



# How are fish assemblages and feeding guilds organized in different tropical coastal systems? Comparisons among oceanic beaches, bays and coastal lagoons

Magda Fernandes de Andrade-Tubino · Marcia Cristina Costa Azevedo ·  
Taynara Pontes Franco · Francisco Gerson Araújo

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**Abstract** Coastal ecosystems can vary considerably in their habitat characteristics and environmental conditions, resulting in divergent fish community structures. However, comparisons among coastal systems, such as oceanic beaches, bays and coastal lagoons, have not been thoroughly evaluated. We test the hypothesis that coastal systems that differ in wave exposure, habitat structure, salinity gradients and productivity show different assemblages and feeding guilds. The fish assemblages were significantly different among the systems. The bays had the largest number of species, whereas the lagoons had the highest numerical abundance and biomass. The planktivorous guild dominated in numerical abundance in all systems, whereas the opportunists dominated in biomass. The benthivores contributed greatly in abundance to the bays, the opportunists to the coastal lagoons, and the hyperbenthivores to the

oceanic beaches. Water transparency and temperature explained a small portion of the variation in the community structure. This study highlighted the complex role that local factors have on the distribution of fishes at the species and trophic levels. These approaches were efficient to describe the structure and functioning of the assemblages in these different coastal systems. This should be viewed as essential for any comparisons of coastal systems, and in particular for conservation planning.

**Keywords** Fish communities · Biodiversity · Coastal zone · Trophic guilds · South-eastern Brazil

## Introduction

Coastal habitats, which include bays, coastal lagoons and oceanic beaches, are among the most productive and utilized environments because they trap matter and energy brought from both continental drainage and the adjacent marine coast. These habitats harbour a large diversity of species that sustain most of the goods and services from their extremely heterogeneous habitats and interconnected compartments, such as mangroves, sandbanks, mudflats and seagrass meadows (Whitfield, 1999; Able, 2005; Sheaves, 2009; Henriques et al., 2017). Fish are the dominant group of species in coastal habitats, playing an

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M. F. de Andrade-Tubino · M. C. C. Azevedo ·  
T. P. Franco · F. G. Araújo (✉)  
Laboratório de Ecologia de Peixes, Universidade Federal  
Rural do Rio de Janeiro, BR 465, Km 7, Seropédica,  
RJ 23897-030, Brazil  
e-mail: gersonufrj@gmail.com

important ecological role by driving energy from lower to higher trophic levels, exchanging energy with neighbouring ecosystems and/or storing energy through the species that inhabit these systems (Beck et al., 2001; Amorim et al., 2017; Schloesser & Fabrizio, 2018). Several authors have emphasized the importance of shallow coastal areas for marine fisheries because many of the world's fisheries target species that spend a portion of their life cycle in these shallow areas (Pauly, 1988; Barletta et al., 1998; FAO, 2011). These habitats are used by different fish assemblages that interact with adjacent marine areas and are of fundamental importance for the preservation of biodiversity (Day & Yáñez-Arancibia, 1985; Mariani, 2001; Ross, 2003; Sheaves, 2016). Understanding the patterns of fish associations in different coastal areas is of paramount importance for identifying habitats for prioritization in conservation programmes aiming to maintain fish populations.

The distribution of fish in coastal areas depends on the intrinsic habitat configuration because each type of coastal system plays a particular role as a nursery area that provides suitable conditions for juvenile recruitment or even as dwelling areas for subadults and adults (Bennett, 1989; Able, 2005; Araújo et al., 2016). Fish assemblages differ in their taxonomic and functional composition according to their habitats or spatial characteristics at the local scale that determine different ecological groups, and they are influenced by both biotic interactions and/or environmental filters (Beck et al., 2001; Mouchet et al., 2013; Azevedo et al., 2017). Comparisons of shallow coastal systems, such as oceanic beaches, bay and coastal lagoons, are very important for understanding the roles of the different habitats and the unique influences on fish species.

Oceanic beaches are very dynamic, where wave energy is the driving force of most of the physical, chemical and biological processes (Bennett, 1989; Defeo et al., 2009). Beaches have high instability and different levels of wave exposure, ranging from calm and protected waters in dissipative beaches to strong and high-energy waters in reflective beaches (McLachlan, 1980; Lasiak, 1981; Beyst et al., 2001). The structures of fish assemblages near sandy beaches vary according to the degree of wave exposure, and the dominance of a few species increases while the species richness decreases as wave exposure increases (Romer, 1990; Clark, 1997). Moreover, the fish communities near surf zones are numerically

dominated by only a few species with marked temporal variations, a high proportion of resident species and a small contribution of transient species. Eventually, the lack of seasonality in the community parameters of oceanic beaches may reflect the fact that short-term variability and spatial differences between sites mask seasonal changes (Beyst et al., 2001). Exposed beaches, mainly those located near estuarine areas, play important roles as rearing grounds or routes for juvenile fish between marine and estuarine areas (Schlacher et al., 2008; Rodrigues & Vieira, 2013).

Bays are generally large, deep and complex water bodies (Blaber et al., 1995; Araújo et al., 2017). Thus, bays can have several compartments, such as mudflats, mangroves and tidal channels, that increase habitat diversity and biological productivity. Tides are among the main driving forces contributing to habitat dynamics in bays. Because of the vast sea connection, bays have a gradually decreasing sea influence from the outer zones to the inner zones, which are calm with diluted waters. The wide connection with the sea favours the entrance of fish as eggs, larvae and young-of-the-year that are brought into bays by tides and currents from spawning areas in the inner platform (Costa & Araújo, 2003; Potter et al., 2010). Inner bay zones act as nursery areas for many species that live mainly offshore as adults. Overall, juvenile fish that are restricted to inshore habitats are the main components of inner bay zones, whereas large juveniles and subadults emigrate to outer bay zones or marine waters (Blaber et al., 1995; Araújo et al., 2016).

Coastal lagoons are characterized as ephemeral systems that form part of a continuum of coastal environments that have narrow sea connections, which limits marine influences and favours a salinity gradient between the mouth and the areas inside the lagoon (Day & Yáñez-Arancibia, 1985; Gray et al., 2011). Because of the narrow sea connection, the entrance of marine fish eggs and larvae into coastal lagoons is limited. Coastal lagoons can range from freshwater to hypersaline conditions depending on freshwater inflow, tidal exchange, rainfall and evaporation rates (Day & Yáñez-Arancibia, 1985; Duck & Da Silva, 2012). Coastal lagoons are highly productive ecotones and provide more ecosystem services and social benefits than other aquatic systems (Elliott & Whitfield, 2011; James et al., 2018). These systems usually have shallow depths and transparent waters that promote high primary productivity, allowing large

fish populations to persist, supporting high diversity of niche specialists (Tittensor et al., 2010; Vasconcelos et al., 2011; García-Seoane et al., 2016). The ichthyofauna of coastal lagoons is predominately small, short-lived species, which could be indicative of previous stress conditions (Gray et al., 2011).

The dynamics of these environments can be driven by processes that occur in both the adjacent coastal region and the continental margin under a wide range of spatial and temporal scales (Mariani, 2001, Vasconcelos et al., 2015; Franco & Santos, 2018). Moreover, the fish assemblages in such areas depend on a variety of environmental variables, such as temperature, salinity, turbidity, depth, the type and complexity of habitats, shelter availability, food and interaction with other species (Blaber et al., 1995, Schloesser & Fabrizio, 2018; Souza et al., 2018). Another important issue that needs to be elucidated is whether the presence of fish assemblages in coastal zones is mediated by seasonal variations because most environmental variables change throughout the year. The changing characteristics of these factors and the mobility of juvenile fish greatly influence the composition of the fish communities in these regions (Olds et al., 2018; Franco et al., 2019b).

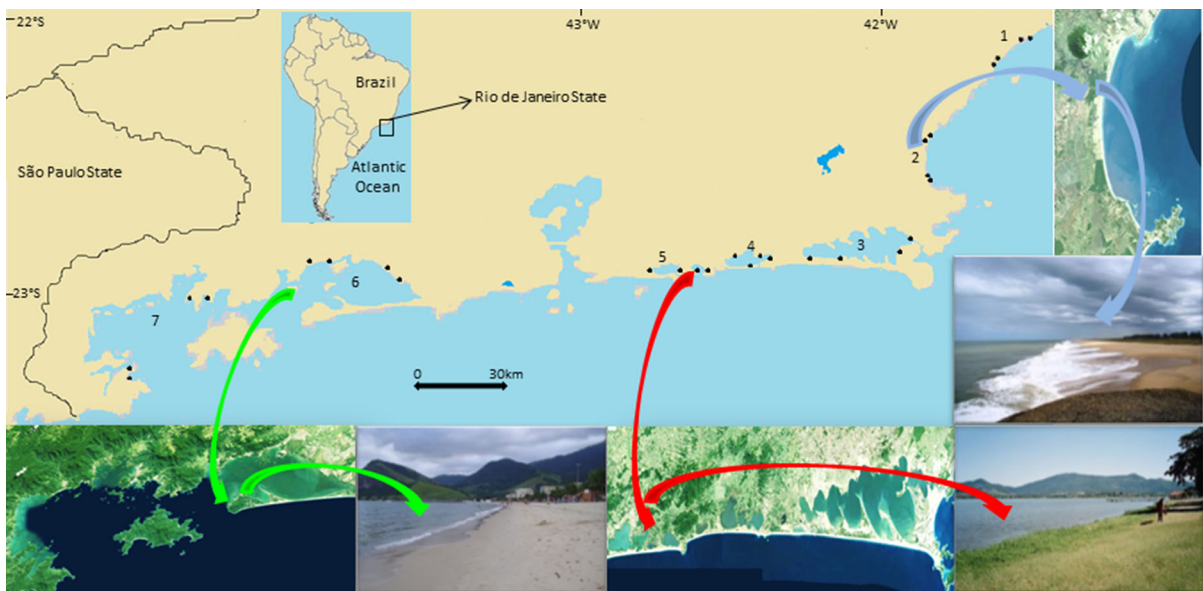
In this study, we aimed to determine and compare the structures of fish assemblages in sandy beaches in

three different coastal systems (oceanic beaches, bays and coastal lagoons) along 650 km of the Rio de Janeiro coast. The tested hypothesis is that the fish assemblages, in terms of species composition and trophic guilds, differ among these three types of coastal systems. The following questions were postulated: (1) Do fish richness and abundance change among these systems? (2) Do differences in the environmental conditions among these three systems result in different fish assemblages and trophic guilds? We expect that bays have greater species richness associated with high habitat diversity, coastal lagoons have high fish abundance and biomass because of the accumulation of high organic loads, and oceanic beaches have a more limited species composition with irregular temporal changes because of the high dynamism of wave exposure.

## Materials and methods

### Study area

The state of Rio de Janeiro has a coastline with great coastal system heterogeneity, such as reflective and dissipative oceanic beaches, bays and coastal lagoons (Fig. 1). In this study, we examined four oceanic



**Fig. 1** Coast of the state of Rio de Janeiro with indication of the sampling sites in the three studied systems (bays, coastal lagoons and oceanic beaches): (1) reflective oceanic beaches;

(2) dissipative oceanic beaches; (3) Araruama Lagoon; (4) Saquarema Lagoon; (5) Maricá Lagoon; (6) Sepetiba Bay; and (7) Ilha Grande Bay

sandy beaches (two reflective and two dissipative), two bays (Sepetiba and Ilha Grande bays) and three coastal lagoons (a hypersaline lagoon, Araruama, with an average salinity of 52 (Kjerfve et al., 1996); a mesohaline lagoon, Saquarema, with an average salinity of 35; and an oligohaline lagoon, Maricá, with an average salinity of 25 (Knoppers et al., 1991, Franco et al., 2019b) (Fig. 1).

The dissipative beaches correspond to flat and shallow shores with a large amount of sand in the submerged portion, whereas reflective beaches form steep shores with a small sand stock (Bastos & Silva, 2000). The average heights of the beaches are 4 m above mean sea level with incipient dunes. The wave heights range between 1 and 2 m.

Sepetiba Bay was formed by an intense sedimentation process brought about by coastal currents that formed an extensive sandbank and an inner zone; the substrate is predominantly muddy and composed of silt and clay with few areas of sand and gravel. Some coastal islands are located near the sea connection, thus enhancing habitat diversity in the bay (Signorini, 1980; Cunha et al., 2006). Ilha Grande Bay is the largest bay in the state of Rio de Janeiro. It has a heavily indented shoreline, and coastal mountains reach the coastline, leaving little space for the formation of coastal plains (Belo et al., 2002; Guerra & Soares, 2009). On the shoreline, there is a predominance of fine sands, with mud sediment restricted to the coves with low hydrodynamics. The coastline is irregular, with alternating stretches of rocky shores, sandy beaches and mangroves that develop in sheltered areas (Belo et al., 2002).

The semi-arid climatic conditions in some regions of the coast favour hypersaline conditions in some of the coastal lagoons (e.g. Araruama coastal lagoon), whereas increased seawater dilution favours the formation of euhaline and mesohaline lagoons, e.g. Saquarema and Maricá coastal lagoon) (Knoppers et al., 1991; Kjerfve et al., 1996).

### Sampling

A beach seine net (12 m long  $\times$  2.5 m high; 8 mm stretched mesh at the wings and 4 mm at the cod end) was used for the fish sampling, which was carried out during the day at neap tide, between 10 and 16 h, twice a year (July, winter; and January, summer) during a two-year period (July 2011, January 2012, July 2012

and January 2013). The hauls were 30 m long and perpendicular to the shore, and they were taken out to a depth of approximately 1.5 m, covering a swept area of approximately 300 m<sup>2</sup>. Two sites in four sandy beaches (two reflective and two dissipative) were sampled with four replicates at each site, totalling 128 samples (4 beaches  $\times$  2 sites  $\times$  2 years  $\times$  2 seasons  $\times$  4 replicates). Four sites were selected in each bay (2 bays  $\times$  4 sites  $\times$  2 years  $\times$  seasons  $\times$  4 replicates = 128 samples) and each coastal lagoon (3 lagoons  $\times$  4 sites  $\times$  2 years  $\times$  2 seasons  $\times$  4 replicates = 192 samples).

The collected fish were fixed in 10% formalin and, after 48 h, preserved in 70% ethanol. For each individual, total length (mm) and weight (g) measurements were obtained. Each species was assigned to one of the six trophic guilds adapted from Elliott et al. (2007) and Araújo et al. (2016), which provided a species list for each guild. Benthivores (BE) feed predominantly on invertebrates associated with the substratum, including animals that live on the sediment (epifauna) or in the sediment (infauna). Hyperbenthivores (HY) feed predominantly on invertebrates that live just above the sediment. Piscivores (PI) feed predominantly on finfish but possibly large nektonic invertebrates. Herbivores (HE) feed predominantly on algae and phytoplankton. Detritivores (DE) feed predominantly on detritus and/or microphytobenthos. Planktivores (PL) feed predominantly on zooplankton. Finally, opportunists (OP) feed on a diverse range of food, and this assignment was used when the species could not be readily assigned to one of the previously specialized feeding modes.

Concurrently with the ichthyofauna sampling, the environmental variables of water temperature (°C), salinity, turbidity (nephelometric turbidity units—NTU), and transparency (cm) were recorded. The environmental variables of temperature, salinity and turbidity were taken with a Horiba U-50 multiprobe (Horiba Trading Co. Ltd., Shanghai) immersed approximately 0.5 m under the water surface. The transparency was measured with a Secchi disc.

### Statistical analyses

Prior to analysis, the biological data were square root transformed to reduce the influence of abundant species but preserve information on their relative abundance. A permutational multivariate analysis of

variance (PERMANOVA, Anderson et al., 2008) was used to compare the differences in the compositions of the fish assemblages and in the trophic guilds (in number and biomass) among the three different systems (three fixed levels: beaches, bays, lagoons) and seasons (two fixed levels: winter and summer) with the sites (random factor) nested within the systems and the environmental variables as predictor covariates. The relative abundance and biomass were expressed as the mean number and weight of fish per 300 m<sup>2</sup> of sampled area. The PERMANOVA was performed using a Bray–Curtis similarity matrix on the previously transformed data. Statistical significance was tested using 9999 permutations of residues under a reduced model of the type I sum of squares (sequential). The environmental variables were standardized (centred to the mean and reduced to units of standard deviation) to eliminate the effects of different units of measurements. A two-way factorial analysis of variance (ANOVA) was used to compare the environmental variables among the three systems and seasons. When ANOVA showed a significant difference, an “a posteriori” Tukey’s HSD test was used to determine the means that were significantly different at the 0.05 level.

A distance-based principal coordinate analysis (PCO) on the fish assemblage and guild data was performed to assess the variability in the samples by plotting the first two axes of the PCO scores. Then, a similarity percentage (SIMPER) analysis was used to determine the species that had the largest contribution to the within-group average similarity for the systems and seasons.

To evaluate the species distribution among systems and seasons, a shadow chart was produced by clustering the samples on the *x*-axis based on the Bray–Curtis similarity. The *y*-axis grouped the common and abundant species based on the association of the Whittaker index (Clarke & Gorley, 2015). Thirty-four species were selected as common or abundant species because they presented frequencies of occurrence or abundance (in weight and number of individuals) higher than 3% in each system. The similarity profile test (SIMPROF) was applied to determine the significance of the differences between the clusters. These analyses were performed using the statistics package PRIMER 6 version 6.1.13. & PERMANOVA + version 1.0.3 (Anderson et al., 2008).

To assess the use of the different systems as nursery areas by a dominant and common fish species, a length-frequency distribution analysis was applied. The species that was used in this analysis (*Atherinella brasiliensis*) was the most widely distributed in the sampled locations of all three systems and was present in more than two-thirds of the samples (69.5%) regardless of the type of system. Comparisons of the length-frequency distribution between the systems and seasons were performed using a non-parametric two-sided Kolmogorov–Smirnov test. This analysis was performed using the Statistica software version 10.0 (StatSoft, 2011).

## Results

### Environmental variables

The water temperature ranged from 18.8 to 34.7°C. Significant differences in the water temperature were found among the systems ( $F = 41.9$ ;  $P = 0.001$ ) and seasons ( $F = 271.5$ ;  $P = 0.001$ ) (Table 1), and the interaction between systems and seasons was also significant ( $F = 7.0$ ;  $P = 0.010$ ). The bays and coastal lagoons had the highest temperature in summer, whereas the bays and oceanic beaches had the lowest temperature in winter (Table 1). The salinity ranged from 8.0 to 54.0. Significant interactions were found between systems and seasons ( $F = 11.5$ ;  $P = 0.001$ ). The oceanic beaches and bays in winter and the coastal lagoons in summer had the highest salinities, whereas the coastal lagoons in winter and the oceanic beaches and bays in summer had the lowest salinity levels (Table 1). The turbidity ranged from 0.64 to 109 NTU, with significant differences among the systems ( $F = 5.1$ ;  $P = 0.007$ ) and seasons ( $F = 4.7$ ;  $P = 0.030$ ), and the interaction between systems and seasons was also significant ( $F = 5.7$ ;  $P = 0.003$ ). The oceanic beaches, coastal lagoons and bays in winter, and the oceanic beaches and coastal lagoons in summer had higher turbidity levels than the bays in summer (Table 1). The water transparency ranged from 10 to 140 cm. Significant differences in the water transparency were found among the systems ( $F = 77.5$ ;  $P = 0.001$ ), and the interaction between systems and seasons was significant ( $F = 9.5$ ;  $P = 0.001$ ). The bays in summer and winter had higher transparencies than the oceanic beaches in

**Table 1** Means and ranges (minimum–maximum) of environmental variables and significant differences from the two-way ANOVA and post hoc Tukey test testing for differences

between systems (oceanic beaches—OB, bays and coastal lagoons—CL) and seasons (winter and summer)

Variable	Oceanic beaches		Bays		Coastal lagoons	
	Winter	Summer	Winter	Summer	Winter	Summer
Temperature (°C)	22.0 (20.9–23.3)	24.4 (18.8–27.7)	22.6 (20.5–27.7)	27.0 (24.1–31.2)	23.8 (20.5–28.3)	28.2 (21.1–34.7)
Salinity	30.9 (18.2–38.0)	30.9 (26.5–33.2)	30.6 (23.5–32.6)	28.1 (19.2–31.6)	29.1 (10.0–53.0)	32.1 (8.0–54.0)
Turbidity (NTU)	20.6 (2.7–48.7)	16.8 (1.6–103.0)	10.7 (1.5–74.5)	9.6 (1.9–34.3)	17.9 (3.3–99.7)	20.9 (1.4–109.0)
Transparency (%)	42.3 (15–90)	55.9 (15–100)	76.3 (25–100)	66.6 (21–100)	42.6 (10–85)	30.3 (10–62)
Post hoc comparisons	Significant differences					
Temperature	Bays and CL in summer > OB in summer and CL in winter > Bays and OB in winter					
Salinity	OB and Bays in winter, CL in summer > OB and Bays in summer and CL in winter					
Turbidity	OB and CL in summer and winter, and Bays in winter > Bays in summer					
Transparency	Bays in summer and winter > OB in summer > OB and CL in winter > CL in summer					

summer, which in turn had higher transparency than the oceanic beaches and coastal lagoons in winter. The coastal lagoons in summer had the lowest transparency.

#### Fish composition

Thirty-seven species were recorded in the dissipative beaches, with the anchovy *Anchoa tricolor* (Spix e Agassiz, 1829), the atherinopsid *Atherinella brasiliensis* (Quoy & Gaimard, 1825), the whitemouth croaker *Micropogonias furnieri* (Desmarest, 1823), the mugilid *Mugil curema* Valenciennes, 1836 and the pompano *Trachinotus carolinus* (Linnaeus, 1766) representing more than 90.0% of the total number of individuals (Table S1 in Supplementary Information). The fish assemblages of the reflective beaches had the lowest species richness (25 species) and abundance of individuals but comparatively high biomass, with more than 80% of the total number of individuals being *Anchoa tricolor* (Table 2). The bays had the greatest numbers of recorded species, with the Rio anchovy *Anchoa januaria* (Steindachner, 1879) representing more than 45% of the total abundance, both in the number of individuals and biomass, in Sepetiba Bay (Table 2). In Ilha Grande Bay, *A. tricolor* and *A. brasiliensis* were the most abundant species.

The coastal lagoons had the greatest abundances in the number of individuals and biomass per sample among all of the studied coastal systems, with the

species richness ranging from 33 in Araruama Lagoon to 34 in Saquarema and Maricá lagoons (Table 2). The assemblages of the coastal lagoons were very similar in their composition and structure, with *A. januaria* and *A. brasiliensis* accounting for approximately 80% of the abundance in the number of individuals and biomass in the three coastal lagoons.

#### Trophic structure

The hyperbenthivores (32 species) followed by the benthivores (24 species) were the dominant guilds in terms of the number of species. The planktivores, which were mainly represented by the Clupeidae and Engraulidae families, had the greatest contributions to the number of individuals and biomass in most of the systems, namely the reflective beaches, the Maricá lagoon and Sepetiba and Ilha Grande bays (Table 2). The detritivorous, herbivorous and piscivorous species were the least representative trophic guilds in both the number of species and the number of individuals and biomass. The opportunistic guild, i.e. species that take advantage of a wide variety of the food available in different habitats, such as *A. brasiliensis*, were well represented in number and biomass in the three coastal lagoons, peaking in Araruama Lagoon (Table 2).

The planktivorous guild dominated the number of individuals and biomass in the reflective beaches, whereas the benthivores, opportunists and piscivores had the greatest contribution to the biomass in the

**Table 2** Mean abundance (MA, individuals per sample) and mean biomass (MB, g per sample) of the selected fish species on the coast of the state of Rio de Janeiro, Brazil

Species	Family	Oceanic Beaches						Coastal Lagoons						Bays						Total	
		Dissipative		Reflective		Araruama		Saquarema		Maricá		Sepetiba		Ilha Grande		MA	MB				
		MA	MB	MA	MB	MA	MB	MA	MB	MA	MB	MA	MB	MA	MB						
<i>Anchoa januaria</i>	Engraulidae	0.6	0.8	0.2	0.1	89.5	57.8	218.9	37.8	99.1	21.9	67.2	10.0	45.2	9.8	74.4	19.7				
<i>Atherinella brasiliensis</i>	Atherinopsidae	4.8	13.8	2.3	19.1	141.6	264.6	84.0	50.3	49.4	78.5	31.4	78.7	9.8	30.0	46.2	76.4				
<i>Anchoa tricolor</i>	Engraulidae	19.0	3.2	31.5	139.1	0.0	0.0	0.0	0.1	0.0	0.0	35.1	8.3	77.7	7.9	23.3	22.7				
<i>Eucinostomus argenteus</i>	Gerreidae	0.0	0.1	0.0	0.0	3.8	5.2	12.2	8.0	0.0	0.0	36.1	15.4	8.8	4.5	11.1	11.9				
<i>Mugil curema</i>	Mugilidae	13.2	0.1	0.8	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.1	1.5	0.0	5.4	6.3				
<i>Brevoortia aurea</i>	Clupeidae	0.0	0.0	0.0	0.0	3.4	4.1	0.5	0.4	31.3	21.7	0.0	0.0	1.8	0.7	5.3	3.8				
<i>Jenynsia multidentata</i>	Anablepidae	0.0	0.0	0.0	0.0	13.5	10.0	5.3	3.4	2.8	3.4	0.0	0.0	0.0	0.0	3.1	2.4				
<i>Micropogonias furnieri</i>	Sciaenidae	9.3	1.0	0.1	0.1	0.1	0.8	1.8	4.2	0.3	7.0	5.5	1.8	4.5	1.6	3.1	2.3				
<i>Mugil liza</i>	Mugilidae	0.0	0.0	0.0	0.0	1.4	4.3	18.7	14.3	17.5	25.4	0.0	0.0	0.0	0.0	2.3	0.0				
<i>Poecilia vivipara</i>	Poeciliidae	0.0	0.0	0.0	0.0	8.3	4.8	5.3	3.0	0.2	0.2	0.0	0.0	0.0	0.0	2.0	1.1				
<i>Trachinotus carolinus</i>	Carangidae	11.5	5.2	0.5	2.2	0.0	0.0	0.0	0.0	0.0	0.0	0.9	1.1	0.4	0.7	1.9	1.3				
Others		5.6	49.7	3.0	39.8	4.0	9.3	13.8	37.9	14.0	25.6	18.8	38.0	11.7	28.3	10.1	32.7				
<b>Trophic Guild</b>	<b>Number of species</b>	<b>37</b>	<b>25</b>	<b>33</b>	<b>34</b>	<b>34</b>	<b>34</b>	<b>49</b>	<b>42</b>	<b>94</b>	<b>42</b>	<b>94</b>	<b>42</b>	<b>94</b>	<b>42</b>	<b>94</b>	<b>94</b>				
Planktivores	11	21.3	8.6	31.7	139.2	92.9	61.9	220.5	44.5	131.6	39.1	104.5	24.0	130.7	22.7	104.7	48.6				
Opportunists	10	5.2	18.4	3.8	38.9	163.5	280.1	95.1	82.3	52.5	69.9	31.4	78.7	10.2	34.7	51.7	86.1				
Benthivores	24	11.8	26.0	0.3	1.5	5.2	9.6	19.4	65.9	23.9	21.0	55.9	36.1	16.5	10.4	19.0	24.4				
Detritivores	3	13.2	0.1	0.8	0.1	1.4	4.7	18.8	25.4	17.5	14.4	0.8	0.1	1.5	0.0	7.7	6.4				
Hyperbenthivores	32	11.8	8.8	1.8	20.2	1.2	0.7	5.3	11.8	3.8	1.4	1.9	6.1	1.6	7.9	3.9	8.1				
Piscivores	10	0.7	11.1	0.1	0.2	1.0	2.5	1.5	2.9	1.5	13.4	1.3	8.1	0.6	7.7	1.0	6.6				
Herbivores	4	0.0	0.9	0.1	0.3	0.4	1.5	0.0	0.7	0.1	0.1	0.1	0.2	0.1	0.0	0.1	0.6				
Mean number of individuals/sample		64.0	73.8	38.5	200.5	265.6	360.9	360.7	159.4	230.9	233.6	195.9	153.4	161.3	83.5	188.1	180.7				

The classification of the trophic guilds is based on Elliott et al. (2007) and Araujo et al. (2016)

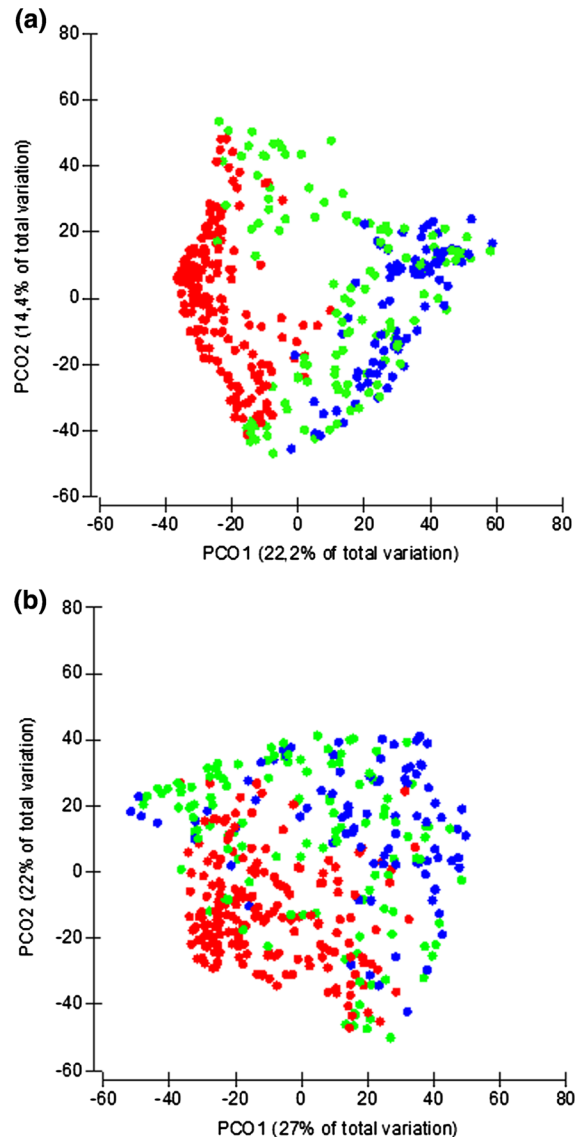
dissipative beaches (Table 2). In the lagoons, the planktivores followed the opportunists in number and biomass, whereas in the bays, the benthivores and opportunists followed the planktivores.

### Spatial–temporal patterns

In number and biomass, the structure of the fish assemblages differed significantly among the three coastal systems (ECV, PERMANOVA, 26.3% of the total variance in number and 23.2% in the biomass), but only the species composition in terms of biomass changed between seasons (6.7%) (Table S2 in the Supplementary Data). The interactions between the sites and seasons were significant for the assemblage structure in terms of the number (12.0%) and biomass (8.8%). There were also significant effects of the sites (nested in the systems) on both the number (20.2%) and biomass (22.3). In addition, a strong relationship was found between the fish assemblages in number and biomass and the covariates of temperature (9.4%, number; 7.7%, biomass) and transparency (13.0% and 9.7%, respectively).

The structure of the trophic guilds also differed significantly in number and biomass among the three coastal systems (20.7% of the total variance in number and 16.6% in the biomass), but, similar to the assemblage structure, only the trophic structure in the biomass changed significantly between seasons (6.5%) (Table S3 in the Supplementary Data). There were no significant interactions between the sites and seasons in the trophic structure in the number or biomass. There was also a significant effect of the sites (nested in the systems) on both the number (18.3%) and biomass (20.7). A weak but significant relationship was detected between the trophic structure and the covariate temperature in the number (3.1%) and biomass (4.3%) and the transparency (4.4%) in the number of individuals.

Differences in the species compositions (Fig. 2a) and trophic guilds (Fig. 2b) between the samples of the coastal lagoons and the oceanic beaches were revealed along the first axis of the principal coordinate analysis (PCO). However, the bay samples were located in an intermediary position, with several samples overlapping with the samples from the oceanic beaches in both species composition and trophic guilds.



**Fig. 2** Plots of the first two axes of the principal coordinate ordination analysis (PCO) on the species composition (a) and trophic guilds (b) with the samples coded by the systems of the state of Rio de Janeiro. Oceanic beaches (blue-filled circle), bays (green-filled circle) and coastal lagoons (red-filled circle)

*Atherinella brasiliensis* contributed most of the within-average similarity for all three systems, accounting for 40.0% in the oceanic beaches, 40.5% in the bays and 49.2% in the coastal lagoons (SIMPER; Table 3). *Anchoa tricolor* contributed 27.5% of the average similarity in the bays, whereas *T. carolinus* and *A. tricolor* contributed 26.6% and 14.7%, respectively, of the average similarity in the oceanic beaches. Moreover, *A. januaria* contributed



14.8% of the average similarity in the bays and 44.2% in the coastal lagoons.

*Anchoa tricolor* was the most abundant species near the oceanic beaches, whereas *A. januaria* and *A. brasiliensis* were the most abundant species in the coastal lagoons (Table 3). *Anchoa januaria* and *A. tricolor* followed by *A. brasiliensis* had the highest abundance in the bays.

The largest contribution to the within-average similarity near the oceanic beaches (Table 3) was recorded for the opportunistic trophic guild (39.0), followed by the hyperbenthivorous (27.9%) and the planktivorous (21.5%) guilds. In the bays, the greatest contribution was recorded for the planktivores (46.6%), followed by the benthivores (26.7%) and the opportunists (22.4%). The opportunistic trophic guild (48.6%) had the highest contribution to the within-average similarity, followed by the planktivorous guild (43.4%) in the coastal lagoons.

The planktivorous guild had the highest numerical abundance in the coastal lagoons, followed by the bays and oceanic beaches (Table 3). Other abundant trophic guilds were the opportunistic guild in the bays (21.3 ind.sample<sup>-1</sup>) and coastal lagoons (103.7 ind.sample<sup>-1</sup>) and the hyperbenthivorous guild near the oceanic beaches (8.4 ind.sample<sup>-1</sup>). The benthivorous guild was well represented near the

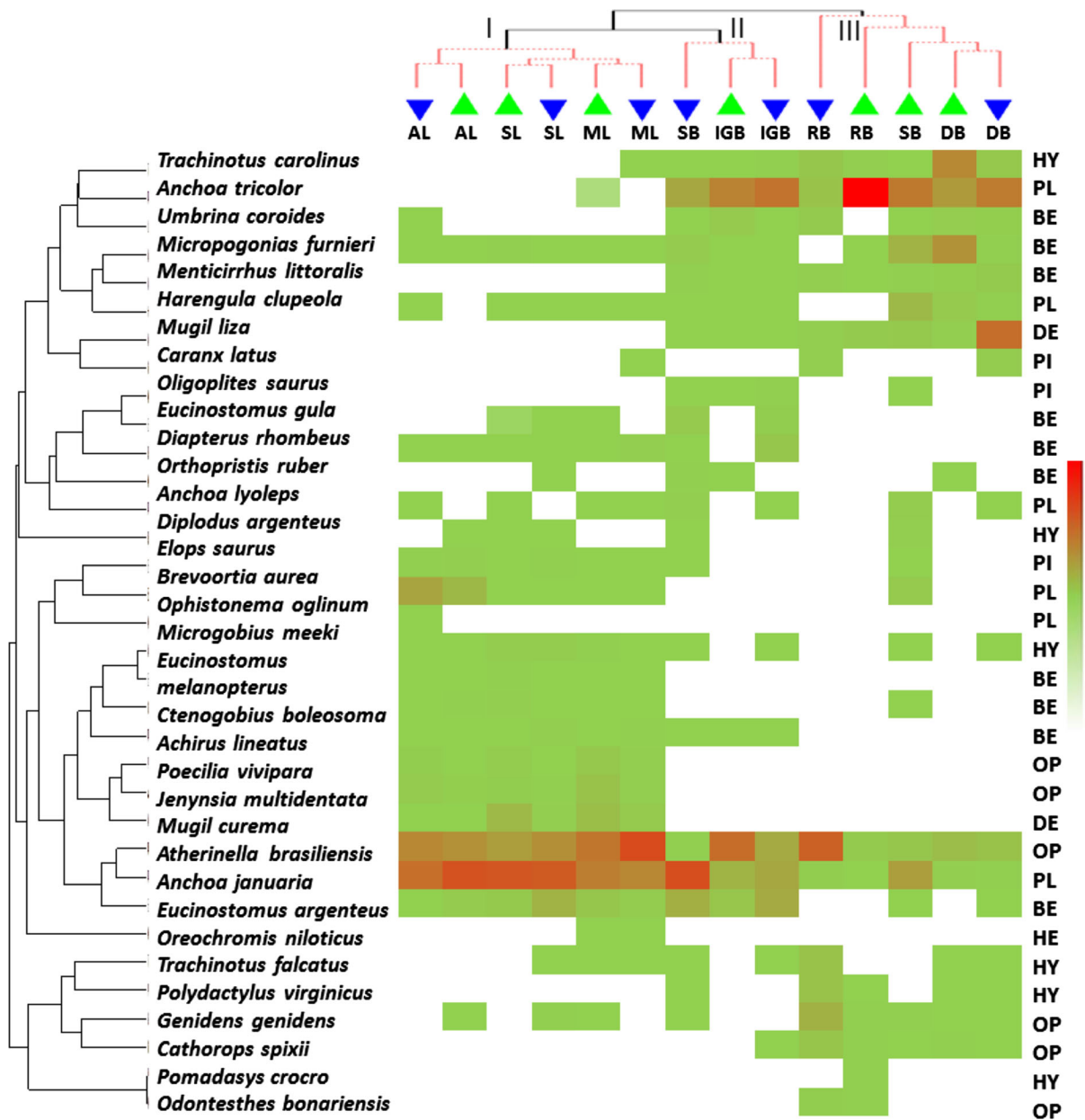
oceanic beaches (7.5 ind.sample<sup>-1</sup>) and in the bays (36.8 ind.sample<sup>-1</sup>).

Differences in the occurrence of species across systems and seasons were detected by cluster analysis, and a shadow diagram based on the abundance of the 34 most commonly selected fish species is shown (Fig. 3). Three different groups were depicted from the axis (systems and seasons): one (I) was formed by the lagoons, with a high abundance of *A. januaria* and *A. brasiliensis* in both winter and summer; a second group (II) was formed by Ilha Grande (both seasons) and Sepetiba Bay during the summer, with the highest abundance of *A. brasiliensis*, *A. januaria* and *A. tricolor*; and the third group (III) was formed by the reflective and dissipative beaches and by Sepetiba Bay in winter, with peaks of *A. tricolor*. The coastal lagoons had more similar assemblage structures, both in winter and summer, with predominance of *A. januaria* and *A. brasiliensis*.

The horizontal axis clustered the species abundance and depicted that the first two groups of species (1 and 2), with eight and six species, respectively, were composed mainly of benthivorous, planktivorous and detritivorous species, with the highest abundances near the beaches and in the bays (Fig. 3). The benthivorous species in group 1 were mainly *M. furnieri*, the planktivorous species were *A. tricolor* and

**Table 3** Average similarity for each system (in brackets) and species average abundance (Av. Ab.) and % contribution to average similarity (Sim. Cont. %) according to the similarity percentage (SIMPER) analysis for the most typical species and trophic guilds in the bays, coastal lagoons and oceanic beaches

Species	Beaches (10.3%)		Bays (10.9%)		Lagoons (31.4%)	
	Av. Ab	Sim. Cont. %	Av. Ab.	Sim. Cont. %	Av. Ab.	Sim. Cont. %
<i>A. brasiliensis</i>	4.9	40.0	21.1	40.5	92.7	49.2
<i>A. januaria</i>			57.1	14.8	117.0	44.2
<i>E. argenteus</i>			14.9	5.8		
<i>A. tricolor</i>	33.9	14.7	57.3	27.5		
<i>M. furnieri</i>			5.1	5.9		
<i>U. coroides</i>	0.7	3.5				
<i>M. liza</i>	0.8	4.2				
<i>T. carolinus</i>	8.0	26.5				
Trophic Guilds	(16.3%)		(21.2%)		(35.8%)	
Benthivores	7.5	7.3	36.8	26.7		
Planktivores	33.2	21.5	119.8	46.6	129.5	43.4
Opportunists	5.6	39.0	21.3	22.4	103.7	48.6
Hyperbenthivores	8.4	27.9				



**Fig. 3** Shade diagram illustrating the distribution of species in the different coastal systems (*DB* dissipative beach, *RB* reflective beach, *AL* Araruama Lagoon, *SL* Saquarema Lagoon, *ML* Maricá Lagoon, *IGB* Ilha Grande Bay, *SB* Sepetiba Bay) and seasons (green-filled triangle winter and blue-filled inverted triangle summer). The upper dendrogram groups the samples based on species composition. The dendrogram on the left

the detritivorous species were *M. liza*. Groups 3 and 4 comprised 14 and 6 species, respectively. Group 3 was mainly composed of planktivorous and opportunistic species that were more abundant in the lagoons but also recorded in the beaches and/or bays with

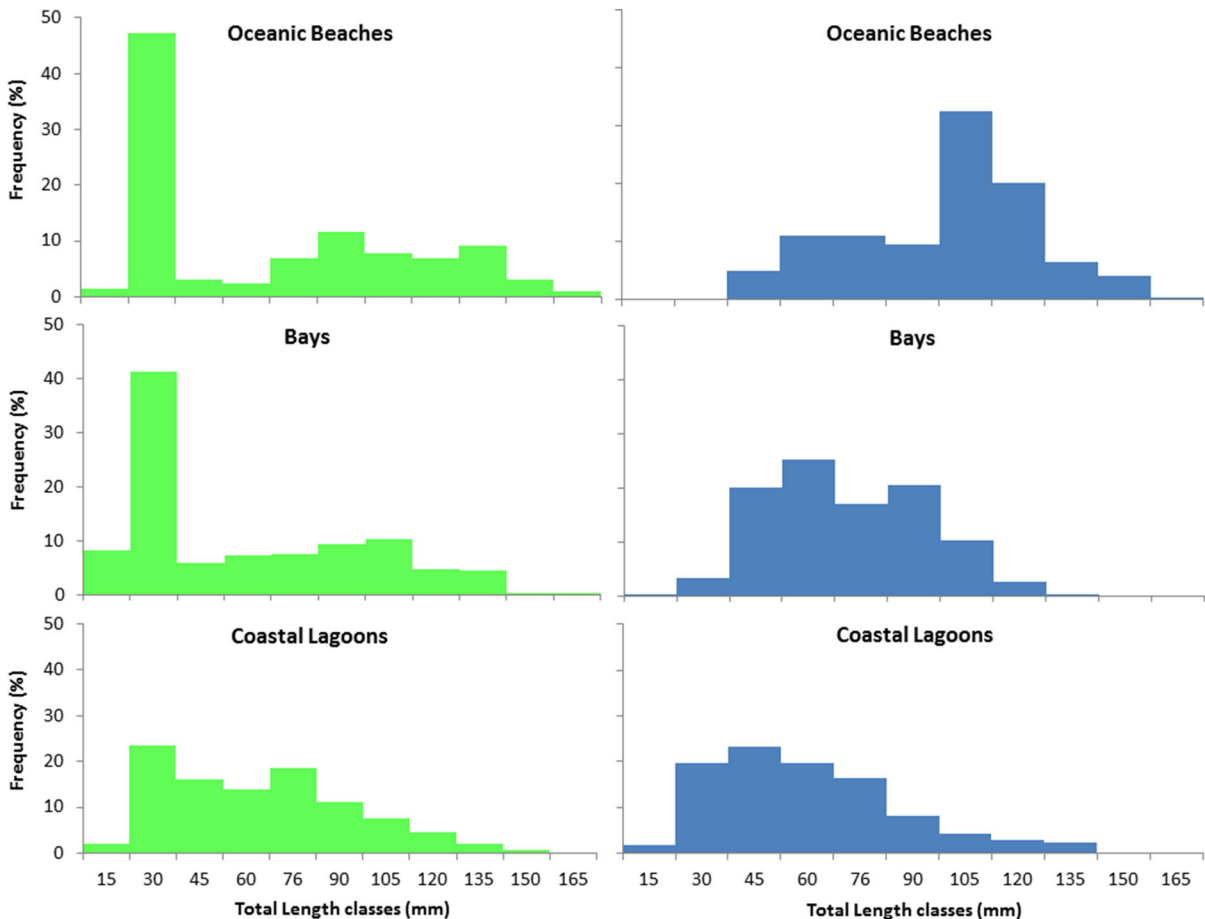
groups is the 34 most common and abundant species. The darker tones in each cell of the matrix represent higher relative abundances ( $\text{ind. sample}^{-1}$ ). A blank indicates the absence of a species (row) in the samples (column). Trophic guilds: *BE* benthivores, *HY* hyperbenthivores, *PI* piscivores, *PL* planktivores, *OP* opportunists, and *DE* detritivores

contributions of some unique species. Group 4 was formed mainly by the opportunistic (*G. genidens*) and hyperbenthivorous (*T. falcatus*) species near the reflective beaches in summer.

## Recruitment and size structure of *Atherinella brasiliensis*

The length-frequency distributions were analysed to evaluate the possible differences in the population structure of *Atherinella brasiliensis*, which is an abundant (46.2 and 76.4 mean abundance in individuals and grams, respectively, per sample) and common species (69.5% frequency of occurrence in all samples), across the different systems and seasons (Fig. 4). The early recruitment of *A. brasiliensis* juveniles (total length  $\leq 30$  mm) was observed in the three systems during winter. The largest size classes (total length (TL)  $> 100$  mm) were dominant in the oceanic beaches in summer. The coastal lagoons

had similar size structures in both seasons, with most individuals having sizes between 30 and 120 mm TL. No significant differences were found in the size structure among the different systems/seasons according to the non-parametric two-sided Kolmogorov–Smirnov test ( $P > 0.05$ ). However, when each system was examined in isolation, large medians were observed in the reflective oceanic beaches, and small medians were observed in Sepetiba Bay, Saquarema Lagoon and the dissipative ocean beaches in winter. During summer, high medians were recorded in the ocean beaches, and low medians were recorded in Maricá and Saquarema coastal lagoons (Fig. S1 in the Supplementary Information).



**Fig. 4** Size structure of the silverside *Atherinella brasiliensis* by the seasons (green-filled square winter and blue-filled square summer) and the coastal systems

## Discussion

Three different fish communities were detected in the three types of coastal systems along the coast of the state of Rio de Janeiro, and these differences were partially explained by the different habitat characteristics and environmental conditions. Other unmeasured features, such as within-habitat characteristics (e.g. sediment composition, slope, wave energy, infaunal and epifaunal biomass), local seascape characteristics (e.g. distance to other habitat types) and degree of marine connectivity (e.g. distance to open ocean), may play a role in explaining part of the data variance (see also, Able, 2005; Sheaves, 2009; Azevedo et al., 2017). The fish assemblages of the oceanic beaches were more similar to those of the bays, whereas the coastal lagoon had the most unique assemblages. The overlap of the samples of the three systems in the PCO plots suggested that several fish species were common to all systems, and the differences were caused by the relative abundance of dominant species and the occurrence of unique species. In coastal lagoons, the degree of isolation or confinement is considered the main factor that structures biological assemblages, which could contribute to differences in assemblages (Day & Yáñez-Arancibia, 1985; Sheaves, 2009; Elliott & Whitfield, 2011). Pérez-Ruzafa et al. (2019) found low connectivity between lagoons and the Mediterranean Sea and asymmetry in the probability of receiving particles, with a lower probability of colonization of the lagoon from the sea than vice versa. On the other hand, estuarine areas with large sea connections (e.g. bays) favour more frequent fish entrances and exits compared with coastal lagoons that have a narrow sea connection (Sheaves, 2009; Vasconcelos et al., 2015; Franco et al., 2019a).

The spatial changes in the assemblage structure and biomass in this study were primarily explained by the site factor on a spatial scale. Sites nested in the systems explained large proportions of the data variance in the numbers and biomass of the fish species and in the trophic guilds. The variability in the tropical estuarine fish assemblages was largely a product of the contrasting spatial patterns displayed by different species, with the patterns seemingly influenced in complex ways by contrasting responses to estuary-level ecological variables, which have greater power in explaining faunal differences than site-specific

physical variables (Sheaves & Johnston, 2009). Different habitat types offer different resources (e.g. food resources or shelter), and the use of these habitats may allow for the more efficient use of the ecosystem as a whole (Sheaves, 2009; Vasconcelos et al., 2015; Loureiro et al., 2016). While the seasonal changes were of minor importance compared with the habitat/system changes, we observed large abundances and biomass of the planktivores *A. tricolor* in the reflective beaches during winter, *H. clupeiola* in the dissipative beaches during summer and *A. januaria* in the lagoons and in the Sepetiba Bay in both seasons. Besides the influences of environmental variables or stochastic events, timing of life history characteristics, such as location, and timing of reproduction and migration influence the seasonal occurrence of these pelagic species (Hagan & Able, 2003).

The highest number of recorded species in the bays is likely associated with the highest habitat diversity in this type of system. This system provides shelters and rearing grounds for larvae and juvenile fish that are brought by currents and tidal movements from the spawning grounds over the adjacent inner shelf (Blaber et al., 1995; Potter et al., 2010; Araújo et al., 2017). Fewer fish species used oceanic beaches than bays and coastal lagoons. Moreover, the dissipative beaches had higher species richness than the reflective beaches. These findings support the idea that the structure of fish assemblages in these systems varies according to the degree of wave exposure, with increased richness in the more protected beaches (Romer, 1990; Clark, 1997). Surf zones in oceanic beaches serve as important foraging areas and might be alternative nurseries to estuaries for certain fish, such as the mullet *Mugil curema*, the pompano *Trachinotus carolinus*, the surf bream of the Sparidae family and grunts of the Haemulidae family (Schlacher et al., 2008; Defeo et al., 2009; Olds et al., 2018). In addition, the use of shallow beaches by various fish species may be influenced by the need to avoid predators, but they must endure wave exposure stress or the possibility of being trapped during reflux (Baker & Sheaves, 2006).

The coastal lagoons had the highest numerical abundance and biomass of fish species. Lagoons act as areas where propagules are retained and resources are concentrated (Day & Yáñez-Arancibia, 1985; Gray et al., 2011). The narrow sea connection that characterizes the coastal lagoons allows for increased

protection of the habitats and accumulation of matter, which favour a greater relative abundance and biomass of fishes in these systems than in bays and oceanic beaches (Abrantes et al., 2015; Azevedo et al., 2017). The effects of high nutrient loads trapped in the lagoons, especially in the euhaline (Saquarema) and mesohaline (Maricá) lagoons (Knoppers et al., 1991; Kjerfve et al., 1996), favour eutrophic conditions associated with continental drainage. Such conditions favour a high abundance and biomass of fish species, most likely as a result of an increased availability of feeding resources.

The planktivores were the dominant feeding guild across the three types of coastal systems, which was mostly due to the predominance of anchovies (e.g. *A. januaria* and *A. tricolor*) and, to a lesser extent, the clupeid *H. clupeiola*. Planktivorous species dominate intertidal habitats and tend to be closely associated with muddy substrates in shallow habitats that provide abundant food resources (Ribeiro et al., 2006; França et al., 2009). A similar pattern was identified by Costa et al. (2013) in an Amazonian estuary, and this study reported high concentrations of phosphate, which probably led to an increase in the availability of food for planktivorous fish. Engraulidae fishes are believed to be a major trophic link in bay food chains through their role in converting planktonic biomass into forage for piscivorous fishes (Hildebrand, 1963). In this study, *A. januaria* was abundant in the bays and coastal lagoons, whereas *A. tricolor* peaked in the bays and oceanic beaches, which indicated that these species tend to partition the use of these systems. *Anchoa januaria* and *A. tricolor* appeared to respond in different ways to environmental conditions, with the former peaking in the less transparent and less saline waters of the inner Sepetiba Bay and the latter peaking in the more transparent and saline waters of the outer bay (Araújo et al., 2008). These two abundant species probably evolved in a differentiated way to adapt to different environmental conditions, avoiding competition, a phenomenon that has been satirically termed “the ghost of competition past” (Connell, 1980). Spatial segregation to optimize resource use and take advantage of rich planktonic coastal waters seems to be the strategy developed by these closely related species to use the area during their early life cycles (Silva et al., 2004).

Large proportions of benthivores were found in the bays, and a large number of hyperbenthivores were

found in the oceanic beaches. High abundances of benthic fauna have been reported in tropical beaches with bare substrates (Guidetti, 2000; Gray et al., 2011). Species in the opportunistic guild were found mainly in the coastal lagoons. The presence of these species seems to be associated with decreases in salinity and transparency in this type of system. The opportunistic cyprinodontid species *J. multidentata* and *P. vivipara* occurred exclusively in the coastal lagoons, presumably reflecting the availability of favourable conditions or food resources brought by inputs of freshwater in these systems (Macedo-Soares et al., 2010). The mesohaline Maricá lagoon receives a greater influx of freshwater than the other lagoons, which results in the wide the local salinity range, and this lagoon is characterized as the most estuarine/brackish of the three lagoons. Many nutrients from the continent are trapped in the sediments of coastal lagoons (Day & Yáñez-Arancibia, 1985; Duck & Da Silva, 2012).

The opportunist silverside *Atherinella brasiliensis* was the only species to contribute significantly to the within-group average similarity in all three coastal systems, being very representative in numerical abundance and biomass, especially in the coastal lagoons. Early recruitment seems to occur in winter, when young-of-the-year are more abundant, mainly in oceanic beaches and bays. During the summer, this species occurs in high abundance in the three coastal systems, with the largest individuals predominating in the oceanic beaches. The different age classes of this species show different habitat use patterns, which may be due to changes in eating habits, increased availability of favourable environments and reduced local hydrodynamics (Neves et al., 2006; Carvalho & Spach, 2015). Pessanha & Araújo (2003) suggested that mangroves are an exporter of *A. brasiliensis* to the nearby sandy beaches in Sepetiba Bay and that connectivity between the Guaratiba mangrove and beaches is important for the life cycle of this species.

The environmental variables had low but significant relationships with the fish assemblages in the studied coastal systems. The environmental correlations of salinity and temperature with the assemblage parameters in tropical and subtropical coastal areas were generally weak (Pichler et al., 2015). Temperature and transparency seem to account for small variations in fish composition (number and biomass) and to a lesser extent trophic guilds. The highest

temperatures in the bays and coastal lagoons in summer and the lowest in the bays and oceanic beaches in winter seem to have species-specific influences on fish, and no seasonal pattern was detected in this study. The highest fish abundance and biomass were found in the lowest transparency waters of the coastal lagoons, but transparency is only one of several variables likely to influence species abundance in coastal systems. Velázquez-Velázquez et al. (2008) noted the inverse correlation between species richness and transparency. Turbid environments may be advantageous for planktivorous fish because they are less vulnerable to predation by piscivores but experience a substantial decrease in their ability to capture zooplankton prey (Robertis et al., 2003; Johnston et al., 2007).

The present study suggests that the assemblages of fish from different systems along the coast of the state of Rio de Janeiro are mediated by different habitat characteristics and environmental conditions. Rather than being random, the differences among the systems are the product of complex interactions of multiple causes and effects at various spatial and temporal scales. Not all habitats are equally suitable for the juvenile stages of fish species, but locations that produce well-conditioned individuals reveal the environmental characteristics associated with high-quality nursery habitats that contribute to species-specific productivity (Ross, 2003; Schloesser & Fabrizio, 2018). The comparative approach adopted in this study provided relevant insights regarding the associations of fish with different coastal systems. An integrated approach is needed to address how these systems are connected to increase the understanding of the mechanisms driving the changes in the composition of fish associations.

A better understanding of the assembly processes associated with coastal fishes in tropical ecosystems is of major relevance to support imperative conservation and management actions, thus reducing the lack of such information for the tropics. Further studies to assess the eventual influences of different human impacts in those systems will contribute knowledge that can be used to address this issue. The implications of habitat alterations for fish include potential changes in the nursery function and the functioning of the fish community (Sheaves, 2016; Amorim et al., 2017). It is likely that most of the changes in the explanatory variables in coastal systems are a combination of

factors, such as increased water temperature, habitat destruction (sand dredging, beach nourishment and fishing) and changes in the trophic structure (Van der Veer et al., 2015; Páez et al., 2018). The management of coastal systems requires the protection of different habitats, and conservation measures should support the heterogeneity of biological assemblages.

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#### Compliance with ethical standards

**Conflict of interest** The authors have no conflict of interest.

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