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To cite this article: Rafaela de Sousa Gomes-Gonçalves & Francisco Gerson Araújo (2022): Relationships between environmental heterogeneity and fish beta diversity in a tropical bay, Marine Biology Research, DOI: [10.1080/17451000.2022.2063902](https://doi.org/10.1080/17451000.2022.2063902)

To link to this article: <https://doi.org/10.1080/17451000.2022.2063902>



Published online: 04 May 2022.



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Relationships between environmental heterogeneity and fish beta diversity in a tropical bay

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ABSTRACT

Estuarine shallow waters have many habitats favouring the colonization and establishment of different fish species. Our study investigated the variability in the composition of these communities by examining beta diversity and evaluated the relationship between fish beta diversity and environmental heterogeneity, which can be dependent on the level of human alteration to which an ecosystem is exposed. Our goal is to provide insights not only on the biodiversity, but also to help develop effective conservation measures. We sampled fish and environmental variables (physicochemical water variables and sediment nutrients and granulometry) in three zones (inner, middle and outer) of Sepetiba Bay, in Southeastern Brazil. The aims of our study were to compare fish communities in the different zones by using beta diversity and to investigate the relationship between environmental heterogeneity and beta diversity. Habitat conditions varied considerably among the zones. Relationships between species and environmental conditions were species-specific, and a weak positive correlation between environmental heterogeneity and beta diversity was found. The highest beta diversity was detected in the inner bay zone, suggesting that relatively more urbanized areas had greater environmental heterogeneity and, thus, higher beta diversity. Our results serve as a 'caution' to reduce the urbanization effects on these environments that sometimes can increase habitat heterogeneity and species richness. The 'weak' relationship suggest that the ecosystems may have been in the 'early stages' of human influences and managers should take into account that anthropogenic impacts would reduce beta diversity because continued degradation would lead to natural habitat reduction.

<http://zoobank.org/urn:lsid:zoobank.org:pub:EBBEA81F-6D4D-4CB3-8796-7E2A578A8B03>

ARTICLE HISTORY

Received 4 February 2021
Accepted 5 April 2022

SUBJECT EDITOR

Roy Kropp

KEYWORDS



Biodiversity; habitat heterogeneity; coastal fish; estuarine areas


Introduction

Knowledge on the distribution of biological communities and their relationships with environmental variables is essential to understand the factors that modulate community organization. In the past few decades, there has been a growing interest in beta diversity (Baselga 2010; Socolar et al. 2015) that can provide insights on how to investigate community organization in space and time. Beta diversity has become increasingly used by environmental managers, mainly because of the emerging need to learn about dynamics of biological community composition and to establish effective conservation measures. Beta diversity measures variation in species composition among habitats, thus providing an overview of the degree of similarity between communities (Whittaker 1972; Olden and Rooney 2006; Gutiérrez-Cortés et al. 2018). The spatial variation in species composition allows testing of hypotheses about the processes

that generate and maintain biodiversity in ecosystems (Legendre and De Cáceres 2013), which is extremely important information to be considered by protected-area planners to establish regions of great interest for conservation (Wiersma and Urban 2005).

The relationship between the diversity of biological communities and environmental heterogeneity has been increasingly investigated since the early 2000s (Heino et al. 2013; Seiferling et al. 2014; López-Delgado et al. 2019). Positive relationships supporting the environmental heterogeneity–biodiversity hypothesis are well documented (MacArthur and Wilson 1967; Levin et al. 2010; López-Delgado et al. 2019), but non-significant and negative relationships are also reported in the literature. A unimodal relationship between environmental heterogeneity and species richness was reported by Allouche et al. (2012), whereas a predominantly negative relationship at small scales (Tamme et al. 2010) or for animal taxa occurring in small to medium level urban

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 Supplemental data for this article can be accessed online at <https://doi.org/10.1080/17451000.2022.2063902>.

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landscapes (McKinney 2008) were also reported, thus increasing the controversies around this topic. Seiferling et al. (2014) evaluated an extensive literature that related environmental heterogeneity and biodiversity and concluded that 'positive relationships predominate in highly modified ecosystems, whereas negative relationships prevail in semi-natural environments (the initial stages of human alterations) and mixed responses in natural ecosystems'. According to such studies, natural ecosystems have intermediate levels of environmental heterogeneity, and based on this assumption, if the amount of modification is increased (becoming a semi-natural environment), initially, new environmental conditions would be created (i.e. low levels of urbanization), resulting in an increase in environmental heterogeneity. At this stage, there may be a decline in biodiversity, as many resident or specialized species may be eliminated because of the new conditions. Thus, at this point, negative relationships between environmental heterogeneity and biodiversity are expected. In highly modified environments, the relationships between heterogeneity and biodiversity tend to be positive, because only a few species can withstand heavily altered environments, with addition of environmental heterogeneity increasing habitats, enabling increases in species richness. This happens when natural habitats become scarce because intensifying human influences shift ecosystems from the initial stages of modification to an intense state of alteration (Seiferling et al. 2014). In this phase, species richness may decline, and reduced environmental heterogeneity may drive losses of biodiversity (Amarasekare 2003). Therefore, anthropogenic impacts can cause the similarity of local communities to increase, decrease or remain unchanged (Socolar et al. 2015). For example, during the initial stages of impacts, loss of localized species and establishment of invaders can cause beta diversity to increase (Socolar et al. 2015). However, in the long run, only generalist species resistant to impacts will be able to remain in the environment, resulting in low beta diversity (Moreno and Halffter 2001). Therefore, the level of human alteration to which an ecosystem is subjected, should be considered in studies of beta diversity.

Estuarine environments are highly dynamic, with high variation in abiotic conditions, such as salinity and turbidity (Elliott and McLusky 2002) and are strongly influenced by tidal action and freshwater discharges that transport a large amount of nutrients (Wolanski et al. 2004). These characteristics are among the factors that affect biological community composition, as species must be tolerant of this fluctuation in environmental conditions (Whitfield 1999; Teichert et al. 2017). Estuarine environments are able to support a great

biological diversity because their high productivity and high environmental heterogeneity favour the establishment of many fish species during different life cycle stages (Whitfield and Pattrick 2015). These environments are among the most important coastal ecosystems, providing valuable resources for the economy with many commercially and recreationally important finfish species that depend on estuaries for survival (Kennish 2002, 2003). Spatial variation in habitats and environmental conditions is of great importance (Anderson et al. 2006; Seiferling et al. 2014) because structurally complex habitats may provide more niches, which contribute to increased species diversity (Bazzaz 1975; Tews et al. 2004). Therefore, beta diversity is expected to be positively related to environmental heterogeneity, as heterogeneous environments increase the probability that different species find suitable conditions according to their environmental preferences (Soares et al. 2015).

Coastal marine systems have undergone considerable environmental degradation caused mainly by anthropogenic activities (Whitfield 1999; Azevedo et al. 2007; Teichert et al. 2017). In addition to the physical destruction of habitats for human occupation, these systems have received pollutants from domestic and industrial wastewaters through the discharge of rivers and drainage channels (Wolanski et al. 2004). These disturbances often result in the introduction of high loads of nutrients and industrial pollutants, among other hazards, threatening ecosystems in several ways, and changing spatial heterogeneity of environmental characteristics (Chi et al. 2018). Several studies (Whitfield and Pattrick 2015; Teichert et al. 2017; Chi et al. 2018) have identified the effects of such disturbances and identified tools to mitigate them. In this sense, beta diversity, among many other parameters, has been widely accepted for decision-making in the development of environmental conservation management policies (Wiersma and Urban 2005; Socolar et al. 2015; López-Delgado et al. 2019).

SePETIBA Bay is an estuarine system located in the south of the State of Rio de Janeiro, Brazil that has suffered the effects of an increase in anthropogenic activities in recent decades, mainly because of the high human population densities and the large industrial park that is located in the region. The bay is adjacent to a continental area that houses part of the population of the city of Rio de Janeiro, including a large port and the largest steel industry in Latin America (Araújo et al. 2016). These anthropogenic activities have contributed to increased degradation of the bay shoreline mainly because of the increase in industrial and municipal effluents discharged into the bay by rivers and drainage

channels, resulting in increases in sedimentation and concentrations of inorganic pollutants (Zn, Cd, Pb and Hg) with eutrophication in the bay (Molisani et al. 2004; 2006). Such changes have affected fish diversity in the bay since the early 90s (Araújo et al. 2002; Pessanha and Araújo 2003; Araújo et al. 2016). Strong urban and industrial growth have caused a series of environmental and biodiversity losses, with significant advances in urbanization replacing mangroves and other vegetated areas along the bay shoreline. Araújo et al. (2017) evaluated changes during the last 30 years of human occupation of the Sepetiba Bay area and concluded that there was a loss of approximately 26% of the mangrove area. In addition, Araújo et al. (2016) evaluated the temporal changes of the ichthyofauna in Sepetiba Bay and reported that most changes occurred in the inner bay zone because of its proximity to sources of impacts. These environmental changes indicate the emerging need for information on the biological composition of fish species and their relationships with environmental variables. This would be useful to provide subsidies for environmental managers aiming to protect the biodiversity.

Assessing the relationship between beta diversity and habitat is an important step to identify components relevant to biodiversity. The objective of this study was to compare the ichthyofauna of three littoral zones (inner, middle and outer) of an impacted tropical bay by measuring beta diversity and relating diversity to environmental heterogeneity. Assuming that the environmental and biological conditions differ among the three bay zones, we investigated whether environmental heterogeneity influences beta diversity. We believe that this information will assist in understanding the general functioning of the ecosystem and contribute to the establishment of measures for the conservation of biodiversity.

Material and methods

Study area

Sepetiba Bay (22°54'–23°40'S, 43°34'–44°10'W) is a 450 km² sedimentary embayment located in the south of the State of Rio de Janeiro (Figure 1). The bay has a narrow connection with the sea in the east side, and a wide connection in the west. Several small rivers and streams flow into the bay, the largest being the Guandu River, which has an average discharge of 190 m³ × s⁻¹ (Leal-Neto et al. 2006). The mean water temperature ranges from 21.5°C in the winter to 26.5°C in summer and average salinity ranges from 29 psu in the inner bay to 33 psu in the

outer bay. This microtidal system has a tidal range of approximately 1 m (Araújo et al. 2002).

We divided Sepetiba Bay into three zones (inner, middle and outer) for this study (Figure 1), according to the environmental conditions and human influences. The inner zone is located near mangrove formations in the innermost part of the bay and is influenced by industrial and urban effluents carried into the bay by streams and rivers, has comparatively higher turbidity and temperature and lower salinity than the other zones, and the substratum is predominantly mud (Araújo et al. 2002; Leal-Neto et al. 2006). The middle zone is located close to the submarine factory and the port, being protected from high hydrodynamic variation (e.g. high waves and tides) by islands close to the beaches, and it has environmental conditions that are intermediate between those of the inner and outer zones. The outer zone is located close to the large opening with the ocean, has relatively less influence of anthropogenic activities and more stable environmental conditions with comparatively lower temperature and higher salinity and transparency than the other zones (Araújo et al. 2016).

Sampling and laboratory analyses

Samples were collected every two months from September 2017 through July 2018 (September and November 2017; January, March, May and July 2018), in the three Sepetiba Bay zones. On each occasion, three sites scattered 'randomly' along the coast in each zone were sampled for fish, physicochemical and sediment analyses with three replicates, totalling 162 samples (6 periods × 3 zones × 3 sites × 3 replicates).

Our study focused on nearshore fish assemblages inhabiting shallow areas with unconsolidated substrate. Fish were collected with a beach seine (12 m long × 2.5 m high; 10-mm mesh size at the wings, with a pocket of 5 mm mesh size in its rear portion). The net was fitted with 30-m hauling ropes and set at approximately 1.5-m depth. The hauls were 30-m long and perpendicular to the shore, performed by two persons, one on each end of the rope, for about 15 min. The total sweeping area was taken to be the distance the net was laid offshore (30 m) multiplied by the mean width of the net opening (10 m), resulting in an effective fishing area of approximately 300 m². The collected fish were fixed in 10% formalin, and after 48 h, preserved in 70% ethanol. Fishes were identified to species level, and voucher specimens were deposited in the Ichthyological Collection of the Laboratório de Ecologia de Peixes of the Universidade Federal Rural do Rio de Janeiro. Larvae of three fish genera (*Anchoa*, *Eucinostomus* and

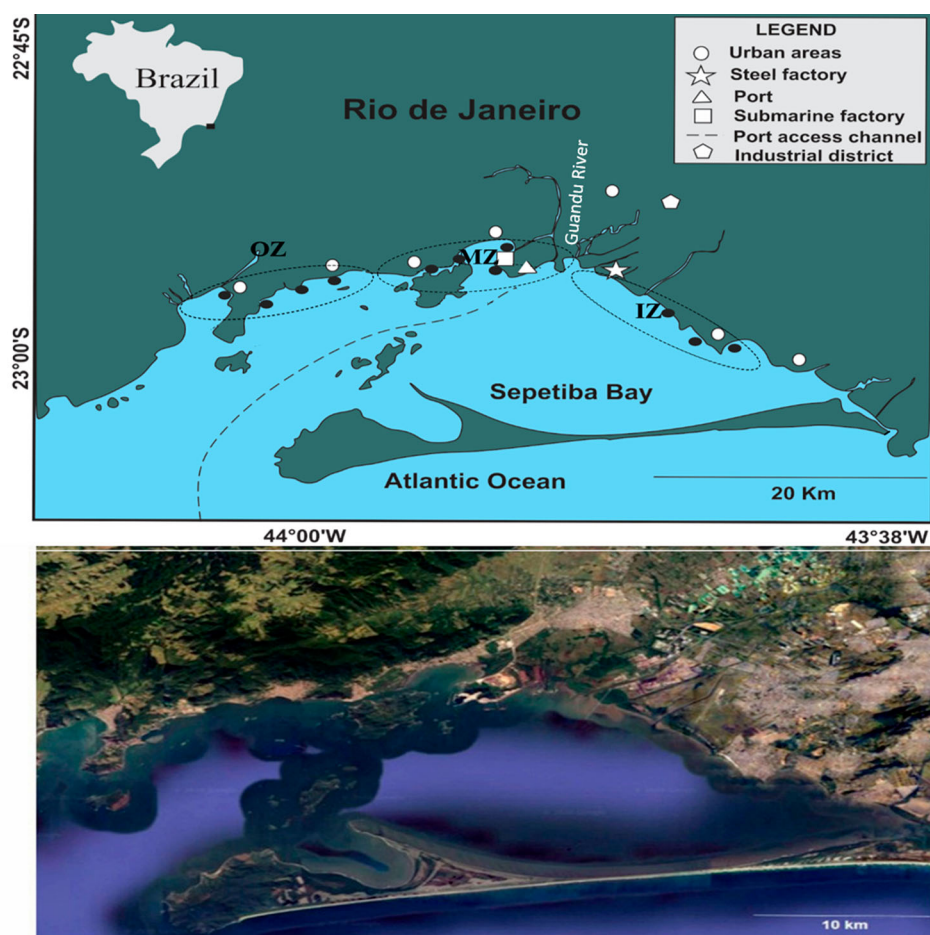


Figure 1. Study area, Sepetiba Bay, Brazil, indicating above, the three studied zones (IZ, inner zone; MD, middle zone; and OZ, outer zone) and the sampling sites (black dots), and below, depicting the land use by anthropogenic activities and urbanization (grey areas) Source: Google Earth (2022).

Mugil) that were difficult to identify were merged as unidentified species, named as Larvae (e.g. Larvae of *Anchoa* spp.) and were included in the analyses.

Water temperature ($^{\circ}\text{C}$) and salinity (psu) were measured at each fish sampling occasion, by using a Horiba W-23 multisensor (Horiba Trading Co. Ltd, Shanghai), whereas transparency (cm) was measured using a Secchi disc. Water measurements were carried out at approximately 50 cm water depth, near the centre of the hauls.

Sediment measurements included granulometric parameters and nutrient concentrations. For granulometric and nutrient analysis, sediment samples were collected using a PVC corer (10 cm in diameter and 50 cm in length) that collected an area of 0.00785 m^2 at 1.5 m of water depth. In the laboratory, the samples were dried and weighed on a precision scale (0.01 g), and 150 and 300 g were removed for nutrient analysis and granulometric analysis, respectively. The determination of the granulometric fractions of the sediment was accomplished by the dry-sieving method proposed by

Suguio (1973) and the average size was determined from the weight of each granulometric fraction retained in each sieve, through analyses with the SysGran software 3.0 (Camargo 2006). The granulometric parameters were calculated according to Folk and Ward (1957) and classified according to Shepard (1954). We considered (1) coarse substrate (%) as the sum of very coarse sand and coarse sand; and (2) fine substrate (%) as the sum of medium sand, fine sand, very fine sand and silt + clay.

The concentrations of the organic carbon (g kg^{-1}), total nitrogen (%) and total phosphorus (mg dm^{-3}) in the sediment were analysed. We analysed nutrients in the sediment rather than in the water column, because sediment accumulates, retains and releases nutrients into the water column, which makes it a more consistent indicator of nutrient loads than the water column, which varies with currents and tides. Organic carbon was measured by oxidation of wet organic matter with potassium dichromate in sulphuric acid medium, employing the heat given off from the sulphuric acid and/or applied heat as the energy source (Walkley and Black 1934). Total

nitrogen concentration (%) was determined using the Kjeldahl nitrogen method with a diffusion camera. Total nitrogen was converted to ammonium sulphate by oxidation with a mixture of CuSO_4 , H_2SO_4 and Na_2SO_4 or K_2SO_4 (mineralization). Later, in alkaline medium, the ammonium sulphate was converted from the organic matter released ammonia, which was complexed in a boric acid solution containing a mixed indicator in a diffusion chamber and was finally determined by using acidimetry (H_2SO_4 or HCl). Total phosphorus concentration (mg dm^{-3}) was determined using a spectrophotometer after digestion with HNO_3 – HCl (3:1, V/V) at 200°C . The solubilization of the mineral and organic phosphate forms was conducted using 1:1 H_2SO_4 (Bowman 1988). The phosphorus contained in the sulphuric extract represented the total concentration of this element.

Data treatment

Prior to multivariate analyses, environmental data were normalized (centred by the mean and reduced to the standard deviation unit) to eliminate the effects of different measurement scales, thus making them dimensionless. In this study, environmental heterogeneity was defined as the variation in abiotic conditions (water physicochemical and sediment variables) among the same set of samples in which fish beta diversity was estimated. A Multivariate Dispersions Homogeneity test (PERMDISP, Anderson et al. 2006) was used to test whether multivariate dispersions within zone differ among the zones, which provides the mean distance to the centroid of environmental data (environmental heterogeneity) from the Euclidean distance matrix. The environmental variables were compared among the zones by using a Permutational Analysis of Variance (PERMANOVA) on the Euclidean distance matrix (Anderson et al. 2006, 2011).

Beta diversity and community structure variation were estimated through a Permutational Analysis of Multivariate Dispersions (PERMDISP). According to Anderson et al. (2006), the variation in species composition for a group of units sampled in a given area can be measured as the average distance from individual units to the group's centroid in a multivariate space. Thus, the results of PERMDISP can be interpreted as a beta diversity measurement, informing the variability in the composition of fish species on a given spatial scale (Anderson et al. 2006). The PERMDISP analysis produces an average of the total beta diversity (presence and absence data) and variation in the community structure (abundance data) at locations within a region. These evaluations were made from similarity matrices

with Sørensen coefficients (qualitative, presence/absence of species) and Bray–Curtis distance (quantitative, abundance data). Fish community composition was also compared among the zones with a Permutational Analysis of Variance (PERMANOVA) on the Sørensen coefficients and Bray–Curtis similarity matrices. PERMANOVA with a Type I (sequential) sum of squares using 999 permutations to calculate *P*-values was used, where biological abundance was the response variable and the zones were the fixed factors.

Differences in the fish community structure among the zones were evaluated using a non-metric Multidimensional Scaling (nMDS) ordination. In addition, the typical species, i.e. those that most contribute to within-group average similarity in each zone were determined by a Similarity Percentage analysis – SIMPER (Anderson et al. 2008).

To detect patterns between environmental variables and fish species, a Detrended Correspondence Analysis (DCA) was performed to determine the gradient length of the first ordination axis of biological data, to select the appropriate direct ordination method (Redundancy or Canonical Correspondence Analysis). In this study, the Canonical Correspondence Analysis (CCA) was used after verifying that the length generated by the DCA analysis was greater than 4, which follows guidelines set by Leps and Smilauer (2003). To perform these analyses, we included species that were found in at least 10 samples because rare taxa can cause pattern distortions in the analysis (Ter Braak 1986). In addition, the Monte Carlo permutation test was applied to determine the significance of the environmental variables on the main ordination axes.

A linear regression analysis was performed to test the null hypothesis that the average distance from biological data to the centroid, calculated by PERMDISP (beta diversity or the variation of the assembly structure) and the average distance from the environmental data to the centroid (environmental heterogeneity) were related. Only the relationships that had significant association ($P < 0.05$) were analysed.

PERMDISP, nMDS, SIMPER and PERMANOVA analyses were performed using PRIMER 6 version 6.1.13 & PERMANOVA+ version 1.0.3 (Clarke and Gorley 2006; Anderson et al. 2008), CCA by using CANOCO FOR WINDOWS 4.5 and regression analyses by using Statistica version 10 (StatSoft 2011).

Results

Environmental characterization

We tested the environmental data and found no significant correlation among these variables. Habitat

Table I. Mean, standard deviation of the environmental variables in the three zones of Sepetiba Bay, Brazil and results of the PERMANOVA (Pseudo-F) and pairwise comparisons in relation to each variable.

	Inner zone (IZ)	Middle zone (MZ)	Outer zone (OZ)	Pseudo-F	Pair-wise comparisons
Sediment nutrient					
P (mg dm ⁻³)	27.3, 15.6	44.4, 22.2	25.1, 18.5	16.6 ***	MZ > IZ; OZ
C (g kg ⁻¹)	0.63, 0.53	0.27, 0.24	0.16, 0.12	28.4***	IZ > MZ > OZ
N (%)	0.14, 0.07	0.11, 0.04	0.10, 0.02	11.3***	IZ > MZ; OZ
Sediment granulometry					
Coarse substrate (%)	57.6, 28.6	68.2, 14.8	35.7, 38.9	17.4***	MZ > IZ > OZ
Fine substrate (%)	42.4, 28.6	31.8, 14.8	64.3, 38.9	17.4***	OZ > IZ > MZ
Water physicochemical parameters					
Temperature (°C)	25.2, 3.33	24.9, 3.57	25.3, 2.76	0.16 ns	–
Salinity (psu)	31.1, 4.72	31.3, 3.54	32.6, 3.05	2.25 ns	–
Transparency (cm)	39.3, 20.93	62.2, 29.2	63.6, 25.1	15.2***	IZ < MZ, OZ

Codes: ns, not significant; *** $P < 0.001$.

conditions varied considerably among zones (Table I). The sedimentary granulometric characterization and nutrient concentrations were significantly different, with the inner zone having higher concentrations of carbon and nitrogen in the sediment than the other zones (Table I), whereas the middle zone had a higher phosphorus concentration and a comparatively higher fraction of coarse sediments than the other zones (Table I). The water temperature and salinity did not differ significantly among the zones, whereas water transparency was lower in the inner zone than in the middle and outer zones (Table I).

PERMANOVA analyses on environmental data showed significant differences among the zones (Pseudo- $F_{(2; 159)} = 12.8$; $P = 0.001$), corroborating the results of the Multivariate Dispersions Homogeneity test (PERMDISP) that showed differences among the zones ($F_{(2; 159)} = 6.75$, $P < 0.003$). The inner zone showed greater environmental heterogeneity (2.80 ± 0.10 s.d.), compared with the middle zone (2.26 ± 0.09) and the outer zone (2.40 ± 0.08). Pairwise comparisons indicated that heterogeneity in the outer and middle zones did not differ significantly ($P > 0.05$).

Ichthyofauna

A total of 38,073 individuals, distributed among 71 species, was recorded (Table S1, Supplementary Material). The middle zone showed the greatest fish abundance, with 23,130 individuals distributed among 33 species. Of these, 52.3% were represented by larvae of *Anchoa* spp. and 14.7% by *Atherinella brasiliensis* (Quoy & Gaimard 1825). The inner zone had 8102 individuals belonging to 44 species, whereas the outer zone had 6841 individuals distributed among 44 species. PERMANOVA analysis showed significant differences in the fish community composition among the zones, for abundance data (Pseudo- $F_{(2; 159)} = 9.2$; $P = 0.01$), and for presence/absence data (Pseudo- $F_{(2; 159)} = 10.6$; $P = 0.001$).

Differences in the species composition among the zones were revealed by the nMDS ordination (Figure 2). However, several samples from different zones overlapped with those of the inner zone having the widest scatter in the diagram. Larvae of *Anchoa* spp. contributed to average similarity for all zones, with greater values in the inner and middle zones compared with the outer zone (Table II). *Atherinella brasiliensis* (Quoy & Gaimard, 1825) contributed most to average similarity in the middle and the outer zones. Other species with high contribution to within-group average similarity were *Genidens genidens* (Cuvier, 1829) in the inner zone, *Eucinostomus argenteus* Baird & Girard, 1855, and *Oligoplites saurus* (Bloch & Schneider, 1801), in the middle zone, and *Trachinotus carolinus* (Linnaeus, 1766) and *Anchoa tricolor* (Spix & Agassiz, 1829) in the outer zone (Table II).

The predominant taxa that occurred in all three zones but were more abundant in the middle zone were anchovy larvae and *Atherinella brasiliensis*. *Anchoa januaria* (Steindachner, 1879), which was also very abundant in the middle zone, predominated in the outer zone (Table II, Table S1, Supplementary

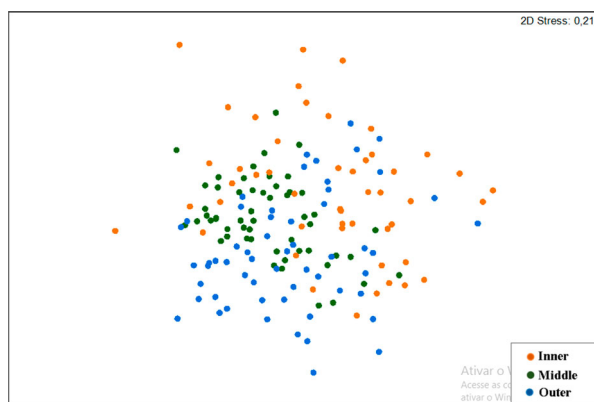


Figure 2. Ordination diagram of non-Metric Multidimensional Scale on species abundance, with samples coded by zones. Codes: Inner zone, yellow circles; Middle zone, green circles; Outer zone, blue circles.

Table II. Zone average similarity (% in parentheses), and species average abundance (Av. abund.) and average similarity (Av. simil.) according to the similarity percentage (SIMPER) analysis for the most typical species in the three zones of the Sepetiba Bay.

Species	Inner (15.8)		Middle (31.3)		Outer (22.2)	
	Av. abund.	Av. simil.	Av. abund.	Av. simil.	Av. abund.	Av. simil.
Larvae of <i>Anchoa</i> spp.	1.08	2.89	1.25	2.85	0.85	2.62
<i>Genidens genidens</i>	0.79	2.96				
<i>Eucinostomus argenteus</i>			0.73	2.70		
<i>Oligoplites saurus</i>			0.64	3.12		
<i>Atherinella brasiliensis</i>			1.92	17.72	1.06	6.60
<i>Trachinotus carolinus</i>					0.73	4.31
<i>Anchoa tricolor</i>					0.61	2.12

Material). Other species with high average abundance in the inner zone were the anchovies *Anchoa lyolepis* (Evermann & Marsh, 1900) and *Cetengraulis edentulus* (Cuvier, 1829) and the marine catfish *Genidens genidens*, whereas the mojarra *Eucinostomus argenteus* had high average abundance in the middle zone, and the white-mouth croaker *Micropogonias furnieri* (Desmarest, 1823) in the outer zone (Table II). The killifish *Jenynsia lineata* (Jenyns, 1842) and *Poecilia vivipara* Bloch & Schneider, 1801, and the herrings *Brevoortia pectinata* (Jenyns, 1842) and *B. aurea* (Spix & Agassiz, 1829) were not abundant, occurring only in the inner zone.

The biological heterogeneity differed among the zones, in which the structural variation of the fish community varied from 48.7 in the middle zone to 59.5 in the inner zone ($F_{(2; 159)} = 18.5; P = 0.001$) (abundance data, Bray–Curtis average of the distance to the centroid of the group), whereas the beta diversity varied from 46.8 in the middle zone to 57.6 in the inner zone ($F_{(2; 159)} = 15.5, P = 0.001$) (presence/absence data, Sørensen average of the distance to the centroid

Table III. Mean, standard deviation distance to the centroid of the group for the data and pairwise comparisons of the fish assemblage in each zone sampled in Sepetiba Bay, Brazil. PERMDISP analyses were based on the presence/absence (Sørensen) or abundance (Bray–Curtis) of fish species. F and P values were obtained from the tests of multivariate dispersions between areas (999 permutations).

Zones	Sørensen	Bray–Curtis
Inner	57.6, 1.3	59.5, 1.1
Middle	46.8, 1.4	48.7, 1.4
Outer	53.0, 1.4	55.1, 1.2
F; P	15.5; 0.001	18.5; 0.001
Pairwise comparisons t (P)		
inner, middle	5.63 (0.001)	5.94 (0.001)
inner, outer	2.40 (0.024)	2.65 (0.008)
middle, outer	3.12 (0.011)	3.43 (0.002)

of the group) (Table III). Each zone differed from the other two (inner > outer > middle) in both analyses (Sørensen and Bray–Curtis and distances).

Environmental effects on ecological descriptors

A significant relationship between the environmental variables and abundance matrices (F-ratio = 4.7, $P = 0.002$ for the first axis, F-ratio = 3.5, $P = 0.007$ for the second axis) was determined by a Monte Carlo test using 500 permutations, applied to the first two CCA ordination axes, confirming that the environmental variables influenced the local ichthyofauna. The first two axes explained 46% of the species–environment relationship, with axis 1 being positively related to sediment nutrients (organic carbon and nitrogen) and coarser sediment fractions, whereas axis 2 was inversely related to temperature and positively to salinity (Figure 3).

The distributions of some species, such as the marine catfish *Genidens genidens* that was more abundant in the inner zone, showed direct correspondence

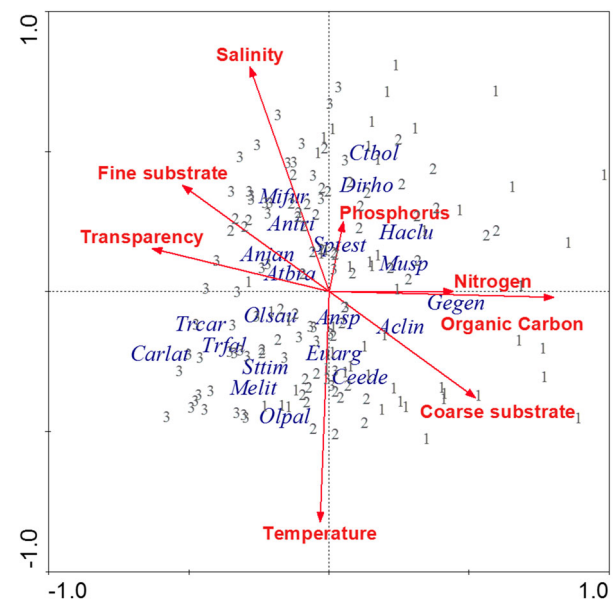


Figure 3. Ordination diagram of the first two axis from Canonical Correspondence Analysis on the fish and environmental variables collected in Sepetiba Bay, Brazil. Codes: 1, inner zone; 2, middle zone; 3, outer zone, Aclin, *Achirus lineatus*; Anjan, *Anchoa januaria*; Ansp, Larvae of *Anchoa* spp.; Antri, *Anchoa tricolor*; Atbra, *Atherinella brasiliensis*; Carlat, *Caranx latus*; Ceede, *Cetengraulis edentulus*; Dirho, *Diapterus rhombeus*; Ctbol, *Ctenogobius boleosoma*; Euarg, *Eucinostomus argenteus*; Gengen, *Genidens genidens*; Haclu, *Harengula clupeiola*; Melit, *Menticirrhus littoralis*; Mifur, *Micropogonias furnieri*; Musp, Larvae of *Mugil* sp.; Olpal, *Oligoplites palometa*; Olsau, *Oligoplites saurus*; Sptest, *Sphoeroides testudineus*; Trcar, *Trachinotus carolinus*; Trfal, *Trachinotus falcatus*; Sttim, *Strongylura timucu*.

with higher concentrations of C and N in the sediment (Figure 3). In contrast, the distributions of species that were common in the outer zone, such as the pompano *Trachinotus carolinus* and the leatherjack *Oligoplites saurus* showed an inverse correspondence with these variables. In addition, greater abundances of the anchovy *Anchoa januaria* corresponded to the predominance of fine sediments and highly transparent waters characteristic of the middle and outer zones, whereas the greater abundance of the whitemouth croaker *Micropogonias furnieri* coincided with high salinity waters of the outer zone (Figure 3).

A weak positive relationship was observed between the biological structure (Bray–Curtis coefficient) and the average of the distances to the centroid of the habitat data group (environmental heterogeneity) ($R^2 = 0.06$; $P = 0.001$; Figure 4A) according to the linear regression analysis. A similar pattern was observed in the comparison of environmental heterogeneity and the average of the distances to the centroid of the fish assemblage data group (beta diversity, Sørensen coefficients) ($R^2 = 0.055$; $P = 0.003$; Figure 4B). In addition, a weak positive relationship was also found between beta diversity and organic carbon ($R^2 = 0.092$; $P = 0.001$; Figure 4C) and nitrogen ($R^2 = 0.03$; $P = 0.02$; Figure 4D).

It can also be observed that the samples from the inner zone (orange circles) had the widest scatter in the diagrams, and many of them are among the higher dissimilarity values (>50) on the y-axis. In contrast, the middle zone samples (green circles) are less dispersed, with most showing lower values on the y-axis. The samples from the outer zone (blue circles) show intermediate values although several samples showed high (>50) dissimilarity (Figure 4).

Discussion

Our results suggest that more heterogeneous environments may have greater fish beta diversity although we detected only a weak relationship between environmental heterogeneity and beta diversity. The inner zone of the Sepetiba Bay showed greater heterogeneity in water physicochemical and sediment variables than the other two zones that did not differ between each other. This zone also had greater fish beta diversity with each zone differing from the other two (inner $>$ outer $>$ middle). Although weak, this pattern is in accordance with those described by Seiferling et al. (2014) in their meta-analysis on environmental heterogeneity–biodiversity relationships. They concluded that this relationship depends

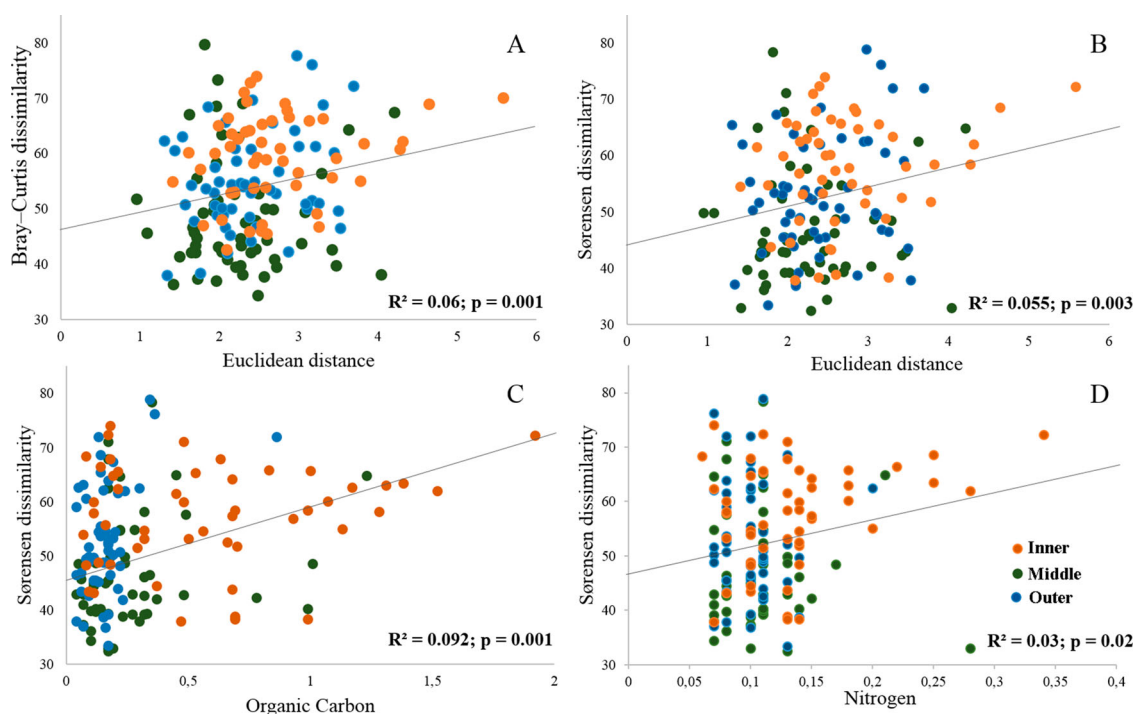


Figure 4. Relationship between habitat heterogeneity (Euclidean distance) and variation in the structure of the fish assemblage collected from Sepetiba Bay, Brazil, based on Bray–Curtis dissimilarity (abundance) (A) and beta diversity based on Sørensen dissimilarity (presence/absence) (B); relationship between beta diversity based on Sørensen’s dissimilarity (presence / absence) and the concentration of organic carbon (C) and nitrogen (D). Samples coded by zones: Inner zone, orange circles; middle zone, green circles; outer zone, blue circles.

on the level of human footprint to which an ecosystem is exposed, and that in highly modified areas there is a predominance of positive environmental heterogeneity–biodiversity relationships. It is widely agreed that more heterogeneous conditions favour the occurrence of a greater number of species compared with more homogeneous environments (Veech and Crist 2007; Bini et al. 2014; Camara et al. 2020), which is in accordance with the MacArthur niche-based hypothesis. Our findings coincided with this novel framework proposed by Seiferling et al. (2014) including the human-caused influences. Although our results point to differences among the bay zones, an indication of the environmental heterogeneity of this system, historical anthropogenic changes such as pollution and habitat degradation must have led to a broad process of homogenization within each zone. It may suggest that the addition of environmental heterogeneity would increase habitat and resources opportunities. However, we should be cautious because this study is essentially correlative and the weak correlation may also be due to a few extreme values and the large sampling size, presumably, thus limiting predictability. We should also bear in mind that environmental heterogeneity is one determinant of the structure of the ichthyofauna at local and regional levels (Camara et al. 2020), and other factors (e.g. biotic interactions, climatic influences, etc.) that were not included in this study may also contribute to fish community structure.

We observed correspondence between environmental variables and some representative species in the study area according to CCA. In estuarine areas, such as the Sepetiba Bay, the characteristics of the habitat seem to act as a filter, with particular species combinations selecting characteristics that allow them to occupy certain areas. Significant differences in the ichthyofauna composition between the inner and outer Sepetiba Bay zones were recorded over three decades (Araújo et al. 2002, 2016; Azevedo et al. 2007), which were attributed in part to differences in environmental conditions that seems to be a key element for maintenance of biodiversity, as suggested in the present study. This spatial partitioning of the bay was confirmed in this study with the occurrences of the killifish *Jenynsia lineata* and *Poecilia vivipara*, the herrings *Brevoortia pectinata*, *B. aurea*, the anchovy *Cetengraulis edentulus*, and the marine catfish *Cathorops spixii* (Agassiz, 1829) and *Genidens genidens* in the inner zone. The inner zone has comparatively higher C and N concentrations, lower transparency and is located near the influences of anthropogenic activities. Alternatively, abundant anchovy larvae

predominated in the middle zone, a more protected area where the proximity of islands decreases the hydrodynamics and thus being suitable for larval development, whereas the jacks *T. carolinus*, and the whitemouth croaker *M. furnieri* predominated in the outer zone, with more marine influence. Most of these fish species in these shallow areas are juveniles that in adult stages use the water column (e.g. herrings, anchovies), or the bottom (e.g. whitemouth croaker, marine catfish) in deeper areas.

Similar to what was observed in relation to environmental heterogeneity, the concentrations of organic carbon and nitrogen showed a weak, but significant, direct relationship with beta diversity. Nutrient-rich sediments can make nutrients available to the water column through the water-sediment interface or bioturbation by benthic invertebrates (Santschi et al. 1983; Sundby et al. 1992; Josefson and Rasmussen 2000; Koch and Wolff 2002). Nutrients are essential for the primary production of the water column, also favouring higher trophic levels, such as fish (Hopkinson 1987; Human et al. 2015). In shallow estuarine areas, such as Sepetiba Bay, this process can favour primary and secondary productivity and also the fish community. Nutrients are usually directly related or associated with higher levels of beta diversity. Higher concentrations of C and N in the inner zone may result from the greater influence of river discharges (Molisani et al. 2004) and probably contribute to higher primary productivity (Leal-Neto et al. 2006; Molisani et al. 2006) and greater beta diversity in this area of the bay. Chase (2010) found that primary productivity seems to be the main driver of biodiversity, with regions with higher productivity generally having more species and greater beta diversity, but the mechanisms underlying this phenomenon are unknown. Similarly, Barcellini et al. (2021) found a positive relationship between total phosphorus concentration and fish species richness, but nevertheless suggested the need for further studies to assess the threshold between positive and negative effects, as high phosphorus concentrations can lead to eutrophication. Cook et al. (2018) evaluated the temporal beta diversity of macroinvertebrates from aquatic environments and observed a decline in this descriptor relative to increased nutrient enrichment, concluding that eutrophication resulting from nutrient inputs leads to temporally more homogeneous communities. Thus, the concentration of nutrients in aquatic environments should be carefully analysed, because high concentrations of nutrients can be harmful to the environment, limiting the occurrence of sensitive species (Bini et al. 2014).

Significant correlations between some fish species and environmental variables suggest a certain degree of association of fish with certain environmental conditions. For example, several species that are representative of the inner zone, such as *Genidens genidens*, showed direct relationships with the concentrations of nutrients in the sediment. These nutrients, which are brought into the bay by rivers and streams that discharge into the inner zone, are initially trapped in organic matter and are released as ions available to primary producers, favouring the entire local food chain (Vanni et al. 2006). The high occurrence of *G. genidens*, mainly in the inner parts of the bay, seems to be related to a series of factors associated with its biology, such as its generalist feeding habit, to which large amounts of particulate organic matter, among other items, were observed in the diet (Denadai et al. 2012). Moreover, marine catfish of the family Ariidae tend to be among the most abundant groups of fish in the inner zones of tropical bays, characterized by muddy substrate and shallow water depths, and low water transparencies and salinities (Azevedo et al. 1999). This pattern can also be related to the reproductive strategy of these species that spawn in low salinity waters, such as lower river reaches and coastal lagoons (Reis 1982; Gomes et al. 1999; Condini et al. 2019).

Anchoa januaria, *A. tricolor* and *Atherinella brasiliensis* were found in high abundance throughout the bay. These high numbers of individuals shows that Sepetiba Bay offers suitable conditions for these fish in their early life stages, mainly in the middle bay zone, which despite the smaller number of recorded species and the lower environmental heterogeneity, contained a remarkably high number of larvae of *Anchoa* spp. and *Atherinella brasiliensis*. This suggests that environmental heterogeneity is not the exclusive driver of fish community structure. The middle bay zone, despite the lower environmental heterogeneity, has certain factors that guarantee to the occurring species, a great possibility of success in their initial stages of life, such as a higher concentration of phosphorus, a main driver to primary productivity (Nakashima et al. 2011). In addition, this zone is relatively better protected against high hydrodynamic variation (e.g. high waves and tides) by islands close to the beaches compared with the other two zones. Such 'stability' may help in the development of larvae and early-stage individuals, thus functioning as efficient nursery areas.

Some species of the family Carangidae, such as the pompano *Trachinotus carolinus* and the leatherjack *Oligoplites saurus* occurred mostly in highly transparent

waters with low sediment nutrient concentrations of the outer bay zone. These species have morphological features adapted to highly hydrodynamic environments that favour their occurrence in bay outer zones and in oceanic beach surf zones (Clark et al. 1996; Palmeira and Monteiro-Neto 2010).

Our results are a step for understanding responses of species to environmental variations at local scale in shallow waters of a tropical bay, which seems to be an important initial approach to investigate the effect of some nearshore anthropogenic activities. Although this study was restricted to the shallow coastal area of the bay (littoral), it brought comprehensive information on the ichthyofauna, as this area is used mostly by juvenile fish, even by those species that in sub-adult and adult stages use the water column in deeper areas. However, we recognize the limitation of extending our findings to other areas of the bay, as well as the methods used, in sampling and statistical treatment, which did not aim at predictive aspects, but rather at the accurate investigation of associations between fish and environmental conditions. Integration between environmental conditions and fish species distribution seems to be a suitable way to generate information to help conserve these resources (Whittaker et al. 2005; Anderson et al. 2011). Despite chronic anthropogenic impacts suffered by tropical estuarine areas, these ecosystems are resilient and still support a relatively rich ichthyofauna, as in the case of the present study. Our results serve as a 'caution' to reduce the urbanization effects on these environments that sometimes can increase habitat heterogeneity and species richness and suggest that strategies for the conservation of biodiversity in tropical bays should take this into account in their policies. The 'weak' relationship suggests that the ecosystems may have been in the 'early stages' of human influences and managers should consider that anthropogenic impacts would reduce beta diversity because continued degradation would lead to natural habitat reduction.

Acknowledgements

The authors thank technicians from the Laboratory of Fish Ecology for helping in fieldwork. We also thank Dr Roy Kropp and two anonymous reviewers for valuable comments that help to strength the quality of the manuscript. This study was supported by the Project Pesquisa Marinha e Pesqueira, a compensatory measure established by Conduct Adjustment Term responsibility of the PetroRio Company, conducted by the Federal Public Ministry – MPF/RJ, with the implementation of the Fundo Brasileiro para a Biodiversidade (FUNBIO, Proc. 016/2017). This research was conducted under SISBIO Collection of Species Permit number10707 issued by ICMBio, Brazilian Environmental Agency.

Ethical approval

All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted (Universidade Federal Rural do Rio de Janeiro, Brazil, Animal Care and Use Committee, Protocol # 11874).


Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This study was part of the Project Pesquisa Marinha e Pesqueira, a compensatory measure established by Conduct Adjustment Term responsibility of the PetroRio Company, conducted by the Federal Public Ministry – MPF/RJ, with the support of the Fundo Brasileiro para a Biodiversidade (FUNBIO, Proc. 016/2017).

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