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Regional patterns in species richness and taxonomic diversity of the nearshore fish community in the Brazilian coast

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ABSTRACT

The nearshore fish assemblage structures and their seasonal changes were compared between two habitats (estuarine and surf zones) in three climatic regions (Tropical, 7˚S; Transition, 23˚S; and Warm Temperate, 32˚S) encompassing ~3200 km in the Brazilian coast. Regional patterns of species richness and taxonomic distinctiveness of the fish community were also described. We expected the highest richness and lowest seasonal variation in the assemblage's structure in the Tropical region and the opposite pattern in the Warm Temperate region. The assemblage structures differed significantly among regions and habitats. In the estuarine habitats, species richness and taxonomic distinctiveness (AvTD) were highest in the Tropical (84 species, AvTD = 92.3) and lowest in the Temperate (31 species, AvTD = 73.9) region. However, in the surf zone the highest species richness and taxonomic distinctiveness were found in the Transition region (49 species, AvTD = 78.5) and the lowest in the Warm Temperate region (19 species, AvTD = 51.9). The two habitats (estuarine and surf zone) differed consistently in the three regions. No seasonal change was found in the structure for the fish assemblage in the Tropical and Transition regions. However, the assemblage structure differed significantly between the spring and summer and between the spring and autumn in the Warm Temperate region. The most significant predictors of the fish community structure were salinity for the Tropical region, temperature and salinity for the Transition region, and transparency and temperature for the Warm Temperate region. The marine fish communities presented low levels of species redundancy in the Warm Temperate region with few species fulfilling key functional roles. The data provided here are references against which to detect future ecological changes at the regional-scale patterns for the Brazilian nearshore fish community and it is important to better inform fisheries management and coastal conservation planning.

1. Introduction

Sandy beaches are the dominant coastal areas of the world and play an important role as rearing grounds for many marine fish species (Brown and McLachlan, 1990; Able et al., 2013; Oliveira and Pessanha, 2014), acting as semi-closed, self-supporting ecosystem and presenting a considerable diversity of communities. Sandy beaches in estuarine habitats are used by juveniles and adults of many resident and estuarine-dependent species for reproduction, foraging and shelter (Patterson and Whitfield, 2000; Beck et al., 2001; Able, 2005; Blaber, 2013). Due to their location between the continent and the sea and their shallow depths, estuarine areas are among the most productive ecosystems (on average $300 \, g \, C \, m^2 \, year^{-1}$, Knoppers, 1994). Surf zones, especially those located in the vicinity of estuarine areas, are also very important as rearing grounds because they can accumulate juvenile fish that may occur in the vicinity of estuary mouths during migrations between marine and estuarine environments (Dahl, 1952; Besyst et al., 1999; Able et al., 2013).

Despite the proximity of estuarine habitats and surf zones, and their roles as rearing grounds or passage areas for fish, studies comparing these two types of habitats are scarce. Clark et al. (1994) compared the ichthyofauna of estuaries and their adjacent surf zones in a temperate region in South Africa and found that juvenile fish were abundant in all areas, numerically constituting 48 and 97% of the estuarine and surf-

zone samples, respectively. Catches and effort of the commercial beach-seine fishery in a temperate bay (False Bay, 34°S) are strongly seasonal, most fish (93%) being caught in late spring, summer and early autumn and only few species being more abundant during winter (Lamberth et al., 1995). Summer peaks in fish abundance have been reported by most studies on surf-zone and nearshore ichthyofauna, and seasonal changes in physical conditions, notably water temperature, being cited as the major determining factor (e.g., Modde and Ross, 1981; Peters and Nelson, 1987; Ross et al., 1987; Vasconcellos et al., 2011). Cycles in fish abundance may also not be attributable to seasonal changes in physical conditions, but merely a result of recruitment, mortality or food availability (Modde and Ross, 1981; Gibson et al., 1993). In addition, the effects of human interference can influence the fish assemblages in different estuarine areas, irrespective of the hydrodynamic influences, thus emphasizing the importance of the sheltered and less anthropogenically affected beaches, as spawning, nursery and growth areas for fish species (Franco et al., 2016).

Estuarine and surf zone have species transient and/or with strong site-fidelity occurring all year round. These habitats support diverse fish assemblages, which are characterized by high numerical dominance (10 species typically comprise 95% of catches), but also show that few families are especially common (Able, 2005; Araújo et al., 2016; Oliveira and Pessanha, 2014). The evolutionary patterns of recruitment and reproduction established in accordance with seasonal fluctuations have made sand beaches important spatial resources for many fish species, which comprise the lower levels of marine food webs (Félix et al., 2007; Able et al., 2013). The composition of assemblages is highly variable, changing with fluctuations in water temperature, wave climate and the biomass of drifting algae or seagrass. Surf zones are not single uniform spatial units but are composed of topographically and hydrodynamically distinct habitats that support correspondingly distinct fish assemblages (Whitfield and Pattrick, 2015; Borland et al., 2017). A clearer understanding of the habitats that serve as nurseries for species, and the factors that make some sites more valuable as nurseries, will allow more efficient use of limited money, time, and effort in conservation and management (Beck et al., 2001; Rishworth et al., 2015).

Most studies that examine patterns of biodiversity use the number of species observed or estimated to occur in an area or a number of indices based on species richness and evenness (Gaston, 2000; Magurran, 2004), which is a simplistic approach to understand the role of biodiversity in ecosystem functioning. The majority of these measures are strongly affected by sample size, sampling effort and natural environmental variability (Rogers et al., 1999; Leonard et al., 2006; Bevilacqua et al., 2011). Recently, taxonomic diversity indices have become a basic tool for community evaluation and have even been used to identify areas of elevated taxonomic diversity relevant for conservation (Walker, 1995; Clarke and Warwick, 2001; Magurran, 2004; Winter et al., 2013). The main assumption of these measures is that taxonomic diversity is greater in a community in which species are phylogenetically more distinct (Walker, 1992; Naeem, 1998; Winter et al., 2013). Therefore, a community in which the species are distributed among many genera is thought to present greater diversity than a community in which most of the species belong to the same genus and therefore may be of greater interest in conservation. Indeed, increases in diversity enhance the resilience of an ecosystem (Loreau and de Mazancourt, 2013; Tilman et al., 2014; Isbell et al., 2015), and it is important that this issue be described based on indices that are suitable for assessing eventual changes in taxonomic diversity.

Assuming that taxonomic diversity translates into ecological diversity, then the taxonomic range of an assemblage may be crucial in maintaining ecosystem stability (Hughes, 1994; Tilman et al., 1996). Although taxonomic redundancy is scarcely referenced in regional studies, it is certainly a proxy for functional redundancy, and communities that have low taxonomic redundancy are jeopardized by disturbances that could lead to losses of ecosystem services and functions. At large scales, species richness should be analysed in consonance with taxonomic redundancy in order to obtain a more holistic picture of the community structure and its role in ecosystem functions.

On the eastern Brazilian coast, tropical conditions are dominant. Moving towards the south, the tropical climate is replaced by a transitional climate, reaching warm temperate conditions in the southernmost part of Brazil (Nobre and Shukla, 1996). This area encompasses two recognized biogeographic provinces (Palacio, 1982; Floeter and Soares-Gomes, 1999): the tropical province in the north, the Paulista province (22°–29° South), which corresponds to the transitional area, and the warm temperate region in the south.

The aims of this study were to assess and compare spatial and seasonal changes in the fish assemblage structure, species richness and taxonomic distinctiveness between two habitats (estuarine and surf zone) in three coastal regions (Tropical, Transition and Warm Temperate) along the Brazilian coast. It is expected: 1) Seasonal variation in the Warm Temperate region but not in the Tropical region; 2) Different assemblage structure between the two habitats (estuary × surf zone); 3) Different fish assemblage structure among the three regions that are dictated by different environmental tolerance; and 4) Higher species richness in the Tropical region compared to the Warm Temperate region.

2. Materials and methods

2.1. Study area

The surveys were carried out at 21 sites in three distinct regions of the Brazilian coast (Fig. 1). In the Tropical region (latitude 6–21° S), samples were taken at four sites in the Mamanguape River estuary and at two sites in the adjacent surf zone (6° 45′ S, 35° 54′ W; Fig. 1). The mouth of the estuary forms a 6 km-wide bay that is nearly closed off by a coastal reef line, which results in calm and quiet waters in the coastal zone (Bezerra et al., 2012). The mean water temperature ranges between 24 and 26 °C, and a well-preserved mangrove stand is present around the main estuarine channel. The sandy beaches display a mesotidal, semi-diurnal tidal regime with the mean tide ranging 2.5 m. On the north-east coast of Brazil, the South Equatorial Current is intercepted by the South American continent, being diverted to the south, forming the Brazil Current (BC). The BC is a warm current (average temperature of 26 °C) that flows to the south along the Brazilian coast (Stramma and England, 1999).

In the Transition region (22°–29° S), samples were taken at five sites in Sepetiba Bay and at two sites in the adjacent surf zone (22° 50′ S, 43° 30' W; Fig. 1). The waters inside the bay are saline (ca. 28–31) and transparent, and the bottom sediment is mainly muddy due to the relatively calm waters (Araújo et al., 2002, 2016). The mean tidal ranges are 1.3 m in spring tides and 0.5 m in neap tides. The surf zone adjacent to Sepetiba Bay was sampled at two different sites with different hydrodynamic characteristics: one on an open-ocean sandy beach with a reflective profile and the other on a sheltered sandy beach with a dissipative profile.

The Warm Temperate region (29–33° S) samples were taken at six sites in the Patos Lagoon Estuary and at two sites in the adjacent surf zone (32° 10′ S, 52° 10′ W; Fig. 1). The Patos Lagoon is the largest choked lagoon in the world, at 250 km long and 60 km wide, covering an area of 10,360 km^2. The sampling sites are restricted to the brackish estuarine area located in the southern portion of the lagoon (ca. 10% of total area), and the mouth of the lagoon is connected to the ocean by a pair of jetties. The adjacent sandy beaches are wave-dominated and classified as dissipative with one or two longshore sandbars (Pereira et al., 2010). The tidal regime is microtidal and semi-diurnal with a mean range of 0.5 m (Seeliger et al., 1997).

The "arc" formed by the coastline between Cape Frio (23° S) near the limit of the Tropical region and Cape Santa Marta (29° S) near the limit of the Warm Temperate region is also referred to as the South American Bight (Rocha et al., 1975) and forms the Transition region.
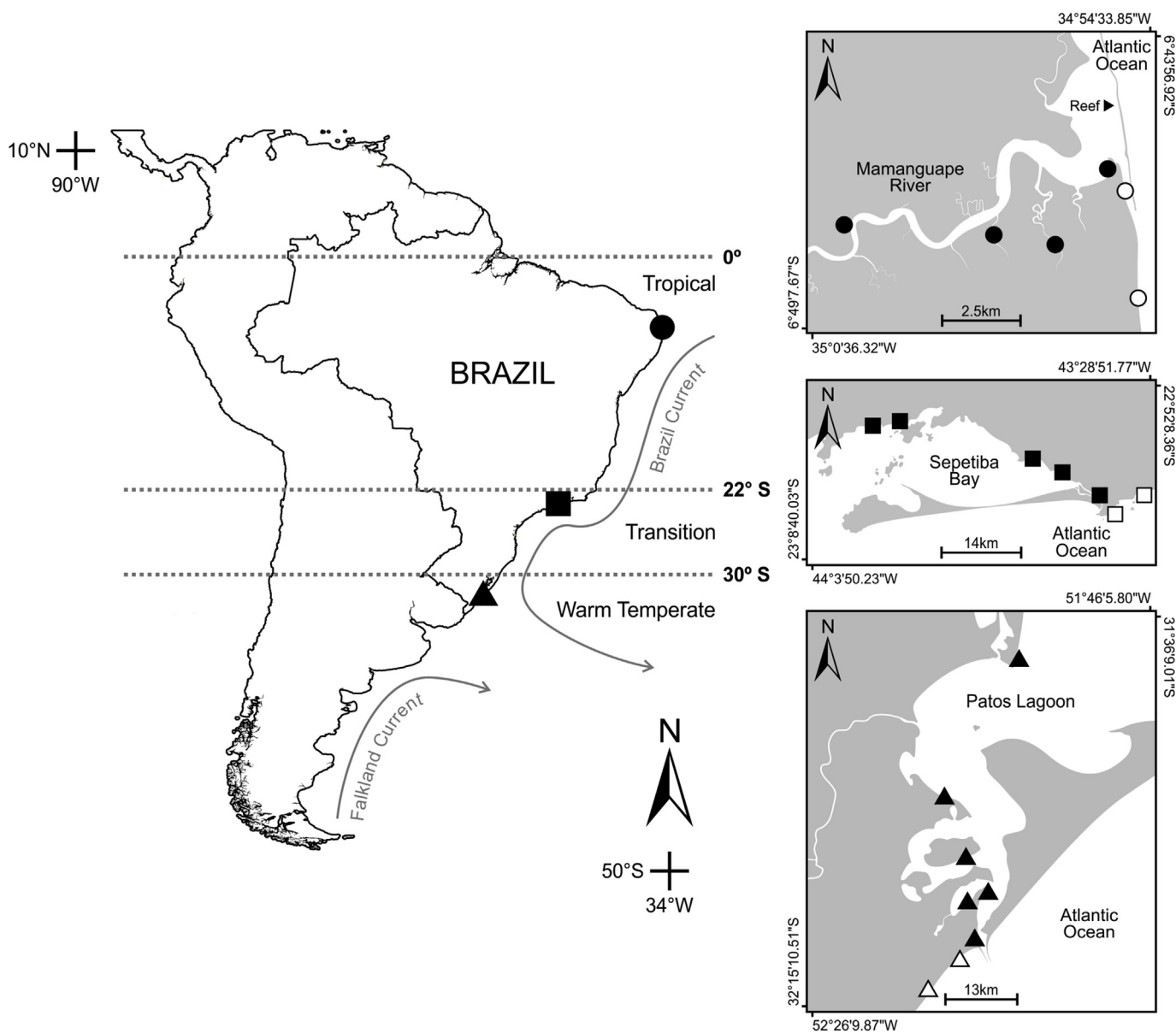
Fig. 1. The study area with indications of the regions and sampled habitats along the coast of Brazil. Circles = Tropical region, Squares = Transition region; Triangles = Warm Temperate region. Black markers = estuarine sites; white markers = adjacent surf zones sites.

For the Transition and the Warm Temperate regions, the presence of South Atlantic Central Waters off the continental shelf plus upwelling phenomena, especially near the northern boundary (Cape Frio, 23° S in Rio de Janeiro State), contribute to an increase in the fishing productivity in this region. In the south, the Subtropical Convergence, formed by the mixing of the Brazil and Falkland currents, provides temperate features that also influence the composition of the local biota (Seeliger et al., 1997).

2.2. Fish sampling

In all geographic regions, fish sampling was conducted monthly between February and December 2011 and bimonthly between January and December 2012 on daytime excursions. In total, 270 samples were collected in the Tropical region, 272 in the Transition region and 450 in the Warm Temperate region for the estuarine habitats, whereas 126 samples were collected in the Tropical region, 118 in the Transition region and 150 in the Warm Temperate region for the surf zone habitats (Table 1). In each different region, fish were collected using a beach

seine net with similar characteristics: Tropical region = 10 × 2.5 m (8-mm mesh), Transition region = 10 × 2.5 m (13-mm and 5-mm mesh), and Warm Temperate region = 9 × 1.5 m (13-mm and 5-mm mesh). Small differences in the mesh size between the nets (only 3 mm) were considered irrelevant, because the fish size structure were similar among the regions and habitats and fish larvae was not considered in this study. Sampling nets were 40 m long, and the net was used at a maximum depth of approximately 1.5 m. The area seined (approximately 300 m^2) and the time (15 min) allocated for each sampling were standardised to allow comparisons among samplings. Samplings were replicated (five samples) at each site. The fish caught were fixed in 10% formalin. All individuals were identified and counted. Fish identification followed keys of Figueiredo (1977), Figueiredo and Menezes (1978, 1980, 2000), and Menezes and Figueiredo (1980, 1985), Fischer et al. (2004) for the Southeast and South regions, and Araújo et al. (2004) for the Northeast region. Environmental variables of sub-superficial water temperature (°C), salinity and transparency (Secchi disk depth in cm) were measured at each site.

Table 1
Number of samples (beach seine) carried out in the two habitats (estuarine and suf-zone) in the three regions (Tropical, Transition and Warm Temperate) along the Brazilian coast between 2011 and 2012.

Year	Month	Tropical		Transition		Warm Temperate	
		Estuarine	Surf-zone	Estuarine	Surf-zone	Estuarine	Surf-zone
2011	February	20	8	20	10	30	10
	March	20	8	16	4	30	10
	April	5	10	16	8	30	10
	May	20	10	16	8	30	10
	June	20	8	16	8	30	10
	July	5	8	16	8	30	10
	August	20	10	16	8	30	10
	Sep	20	8	20	8	30	10
	Oct	20	8	16	8	30	10
	Nov	20	8	20	8	30	10
	Dec	20	8	20	8	30	10
2012	February	20	8	20	8	30	10
	May	20	8	20	8	30	10
	August	20	8	20	8	30	10
	Nov	20	8	20	8	30	10
Total		270	126	272	118	450	150

2.3. Data analysis

Before the analyses, all counts data were checked for the presence of outliers. Only in the Transition region, two outliers were identified for the surf zone and adjusted to the average of the largest five catches (large captures of *Harengula clupeola* and *Diplodus argenteus*). After this treatment of the raw data, the species abundance at each site was standardised by the number of fish caught per sample (CPUE, i.e., number of individuals/300 m^2/15 min) by month and transformed to log (CPUE + 1) to perform multivariate analysis.

For each site, the CPUE values were converted into percentages (CPUE%) obtained from the ratio between the CPUE of one species over the sum of CPUE values of all species collected at a given site multiplied by 100. The relative frequency of occurrence by species (FO%) was also estimated from the ratio between the number of samples in which the species occurred and the total number of samples collected at a given site multiplied by 100. After the calculation of CPUE% and FO%, the relative importance of each species at each site was determined. Using the combination of CPUE% and FO% values compared to their means (μ), each species was classified as follows: abundant and frequent (CPUE% ≥ μ CPUE%, FO% ≥ μ FO%); abundant and non-frequent (CPUE% ≥ μ CPUE%, FO% < μ FO%); non-abundant and frequent (CPUE% < μ CPUE%, FO% ≥ μ FO%); and present (CPUE% < μ CPUE%, FO% < μ FO%). The species identified as abundant and frequent were considered to be dominant (Garcia and Vieira, 2001; Burns et al., 2006; Ceni and Vieira, 2013).

Diversity analysis was based on species rarefaction (E$_S$) and evenness (Pielou's Index). Rarefaction was used to compare the number of species in each habitat/geographical region, and the number of individuals caught was reduced to a specified expected number of individuals caught, in our case equal to 501 individuals. This approach allows comparisons amongst communities with unequal sampling efforts and individuals caught using the number of individuals caught in the smallest sample (Hurlbert, 1971; Magurran, 2004). Species evenness was calculated using Pielou's index, J = H'/Hmax, where Hmax represents the natural log of S and H′ is the Shannon index.

Multivariate analyses were used to investigate whether fish assemblages varied seasonally (4 levels, summer, autumn, winter and spring) and between habitats (2 levels, estuary and surf zone) and geographic regions (3 levels, Tropical, Transition and Warm Temperate). The Bray-Curtis dissimilarity matrix (square root transformed), derived from the transformed CPUE data of all species at the different sites was used for multivariate analyses. A hierarchical cluster analysis was performed using group average linkage in combination with the similarity profiles (SIMPROF) test. The results of the SIMPROF test allow for hypothesis testing, and the findings were considered to be significantly clustered if the test statistic (π) was larger than 95% (P < 0.5) of the 9999 permutations of the null distribution of randomly simulated similarities (Anderson et al., 2008). The cluster analysis grouped samples using the grouped average similarities to determine whether discernible patterns were apparent in the samples with regard to sampling region/habitat. Multivariate patterns were visualized with a non-metric multi-dimensional scaling (nMDS) ordination and possible differences in assemblage structure among regions, seasons and between habitats. For each region, seasons and habitats changes were determined through a permutational analysis of variance (PERMANOVA), with seasons and habitats as fixed factors, and months (nested in seasons) and sites (nested in habitats) as random factors. When significant differences were detected (P < 0.01), pairwise comparisons between groups were conducted and a similarity percentage (SIMPER; Clarke and Warwick, 1998) analysis was used to determine species that most contributed to within-group average similarity for habitats and seasons.

To determine the taxonomic structure of the communities, the average taxonomic distinctness (AvTD, Δ+), which addresses the taxonomic aspects of community structure (Clarke and Warwick, 1998) was used. The AvTD was based on presence/absence data, using four taxonomic levels: species, genus, family and order. This index is calculated by summing the path lengths through a taxonomic Linnaean tree connecting every pair of species in the list, and dividing by the number of paths. Equal step lengths are assumed between each level in the hierarchy (species to genus, genus to family, etc.). Then, they are standardised so that the distinctness of 2 species connected at the highest level (the taxonomically most distant pairing used in a batch of analyses) is set equal to 100. The species list identified for the three geographic regions was plotted against the number of species in each habitat/geographic region. To identify the average number of species expected (under the null hypothesis that all fish assemblages are constrained by the species list), a 95% confidence funnel was generated. The null hypothesis assumes that each sample contains species randomly selected from the global list and that it should thus fall within the 95% confidence intervals. Since the theoretical mean remains constant while the variance decreases as the number of species increases, the 95% confidence intervals take the form of a funnel. The AvTD values are independent of the number of species, whereas their

variability around the average value is dependent on the number of species (i.e., the higher the number of species, the lower the expected variability, and vice versa) (Clarke and Warwick, 1998; Warwick and Clarke, 2001). The values of AvTD were calculated for each sample and plotted against the corresponding number of species. The species richness and the AvTD calculated for each site and region were compared with PERMANOVA on the Euclidean distance and permutation of residuals under a reduced model to test for differences among regions and habitats. Significant differences among the factors were followed by PERMANOVA pairwise comparison tests. Analyses were performed in PRIMER v. 6.1.13 & PERMANOVA + v. 1.0.3 software (Anderson et al., 2008).

3. Results

3.1. Fish fauna

In total, 174,390 fish individuals belonging to 141 species, 96 genera, 47 families and 17 orders were caught from both estuarine and surf zones at the 21 sites between February 2011 and December 2012 (Table S1 in the Supplement). Perciformes was the most representative order in both habitats of the three regions. The families that included a great number of species were Sciaenidae (16 species, 11.34% of all recorded species), Carangidae (11), Tetraodontidae (9), Gobiidae (9), Clupeidae (8), Engraulidae (8) and Gerreidae (7). These taxa composed 49% of the observed fishes in terms of the number of species. However, 24 families were represented by a single species (Table S1 in the Supplement).

More species were observed at the estuarine sites than at the surf zones (Fig. 2). Of the 141 species recorded, 125 were from the estuarine zone and 80 were from the surf zone, with 61 exclusively estuarine, 16 recorded in surf zones only, and 64 species common in both habitats (Fig. 2; Table S1 in the Supplement).

The richest region was the Tropical region, with 96 species, of which 84 were observed in the estuarine habitat, 39 in the surf zone, and 27 were recorded in both habitats (Fig. 2; Table S1 in the Supplement). In the Transition region, 84 species were caught, with 72

being observed in the estuary, 49 in the surf zone, and 37 common in both. In the Warm Temperate region, a total of 37 species was recorded, with 31 in the estuary, 19 in the surf zone, and 13 common in both habitats (Fig. 2).

Fish assemblages based on the mean CPUE of each fish species at each site were grouped by geographical regions and habitats. The cluster and SIMPROF analyses based on log (CPUE + 1) identified four clusters within which the structure of the fish assemblages was similar (π = 8.7; P < 0.01). Overall, the sites were grouped by geographical regions (Fig. 3), with the two different habitats being clustered within each region. The only exception was found in the Tropical region, where sites located in the estuary and surf zone were placed into different branches in the cluster, indicating a clear distinction between the fish assemblage structures.

The richness of the different taxonomic groups (order, family, genus and species) had a clear regional difference with the highest values in the Tropical region and the lowest in the Warm Temperate region in the estuarine habitats (Fig. 4). In the surf zone, the highest numbers of species, genera and families were recorded in the Transition region, followed by the Tropical region, whereas the Warm Temperate region had the lowest species richness.

The expected richness determined by rarefaction decreased from the Tropical region to Warm Temperate region in both habitats (Tables 2 and 3). In addition, the estuarine habits had higher values compared with the surf zone habitat for the Tropical and Transition region, but not for the Warm Temperate region. In the Tropical region, the estimated species richness was 39.7 ± 2.8 s.d. for the estuarine habitats and 36.5 ± 1.6 for the surf zones. In the Warm Temperate region, the estimated richness was 10.6 ± 1.2 for the estuarine habitats and 10.5 ± 1.5 for the surf zone (Tables 2 and 3). CPUEs were higher in the Transition region (372.05 individuals/300 m^2/15 min) than in the Warm Temperate (84.57) and Tropical region (54.30) in the estuarine habitats. In the surf zones CPUEs were also higher the Transition region (466.20), decreased in the Warm Temperate region (53.03), and had the lowest values in the Tropical region (7.15). In the Tropical region and Warm Temperate regions, equitability was higher in the surf zone than in the estuarine habitats, whereas in the Transition region these
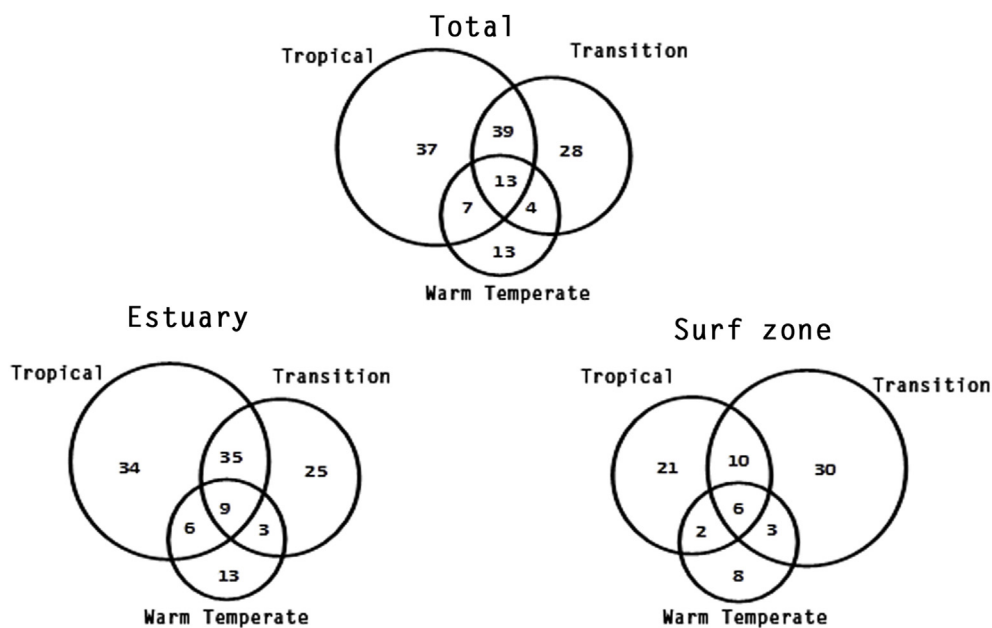

Fig. 2. Venn's diagram representing the total number of species in the three different regions (Tropical, Transition and Warm Temperate) and the two habitats (Estuary and Surf zone).
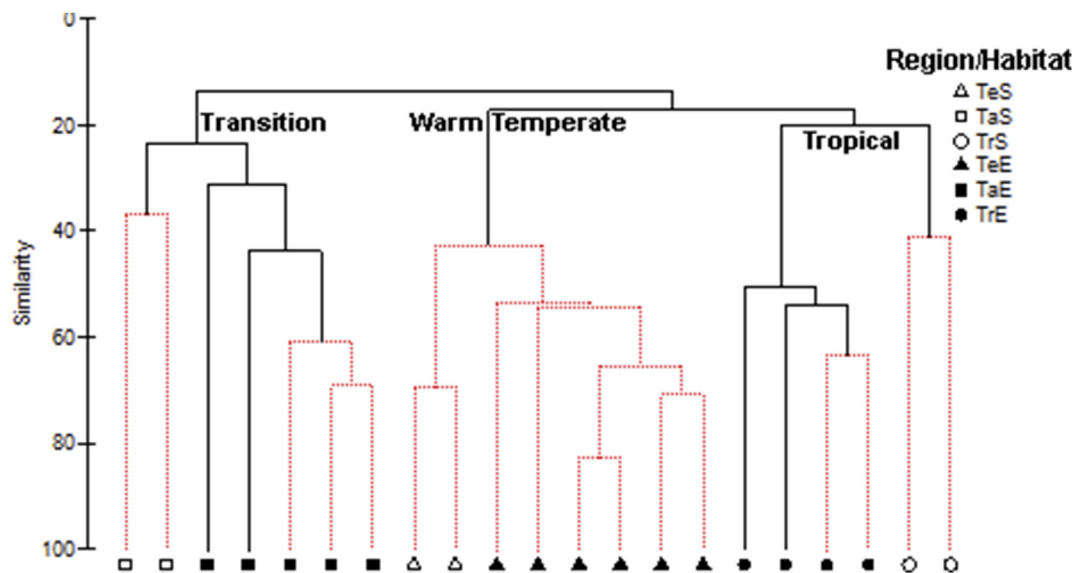
Fig. 3. Cluster with SIMPROF showing fish assemblages structure among regions (Tr, Tropical; Ta, Transition; Te, Warm Temperate) and habitats: estuary (E = dark simbols) and surf zone (S = hollow simbols).
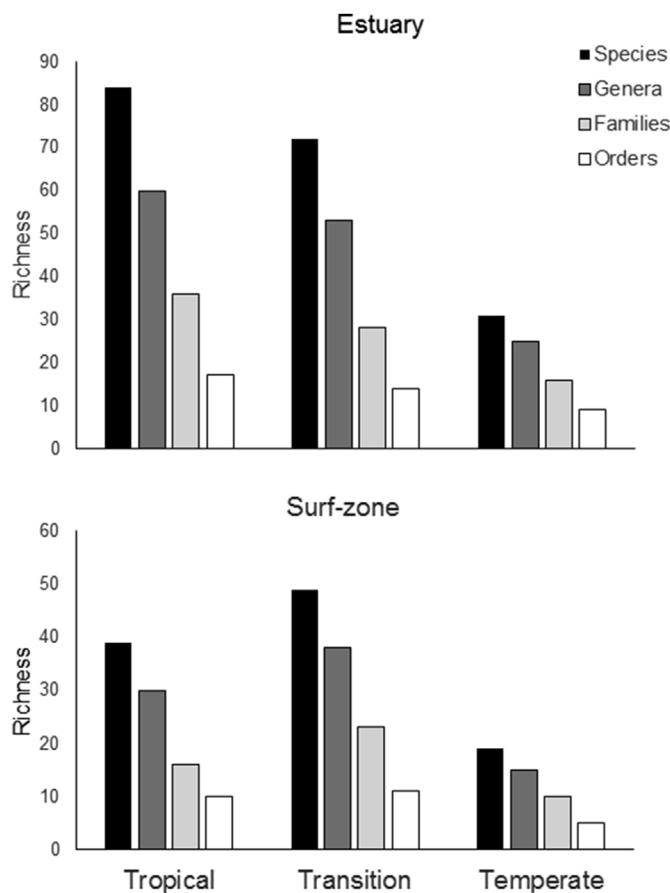

Fig. 4. Taxonomic richness (total number of taxa) of the two habitats (estuary and surf zone) in the three regions (Tropical, Transition and Warm temperate).

values were comparatively lower with 0.34 ± 0.1 in both the estuarine and surf zone habitats (Tables 2 and 3).

3.2. Regional patterns of fish assemblages

The assemblage structure varied significantly among the three regions (*Pseudo-F* = 12.08; P < 0.001), and between the habitats nested

in seasons (nested in region) (*Pseudo-F* = 5.16; P < 0.001), but not between seasons (*Pseudo-F* = 0.53; P = 0.99), (Table 4), therefore each region was analysed separately. *Post-hoc* pairwise testing among the regions showed that assemblages were statistically distinct from one another (Table 4). The nMDS plots for each habitat indicated that assemblages were markedly distinct in the three regions (Fig. 5).

3.3. Tropical region

The estuarine habitats in the Tropical region had 16 dominant species, with peaks for *Rhinosardinia bahiensis* (CPUE = 17.26 individuals per sample), *Lycengraulis grossidens* (CPUE = 7.43) and *Atherinella brasiliensis* (CPUE = 6.21) (Table 2). In the surf zone, seven species were dominant (Table 3), with *M. liza* (CPUE = 1.39) and *L. grossidens* (CPUE = 1.46) being the most abundant species. Distinct fish communities were detected for each habitat in the Tropical region, according to nMDS ordination but no seasonal changes in the fish community structure for each habitat were found (Fig. 6).

3.4. Transition region

Seven species were dominant in the estuarine habitats, with *Anchoa tricolor* and *Anchoa januaria* having the greatest abundance (CPUE = 237.9 and 55.7, respectively) and another five species (*Harengula clupeola, Micropogonias furnieri, Mugil liza, Atherinella brasiliensis* and *Anchoa lyolepis*) being caught with CPUEs between 5 and 20.0 (Table 2). Six species were dominant in the surf zone: *Harengula clupeola* (CPUE = 303.9), *Diplodus argenteus* (CPUE = 51.2), *Pomadasys corvinaeformes* (CPUE = 39.8) and *Trachinotus carolinus* (CPUE = 23.3), while *Sardinella brasiliensis* (CPUE = 17.59) and *A. brasiliensis* (CPUE = 11.6) were caught in comparatively lower abundance (Table 3). Different fish communities were detected for each habitat, but no seasonal changes were found (Fig. 6).

3.5. Warm temperate region

Four species were dominant in the estuarine habitats. *Mugil liza* and *A. brasiliensis* had the greatest abundance, with CPUE = 46.1 and 21.2, respectively. *Jenynsia multidentata* and *Brevoortia pectinata* were the other two frequent and abundant species, but they were caught in lower abundance (CPUE = 6.6 and 5.0, respectively) (Table 2). In the surf zone, only four species were frequent and abundant. *Mugil liza* and

Table 2

Species composition, Capture Per Unit Effort (CPUE, number of individuals per/300 m²/15 min) and the relative importance (color scale) of each species for the estuarine habitats in the three geographic regions, and site average (± standard deviation) for diversity attributes and environmental variables. Color scale associated with CPUE values represent the importance of each species in each region, as follow: black shading (frequent and abundant), dark gray (not-frequent but abundant) and light gray (frequent and not-abundant).

Species	Tropical CPUE	Transition CPUE	Warm Temperate CPUE
Mugil liza	1.68	6.19	46.05
Atherinella brasiliensis	6.21	6.04	21.16
Mugil curema	0.85		2.65
Brevoortia pectinata		0.03	4.99
Jennynsia multidentata			6.58
Micropogonias furnieri	0.01	11.03	0.22
Harengula clupeola	0.15	19.23	< 0.01
Anchoa tricolor		237.86	
Anchoa januaria	0.11	55.72	
Pomadasys corvinaeformes	0.02	0.80	
Trachinotus carolinus	0.01	0.55	
Sardinella brasiliensis		6.02	
Rhinosardinia bahiensis	17.26		
Lycengraulis grossidens	7.43		0.05
Anchoa lyolepis		5.62	
Ctenogobius boleosoma	0.65	4.58	
Menticirrhus littoralis	0.03	0.83	
Eucinostomus argenteus	1.20	1.37	< 0.01
Eucinostomus melanopterus	1.52	0.15	0.36
Eugerres brasilianus	2.11		
Sphoeroides testudineus	2.00	0.03	
Achirus lineatus	1.67	0.04	
Sciades herzbergii	1.32		
Symphurus tesselatus	1.16	0.03	
Hyporhamphus unifasciatus	0.87	0.03	
Citharichthys macrops	0.69		
Anchovia clupeoides	0.66		
Others (93 species)			
Total abundance	10146	71433	27980
Effort	190	192	330
CPUE	53.40	372.05	84.57
Rarefaction (501)	39.7 ± 2.8	22.0 ± 2.3	10.6 ± 1.2
Equitability (J')	0.60 ±0.2	0.34±0.1	0.39±0.1
Salinity	23.3 ± 10.1	29.4 ± 5.0	11.2 ± 10.0
Transparency (cm)	38.7 ± 19.8	66.6 ± 39.3	46.0 ± 27.8
Temperature (ºC)	29.4 ± 2.4	24.5 ± 2.8	19.8 ± 5.1

Trachinotus marginatus had the greatest abundances, with CPUE = 21.1 and 17.0, respectively (Table 3). *Mugil curema* and *B. pectinata* were the other two frequent and abundant species, but they were caught in relatively lower abundances (CPUE = 7.5 and 5.3, respectively). Distinct fish assemblage structures were detected between the estuarine and surf zone habitats, and indications of seasonal change were found between the spring and the summer, and between the spring and autumn. Samples from summer and autumn overlapped in the nMDS plots

(Fig. 6). The SIMPER analysis revealed the species that most contributed to the within-group similarity in each habitat and season (Table S2 in the Supplement). In the Warm Temperate region, *Mugil liza* and *A. brasiliensis*, were the species that made the biggest contribution to within-group average similarity during all seasons. *Jenynsia multidentata* and *M. curema* contributed most to within-group average similarity in summer and autumn, whereas *Odontesthes argentinensis* was typical of the spring (Table S2 in the Supplement).

Table 3
Species composition, Capture Per Unit Effort (CPUE, number of individuals per 300 m²/15 min) and the relative importance (color scale) of each species for the surf zone habitats in the three geographic regions, and site average (± standard deviation) for diversity attributes and environmental variables. Color scale associated with CPUE values represent the importance of each species in each region, as follow: black shading (frequent and abundant), dark gray (not-frequent but abundant) and light gray (frequent and not-abundant).

	Tropical	Transition	Warm Temperate
Species	CPUE	CPUE	CPUE
Mugil liza	1.39	2.12	21.08
Atherinella brasiliensis	0.12	11.67	0.12
Trachinotus marginatus			17.02
Mugil curema	0.04		7.53
Brevoortia pectinata			5.25
Micropogonias furnieri		1.26	0.03
Harengula clupeola		303.92	0.02
Anchoa januaria	0.22		
Diplodus argenteus		51.15	
Pomadasys corvinaeformes	0.01	39.84	
Trachinotus carolinus	0.35	23.29	0.01
Sardinella brasiliensis		17.59	
Lycengraulis grossidens	1.46		0.03
Anchoa lyolepis		3.10	
Menticirrhus littoralis	0.30	3.62	0.19
Mugil hospes	0.46		0.07
Polydactylus virginicus	0.6	0.03	
Trachinotus goodei	0.23	0.53	
Others (49 species)			
Total abundance	672	40093	5834
Effort	94	86	110
CPUE	7.15	466.20	53.03
Rarefaction (501)	36.5 ± 1.6	15.1 ± 1.7	10.5 ± 1.5
Equitability (J')	0.73±0.2	0.34±0.1	0.46±0.2
Salinity	34.9 ± 6.1	34.1 ± 2.7	29.4 ± 5.9
Transparency (cm)	36.3 ± 14.7	102.4 ± 32.8	40.0 ± 27.3
Temperature (ºC)	28.9 ± 1.6	22.6 ± 2.7	19.2 ± 4.0

Table 4
Results of PERMANOVA testing for differences in the fish assemblage structure among the three regions (fixed factor) with seasons and habitat nested in region (random factors). *t*-test values are shown for *post-hoc* pairwise tests between regions. df, degrees of freedom; MS, mean sum of squares; *ECV*, percent estimated components of variation; F, *Pseudo-F*; * = p < 0.05; ** = p < 0.01; ***p < 0.001; n.s. = non-significant.

Source	df	MS	*Pseudo*-F	*ECV*(%)
Region (R)	2	80272	12.08***	31.2
Season - S (nested in R)	9	6797	0.53n.s.	17.4
Habitat (nested in S (nested in R))	12	12933	5.16***	32.3
Residuals	267	2505		50.1
Total	290	1.1112E6		

Pair wise test for the fixed factor (Region)	t		P
Tropical × Transition	3.47**		0.003
Tropical × Warm Temperate	3.33*		0,028
Transition, × Warm Temperate	3,.60**		0,008

3.6. Environmental influences on the community structure

3.6.1. Tropical region

PERMANOVA detected significant differences in the fish community structure between the habitat (*Pseudo-F* = 4.03, P = 0.001) but not

among the seasons (*Pseudo-F* = 1.26, P = 0.06) (Table 5). In addition, significant changes among the sites (nested in habitats) were also found (*Pseudo-F* = 2.48, P = 0.001). The three explanatory environmental variables explained a significant proportion of the variance (*Pseudo-F* ranging from 2.62 to 5.97). Salinity was the variable to show the most significant effect on the fish community structure accounting for 17.2% of the estimate of components of variation (*ECV*), whereas temperature had the lowest influence with 8.4% *ECV* (Table 5).

The first distance based redundancy analysis (dbRDA) axis accounted for 12.4% of the total variation in fish assemblages and distinguished sites from the surf zone with higher salinity and lower temperature from sites from the estuarine habitats with the opposite pattern (Fig. 7).

3.6.2. Transition region

Significant differences in the fish community structure between the habitats (*Pseudo-F* = 2.84, P = 0.001) but not among the seasons (*Pseudo-F* = 1.12, P = 0.22) were found according to PERMANOVA (Table 5). Significant *Pseudo-F* value was found for the sites (nested in the habitats), suggesting strong among-site differences. Temperature (*Pseudo-F* = 4.12, P = 0.001) followed by salinity (*Pseudo-F* = 2.84, P = 0.003) were the best predictors of the fish community structure.

The first distance based redundancy analysis axis (dbRDA1) accounted for 6.4% of the total variation in the fish assemblage structure and distinguished sites from the surf zone with higher with higher salinity and transparency from sites from the estuarine zone with the opposite pattern (Fig. 7).
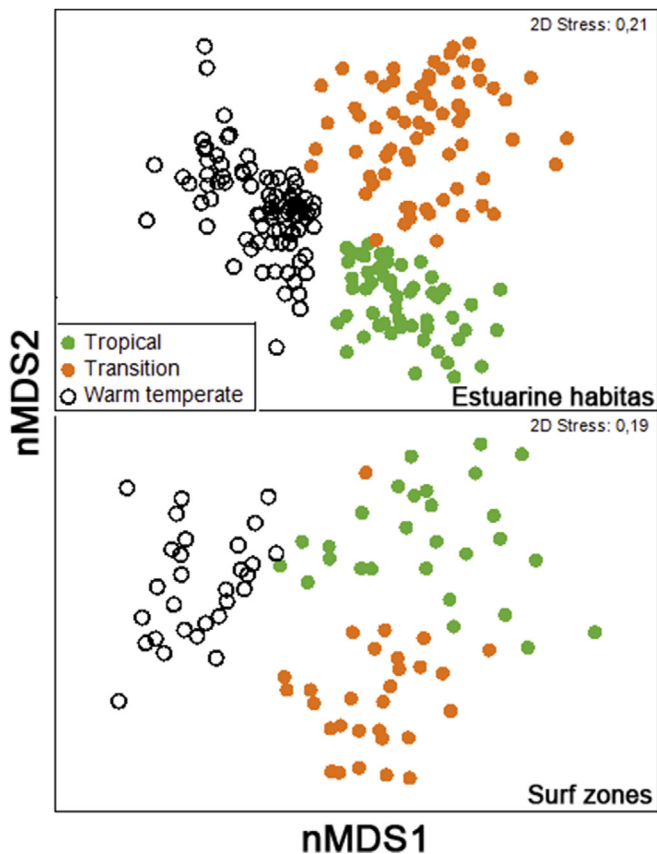
Fig. 5. Ordination diagrams of non-Metric Multidimensional Scale on fish assemblage for each habitat (estuary and surf zone). Samples coded by regions.

3.6.3. Warm temperate region

PERMANOVA detected significant differences in fish community structure between the habitats (*Pseudo-F* = 2.24, P = 0.003) and to a lesser extent between seasons (*Pseudo-F* = 1.47, P = 0.02) (Table 5). Changes among the sites (nested in habitats) were also found (*Pseudo-F* = 4.08, P = 0.001). Seasonal change in fish assemblage structure was found between autumn and spring (t = 1.32; P = 0.04) and between summer and spring (t = 1.50; P = 0.03) only. Two explanatory environmental variables (Transparency, *Pseudo-F* = 6.64; P = 0,001; Temperature, *Pseudo-F* = 4.37; P = 0.001) explained a significant proportion of the variance and accounted for 10.6–11.7% *ECV* (Table 5).

The first distance based redundancy analysis axis (dbRDA1) accounted for 7.8% of the total variation in the fish assemblage structure and distinguished sites from the estuarine habitats with higher transparency and lower salinity, from the sites from the surf zone, with higher salinity and lower transparency (Fig. 7).

3.7. Species richness and taxonomic distinction

Forty-seven families were recorded in both habitats (estuarine and surf zones) of the three coastal regions, with remarkable differences in richness and taxonomic distinctiveness among the regions (Figs. S1 and S2 in the Supplement).

3.7.1. Tropical region

In the estuarine habitats, the Tropical region had the highest species richness (84) and taxonomic distinctiveness (AvTD = 92.3), with 9 orders being represented by only one species and 21 of the 35 families were also represented by only one species. In the surf zone, four of the 10 orders and 8 of the 16 families were represented by only one species.

3.7.2. Transition region

Seven orders were represented by only one species and 13 of the 28 families were also represented by only one species in the estuarine habitats. In the surf zone habitats, we recorded a high richness (49 species) and taxonomic distinctiveness (AvTD = 78.5), with 7 of the 11 orders and 15 of the 23 families represented by only one species.

3.7.3. Warm temperate region

The estuarine habitats presented only 31 species and low taxonomic distinctiveness (AvTD = 73.9), with 8 of the 16 families being represented by only one species. The lowest species richness (19) and taxonomic distinctiveness (AvTD = 51.9) was recorded in the surf zone, with 5 of the 10 families being represented by only one species (Figs. S1 and S2 in the Supplement).

Similar to the estuarine habitat, the surf zone in the Warm Temperate region had the lowest richness and redundancy, whereas the Transition and Tropical regions had comparatively high richness and taxonomic redundancy. Therefore, few species and genera were recorded for the families in the Warm Temperate region, whereas the Tropical and the Transition regions were richer in species and had comparatively higher taxonomic redundancy.

The species richness (number of species per sample) changed significantly among the regions (Table 6), with the Tropical estuarine Region presenting more species richness than the Warm Temperate estuarine and surf zones. Moreover, the Transition estuarine zone was more species rich than the Warm Temperate estuarine zone. All the pair-wise comparisons of species richness between the regions and habitats differed significantly except for the Warm Temperate surf zone × Tropical surf zone and the Transition estuary × Transition surf zone (Fig. S2 in the Supplement).

The AvTD was significantly higher in the Tropical estuarine zone compared with the Transition estuarine zone. For the surf zone, the Transition region had the highest AvTD compared with the other two regions (Table 6). Again, all pair-wise comparisons of AvTD between regions/habitats showed significant differences except for the Warm Temperate estuary × Transition surf zone and the Warm Temperate estuary × Tropical surf zone (Fig. S2 in the Supplement).

4. Discussion

The fish assemblage structure differed significantly among the three regions and, to a lesser extent, between the two habitats within each region. More evident, was the distinct segregation in samples between assemblages in the Tropical (7° S) and Warm Temperate (32° S) regions. These changes in assemblage structure were consistent and may correspond to shifts in dominant environmental conditions, mainly the temperature. Vilar et al. (2013), comparing fish assemblages among different estuaries along the Brazilian coast, found that at the regional scale, the assemblages are simultaneously determined by environmental filters and species dispersal capacity, while at the local scale, the effects of environmental factors should vary depending on estuary-specific physical and hydrological characteristics. It is likely that regional influences on species richness covary with environmental filters and local factors thus reflecting the net result of processes operating during evolution.

Species richness changed significantly between the Tropical (84 species) and the Warm Temperate (31 species) regions in the estuarine habitat, and from the Transition region (49 species) to the Warm Temperate region (19 species) in the surf zone habitat. These changes are much more pronounced than the findings of Macpherson and Duarte (1974) based on a compilation of data for fish species of the East Atlantic, regardless of habitat. According to Hillebrand (2004), regional differences are more pronounced in richer taxa (i.e., taxa with more species).

Although the structure of the fish community differed consistently in the three regions, seasonal changes were detected only for the Warm
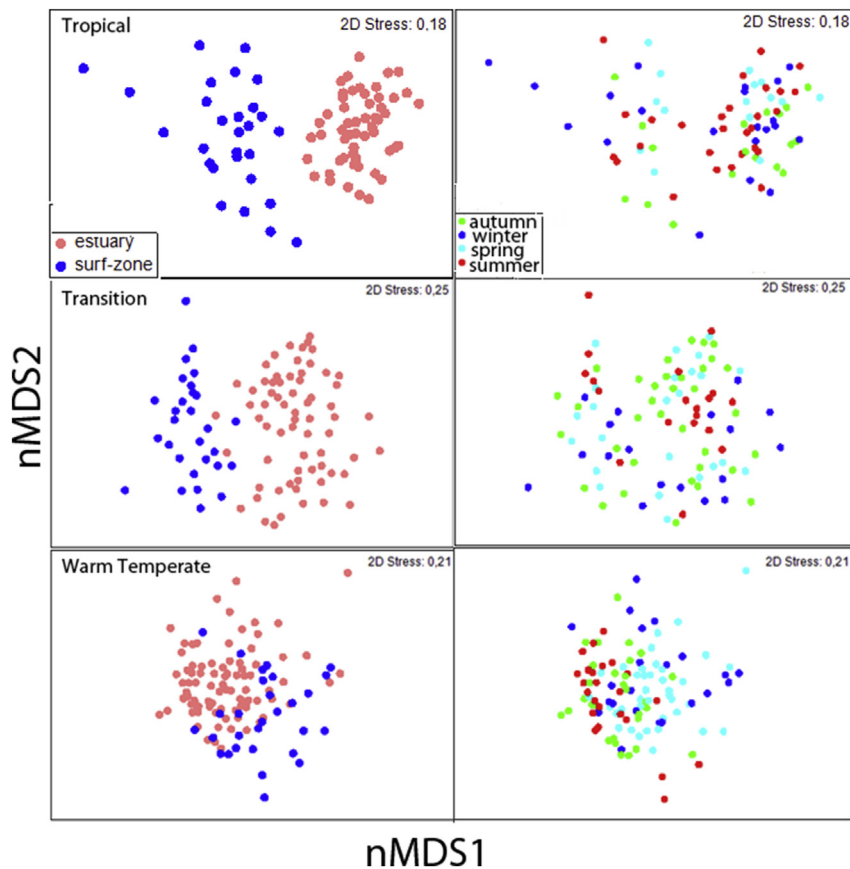
Fig. 6. Ordination diagrams of non-Metric Multidimensional Scale on fish assemblage for each habitat (estuary and surf zone) and seasons in each region.

Temperate region. Moreover, the three examined environmental variables differed on their importance to predict the fish community according to the region. While salinity was the best predictor of fish community structure in the Tropical region, temperature had the most important influence to structure fish community in the Transition region. In the Warm Temperate region, temperature and transparency were the best predictor of fish community structure. Seasonal ecological effects caused by temperature and photoperiod are typically considered minimal in the tropics and seasonality is heavily determined by precipitation which generates dry and rainy seasons (Lowe-Mcconnell, 1999). There is a seasonal pattern in the structure of demersal fish assemblage of estuaries on the Brazilian coast related to variation in salinity that is influenced by the rainfall (Andrade-Tubino et al., 2008). Such patterns are more conspicuous in the tropical areas. Spatial differences in the structure for fish assemblages among three tropical beaches are strongly influenced by wave action in a tropical the estuary of northeastern Brazil with dissipative beaches harboring the most diverse and abundant fish assemblage, whereas reflective beaches harbored the lowest densities of fishes (Oliveira and Pessanha, 2014). Salinity and transparency played an important role determining spatial variations in fish abundance in those beaches.

In the Warm Temperate region, the fish community in the spring differed significantly from those in the summer and autumn, and temperature and transparency were the best predictor of such changes. Seasonal changes in a sandy beach fish assemblage in Southern Brazil is characterized by strong seasonality in which greater abundances, biomass, richness and diversity are found in summer months (Barreiros et al., 2004; Rodrigues and Vieira, 2013). The hydrodynamics of the Patos Lagoon estuary in southern Brazil is mainly determined by the contribution of freshwater from the large drainage basin, mainly depending on the relationships between the river discharges and the wind action (Möller and Fernandes, 2010). Other estuaries in South America

also change seasonally structure of fish community. The composition of fish assemblages in the Rıo de la Plata estuary, Argentina, was associated to temperature (Jaureguizar et al., 2004). Changes in fish community of a small temperate estuaries on the Argentinian and Uruguayan coasts were linked to spatial variation in salinity, which was consistently influenced by discharge and local precipitation (Plavan et al., 2010; Solari et al., 2015). The number of species present in the temperate and subtropical estuaries presents peaks according to the annual temperature patterns, while the seasonal cycles of the tropical systems are related to the salinity variations, influenced by the pluviometric regime of the drainage basin (Barletta et al., 2005; Passos et al., 2016; Souza et al., 2018). Our findings corroborate this pattern of differential influence of the environmental variables for different climatic regions.

Unlike the estuarine habitat that had the highest species richness and rarefaction in the Tropical region, in the surf zone the highest number of species observed in the Transition region did not coincide with the highest rarefaction that peaked in the Tropical region. A probable explanation for this unexpected low rarefaction in the Transition region is the occurrence of some very abundant samples with large numbers of *Harengula clupeola* and *Diplodus argenteus* that contributed to decrease the expected number of species for a given number of individuals. Other causes may be associated with eventual differences in community structure, sampling effort, or habitats. Rarefaction should be more appropriate to compare collections from communities that are taxonomically similar, from similar habitats (Tipper, 1979).

In the present study, the highest number of individuals and species in surf zone habitats in the Transition region could be associated with the high primary productivity (Ciotti et al., 1995), since there are several upwelling events that occur in Cape Frio (23° S), São Sebastião Isle (24° S) and Cape Santa Marta (28.5° S) (Signorini, 1978). The productivity–richness hypothesis suggests a positive effect of primary

Table 5

Results of PERMANOVA testing for differences in fish assemblage structure, in response to salinity, transparency and temperature (covariates), regions (fixed factor) and season, habitat, month and site (random factors) and interaction effects. (df, degrees of freedom; MS, mean sum of squares; ECV, percent estimated components of variation; F, Pseudo-F; *p < 0.05; ** = p < 0.01; ***p < 0.001; n.s. = non-significant).

Tropical region Source	df	MS	Pseudo-F	ECV(%)	Pair wise test (Significant differences)
Salinity	1	28921	5,97***	17.2	
Transparency	1	11075	3,07***	9.7	
Temperature	1	8971	2,62***	8.4	
Season (S)	3	5124	1,26n.s.	9.8	n.s.
Habitat (H)	1	29074	4,03***	34.2	Estuarine ≠ surf zone (t = 2,02; p = 0.001)
Month (nested in S)	7	3106	1,53	12.8	
Site (nested in H)	4	5300	2,48***	17.8	
H x S	3	4132	1,38*	15.2	
H x Month (S)	7	2203	1,15	8.1	
Residuals	19	2330		45.1	
Total	81	2,7187E5			
Transition region					
Salinity	1	15827	2,84***	10.4	
Transparency	1	13881	2,31**	9.6	
Temperature	1	11238	4,12***	10.8	
Season (S)	3	4734	1,12	7.0	n.s.
Habitat (H)	1	301333	2,89***	28.8	Estuarine ≠ surf zone (t = 1,71; p = 0.001)
Month (nested in S)	8	2994	1.29ns	10.2	
Site (nested in H)	5	8521	3.97*	24.1	
H x S	3	3512	1.18*	10.5	
H x Month (S)	7	2154	1,09	1.0	
S x Site (H)	15	2511	1.17ns	11.0	
Residuals	21	2388		46.3	
Total	95	3,2215E5			
Warm Temperate region					
Salinity	1	8939	1,90n.s.	6.3	
Transparency	1	17508	6,64***	11.7	
Temperature	1	14275	4,37***	10,6	Spring ≠ Summer* (t = 1.50; p = 0.03)
Season (S)	3	6310	1,47*	11.3	Spring ≠ Autumn* (t = 1.32; p = 0.04)
Habitat (H)	1	14774	2,24***	20.4	Estuarine ≠ surf zone (t = 1.50; p = 0.01)
Month (nested in S)	13	2510	1,35	11.4	
Site (nested in H)	7	6386	4,08***	21.8	
H x S	3	3445	1,03	3.7	
H x Month (S)	7	1943	1,36	12.5	
S x Site (H)	19	2536	1,68***	19.2	
Month(S) x Site (H)	36	1403	1,0523	7.8	
Residuals	20	1333		36.5	
Total	112	3,0109E5			

productivity on species richness by allowing larger populations to persist, thereby reducing extinction risk and supporting a higher diversity of niche specialists (see Willig et al., 2003). However, productivity is also not consistently correlated with species diversity. The productivity is low, for example, in some tropical seas with high diversity (Miloslavich et al., 2011; Vallina et al., 2014). On the other hand, some authors have recorded high levels of diversity at intermediate levels of productivity (see Begon et al., 1986). In the study area, freshwater input in estuarine habitats is lowest in the Tropical region, which has the lowest annual accumulated rainfall of 1000 to 1200 mm/year (Hastenrath and Heller, 1977), compared with the Transition region, which has an accumulated rainfall of 1500 to 2000 mm/year, and the Warm Temperate region, with 1250 to 2000 mm/year (Nobre and Shukla, 1996). Moreover, the tropical waters on the Brazilian coast are predominantly oligohaline in the Tropical region, compared with the richer Transition and Warm Temperate regions (Signorini, 1978). The large number of individuals and taxa recorded in the surf zone of the Transition region compared with the
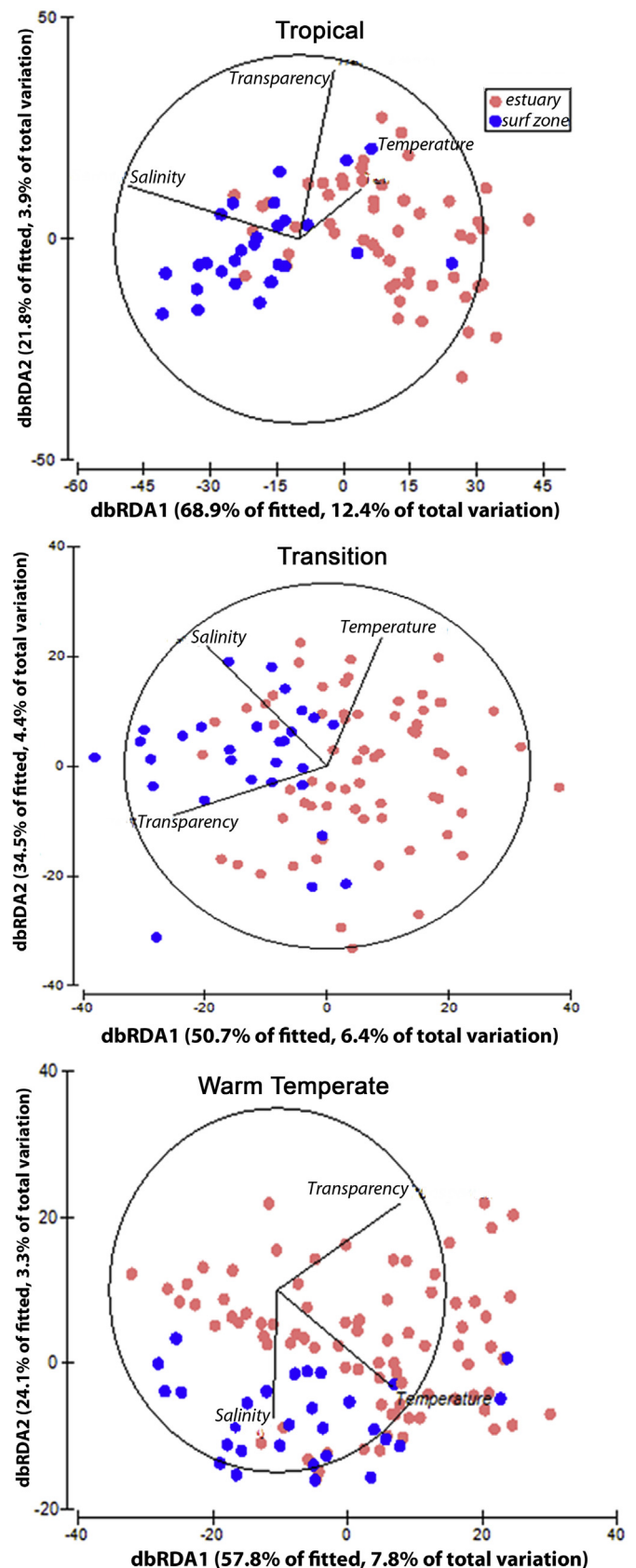

Fig. 7. Distance-based redundancy analysis (dbRDA) on the relationships between fish assemblage structure and the covariates (temperature, salinity and transparency). Sampling sites were indicated according to the habitat (estuary and surf zone).

Table 6

Results of PERMANOVA for the effects of regions and habitats for richness and average taxonomic distinctness - AvTD. Regions: Tr, Tropical; Ta, Transition and Te, Warm Temperate. Habitats: E, estuary and S, surf zone.

Richness				
Source of variation	df	MS	*Pseudo*-F	P
Region	2	36.8	100.9	< 0.001
Habitat	1	39.5	111.3	< 0.001
Region × Habitat	2	16.4	46.2	< 0.001
Residuals	928	0.4		
Total	933			
AvTD index				
Region	2	360.4	33.8	< 0.001
Habitat	1	611.6	57.3	< 0.001
Region × Habitat	2	48.7	4.6	0.011
Residuals	928	10.7		
Total	933			

Tropical region could also be related to eventual differences in the sampling efficiency. Although we have tried to standardise the sampling effort by carrying out the samplings under better weather conditions, the comparatively high tide range in the mesotidal tropical oceanic surf zone (ca. 2.5 m) could make the beach seines less efficient when compared to the microtidal oceanic beaches in the Transition and Warm Temperate regions (tidal range 0.5–1.3 m).

An alternative hypothesis, the climate harshness hypothesis (Currie et al., 2004) or climate stability hypothesis, suggests that regional differences in species diversity is explained by fluctuation in environmental conditions. According to this hypothesis, fluctuations in environmental conditions increase the extinction rate or preclude specialization, whereas a constant environment can allow species to specialize on predictable resources, allowing them to have narrower niches, facilitating speciation (Brown, 1981; Rohde, 1992; Feary et al., 2014). Since the Warm Temperate region is more seasonally variable, the lower species richness and diversity found in this area compared with the Tropical and Transition regions are in accordance with the climate harshness hypothesis. However, the debate over the cause of the regional diversity gradient will continue until there is a general consensus that multiple factors contribute to this pattern.

Species richness and taxonomic distinctness were positively correlated and were lowest in the Warm Temperate region. A reduction in the average taxonomic range of the benthic fish community sampled by beam trawl surveys between the western waters of the UK and the southern North Sea was consistent with the general decline in species richness observed between these regions and suggests that these two factors may be spatially positively correlated (Rogers et al., 1999). Our findings of higher AvTD in the Tropical and Transition regions compared with the Warm Temperate region, also coincide with a decreasing in the number of species. Another similar trend of decreasing AvTD and species richness was found by Xavier and Van Soest (2012) based on compiling data for the Mediterranean Sea and the north-east Atlantic. Taxonomic measures of diversity and distinctness are sensitive indicators of ecological conditions fish community (Campbell et al., 2011). Hall and Greenstreet (1998) observed that, for bottom-dwelling fish from the northern North Sea, trends in taxonomic distinctness and diversity were identical, suggesting that assemblages that are more diverse and species-rich always contain species that have a wider average taxonomic range than assemblages that are less diverse.

High fish redundancy was detected in both habitats for the Tropical and Transition regions compared with the Warm Temperate region, where a low number of species was found for each genus or higher taxonomic level. Seven of the 16 families in estuarine habitats and five of the 10 families in the surf zone of the Warm Temperate region were represented by only one species. This low redundancy associated with low species richness in the Warm Temperate region raises concerns in terms of conservation of ecosystem services in case of disturbances in the Warm Temperate region.

Regional-scale patterns of the nearshore fish community encompassing ~ 3200 km of the Brazilian coast were described in this study. These patterns provide a baseline against which to detect and monitor future ecological changes in the nearshore fish assemblage structure and diversity. However, cautions should be taken in interpreting these patterns because we have only three region investigated, although with large number of samples collected during two years. Species richness is also influenced by more regional and local parameters that can further affect the process of community colonization in an estuary including the connectivity of the estuary with the adjacent marine habitat, and, over smaller spatial extents, the size of these habitats (Barletta et al., 2010; Vasconcelos et al., 2015). Understanding patterns of diversity help us to understand large scale ecological processes and represent the first steps towards developing a more complete picture of nearshore fishes of the Southwestern Atlantic coast. However, it is necessary the development of analyses that rigorously and quantitatively assess the extent to which the distribution of species occur. It is a difficult conceptual challenge that worth confronting.

Acknowledgements

Appendix A Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ecss.2018.04.027.

References

Able, K.W., 2005. A re-examination of fish estuarine dependence: evidence for connectivity between estuarine and ocean habitats. Estuar. Coast Shelf Sci. 64, 5–17. http://dx.doi.org/10.1016/j.ecss.2005.02.002.

Able, K.W., Wuensche, M.J., Grothues, T.M., Vasslides, J.M., Rowe, P.M., 2013. Do surf zones in New Jersey provide "nursery" habitat for southern fishes? Environ. Biol. Fish. 96, 661–675. http://dx.doi.org/%2010.1007/s10641-012-0056-8.

Anderson, M., Gorley, R., Clarke, K., 2008. Permanova+ for Primer. Primer-E Ltd, Plymouth.

Andrade-Tubino, M.F., Ribeiro, A.L.R., Vianna, M., 2008. Organização espaço-temporal das ictiocenoses demersais nos ecossistemas estuarinos brasileiros: Uma síntese. Oecol. Bras 12, 640–661 https://doi.org/10.4257/oeco.%3ca href= > https://doi.org/10.4257/oeco.2008.1204.05.

Araújo, F.G., Azevedo, M.C.C., Pessanha, A.L.M., Silva, M.A., Gomes, I.D., Cruz-Filho, A.G., 2002. Environmental influences on the demersal fish assemblages in the Sepetiba Bay, Brazil. Estuaries 25 (3), 441–450. http://doi.org/10.1007/BF02695986.

Araújo, M.E., Texeira, J.M., Oliveira, A.M.E., 2004. Peixes estuarino-marinhos do nordeste do Brasil: Guia Ilustrado. Fortaleza: Editora da Universidade Federal do Ceará. pp. 260.

Araújo, F.G., Azevedo, M.C.C., Guedes, A.P.P., 2016. Inter-decadal changes in fish communities of a tropical bay in southeastern Brazil. Reg. Stud. Mar. Sci. 3, 107–118. http://doi.org/10.1016/j.rsma.2015.06.001.

Barletta, M., Barletta-Bergan, A., Saint-Paul, U., Hubold, G., 2005. The role of salinity in structuring the fish assemblages in a tropical estuary. J. Fish. Biol. 66, 45–72. https://doi.org/10.1111/j.0022-1112.2005.00582.x.

Barletta, M., Jaureguizar, A.J., Baigun, C., Fontoura, N.F., Agostinho, A.A., Almeida-Val, V.M.F., Val, A.L., Torres, R.A., Jimenes-Segura, L.F., Giarrizzo, T., Fabré, N.N., Batista, V.S., Lasso, C., Taphorn, D.C., Costa, M.F., Chaves, P.T., Vieira, J.P., Corrêa, M.F.M., 2010. Fish and aquatic habitat conservation in South America: a continental overview with emphasis on Neotropical systems. J. Fish. Biol. 76, 2118–2176. http://dx.doi.org/10.1111/j.1095-8649.2010.02684.x.

Barreiros, J.P., Figna, V., Hostim-Silva, M., Santos, R.S., 2004. Seasonal changes in a sandy beach fish assemblage at Canto Grande, Santa Catarina, south Brazil. J. Coast Res. 20 (3), 862–870. http://www.jstor.org/stable/4299344.

Beck, M.W., Heck, K.L., Able Jr., K., Childers, D., Eggleston, D.B., Gillanders, B.M.,

Halpern, B., Hays, C.G., Hoshino, K., Minello, T.J., Orth, R.J., Sheridan, P.F., Weinstein, M.P., 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51, 633–641 http://dx.doi.org/10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2.

Begon, M., Harper, J.L., Townsend, C.R., 1986. Ecology. Individuals, Populations and Communities. Blackwell, Oxford.

Besyst, B., Cattrijsse, A., Mees, J., 1999. Feeding ecology of juvenile flatfishes of the surf zone of a sandy beach. J. Fish. Biol. 55, 1171–1186. http://dx.doi.org/%2010.1111/j.1095-8649.1999.tb02068.x.

Bevilacqua, S., Fraschetti, S., Musco, L., Guarnieri, G., Terlizzi, A., 2011. Low sensitiveness of taxonomic distinctness indices to human impacts: evidences across marine benthic organisms and habitat types. Ecol. Indicat. 11, 448–455. http://doi.org/10.1016/j.ecolind.2010.06.016.

Bezerra, D.M.M., Nascimento, D.M., Ferreira, E.N., Rocha, P.D., Mourão, J.S., 2012. Influence of tides and winds on fishing techniques and strategies in the Mamanguape River estuary, Paraíba state, NE Brazil. An. Acad. Bras. Cienc 84, 775–787. https://doi.org/10.1590/S0001-37652012005000046.

Blaber, S.J.M., 2013. Fishes and fisheries in tropical estuaries: the last 10 years. Estuar. Coast Shelf Sci. 135, 57–65. https://doi.org/10.1016/j.ecss.2012.11.002.

Borland, H.P., Schlacher, T.A., Gilby, B.L., Connolly, R.M., Yabsley, N.A., Olds, A.D., 2017. Habitat type and beach exposure shape fish assemblages in the surf zones of ocean beaches. Mar. Ecol.: Prog. Ser. 570, 203–211. https://doi.org/10.3354/meps12115.

Brown, J.H., 1981. Two decades of homage to Santa Rosalia: towards a general theory of diversity. Am. Zool. 21, 877–888. http://doi.org/10.1093/icb/21.4.877.

Brown, A.C., McLachlan, A., 1990. Ecology of Sandy Shores. Elsevier/New York.

Burns, M.D.M., Garcia, A.M., Vieira, J.P., Bemvenuti, M.A., Marques, D.M.L.M., Condini, V., 2006. Evidence of habitat fragmentation affecting fish movement between the Patos and Mirim coastal lagoons in Southern Brazil. Neotrop. Ichthyol. 4, 69–72. https://doi.org/10.1590/S1679-62252006000100006.

Campbell, N., Neat, F., Burns, F., Kunzlik, P., 2011. Species richness, taxonomic diversity, and taxonomic distinctness of the deep-water demersal fish community on the Northeast Atlantic continental slope (ICES Subdivision VIa). ICES J. Mar. Sci. 68 (2), 365–376. http://dx.doi.org/10.1093/icesjms/fsq070.

Ceni, G., Vieira, J.P., 2013. Looking through a dirty glass: how different can the characterization of a fish fauna be when distinct nets are used for sampling. Zool 30, 499–505. https://doi.org/10.1590/S1984-46702013000500005.

Ciotti, A.M., Odebrecht, C., Fillman, G., Moller Jr., O.O., 1995. Freshwater outflow and subtropical convergence influence on phytoplankton biomass on the southern Brazilian continental shelf. Continent. Shelf Res. 15, 1737–1756. http://doi.org/10.1016/0278-4343(94)00091-Z.

Clark, B.M., Bennett, B.A., Lamberth, S.J., 1994. A comparison of the ichthyofauna of two estuaries and their adjacent surf zones, with an assessment of the effects of beach-seining on the nursery function of estuaries for fish. S. Afr. J. Mar. Sci. 14 (1), 121–131. http://dx.doi.org/10.2989/025776194784286941.

Clarke, K.R., Warwick, R.M., 1998. A taxonomic distinctness index and its statistical properties. J. Appl. Ecol. 35 (4), 523–531. http://dx.doi.org/10.1046/j.1365-2664.1998.3540523.x.

Clarke, K.R., Warwick, R.M., 2001. A further biodiversity index applicable to species lists: variation in taxonomic distinctness. Mar. Ecol. Prog. Ser. 216, 265–278. http://dx.doi.org/10.3354/meps216265.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Kaufman, D.M., Kerr, J.T., Oberdorff, T., 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecol. Lett. 7, 1121–1134. http://dx.doi.org/10.1111/j.1461-0248.2004.00671.x.

Dahl, E., 1952. Some aspects of the ecology and zonation of the fauna on sandy beaches. Oikos 4, 1–27. http://dx.doi.org/%2010.2307/3565072.

Feary, D.A., Pratchett, M.S., Emslie, M.J., Fowler, A.M., Figueira, W.F., Luiz, O.J., Nakamura, Y., Booth, D.J., 2014. Latitudinal shifts in coral reef fishes: why some species do and others do not shift. Fish Fish. 15, 593–615. http://dx.doi.org/%2010.1111/faf.12036.

Félix, F.A., Spach, H.L., Moro, P.S., Schwarz Jr., R., Santos, C., Hackradt, C.W., Hostim-Silva, M., 2007. Utilization patterns of surf zone inhabiting fish from beaches in Southern Brazil. Pan Am. J. Aquat. Sci. 2, 27–39.

Figueiredo, J.L., 1977. Manual of Marine Fish from Southeastern Brazil. I. Introduction: Sharks, Rays and Chimaeras. Zoology Museum. São Paulo, Brazil in Portuguese.

Figueiredo, J.L., Menezes, N.A., 1978. Manual of Marine Fish from Southeastern Brazil. II Teleostei (1). Zoology Museum. São Paulo, Brazil in Portuguese.

Figueiredo, J.L., Menezes, N.A., 1980. Manual of Marine Fish from Southeastern Brazil. III. Teleostei (2). Zoology Museum. São Paulo, Brazil in Portuguese.

Figueiredo, J.L., Menezes, N.A., 2000. Manual of Marine Fish from Southeastern Brazil. III. Teleostei (5). Zoology Museum. São Paulo, Brazil in Portuguese.

Fischer, L.R., Pereira, L.E., Vieira, J.P., 2004. In: Peixes Estuarinos e Costeiros, 1. ed. pp. 125 Rio Grande: Ecoscientia.

Floeter, S.R., Soares-Gomes, A., 1999. Biogeographic and species richness patterns of Gastropoda on the southwestern Atlantic. Rev. Bras. Biol. 59, 567–575. https://doi.org/10.1590/S0034-71081999000400006.

Franco, A.C., Chaves, M.C.N.R., Castel-Branco, P.B.M., Santos, L.N., 2016. Responses of fish assemblages of sandy beaches to different anthropogenic and hydrodynamic influences. J. Fish. Biol. 89 (1), 921–938. http://dx.doi.org/10.1111/jfb.12889.

Garcia, A.M., Vieira, J.P., 2001. The increase in diversity of the fish estuarine assemblage in the Patos Lagoon estuary during the El Niño 1997–1998 event. Atlantica 23, 133–152. http://doi.org/10.1007/BF02803417.

Gaston, K.J., 2000. Global patterns in biodiversity. Nature 405, 220–227. http://dx.doi.org/10.1038/35012228.

Gibson, R.N., Ansell, A.D., Robb, L., 1993. Seasonal and annual variations in abundance and species composition of fish and macrocrustacean communities on a Scottish sandy beach. Mar. Ecol. Prog. Ser. 98, 89–105.

Hall, S.J., Greenstreet, S.P.R., 1998. Taxonomic distinctness and diversity measures: responses in marine fish communities. Mar. Ecol. Prog. Ser. 166, 227–229. http://dx.doi.org/%2010.3354/meps166227.

Hastenrath, S., Heller, L., 1977. Dymamics of climatic hazard in the Northeast Brazil. Quart. J. Roy. Meteor. Soc. 103, 77–92. http://dx.doi.org/%2010.1002/qj.49710343505.

Hillebrand, H., 2004. Strength, slope and variability of marine latitudinal gradients. Mar. Ecol. Prog. Ser. 273, 251–267. http://www.jstor.org/stable/24867490.

Hughes, T.P., 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265, 1547–1551. http://dx.doi.org/%2010.1126/science.265.5178.1547.

Hurlbert, S.H., 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52, 577–586. http://dx.doi.org/%2010.2307/1934145.

Isbell, F., Craven, D., Connolly, J., Loreau, M., et al., 2015. Biodiversity increases the resistance of ecosystem productivity to climate extremes. Nature 526, 574–577. http://dx.doi.org/10.1038/nature15374.

Jaureguizar, A.J., Mennic, R., Guerrero, R., Lasta, C., 2004. Environmental factors structuring fish communities of the Río de la Plata estuary. Fish. Res. 66, 195–211. http://dx.doi.org/10.1016/S0165-7836(03)00200-5.

Knoppers, B., 1994. Aquatic primary production in coastal lagoons. In: Kjerfve, B. (Ed.), Coastal Lagoon Processes. Elsevier Oceanography Series 60, pp. 243–286. http://doi.org/10.1016/S0422-9894(08)70014-X.

Lamberth, S.J., Clark, B.M., Bennett, B.A., 1995. Seasonality of beach-seine catches in False Bay, South Africa, and implications for management. S. Afr. J. Mar. Sci. 15, 157–167. https://doi.org/10.2989/025776195784156386.

Leonard, D.R.P., Clarke, K.R., Somerfield, P.J., Warwick, R.M., 2006. The application of an indicator based on taxonomic distinctness for UK marine biodiversity assessments. J. Environ. Manag. 78, 52–62. http://dx.doi.org/%2010.1016/j.jenvman.2005.04.008.

Loreau, M., de Mazancourt, C., 2013. Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. Ecol. Lett. 16 (Suppl 1), 106–115. http://dx.doi.org/%2010.1111/ele.12073.

Lowe-Mcconnell, R.H., 1999. Estudos ecológicos de comunidade de peixes tropicais. São Paulo: Edusp.

Macpherson, E., Duarte, C.M., 1974. Patterns in species richness, size, and latitudinal range of East Atlantic fishes. Ecography 17, 242–248. http://dx.doi.org/%2010.1111/j.1600-0587.1994.tb00099.x.

Magurran, A.E., 2004. Measuring Biological Diversity. Blackwell Science Ltd, Oxford.

Menezes, N.A., Figueiredo, J.L., 1980. Manual of Marine Fish from Southeastern Brazil. IV. Teleostei (3). Zoology Museum. São Paulo, Brazil in Portuguese.

Menezes, N.A., Figueiredo, J.L., 1985. Manual of Marine Fish from Southeastern Brazil. IV. Teleostei (4). Zoology Museum. São Paulo, Brazil in Portuguese.

Miloslavich, P., Klein, E., Díaz, J.M., Hernández, C.E., Bigatti, G., Campos, L., Artigas, F., Castillo, J., Penchaszadeh, P.E., Neill, P.E., Carranza, A., Retana, M.V., Astarloa, J.M.D., Mirtha, L., Yorio, P., Piriz, M.L., Rodriguez, D., Yoneshigue-Valentin, Y., Gamboa, L., Martín, A., 2011. Marine biodiversity in the Atlantic and Pacific coasts of South America: knowledge and gaps. PLoS One 6, e14631. http://dx.doi.org/%2010.1371/journal.pone.0014631.

Modde, T., Ross, S.T., 1981. Seasonality of fishes occupying a surf zone habitat in the northern Gulf of Mexico. Fish. Bull. 78, 911–922.

Möller, O., Fernandes, E., 2010. Hidrologia e hidrodinâmica. In: Seeliger, U., Odebrecht, C. (Eds.), O estuário da Lagoa dos Patos: um século de transformações. FURG, pp. 17–30.

Naeem, S., 1998. Species redundancy and ecosystem reliability. Conserv. Biol. 12, 39–45. http://dx.doi.org/%2010.1111/j.1523-1739.1998.96379.x.

Nobre, P., Shukla, J., 1996. Variations of sea surface temperature, wind stress and rainfall over the Tropical Atlantic and South America. J. Clim. 9, 2464–2479 http://doi.org/10.1175/1520-0442(1996)009 < 2464:VOSSTW > 2.0.CO;2.

Oliveira, R.E.M.C.C., Pessanha, A.L.M., 2014. Fish assemblages along a morphodynamic continuum on three tropical beaches. Neotrop. Ichthyol. 12 (1), 165–175. https://doi.org/10.1590/S1679-62252014000100018.

Palacio, F.J., 1982. Revisión zoogeográfica marina del sur del Brasil. Bol. Inst. Oceanogr. 31, 69–92. https://doi.org/10.4067/S0716-078X2000000400007.

Passos, C.V.B., Fabré, N.N., Malhado, A.C.M., Batista, V.S., Ladle, R.J., 2016. Estuarization increases functional diversity of demersal fish assemblages in tropical coastal ecosystems. J. Fish. Biol. 89, 847–862. http://doi.org/10.1111/jfb.13029.

Patterson, A.W., Whitfield, A.K., 2000. Do the shallow-water habitats function as refugia for juveniles fishes? Estuar. Coast Shelf Sci. 51, 359–364. http://doi.org/10.1006/ecss.2000.0640.

Pereira, P.S., Calliari, L.J., Barletta, R.C., 2010. Heterogeneity and homogeneity of southern Brazilian beaches: a morphodynamic and statistical approach. Continent. Shelf Res. 30, 270–280. http://doi.org/10.1016/j.csr.2009.11.007.

Peters, D.J., Nelson, W.G., 1987. The seasonality and spatial patterns of juvenile surf zone fishes of the Florida east coast. Fla. Scient 50, 85–99.

Plavan, A.A., Passadore, C., Gimenez, L., 2010. Fish assemblage in a temperate estuary on the Uruguayan coast: seasonal variation and environmental influence. Braz. J. Oceanogr. 58 (4), 299–314. http://doi.org/10.1590/S1679-87592010000400005.

Rishworth, G.M., Strydom, N.A., Potts, W., 2015. Fish utilization of surf-zones. Are they changing? A case study of the Sheltered, warm-temperate King's Beach. Afr. Zool. 49 (1), 5–21. http://dx.doi.org/10.1080/15627020.2014.11407616.

Rocha, J.M., Milliman, J.D., Santana, C.I., Vicalvi, M.A., 1975. Southern Brazil. In: COntributions to Sedimentology, Upper Continental Margin Sedimentation off Brazil, Stuttgart 4, pp. 117–150.

Rodrigues, F.L., Vieira, J.P., 2013. Surf zone fish abundance and diversity at two sandy

beaches separated by long rocky jetties. J. Mar. Biol. Assoc. U. K. 93 (4), 867–875. http://dx.doi.org/10.1017/S0025315412001531.

Rogers, S., Clarke, K.R., Reynolds, J.D., 1999. The taxonomic distinctness of coastal bottom-dwelling fish communities of the North-east Atlantic. J. Anim. Ecol. 68, 769–782. http://www.jstor.org/stable/2647315.

Rohde, K., 1992. Latitudinal gradients in species diversity: the search for the primary cause. Oikos 65, 514–527. http://dx.doi.org/%2010.2307/3545569.

Ross, S.T., Mcmichael, R.H., Ruple, D.L., 1987. Seasonal and die I variation in the standing crop of fishes and macroinvertebrates from a Gulf of Mexico surf zone. Estuar. Coast Shelf Sci. 25, 391–412.

Seeliger, U., Garcia, V.M.T., Gianuca, N.M., Castello, J.P., Haimovici, M., Odebrecht, C., Vooren, C.M., 1997. Relationships and function of coastal and marine environments. In: Seeliger, U., Odebrecht, C., Castello, J.P. (Eds.), Subtropical Convergence Environments: The Coast and Sea in the Southwestern Atlantic. Springer-Verlag Berlin Heidelberg, pp. 161–178. http://doi.org/10.1007/978-3-642-60467-6_7.

Signorini, S.R., 1978. On the circulation and the volume transport of the Brazil current between the Cape of São Tomé and Guanabara bay. Deep-Sea Res. 25 453–443. http://doi.org/10.1016/0146-6291(78)90556-8.

Solari, A., Jaureguizar, A.J., Milessi, A.C., García, Mirta L., 2015. Fish assemblages in a small temperate estuary on the Argentinian coast: spatial variation, environmental influence and relevance as nursery area. Braz. J. Oceanogr. 63, 181–194. https://doi.org/10.1590/S1679-87592015085106303.

Souza, C.D., Batista, V.S., Fabré, N.N., 2018. What are the main local drivers determining richness and fishery yields in tropical coastal fish assemblages? Zool 35, e12898. http://dx.doi.org/10.3897/zoologia.35.e12898.

Stramma, L., England, M., 1999. On the water masses and mean circu1ation of the South Atlantic Ocean. Geophys. Res. 104, 20863–20883. http://dx.doi.org/%2010.1029/1999JC900139.

Tilman, D., Wedin, D., Knops, J., 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379, 718–720. http://dx.doi.org/10.1038/379718a0.

Tilman, D., Isbell, F., Cowles, J.M., 2014. Biodiversity and ecosystem functioning. Annu. Rev. Ecol. Evol. Syst. 45, 471–493. http://doi.org/10.1146/annurev-ecolsys-120213-091917.

Tipper, J.P., 1979. Rarefaction and rarefiction-—the use and abuse of a method in paleoecology. Paleobiology 5, 423–434. http://doi.org/10.1017/S0094837300016924.

Vallina, S.M., Follows, M.J., Dutkiewicz, S., Montoya, J.M., Cermeno, P., Loreau, M., 2014. Global relationship between phytoplankton diversity and productivity in the ocean. Nat. Commun. 5 (4299), 1–10. http://dx.doi.org/%2010.1038/ncomms5299.

Vasconcelos, R.P., Henriques, S., Franca, S., Pasquaud, S., Cardoso, I., Laborde, M., Cabral, H.N., 2015. Global patterns and predictors of fish species richness in estuaries. J. Anim. Ecol. 84, 1331–1341. http://dx.doi.org/10.1111/1365-2656.12372.

Vasconcellos, R.M., Araújo, F.G., Santos, J.N.S., Silva, M.A., 2011. Diel seasonality in fish biodiversity in a sandy beach in south-eastern Brazil. J. Mar. Biol. Assoc. U. K. 91, 1337–1344.

Vilar, C.V., Joyeux, J.C., Giarrizzo, T., Spach, H.L., Vieira, J.P., Vaske-Junior, T., 2013. Local and regional ecological drivers of fish assemblages in Brazilian estuaries. Mar. Ecol. Prog. Ser. 485, 181–197. http://doi.org/10.3354/meps10343.

Walker, B.H., 1992. Biodiversity and ecological redundancy. Conserv. Biol. 6, 18–23.

Walker, B.H., 1995. Conserving biological diversity through ecosystem resilience. Conserv. Biol. 9, 747–752. http://dx.doi.org/%2010.1046/j.1523-1739.1995.09040747.x.

Warwick, R.M., Clarke, K.R., 2001. Practical measures of marine biodiversity based on relatedness of species. Oceanogr. Mar. Biol. Annu. Rev. 39, 207–231. http://www.researchgate.net/publication/268976744.

Whitfield, A.K., Pattrick, P., 2015. Habitat type and nursery function for coastal marine fish species, with emphasis on the Eastern Cape region, South Africa. Estuar. Coast Shelf Sci. 160, 49–59. http://dx.doi.org/10.1016/j.ecss.2015.04.002.

Willig, M.R., Kaufmann, D.M., Stevens, R.D., 2003. Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. Annu. Rev. Ecol. Syst 34, 273–309. http://doi.org/10.1146/annurev.ecolsys.34.012103.144032.

Winter, M., Devictor, V., Schweiger, O., 2013. Phylogenetic diversity and nature conservation: where are we? Trends Ecol. Evol. 28, 199–204. http://dx.doi.org/10.1016/j.tree.2012.10.015.

Xavier, J.R., Van Soest, R.W.M., 2012. Diversity patterns and zoogeography of the Northeast Atlantic and Mediterranean shallow-water sponge fauna. Hydrobiologia 687, 107–125. http://dx.doi.org/10.1007/s10750-011-0880-4.