish community or two-thirds of all recorded species, and this was the reason why we did not include such data in this work. Although excluding rare species could be done for statistical reasons, this could lead to lack of ecological information. In the present work, only a few excluded species showed a trend for spatial patterns; these species were mainly occasional marine visitors limited to the outer zone. The great majority of rare species did not show either spatial or temporal patterns, but merely increased noise and unexplained variance in the statistical multivariate analyses.

Although it is impossible to measure both biotic and environmental constraints that are relevant in an ecological study, the amount of variation involved in the largely explained trends of the Sepetiba Bay data sets may seem proportionally low. The large amount of unexplained variance could be owed

to factors that were not measured or that were not explained by the space, environmental, or temporal structure described in this model. Nevertheless, the underlying causes of species variation found to be significant can still be considered as important in the structuring of fish assemblages. Species and environmental variables showed similar spatial structure. The spatial effect, not the seasonal, explained the highest part of species variations.

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