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Spatial patterns of beta diversity in marine benthic assemblages from coastal areas of southern Brazil and their implications for conservation

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ABSTRACT

Beta diversity helps to understand changes in species composition over space and time, with two key components: nestedness (hierarchical pattern in richer sites) and turnover (species replacement due to niche or dispersal differences). It measures the loss or gain of species (nestedness) and species replacement (turnover) when comparing two or more spatial/temporal/environmental units. As both components require different species conservation strategies, assessing which of them the communities are organized is an important tool for this purpose. Our study aimed to evaluate which two components of beta diversity (nestedness or turnover) are responsible for structuring invertebrate and fish assemblages on the southern coast of Brazil. This region is historically recognized as a shrimp trawling area, a type of fishing with negative impacts on marine biota, such as the removal of species and habitat destruction. Our results suggest that the overall beta diversity values demonstrated a high environmental heterogeneity among the sampled areas. The most significant fraction of the general beta diversity for both assemblages is explained by the spatial turnover component. As depth increased, there was a significant rise in overall beta diversity and species turnover for fish and invertebrate assemblages. In contrast, there were no significant correlations among the nestedness component, the geographical distance and depth. In water mass conditions, fish assemblage decreased with rising chlorophyll and decreasing temperature. Elevated marine phosphate and thick sediments adversely impacted invertebrate composition. Additionally, invertebrate richness showed a positive correlation with fine sand grains. The research conducted along the southern coast of Brazil suggests the utmost importance of these regions in terms of species conservation. Here, the dominant influence of the turnover component shapes the organization of subtropical marine benthic assemblages. Furthermore, these areas receive frequent visits from migratory species, further accentuating their ecological significance.

1. Introduction

Beta diversity serves as a valuable tool for comprehending spatial and temporal variations in species composition, providing insights into the underlying processes shaping communities (Whittaker, 1972; Si et al., 2015). These variations can be attributed to two distinct components: nestedness and turnover. Nestedness occurs when sites with lower taxonomic richness are subsets of those with higher richness, displaying a hierarchical pattern (Wright et al., 1997; Ulrich and Gotelli, 2007). In contrast, turnover refers to the replacement of species across different sites, arising from differences in niche characteristics and/or dispersal abilities (Si et al., 2015). Distinguishing between these two components is crucial for effective management, as they may require different conservation strategies. Prioritizing locations with high taxonomic richness is beneficial when nestedness is prominent, whereas conserving multiple distinct areas, regardless of richness, becomes important in the case of

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turnover (Wright et al., 1997; Baselga, 2010).

In response to global concerns about habitat loss, many studies have employed beta diversity components to evaluate the processes shaping communities within their respective ecosystemsand to discern underlying patterns. These studies have concluded that beta diversity components in vertebrate and invertebrate communities are influenced by specific factors, including habitat isolation, habitat richness, geographical distances between areas, and the dispersal capacity among species (Angeler, 2013; Si et al., 2015; Iacarella et al., 2018; Pinheiro et al., 2019). However, a critical knowledge gap persists regarding the structure of species communities in coastal ecosystems (Iacarella et al., 2018). These environments are globally paramount, sustaining a significant portion of the world's population through the provision of essential food resources, access to maritime trade and transport, and fertile agricultural land, all while facing substantial threats (Hugo, 2011; Neumann et al., 2015; Iacarella et al., 2018). For instance, bottom trawling disrupts seabed habitats and communities that rely on these sites for survival (Blanchard et al., 2004; Barrilli et al., 2021). These impacts involve substantial alterations in the substrate, disrupting both the composition of benthic communities and the essential processes of matter and energy transfer within coastal ecosystems. (Bellido et al., 2011; Pusceddu et al., 2014; Keledjian et al., 2014). Moreover, intensive fishing can impact species abundance, biomass, and behaviour, decrease biodiversity, favour the dominance of generalist species, and lead to the disappearance of more sensitive ones (Barrilli et al., 2021).

On the southern coast of Brazil, numerous localities have traditionally depended on small-scale trawling, with shrimp being the primary resource harvested by fishing communities (Pezzuto et al., 2008; Branco et al., 2013; Serafini et al., 2014). This fishery occurs place in regions with depths of up to 30 m, and is carried out extensively along the coast, playing a vital sociol-economic role in many coastal communities (Graça-Lopes et al., 2007; Branco et al., 2013). These areas are characterized by high species richness, an abundance of young individuals, and similar oceanographic conditions, yet the composition of catches varies considerably across fishing sites (Bernardes-Júnior et al., 2011; Branco et al., 2015). Hence, there is a need to understand the mechanisms that shape species communities in regions affected by fishing.

Therefore, this study aims to comprehensively assess the spatial patterns of beta diversity and its components (nestedness and turnover) in benthic macroinvertebrate and fish communities along the southern coast of Brazil, supporting monitoring and conservation efforts. To achieve this, we utilized data from species compositions in these areas to: 1 - Detect general beta diversity and its components for the benthic fish and invertebrate assemblages; 2 - Assess how beta diversity components change with depth and geographic distance; and 3 - Evaluate both beta diversity and taxonomic richness in relation to environmental variables related to water mass and sediment seabed.

2. Material and methods

2.1. Study area

The study area covers the northern region of the central coast of Santa Catarina, specifically the municipal boundaries of Balneário Barra



Fig. 1. Study locations along the central-northern coast of Santa Catarina State (Southern Brazil). Sampled areas: I- Balneário Barra do Sul, II- Penha and, III- Porto Belo. Letters - sampling at different sites.

do Sul, Penha and Porto Belo (Fig. 1). Notably, this area is significant for artisanal fishing of the shrimp *Xyphopenaeus kroyeri* along the Brazilian coast (Branco, 2005). The prevailing wind patterns in the study area are south-westerly during the winter and north-easterly during the rest of the year (Araújo et al., 2006). The regional water mass is characterized by coastal waters that receive substantial inputs of nutrients from the rivers Santa Catarina state. Also, the Brazilian tropical waters current influence the area during the summer and fall, while the Central Water of the South Atlantic (ACAS) is observed in the lower layers of the water column during the summer months (Resgalla and Schettini, 2006). Finally, the bottom sediment composition is quite variable, causing great habitat heterogeneity along Barra do Sul to Porto Belo (Barrilli et al., 2021).

2.2. Samplings

Between 2009 and 2010, we collected samples of fish and benthic invertebrates at 18 sampling points along 80 km between the marine areas belonging to Barra do Sul (A - F), Penha (G - L) and Porto Belo (M -R). Sampling was carried out quarterly in all sampling points (n = 36)using an artisanal trawler equipped with double doors (Double-rig) at depths varying between 10 and 30 m, in accordance with the methodology used in previous studies (Sedrez et al., 2013; Branco et al., 2015; Barrilli et al., 2021). At each sampling point, bottom water samples were taken with a vertical van Dorn bottle, and temperature and salinity measurements were obtained with a thermometer (accurate to 0.1 °C) and a refractometer (accurate to 0.5 %). Finally, the benthic samples were carefully preserved in ice coolers and transported, along with water and sediment samples, to the biology laboratory at the Technological Sciences Center of the Earth and Sea. (Univali - Itajaí - SC). There, with the invaluable assistance of specialists, the samples were meticulously sorted and identified to the finest taxonomic resolution possible. This entire procedure was authorized by the SISBIO license (nº 324,642).

2.3. Data analysis

2.3.1. Environmental variables

Seven parameters were analysed in the water samples, including bottom temperature, salinity, silicon dioxide (SiO₂), ammonia (NH₄⁺), nitrite (NO₂⁻), phosphate (PO₄³⁻) following the method described in APHA (1998), and chlorophyll - a analysis according to Mantoura et al. (1997). For sediments analysis, the screening and pipetting methods described by Suguio (1973) were employed, and the particle size measurements followed the parameters established by Folk and Ward (1957), as well as the texture classification proposed by Shepard (1954). To quantify the calcium carbonate and organic matter, the gravimetric method was applied (Suguio, 1973) and to quantify the carbonate content, 100 g of sample were exposed to a solution of hydrochloric acid (HCl - 10%). Finally, the organic matter content was determined by loss on ignition (8 h at 800 °C). To assess statistical differences in environmental conditions between the municipal limits, depths, water and sediment data were subjected to the PERMANOVA (Two-way) analysis (Anderson, 2001), using the Euclidean distance method, with 999 permutations.

2.3.2. Species composition

To classify the species based on their occurrences, the adapted modified constancy index (Dajoz, 1983) was employed, categorizing the species into the following groups: constant species - present in over 50% of the samples; common species - present in 25–50% of the samples; and rare species - present in less than 25% of the samples.

2.3.3. Partitioning the turnover and nestedness components of beta diversity Beta diversity was partitioned into two distinct components based on the average dissimilarity among the 18 collection sites, following the methodology outlined in Baselga (2010). Using a presence/absence

matrix of collected species, this approach separates Sørensen's dissimilarity (β_{sor}) between assemblages into two additive components. These components capture spatial turnover (β_{sim}) and dissimilarities resulting from nestedness (β_{nes}). Simpson's dissimilarity index (β_{sim}) quantifies species turnover independent of richness gradients (McKnight et al., 2007; Si et al., 2015). When nestedness is absent, β_{sor} and β_{sim} have equal values, and their difference represents the component obtained by subtraction beta diversity, denoted as $\beta_{nes} = \beta_{sor} - \beta_{sim}$ (see Baselga, 2010). To compare dissimilarity in fish and marine invertebrates assemblages between the areas, a standard resampling procedure based on Baselga's analysis was performed, involving 100 random samples drawn from the entire set of 18 sampled areas. This procedure was conducted separately for the fish and invertebrate matrices, resulting in average beta diversity values (β_{sor}) and its components (β_{sim} and β_{nes}) (Baselga, 2012; Si et al., 2015). Subsequently, the proportion of the nestedness component was calculated for each assemblage to assess the relative contribution to overall beta diversity: $\beta_{ratio} = \beta_{nes} / \beta_{sor}$. A β ratio value <0.50 indicates that beta diversity is primarily driven by species turnover, while a $\beta_{ratio} > 0.50$, indicates that nestedness plays a role (Dobrovolski et al., 2012; Si et al., 2015). The calculation of beta diversity and its components was performed using the "betapart" statistical package (Baselga and Orme, 2012) in the R software environment (R Development Core R Core Team, 2020).

Generalized linear models were employed to investigate the potential spatial effects of depth and geographic distance on beta diversity and its components across the sampled sites. Furthermore, we used GLMs to look for the relationship between beta diversity and taxonomic richness with environmental variables related to water mass and bottom sediment composition (grain size). For this, we used the *glm* function from the "MASS" package, assuming a Gaussian distribution with a log link and quasipoisson distribution (Oksanen et al., 2020) to spatial and environmental variables, respectively. Additionally, pseudo R2 values were calculated using the *pR2* function from the "pscl" package for spatial glm analyses. Analyses were conducted in the R software environment (R Development Core R Core Team, 2020).

3. Results

3.1. Environmental variables

Based on the mean values of water and sediment variables (Table A1), our Permanova analysis found no significant differences between the sites and the depths in the water mass (Table 1). However, we did detect significant differences in mean sediment grain sizes between locations and depths. Specifically, we found that grain sizes were larger in Balneário Barra do Sul compared to Penha (F = 10.34, p < 0.01) and Porto Belo (F = 12.47, p < 0.01). Furthermore, our analysis revealed that the average grain sizes at a depth of 10 m were significant larger than those at a depth of 30 m (F = 4.20, p = 0.02). However, there

Table 1

Results of the multivariate analysis of variance (PERMANOVA - two-way) of the water and sediment parameters between the areas and seasons sampled. * Significant (p < 0.05).

Water Mass	Sum of sqrs	df	Mean square	F	Р
Areas	12,392	8	1549.1	0.074	0.575
Depths	826.64	2	413.3	0.020	0.914
Interaction	1.4298E05	16	8936.3	0.424	0.087
Residual	1.8954E05	9	21060.0		
Total	59,777	35			
Grain size	Sum of sqrs	df	Mean square	F	Р
Areas	0.12749	2	0.063744	2.072	0.0001*
Depths	0.036839	2	0.018419	5.986	0.0039*
Interaction	0.066361	4	0.01659	5.392	0.0021*
Residual	0.083075	27	0.0030769		
Total	0.31376	35			

were no significant differences between the average grain sizes at depth of 10 vs. 20 m (F = 2.14, p = 0.20) or depth of 20 vs. 30 m (F = 0.80, p = 0.38). Our analysis found no significant differences in water conditions between sites and depths, but significant differences in sediment grain sizes were detected.

3.2. Species composition

Our study found that the invertebrate assemblages varied from 5 to 25 (16.5 \pm 5.5) species between the sampled areas, totalling 41 different species. Among the registered species, 34.0% were constant, 27.0% common, and 39.0% rare (Table A2). Notably, Porto Belo had the highest number of invertebrate species sampled, with a total of 90.2%, followed by Penha (75.6%) and Balneário Barra do Sul (68.3%).

Similarly, our analysis of fish assemblages found that they ranged from 12 to 40 (25.8 ± 8.0) species between the sampled areas with a total of 21% constant, 24% common, and 55% rare species recorded (Table A3). Samples in Porto Belo represented the highest percentage of all fish species collected between the areas at 78.2%, followed by Balneário Barra do Sul at 64.4%, and Penha at 57.5%.

3.3. The beta diversity (β_{sor}) components: nestedness (β_{nes}) and turnover (β_{sim})

For the invertebrate assemblages (Fig. 2 a - c), our analysis revealed that the sites with the highest beta diversity (β_{sor}) and nestedness component (β_{nes}) values were among the groups with the lowest species richness specifically the Balneário Barra do Sul group (C_{20} , E_{30} and F_{30}) and other sites. Interestingly, we found that the turnover component (β_{sim}) was higher among the Porto Belo groups (Q_{30} and R_{30}).

Similarly, for the fish assemblages (Fig. 2 d – f), our analysis showed that the Balneário Barra do Sul (E_{30} and F_{30}) and Penha (K_{30} and L_{30}) groups had higher β_{sor} and β_{sim} values compared to each other and to other sites. The nestedness component (β_{nes}) was also higher among the group formed by samples from Barra do Sul and Porto Belo areas (C_{20} , Q_{30} , N_{10} M_{10} , R_{30}).

The average beta diversity values (β_{sor}) were found to be lower for invertebrate assemblages (0.70 \pm 0.02) than for fish assemblages (0.75 \pm 0.02) (Table 2). The spatial turnover component (β_{sim}) was found to be the main contributor to the total dissimilarity in both fish and marine invertebrate assemblages, with a higher value for fish (0.67 \pm 0.03) compared to marine invertebrates (0.56 \pm 0.03). Conversely, the nest-edness component (β_{nes}) resulted in a lower value for the fish assemblage (0.08 \pm 0.02) compared to marine invertebrates (0.13 \pm 0.02). Interestingly, due to the high turnover values, the ratio between the



Fig. 2. Beta diversity (β_{sor}) , turnover (β_{sim}) and nestedness (β_{nes}) clusters between the invertebrates (a, b, c) and fish (d, e, f) assemblages.

Table 2

Results of the beta diversity metric (β_{sor}), nestedness (β_{nes}) and Turnover (β_{sim}) components, between the sampled areas and standard deviation. β_{ratio} - Ratio between β_{nes} and β_{sor} ($\beta_{ratio} = \beta_{nes/} \beta_{sor}$).

Assemblages	B _{sor}	β_{nes}	β_{sim}	β_{ratio}
Invertebrates Fish	$\begin{array}{c} 0.70\pm0.02\\ 0.75\pm0.02\end{array}$	$\begin{array}{c} 0.13\pm0.02\\ 0.08\pm0.02\end{array}$	$\begin{array}{c} 0.56 \pm 0.03 \\ 0.67 \pm 0.03 \end{array}$	$\begin{array}{c} 0.19\pm0.04\\ 0.11\pm0.02\end{array}$

nestedness component and the beta diversity was less than 0.50 in both groups, resulting in a lower value for fish assemblages (0.11 \pm 0.02) compared to marine invertebrates (0.19 \pm 0.04).

In our analysis, both the invertebrate (Fig. 3) and fish (Fig. 4) assemblages exhibited similar patterns concerning beta diversity values (β_{sor}) and the turnover component (β_{sim}). We observed non-significant correlations between distance and significant correlations observed with depth. Interestingly, the nestedness component (Fig. 3b and e) did not result in significant correlations when considering distances and depths between the areas. Furthermore, the beta diversity of fish assemblages varied significantly as a function of temperature and chlorophyll *a*, while the beta diversity of marine invertebrates varied as a function of marine phosphate and grain size (Table A4). Finally, invertebrate taxonomic richness demonstrated a significant relationship with sediment grain size, while fish richness did not result in significant relationships with any environmental variable.

4. Discussion

Our results reveal that the composition and diversity of fish and

invertebrate assemblages are primarily characterized by rare species confined to specific sites. Furthermore, our findings indicate that turnover plays a central role in shaping beta diversity within these sites. This result demonstrates a significant shift in composition of marine assemblages between locations, primarily driven by species substitution and, to a lesser extent, differences in species richness (Si et al., 2015).

In the present study, turnover, referring to the replacement of species in different locations, is likely influenced by different microhabitats resulting from disparities in the structure of the sediments between these sites. The sediment differences between locations form a gradient of environmental quality along the Balneário Barra do Sul (low quality) to Porto Belo (high quality), in addition, the sediment to positively influencing species diversity with smaller sand grain sizes and large quantities of organic matter on the seabed (Barrilli et al., 2021). In our findings, the site with the largest grain of sand (Barra do Sul) had lower species richness compared to Penha and Porto Belo. These results demonstrate that substrates with low heterogeneity in the sediment (more sand and little organic matter) harbor fewer species. This occurs because benthic fauna is positively influenced by heterogeneous sediments (i.e. finer sand and more organic matter), as they have essential resources involved in the feeding and shelter processes of most species (Mayor et al., 2012: Pusceddu et al., 2014; Barrilli et al., 2021).

Ecological interactions between species may also contribute to the heterogeneity of species composition. Higher trophic levels of marine benthic assemblages, such as fish and some macroinvertebrates, are more influenced by competition (Menge and Sutherland, 1976). In instances of intense competition, species tend to repel each other, resulting in less overlap between them and, consequently, a more significant



Fig. 3. Relationships of beta diversity (β_{sor}) and its componentes, nestesdness (β_{nes}) and turnover (β_{sim}), with the geographical distance between the areas and depths sampled for the marine invertebrate assemblages.



Fig. 4. Relationships of beta diversity (β_{sor}) and its componentes, nestesdness (β_{nes}) and turnover (β_{sim}), with the geographical distance between the areas and depths sampled for the marine fish assemblages.

change in composition (species turnover) along the environmental gradient (Wei et al., 2012). Sedrez et al. (2013) and Sabinson et al. (2015) have already reported competition over the same resources in these areas among different groups of organisms such as fish and invertebrates that compete for breeding grounds and are subject of common predation by small invertebrates like polychaetes, molluscs and crustaceans. Trawl fishing, which targets shrimp as the main catch, can also act as a competitive force in the marine benthic ecosystem, promoting the selection of benthic species. This fishing modality can act as a top-down control by removing dominant organisms, which promotes a change in competitive interactions between species (Blanchard et al., 2004; Van Denderen et al., 2013). As a result, trawl fishing may contribute to changes in the composition and diversity of benthic assemblages (Barrilli et al., 2021).

In our study, a large portion of the fish we sampled are either estuarine-opportunistic or rare species. This might lead to more turnover of species in these areas. Interestingly, the β ratio value was relatively lower for fish compared to invertebrates, possibly suggesting their greater dispersal capability compared to marine invertebrates. Species with higher mobility are more likely to spread to new places and overcome ecological barriers. Greater dispersal capacity can lead to differences in species composition among sites (Si et al., 2015). Regarding nesting components, there was a tendency for higher values in the invertebrate assemblages. Consequently, the invertebrate community may be more susceptible to extinctions resulting from habitat loss (Si et al., 2015). Additionally, the small proportion of nested estuarine-opportunistic ichthyofauna may also be impacted.

We observed that beta diversity increased significantly with depth in

both assemblages. Notably, only the fish assemblages showed a significant positive correlation between spatial turnover and depth. Conversely, no significant relationship was observed between the nestedness components and geographical distance between the areas for either assemblage. These results confirm findings that geographical distance has a weaker impact on species composition than depth, as shown by Zintzen et al. (2017) in their study on marine beta diversity. The authors further assert that shallow environments tend to be more heterogeneous because they are geologically unstable, promoting species rotation. Furthermore, several limiting physical and biological factors (e.g., competition, predation, temperature, and hydrostatic pressure) are correlated with water depth (Rex et al., 2006; Wei et al., 2010, 2012). The relationship between beta diversity and environmental variables showed in our study showed that high chlorophyll concentrations and low temperatures tend to homogenize fish assemblages (i.e., decrease fish assemblages), while high marine phosphate concentrations and thick sediments tend to homogenize invertebrate assemblages. Furthermore, the richness of invertebrates was greater in finer grains, aligning with results from Costa et al., (2007); Kolling and Ávila-da Silva (2014), demonstrating aggregations of species in finer sediments.

The dominance of turnover suggests that all sampled areas possess high conservation value and should be prioritized accordingly. In this case, we recommend selecting areas with the highest richness, combining them with those of lower richness but exhibiting high levels of spatial turnover to represent all species. It is crucial to note that trawling impacts various groups, not solely the target species (shrimp), potentially leading to local extinctions in the future. Moreover, we also

recommend additional studies on the life history of marine species (e.g., life cycle, growth, feeding and reproduction) since many species represented in our analysis lack this type of information. Therefore, we suggest that conservation strategies utilize the beta diversity partition as an analytical tool and incorporate species' conservation status as a criterion for prioritizing areas.

CRediT authorship contribution statement

Germano Henrique Costa Barrilli: Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Formal analysis, Conceptualization. Julia Gomes do Vale: Writing – review & editing, Validation. Samira Chahad-Ehlers: Writing – review & editing. José Roberto Verani: Visualization, Supervision, Resources, Funding acquisition, Conceptualization. Joaquim Olinto Branco: Supervision, Resources, Project administration, Investigation, Funding acquisition.

Appendix A

Table A1

Mean and standard deviations values of abiotic variables in study areas

Declaration of competing interest

The author(s) declare(s) that they have no conflict of interest related to the publication of this manuscript.

Data availability

No data was used for the research described in the article.

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	Balneário Barra	do Sul		Penha			Porto Belo		
	10 m	20 m	30 m	10 m	20 m	30 m	10 m	20 m	30 m
Salinity (%)	$\textbf{32.08} \pm \textbf{1.19}$	33.95 ± 0.69	33.48 ± 1.07	32.88 ± 1.20	34.63 ± 0.71	32.68 ± 0.40	33.35 ± 0.53	33.25 ± 2.11	32.60 ± 0.62
Temperature (°C)	21.50 ± 1.29	20.25 ± 0.50	15.88 ± 1.44	23.38 ± 1.80	20.03 ± 0.05	16.63 ± 1.97	$\textbf{22.38} \pm \textbf{1.49}$	19.75 ± 1.50	18.88 ± 0.25
Chlorophyl a (mg. L^{-1})	$\textbf{2.58} \pm \textbf{1.81}$	1.86 ± 1.54	1.48 ± 1.76	1.83 ± 0.34	1.09 ± 0.49	$\textbf{2.02} \pm \textbf{1.26}$	1.21 ± 0.72	0.93 ± 0.32	$\textbf{0.76} \pm \textbf{0.25}$
SiO_2 (mg.L ⁻¹)	46.85 \pm	$47.27~\pm$	$37.54 \pm$	57.88 \pm	$28.66~\pm$	$47.87~\pm$	$39.31~\pm$	72.87 \pm	$63.94 \pm$
	26.06	21.18	35.84	18.02	12.17	26.72	37.54	55.51	60.18
$NH4+(mg.L^{-1})$	$25.22 \pm$	15.29 ± 7.24	55.62 \pm	15.85 ± 7.96	$21.32~\pm$	13.76 \pm	$26.29~\pm$	42.13 \pm	$\textbf{28.24} \pm$
	16.02		30.34		11.34	10.84	10.95	42.34	24.35
NO_2 -(mg.L ⁻¹)	0.16 ± 0.14	0.11 ± 0.07	0.23 ± 0.22	0.26 ± 0.24	0.53 ± 0.35	0.35 ± 0.26	0.16 ± 0.08	0.55 ± 0.34	0.09 ± 0.03
PO4 ³⁻ (mg.L ⁻¹)	$\textbf{0.48} \pm \textbf{0.11}$	0.56 ± 0.19	0.65 ± 0.15	$\textbf{0.48} \pm \textbf{0.11}$	0.51 ± 0.11	0.72 ± 0.20	$\textbf{0.60} \pm \textbf{0.18}$	0.53 ± 0.15	$\textbf{0.78} \pm \textbf{0.18}$
Grain size (mm)	$\textbf{0.03} \pm \textbf{0.01}$	$\textbf{0.16} \pm \textbf{0.09}$	$\textbf{0.25}\pm\textbf{0.14}$	$\textbf{0.02} \pm \textbf{0.01}$	$\textbf{0.02} \pm \textbf{0.00}$	$\textbf{0.04} \pm \textbf{0.01}$	$\textbf{0.03} \pm \textbf{0.02}$	$\textbf{0.00} \pm \textbf{0.01}$	$\textbf{0.01} \pm \textbf{0.01}$

Table A2

Invertebrate species composition in shrimp trawling areas. Legend: Areas – Balneário Barra do Sul (A-F), Penha (G-L) and Porto Belo (M-R); Depths – 10 m, 20 m, and 30 m. Letters - sampling at different sites.

Balneário Barra do Sul Penha Porto Belo		
10 m 20 m 30 m 10 m 20 m 30 m 10 m 20 m 30 m		
Taxon A B C D E F G H I J K L M N O P O	<u>)</u> R	%
CNIDARIA		
CHIROPSALMIDAE		
Chiropsalmus quadrumanus (Müller, 1859) x x x x x x x x x x x x x x x x x x x		38.9
Lychnorttiza lucerna Haeckel, 1880 x		5.6
OLINDIIDAE		
Olindias sambaquiensis Muller, 1861 x x		11.1
PELAGIIDAE		
Chrysaora lactea Eschscholtz, 1829 x		5.6
RENILLIDAE		
Renilla muelleri Kölliker, 1872 x x x x x x x x x x x x x x x x x x x	x	88.9
Rhizostoma sp x		5.6
ARTHROPODA (Crustacea)		
AETHRIDAE		
Hepatus pudibundus (Herbst, 1785) x x x x x x x x x x x x x x x x x	х	77.8
ALPHEIDAE		
Alpheus sp x x x x x		22.2
DIOGENIDAE		
Dardanus insignis (de Saussure, 1858) x x x x x x x x x x x x x x x x x x x	х	77.8
Dardanus venosus (H. Milne Edwards, 1848) x x x x x x		22.2

Table A2 (continued)

	Shri	mp Tra	awling	areas															
	Balr	neário I	Barra d	o Sul			Pen	ha					Por	to Belo					
	10 r	n 20 m	30 m				10 r	n 20 m	30 m				10 r	n 20 m	30 m				
Taxon	A	В	С	D	Е	F	G	Н	Ι	J	К	L	М	Ν	0	Р	Q	R	%
Loxopagurus loxochelis (Moreira, 1901)			x						x						x	x			22.2
EPIALTIDAE																			
Libinia spinosa (H. Milne Edwards, 1834) HIPPOLYTIDAE							x						х				х	x	22.2
Exhippolysmata oploforoides (Holthuis, 1948) LEUCOSIIDAE	х	х					х	х							х			х	33.3
Persephona lichtensteinii Leach, 1817							х						х	х	х	х	х		33.3
Persephona mediterranea (Herbst, 1794)			х			х	х		x	х			х	х	х	х			50.0
Persephona punctata (Linnaeus, 1758) PENAEIDAE	х						x		x	х				х		х			33.3
Artemesia longinaris (Bate, 1888)		х	х				х	х					х	х	х	х	х	х	55.6
Farfantepenaeus brasiliensis (Latreille, 1817)				х			х			х			х	х	х	х	х	х	50.0
Litopenaeus schmitti (Burkenroad, 1936)	х		х										х	х	х	х		х	38.9
Rimapenaeus constrictus (Stimpson, 1871)														х			х	х	16.7
Xiphopenaeus kroyeri (Heller, 1862)	х	х	х		х	х	х	х	х		x	х	х	х	х	х			77.8
PORCELLANIDAE																			
Porcellana sayana (Leach, 1820) PORTUNIDAE										х	х				х				16.7
Arenaeus cribarius (Lamarck, 1818)	х	x	x								x			x					27.8
Callinectes danae (Smith, 1869)	х				х		х	x	x	х	x	x	х	x	x	x			66.7
Callinectes ornatus (Ordway, 1863)	х	x	x	х	х	х	х	x	x	х	x	x	х	x	x	x	x	x	100.0
Callinectes sapidus Rathbun, 1896																	x		5.6
Portunus spinicarpus (Stimpson, 1871)										х		x				x	x	x	27.8
Portunus spinimanus (Latreille, 1819) SERGESTIDAE			x		x			х	x				x	x		x	x	x	50.0
Acetes americanus (Ortmann, 1893) SICYONIIDAE							x								x	x			16.7
Sicyonia dorsalis (Kingsley, 1878) SOLENOCERIDAE		x	х				x		x	х			х	х	x	x	x	x	61.1
Pleoticus muelleri (Bate, 1888)	x	x	x				x	x					x		x	х	х	x	55.6
SQUILIIDAE Sauilla empusa							x												5.6
ECHINODERMATA																			0.0
ARBACIIDAE																			
Arbacia punctulata (Lamarck, 1816) ASTROPECTINIDAE														x					5.6
Astropecten brasiliensis Muller and Troschel, 1842																	x	x	11.1
Astropecten marginatus (Gray, 1840) LUIDIIDAE	х						x	х	x	x	х	х	x	x	x	x	х	x	72.2
Luidia senegalensis (Lamarck, 1816)								х		х			х						16.7
MOLLUSCA																			
LOLIGINIDAE																			
Lolliguncula brevis (Brainville, 1823)	х	x	x	х	х		х	x	x	х	x	x	х	x	x	x	x	x	94.4
Dorytheuthis sanpaulensis (Brakoniecki, 1984)			х				х	х	х	х	x	х				х	х	х	55.6
Dorytheuthis plei (Blainville, 1823) NASSARIIDAE			х	х	х		х				х	х					х	х	44.4
Buccinanops gradatum (Deshayes, 1844) OLIVIDAE	x	x					x	x	x	x	x	x	x		x	x	x	x	72.2
Olivancillaria urceus (Röding, 1798)	х	x	x				x	х	x	x	х	х			x				55.6
RICHNESS (S)	18	14	18	7	9	5	25	17	16	17	14	13	21	19	23	23	18	20	

Table A3

Fish species composition in shrimp trawling areas. Legend: Areas – Balneário Barra do Sul (A-F), Penha (G-L) and Porto Belo (M-R); Depths – 10 m, 20 m and 30 m. Letters - sampling at different sites.

	Shrin	np Tra	wling ar	eas															
	Balne	eário B	arra do	Sul			Penh	a					Porto	Belo					
	10		20		30		10		20		30		10		20		30		
	m		m		m		m		m		m		m		m		m		
Taxon	A	в	С	D	E	F	G	н	I	J	К	L	М	N	0	Р	Q	R	%
CHONDRICHTHYES																			
ARHYNCHOBATIDAE																			
Atlantoraja cyclophora Regan 1903										x		х				х	x	x	27.8
Rioraaja agassizi Müller and Henle,					x	х											x	x	22.2
1841																			
RHINOBATIDAE																			

(continued on next page)

Table A3 (continued)

	Shrin	np Trav	vling ar	eas															
	Balne	ário Ba	arra do	Sul			Penh	a					Porto	o Belo					
	10 m		20 m		30 m		10 m		20 m		30 m		10 m		20 m		30 m		
Taxon	A	В	С	D	Е	F	G	Н	I	J	K	L	М	N	0	Р	Q	R	%
Zapteryyx brevirostris			х	х		x					x			х	x				33.3
RHINOPTERIDAE																	v		E 6
OSTFICHTHYES																	x		5.0
ACHIRIDAE																			
Achirus declivis (Chabanaud, 1940)	x		х				х						х	х					27.8
Achirus lineatus (Linnaeus, 1758)			х		х								х	х		х			27.8
Gymnachirus nudus Kaup 1858												х							5.6
ARIIDAE Arius spivii (Agassiz 1829)															v				5.6
Genidens barbus (Lacepède, 1803)							x	x						x	x	х	x		33.3
Genidens genidens (Valenciennes,							х						х						11.1
1829)																			
BALISTIDAE																			
Balistes capriscus Gmelin, 1789						х													5.6
Porichthys porosissimus (Cuvier 1829)								x	x	x		x	x		x	x	x	x	50.0
CARANGIDAE																			
Caranx crysos (Mitchill, 1815)										x									5.6
Chloroscombrus chrysurus (Linnaeus,													х						5.6
1766)																			- (
Schneider 1801)																х			5.6
Selene setapinnis (Mitchill, 1815)	x	x	x	х		x	x	x	x	x		x	x	x	x		x		77.8
Selene vomer (Linnaeus, 1758)	x	x					x	x	x				x	x					38.9
CLUPEIDAE																			
Harengula clupeola (Cuvier, 1829)							х	х											11.1
Sardinella brasiliensis (Steindacher,																	х		5.6
1879) CONGRIDAE																			
Conger orbignyanus (Valenciennes,			х												x		x	x	22.2
1837)																			
CYNOGLOSSIDAE																			
Symphurus tessellatus (Quoy and																х		х	11.1
Gaimard, 1824)																			
Dactylopterus volitans (Linnaeus,										x	x		x	x					22.2
1758).																			
DIODONTIDAE																			
Cyclichthys spinosus (Linnaeus, 1758)			х					х			х	х			х		х		33.3
ENGRAULIDAE	v							v											11 1
Anchoviella lepidentostole (Fowler.	А						x	x	x	x						x		x	33.3
1991)																			
Lycengraulis grossidens (Agassiz, 1829)			х										х		х				16.7
EPHIPPIDAE																			- (
(Broussonet,														х					5.6
FISTULARIDAE																			
Fistularia petimba Lacepède, 1803																		x	5.6
GERREIDAE																			
Diapterus rhombeus (Cuvier, 1829)			х	х						х				х		х	х	х	38.9
<i>Eucinostomus argenteus</i> (Baird and						х													5.6
Eucinostomus gula (Quoy and Gaimard.					x	x				x	x	x	x	x			x	x	50.0
1824)										-		-						-	
Eucinostomus melanopterus (Bleeker,																х			5.6
1863)																			
HAEMULIDAE			v																16 7
Orthopristis ruber (Cuvier, 1830)			x	x								х		x					16.7
Pomadasys corvinaeformis			x							x		x	x	x	x		x		38.9
(Steindachner, 1868)																			
LABRIDAE																			. .
<i>Xyrichtys novacula</i> (Linnaeus, 1758)					х														5.6
Stephanolenis hispida (Lippoous, 1766)		v	v			v			v	v	v	v	v	v		v	v	v	66 7
MULLIDAE		А	А			л			А	л	А	л	А	л		л	А	л	00.7
Mullus argentinae (Hubbs and Marini,										x									5.6
1935)																			

(continued on next page)

Table A3 (continued)

	Shrin	np Trav	wling ar	eas															
	Balne	eário B	arra do	Sul			Penh	ia					Port	o Belo					
	10 m		20 m		30 m		10 m		20 m		30 m		10 m		20 m		30 m		
Tayon		B				F		ц		T		T	M	N		D		D	06
	л	Б	C	D	Б	г	G	11	1	5	K	г	191	IN	0	r	Q	K	70
Gvmnothorax ocellatus (Agassiz, 1831)			x									x	x		x	x	x	x	38.9
OGCOCEPHALIDAE																			
Ogcocephalus vespertilio		х																	5.6
(Linnaeus, 1758) OPHICHTIDAE																			
Ophichthus gomesìi (Castelnau, 1855)		x					х	х									x		22.2
Ophidion holbrookii (Putmam, 1874)			х																5.6
Raneya brasiliensis (Ribeiro, 1903)														x					5.6
Citharichthys macrons Dresel, 1885		x	x	x	x	x													27.8
Citharichthys spilopterus (Günther,			x														x	x	16.7
1862)																			
Cyclopsetta chittendeni Bean, 1895																	x	x	11.1
Etropus crossotus (Jordan and Gilbert,			x	x					x	x	x	x	x	x		x	x x	x	61.1
1882)																			
Etropus longimanus Norman, 1933												х						х	11.1
Paralichthys brasiliensis (Ranzani,												x							5.6
Paralichthys patagonicus Jordan. 1890										x							x	x	16.7
Syacium micrurum Ranzani, 1842				x	х	x													16.7
Syacium papillosum (Linnaeus, 1758)			х	х	х	х		х			х	х						х	44.4
PHYCIDAE Urophycis brasiliensis (Kaup, 1858)			v				v		v				v			v	v	v	38.9
PINGUIPEDIDAE			л				л		л				л			л	л	л	30.9
Pseudopercis semifasciata (Cuvier,														х		х	x	х	22.2
1829)																			
POLYNEMIDAE Polydactilus virginicus (Linnaeus, 1758)			x										x	x	x	x			27.8
PRISTIGASTERIDAE																			_,
Chirocentrodon bleekerianus (Poey,	x		х														х		16.7
1867) Pellong harroweri (Fowler, 1917)	v	v	v	v			v	v	v	v			v	v	v	v		v	70.0
SCIANIDAE	А	А	А	А			А	А	А	А			А	А	А	А		А	, 2.2
Ctenosciaena gracilicirrhus (Metzelaar,	x		х	x	х	х		х	х	х	х	x	x	x	х	х		х	83.3
1919) Davelonchurus brasiliansis	v	v	v	v		v	v		v	v		v			v		v	v	<u> </u>
(Steindachner, 1875)	х	х	х	х		х	х	х	х	х		х	х	х	х	х	х	х	00.9
Cynoscion jamaiscensis (Vaillant and	x	х	х	x			х	х	х	x			x	x	х	х	х	х	77.8
Boccourt, 1883)																			
Cynoscion leiarchus (Cuvier, 1830)	x	v	v	v			v	v	v			v	v	v	v	v	v	v	5.6 77.8
Larimus breviceps (Cuvier, 1830)	x	x	x	x			x	x	x	x		л	x	x		x	x	x	72.2
Macrodon ancylodon (Bloch and	x	х	х				х					x	x		х		х		44.4
Schneider, 1801)																			FF 6
1758)		х	х	х						х			х	х	х	х	х	х	55.0
Menticirrhus littoralis (Holbrook, 1860)	x		x	x	x				x	x		x		x				x	50.0
Micropogonias furnieri (Desmarest,	х		х	х	х		х		х	х			х	х	х	х	х	х	72.2
1823) Stallifar braziliansis (Schultz, 1045)	v	v	v	v			v	v	v	v			v	v	v	v	v	v	77.9
Stellifer sp.	x	x	x	л		x	x	x	x	x			x	x	x	л	л	л	61.1
Stellifer (Bloch, 1790)	x	x						х					х	x					27.8
Stellifer rastrifer (Jordan, 1889)	x	х	х		х		х	х	х		х		х	х	х	х			66.7
SCORPAENIDAE Scorpaena isthmensis (Meeke and													v						5.6
Hildebrand, 1928)													А						0.0
Scorpaena plumieri Bloch, 1789											х								5.6
SERRANIDAE																			E 6
Diplectrum formosum (Linnaeus, 1766) Diplectrum radiale (Quoy and Gaimard				x	х								x						5.6 11.1
1824)																			
Dules auriga (Cuvier, 1829)												х					х	х	16.7
<i>kypticus randalli</i> Courtenay, 1967 STROMATEIDAE			х																5.6
Peprilus paru (Linnaeus, 1758)														x	х		x		16.7
SYNODONTIDAE																			
Synodus foetens (Linnaeus, 1766)					х	х											х		16.7

(continued on next page)

Table A3 (continued)

	Shrim	ıp Trav	vling are	eas															
	Balne	ário Ba	rra do S	Sul			Penha	1					Porto	Belo					
	10		20		30		10		20		30		10		20		30		
	m		m		m		m		m		m		m		m		m		
Taxon	A	В	С	D	E	F	G	Н	I	J	К	L	М	Ν	0	Р	Q	R	%
Synodus intermedius (Spix and Agassiz, 1829)					x														5.6
Trachinocephalus myops (Forster, 1801) TETRAODONTIDAE					x	x											x		16.7
Lagocephalus laevigatus (Linnaeus, 1766)	x	x	х		x			х					x	x	x		x	x	55.6
Sphoeroides greeleyi (Gilbert, 1900)			x	x	x	х			x	х		х					x	x	50.0
Sphoeroides testudineus (Linnaeus, 1758)		x	x			x	x		x	x	x	x	x	x	x	x	x	x	77.8
TRIGLIDAE																			
Prionotus punctatus (Bloch, 1793) TRICHIURIDAE			x					x	x		х	x	x		x	x	х	x	55.6
Trichiurus lepturus (Linnaeus, 1758)	х	х	x	x		х	х	х	х	х			х	х	х	х		x	77.8
RICHNESS (S)	21	20	40	22	17	18	21	23	22	26	12	23	35	34	27	28	39	36	

Table A4

Generalized linear models with relationships between beta diversity and taxonomic richness with environmental variables of fish and invertebrate assemblages sampled in the studied areas.

Beta diversity									
Fish assemblages					Invertebrates asse	emblages			
	Estimate	SE	t-value	p-value		Estimate	SE	t-value	p-value
(Intercept)	-0.681	0.050	-13.510	0.000	(Intercept)	-0.731	0.040	-18.164	0.000
Temperature	-0.185	0.078	-2.365	0.046	Temperature	-0.005	0.063	-0.079	0.939
Salinity	-0.085	0.061	-1.389	0.202	Salinity	-0.037	0.050	-0.747	0.476
Chlorophyl	0.129	0.050	2.610	0.031	Chlorophyl	0.001	0.042	0.020	0.984
SiO ₂	0.045	0.063	0.715	0.495	SiO ₂	-0.018	0.051	-0.351	0.734
NH_4^+	0.027	0.068	0.404	0.697	NH_4^+	0.090	0.055	1.633	0.141
NO_2^-	0.101	0.064	1.594	0.150	NO_2^-	-0.003	0.054	-0.059	0.955
PO4 ³⁻	0.087	0.070	1.233	0.253	PO4 ³⁻	0.141	0.056	2.512	0.036
Grain size	0.087	0.079	1.096	0.305	Grain size	0.138	0.063	2.406	0.048
Taxonomic Richne	ess								
Fish assemblages					Invertebrates asse	emblages			
-	Estimate	SE	t-value	p-value		Estimate	SE	t-value	p-value
(Intercept)	3.189	0.064	49.952	0.000	(Intercept)	2.744	0.067	41.207	0.000
Temperature	0.105	0.100	1.048	0.325	Temperature	0.163	0.093	1.740	0.120
Salinity	0.069	0.079	0.869	0.410	Salinity	0.036	0.088	0.407	0.694
Chlorophyl	0.038	0.064	0.591	0.571	Chlorophyl	-0.051	0.088	-0.579	0.578
SiO ₂	-0.005	0.087	-0.056	0.957	SiO ₂	0.078	0.089	0.874	0.407
NH_4^+	-0.019	0.089	-0.210	0.839	NH_4^+	0.004	0.094	0.048	0.963
NO_2^-	0.003	0.085	0.037	0.972	NO_2^-	0.040	0.077	0.517	0.619
PO4 ³⁻	-0.063	0.087	-0.719	0.492	PO4 ³⁻	0.087	0.089	0.983	0.355
Grain size	0.178	0.093	1.916	0.092	Grain size	-0.228	0.108	-2.113	0.049

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