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PRIMARY RESEARCH PAPER

Better with more or less salt? The association of fish assemblages in coastal lagoons with different salinity ranges

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Abstract Coastal lagoons are naturally stressed systems and experience changes in environmental conditions because freshwater inputs change environmental variables, mainly the salinity. We hypothesized that fish assemblages would change in structure and richness in three tropical lagoons that had different salinity ranges (a hyperhaline lagoon, 36–54; a euhaline lagoon, 16–40; and a mesohaline lagoon, 8–34). The assemblage structure differed among the three lagoons, and changed seasonally only in the mesohaline lagoon with the biomass being comparatively higher in summer than that in winter. The four environmental variables (salinity, temperature, turbidity and depth) explained a significant proportion of the variance, with salinity having the most significant effect ($\approx 10\%$ of the explained variation) on fish assemblage structure. The mesohaline lagoon, with the widest salinity range (from estuarine to marine conditions) and more loads of nutrient brought by small rivers' inflows, was the most abundant (in fish number and biomass) system. The euhaline lagoon, with a salinity range closest to marine conditions, had the highest species richness as opposed to the hyperhaline lagoon that appeared to limit species abundance and richness, probably due to the stress of high salinity.

Keywords Assemblage composition · Biodiversity · Ichthyofauna · Spatial variability · Shallow water habitats · Transitional waters

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Introduction

Fish–habitat relationships in transitional waters such as coastal lagoons are complex due to strong fluctuations in salinity, temperature and degree of connectivity with the sea, among other factors. As a result, differences in the fish fauna between these habitats are often spatially and temporally difficult to predict. Salinity followed by the degree of separation from the marine domain appears to be the major driving factor influencing the performances of organisms along habitat and environmental gradients (Telesh &

Khlebovich, 2010; Telesh et al., 2013). Salinity ranges act as both an external ecological factor and physiological characteristic of the internal environments of aquatic organisms; it divides living conditions appropriate for freshwater and marine faunas, separates communities with different osmotic regulation types, and defines the distribution range of species (Telesh & Khlebovich, 2010). Changes in salinity influence fish distribution, where specific species are often more prevalent in either brackish or saline waters (Yanez-Arancibia et al., 1994; Potter & Hyndes, 1999; Harrison & Whitfield, 2006). Salinity is very important at a local scale, especially because it is capable of promoting differences in the distribution patterns of aquatic communities, especially for juveniles and small-sized species that use these habitats (Perez-Ruzafa et al., 2007; Franco et al., 2008; Pérez-Ruzafa et al., 2013). The number of marine species reaches a maximum at normal seawater conditions (salinity 36) and then decreases with hypersaline conditions (Khlebovich, 1990; Telesh & Khlebovich, 2010). In addition, the diversity of life history strategies significantly decreases from euhaline to oligohaline conditions and along the gradient of human disturbances (Teichert et al., 2017).

Coastal lagoons are shallow and microtidal systems with limited riverine input and openings to the ocean and support diverse habitats, which are susceptible to anthropogenic activities (Kjerfve, 1994; Yanez-Arancibia et al., 1994; Haines et al., 2006; Franco et al., 2008). These coastal systems can have different salinity gradients depending on the geographical position, hydrological balance, and width of the sea connection among other factors, which influence the structures of fish assemblages (Knoppers, 1994; Barletta et al., 2005; Becker et al., 2016). They are short-lived systems that usually trap inorganic sediment and organic matter, with an existence intrinsically linked to filtering efficiency (Knoppers et al., 1991; Knoppers, 1994). Coastal lagoons have usually low depth and transparent waters that promote high primary productivity allowing large fish populations to persist, supporting a higher diversity of niche specialists (Willig et al., 2003; Tittensor et al., 2010; Vasconcelos et al., 2015). Freshwater inputs deliver sediment and nutrients that increase productivity being major drivers of ecological and biogeochemical processes in costal lagoons (Knoppers, 1994; Teichert et al., 2017). In addition, winds, solar radiation, and evaporation favour a range of interacting biogeochemical processes (Camacho-Ibar & Rivera-Monroy, 2014).

Knowledge of the spatial and temporal associations of fish with transitional habitats such coastal lagoons is essential for understanding and assessing the potential impacts of environmental and human perturbations on populations and assemblages and for managing key habitats for the conservation and maintenance of biodiversity. Few studies have tested the consistencies of such associations across distinct lagoons or between different lagoons and through time (e.g. França et al., 2011; Gray et al., 2011). Therefore, coastal lagoons with different salinity ranges provide a good opportunity to assess richness and assemblage structure patterns associated with gradual changes in environmental variables and relatively stable isohalines.

The aim of this study was to assess the ichthyofauna and their eventual changes in relation to environmental variables, mainly the salinity, in three tropical choked lagoon systems in the coast of Rio de Janeiro State that differed in salinity range, i.e., a hyperhaline lagoon with salinity 36–54; an euhaline lagoon, with 16–40; and a mesohaline lagoon with 8–34. The hypothesis is that fish assemblages differed among the lagoons and that species richness is closely associated with salinity with an optimum at normal marine water (36) and that changes above or below this value can limit the occurrence of stenohaline species. In addition, we expect that mesohaline lagoons are more abundant in number of fish and biomass because their comparatively higher freshwater inputs increase the range of salinity and bring organic loads into the system.

Materials and methods

Study area

Three tropical coastal lagoons (Maricá, Saquarema and Araruama) on the southeastern Brazilian coast were studied (Fig. 1). The lagoons are located less than 50 km from each other and have low tide amplitudes. All lagoons have a permanent connection with the sea and are characterized as choked systems (sensu Kjerfve, 1994) because they have long turnover times with winds usually as the dominant factor causing circulation, mixing and water exchange with
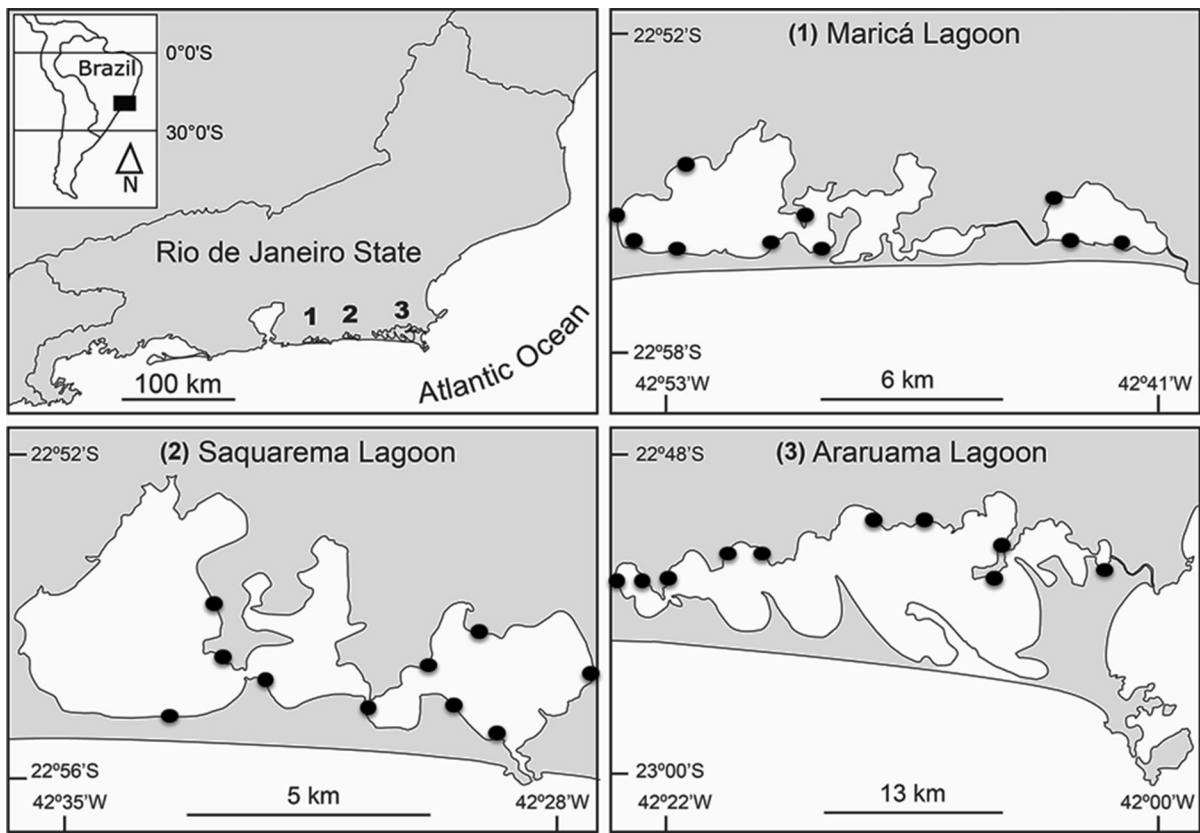
Fig. 1 Map of the study area lagoons with indication of the sampling sites in the mesohaline (1, Maricá), euhaline (2, Saquarema), and hyperhaline (3, Araruama) lagoons

the ocean, and the lagoons largely depend on the hydrological cycle. They have minimal riverine input and constricted entrances to the sea. The shallow margins (50–100 m width) of all the lagoons are covered by a mosaic of vegetated and bare substrata in populated areas, whereas the deeper (> 2 m) central basins consist mostly of bare sand and mud substrata (Kjerfve et al., 1990, 1996).

Mesohaline lagoon The Maricá lagoon system (22°58′S, 42°40′°W) consists of four interconnected lagoons, with a total surface area of 34.7 km² and an average depth of 1.2 m. The renewal times for 50% of the water of the inner zone and outer zone are 27 and 7 days, respectively (Kjerfve et al., 1990; Knoppers, 1994). The Maricá lagoon receives more freshwater input and human effluent discharge that the other two lagoons (Knoppers et al., 1991). This lagoon has a range of salinities between 8 and 38, with an average of 18, and the salinity depends on the influx of freshwater from the small rivers that discharge into

this system. The lagoon is connected to the sea by a single canal that is 1,000 m in length and from 20 to 30 m in width.

Euhaline lagoon The Saquarema lagoon complex (22°55′S, 42°34′W) is formed by four interconnected shallow lagoons, with an area of 21.2 km² and an average depth of 1.2 m. The canal that connects the lagoon to the sea is 500 m in length and approximately 70 m in width. The lagoon has an average salinity of 35, which is close to the salinity of seawater. Knoppers (1994) calculated the renewal times for 50% of the water in the inner zone and outer zone as 23 and 6 days, respectively.

Hyperhaline lagoon The Araruama lagoon (22°53′S, 42°23′W) has an area of 210 km², with an average depth of 3 m and a maximum depth of 17 m. This lagoon has a mean salinity of 52 (Knoppers et al., 1991; Kjerfve et al., 1996), as result of semi-arid climatic conditions. The lagoon consists of seven elliptical cells of varying sizes and is connected to the

ocean by a single canal that is 4 km in length and 50–60 m in width. Small intermittent streams flow in from the west (Kjerfve et al., 1996). The renewal time for 50% of the water in the entire lagoon takes approximately 84 days (Kjerfve, 1994). The banks of the lagoon are primarily used as residences (houses), and saline extraction companies favour by the hyper-haline condition of the lagoon.

Sampling

The fish assemblages were sampled during the day, between 10 and 16 h, twice a year (July, winter; and January, summer), during a two-year periods (July-2011, January-2012, July-2012 and January-2013). All samplings were conducted between the first and last quarter of the moon, and it took 2 days to sample each lagoon. The sampling sites were distributed across the whole coastal lagoon, covering the inner and outer zones. The sample design contained a total of 360 samples (3 lagoons × 10 sites × 2 years × 2 seasons × 3 replicates). Some samples were missing because of inclement weather conditions. The beach seine (12 × 2.5 m; 5-mm mesh size) had panels made of polyamide multifilament nylon. The net was fitted with 30-m hauling ropes and set perpendicular to the shore at approximately a 1.5-m depth. The position where the beach seine was deployed at each site was not the same each sampling time; rather, the hauls were simply carried out within a general area at each site each sampling time. Seine hauls were performed by two people, one at each end of the rope, covering a length of approximately 30 m; hauling lasted an average of 15 min. The distance seined and the time required for each haul were standardized, thus allowing comparisons among samplings. The total sampled area was taken to be the distance the net was laid offshore multiplied by the mean width of the haul, resulting in an effective fishing area of approximately 300 m^2.

A sampling design was used to examine the differences in the structures of the fish assemblages among the three lagoons and seasons. Ten sites were distributed across the whole lagoon. The order in which each lagoon, and sites within a lagoon, were sampled was randomized during each sampling. Fish caught in each net were identified, counted, measured to total length (nearest 0.5 cm) and weighed (g). During each fish sampling, the environmental

measurements of water temperature (degree C), salinity (psu), depth (cm) and turbidity (NTU) were recorded. Temperature, salinity and turbidity were measured by means of a Horiba W-21 multiprobe (Horiba Trading Co. Ltd., Shanghai) immersed approximately 0.5 m under the water surface. Depth was measured with a Speedtech model SM-5 digital sounder.

Data analysis

A two-way factorial analysis of variance (ANOVA) was used to compare the environmental variables of the three lagoons and the two seasons. Where the ANOVA showed a significant difference, an a posteriori Tukey HSD test was used to determine which means were significantly different at the 0.05 level. Pairwise correlation coefficients were calculated between the environmental variables to detect eventual co-linearity ($r < 0.7$; Sleeman et al., 2005; Leathwick et al., 2006), but no significant associations were found among these variables. Further, a principal component analysis (PCA) was applied on the standardized environmental data to identify spatial patterns, i.e., groups of samples coded by lagoons and seasons according to the environmental variables. Because environmental data have different units of measurements, they were transformed to standard z-scores (Larsen & Marx, 2000), i.e., they became dimensionless before submit to multivariate analysis.

Species richness was compared among the lagoons by using rarefaction of the individuals. The individual-based rarefaction curves that represented the means of repeated re-sampling of all pooled individuals (Gotelli & Colwell, 2001) were computed using EstimateS v. 7.5.2 (Colwell, 2000).

Fish assemblage structure expressed as the number or biomass (g) of individuals per species was square root transformed to perform comparisons among the lagoons and between the seasons using a permutational analysis of variance (PERMANOVA) with 999 permutations of residuals under a reduced model (Anderson et al., 2008). A Bray–Curtis similarity matrix was used on the transformed data with a type I (sequential) sum of squares to calculate the p-values. The fish assemblages as numbers of individuals per species or as biomass were the response variables, the environmental variables (temperature, salinity, turbidity and depth) were the covariates, the lagoons (3

levels: mesohaline, euhaline and hyperhaline) and the seasons (2 levels, summer and winter) were the fixed factors, and the sites (random factors) were nested in the lagoons. Previously to test this model, we introduced year as a fixed factor, but as no significant difference were found for year (pseudo-F = 1.41; P = 0.145), we did not consider year in the model. A similarity percentage (SIMPER analysis) was used to determine the species that had the largest contribution to the within-group average similarity for the lagoons and seasons. Moreover, a distance-based redundancy analysis (dbRDA) was used to detect relationships between the environmental variables and fish assemblages with samples coded by lagoon and season. Rare species, i.e., those that had < 1% of the total individuals and 1% of frequency of occurrence in the samples, were not considered in the multivariate analyses.

A PERMANOVA on the Euclidian distance was used to test for differences in the fish richness, number of individuals and biomass among the lagoons and seasons (fixed factors) with the sites (random factors) nested in the lagoons. Significant differences among the factors were followed by a PERMANOVA pairwise comparisons test.

The relationship between the abundance of the discriminant fish species determined by SIMPER with the explanatory environmental variables (predictors) were analysed. A distance-based linear model (DistLM; Legendre & Anderson, 1999; McArdle & Anderson, 2001) on a square-root Euclidean distance matrix was used. The marginal test was used to determine the pseudo-F values and the explained variance for the final model (R^2). All statistical analyses were performed using the statistical packages PRIMER 6 v. 6.1.13 and PERMANOVA + v. 1.0.3.

We also selected the two fish species that were common and abundant in all three systems to assess and compare their size structure among the three lagoons in each season (summer and winter). Fishes were allocated to different size classes according to their body size: < 2.4 cm, 2.5–3.4 cm, 3.5–4.4 cm, 4.5–5.4 cm, 5.5–6.4 cm, 6.5–7.4 cm, 7.5–8.4, 8.5–9.4, 9.5–10.4, > 10.4 cm. The body size structure (% of fish abundance per size class) were compared among the systems for each season using a nonparametric test (Wilcoxon's matched pairs test) on pairs of length frequency distribution (P < 0.05). This

analysis was performed using the Statistica v. 7.0 software (StatSoft, 2011).

Results

Environmental variables

The salinity ranged from 8 to 54. The salinity of the mesohaline lagoon ranged from 8 to 25 (15.4 ± 5 SD) in the winter to 8 to 34 (mean 20.5 ± 8 SD) in the summer. The salinity of the euhaline lagoon ranged from 16 to 40 (27.3 ± 4.5 SD) in the winter to 25 to 35 (33 ± 5) in the summer, whereas the salinity of the hyperhaline lagoon ranged from 36 to 54 (46.4 ± 6) in the winter to 42 to 54 (48.5 ± 3 SD) in the summer. Significant differences were found among all comparisons between the lagoons (F = 46.7 P = 0.0001) and zones (F = 708.0, P = 0.0001), except for the hyperhaline lagoon, between the winter and summer (P = 0.396). The interaction lagoon × season was non-significant (F = 0.31, P = 0.05) (Table 1). The hyperhaline lagoon had the highest average salinity (48.5 ± 4.7 SD) in the summer, whereas the mesohaline lagoon had the lowest average salinity (15.4 ± 5.1 SD) in the winter.

The water temperature ranged from 19.6 to 34.7°C. Significant differences in the water temperatures were found among the lagoons (F = 24.5; P = 0.0001) and the seasons (F = 263.3, P = 0.001) (Table 1). The euhaline lagoon had the highest temperature (mean = 29.4 ± 3.6°C SD) in the summer, whereas the hyperhaline lagoon had the lowest temperature (23.1 ± 1.6°C SD) in the winter.

The turbidity ranged from 1.4 to 48.3 NTU. Significant differences were found in the turbidity of the lagoons (F = 15.2, P = 0.001) but not between the seasons (F = 1.2, P = 0.27) or the interaction lagoon × season (F = 0.8, P = 0.5). The mesohaline lagoon during the winter (17.3 ± 9.2 SD) and the summer (17.6 ± 7.0 SD) had a significantly higher turbidity compared with the turbidity of the hyperhaline lagoon in the winter (12.1 ± 6.2 SD) and in the summer (12.2 ± 8.3) and the euhaline lagoon in the winter (12.0 ± 7.0 SD).

The depth at the sampling sites ranged from 18 to 95 cm. Significant differences in depth were found among the lagoons (F = 20.1, P = 0.0001) and between the seasons (F = 54.7, P = 0.0001) and to a

Table 1 F-values from two-way ANOVA and significant differences (Tukey test) for environmental variables among the lagoons and seasons

Environmental variables	Lagoon	Season	Lagoon × season	Significant differences (mean ± SD)
Temperature (°C)	24.5**	263.3***	4.6*	Euhaline (27.1 ± 3.6), mesohaline (26.0 ± 3.3) > hyperhaline (24.7 ± 3.3)
				Summer (28.1 ± 3.4) > Winter (23.7 ± 1.7)
Salinity	708.0***	46.7**	0.31ns	Hyperhaline (46.5 ± 5.0) > euhaline (30.1 ± 5.6) > mesohaline (18.1 ± 7.4)
				Summer (26.3 ± 4.7) > winter (21.1 ± 3.3) (except for hyperhaline that did not differ seasonally (Sum, 47.5 ± 4.7; Win. 45.5 ± 5.1)
Turbidity (NTU)	15.2**	1.2ns	0.8ns	Mesohaline (17.4 ± 8.1) > euhaline (13.1 ± 6.9), Hyperhaline (12.1 ± 7.2)
Depth (cm)	20.1**	54.7**	4.4*	Hyperhaline (65 ± 12) > euhaline (55 ± 19), mesohaline (55 ± 12)
				Winter (64 ± 15) > summer (53 ± 13)

Average ± standard deviation (SD) of environmental variables in brackets

Significant differences: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; *ns* non-significant

lesser extent for the lagoon × season interaction ($F = 4.4$, $P = 0.01$). A higher depth average was recorded in the hyperhaline lagoon in winter (67.7 ± 14.9 SD) than in the summer (62.2 ± 7.5 SD). Similarly, a higher depth in the euhaline (62.8 ± 19.3 SD) and mesohaline (62.8 ± 19.3) lagoons occurred in the winter when compared with the euhaline (46.5 ± 15.0) and mesohaline (49.6 ± 10.2 SD) lagoons in the summer.

With some widespread samples across the PCA diagram (Fig. 2), it was possible depict a spatial pattern (differences among the lagoons) in the environmental data, with the hyperhaline and mesohaline lagoons in opposite positions and the euhaline lagoon in an intermediate position between these two other lagoons. The first two axes explained almost 70% of the data variances, with the hyperhaline lagoon having a higher salinity, as expected, the mesohaline lagoon having the highest turbidity and the euhaline lagoon having the highest temperature. Seasonally, the diagram contrasted the higher depth in the winter and the higher temperature in summer.

Species composition

A total of 50 species in 43 genera, 25 families and 13 orders were recorded in the three coastal lagoons with the Perciformes (27 species) and Clupeiformes (7 species) contributing the highest number of species

(Table S1 in the Supplementary information). The silverside *Atherinella brasiliensis* (Quoy & Gaimard, 1825) and the engraulid *Anchoa januaria* (Steindachner, 1879) were common and abundant in all lagoons and seasons with both having the highest biomass in the mesohaline lagoon (Tables S2–S3 in the Supplement information). Other species that had great contribution to the number of fish and biomass were the cyprinodontids *Jenynsia multidentata* (Jenyns, 1842) and *Poecilia vivipara* Bloch & Schneider, 1801 in the mesohaline lagoon, the mojarra *Eucinostomus argenteus* Baird & Girard, 1855 in the euhaline lagoon, the clupeid *Brevoortia aurea* (Spix & Agassiz, 1829) in the hyperhaline lagoon and the mullet *Mugil curema* (Valenciennes, 1836) in the mesohaline and euhaline lagoons. The gobiid *Microgobius meeki* (Valenciennes, 1836) occurred in high numbers but with a low biomass in the mesohaline and euhaline lagoons (Tables S2–S3 in the Supplementary information).

Descriptions of the assemblage structure

The highest number of recorded species was found in Saquarema (33, euhaline lagoon) followed by Maricá (32, mesohaline lagoon) and Araruama (30, hyperhaline lagoon). The individual rarefaction curve for the euhaline lagoon was well above the corresponding curve for the hyperhaline lagoon, whereas the
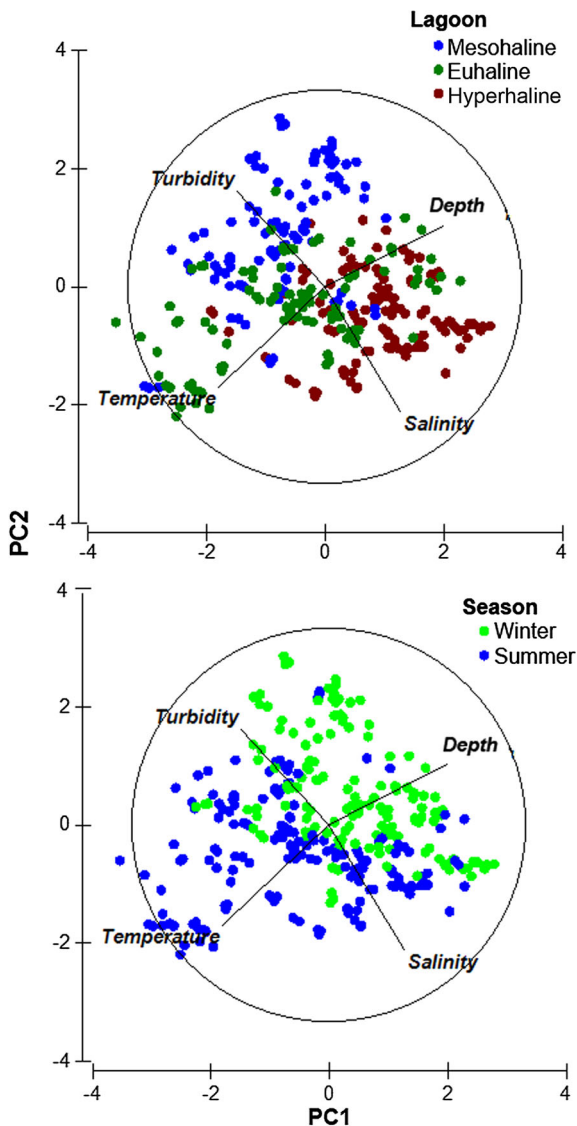
Fig. 2 Ordination diagram from the first two axes of the principal component analysis on environmental variables. Samples coded by lagoons (above) and seasons (below)

Fig. 3 Individual-based rarefaction curves for species richness by lagoons

mesohaline had intermediate values between these two lagoons (Fig. 3).

Species richness changed significantly among the lagoons (pseudo-F = 4.86, P = 0.017) but not between seasons (pseudo-F = 2.59, P = 0.131) or the lagoon × season interaction (pseudo-F = 1.34, P = 0.26) according to PERMANOVA (Table 2). The euhaline lagoon had comparatively more fish species than that of the hyperhaline lagoon.

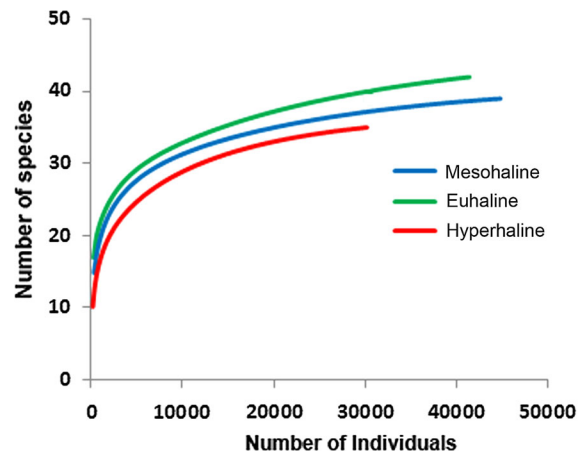The fish abundance also changed significantly among the lagoons (pseudo-F = 5.92, P = 0.004) but not between seasons (pseudo-F = 1.87, P = 0.177) or the lagoon × season interaction (pseudo-F = 0.39, P = 0.736) (Table 2). The mesohaline and euhaline lagoons had higher numbers of fish than the hyperhaline lagoon. In all lagoons, there was a non-significant trend of higher fish abundance in the summer compared with the winter.

The fish biomass changed significantly among the lagoons (F = 4.68, P = 0.014) and seasons (F = 12.44, P = 0.002) but not for the lagoon × season interaction (pseudo-F = 2.66, P = 0.081)). The mesohaline lagoon had higher fish biomass than the hyperhaline lagoon (Table 2), and the fish biomass was higher in the summer compared with that in the winter.

Spatial and temporal patterns in fish assemblages

PERMANOVA detected significant differences in fish assemblage structures among the lagoons and seasons in terms of both numerical abundance and biomass. Moreover, significant pseudo-F values for the sites nested in the lagoons were also detected. The most pronounced changes were found among the lagoons (ECV, percent estimated components of variation was 18.2% in number and 18.3% in biomass) and for the sites (ECV 20.6% in numbers and 20.9% in biomass), suggesting substantial changes in site species composition among the samples (Table 3).

Seasonal differences in the structures of fish assemblages were detected for the mesohaline lagoon, with significant differences between the winter and

Table 2 Mean ± standard errors for descriptors of the fish assemblage and significant differences from PERMANOVA among lagoons and seasons

Descriptors	Mesohaline		Euhaline		Hyperhaline	
	Winter (48)	Summer (54)	Winter (57)	Summer (54)	Winter (60)	Summer (57)
Number of species	6.0 ± 0.4	5.9 ± 0.2	8.2 ± 0.3	6.9 ± 0.3	5.6 ± 0.3	5.2 ± 0.3
Number of individuals	325 ± 38	428 ± 48	143 ± 16	286 ± 39	135 ± 14	192 ± 18
Biomass	344 ± 30	360 ± 52	276 ± 33	271 ± 28	226 ± 27	189 ± 26
PERMANOVA comparisons	Pseudo-*F*		*P*-values		Significant differences	
Number of species	4.86		0.017		Euhaline > hyperhaline	
Number of individuals	5.92		0.004		Mesohaline > euhaline > hyperhaline	
Biomass—lagoon	4.68		0.014		Mesohaline > hyperhaline	
Biomass—season	12.44		0.002		Summer > winter	

Number of samples indicated in brackets

Table 3 Results of PERMANOVA testing for differences in fish assemblage structure, in response to temperature, salinity, turbidity, depth (covariates), lagoons and seasons (fixed factors), and sampling sites (random factor nested in lagoons)

Numerical abundance	df	Pseudo-*F*	*P* (perm)	ECV	
				Estimate	Square root
Salinity	1	7.4	0.0001	94.4	9.7
Turbidity	1	6.2	0.0001	47.1	6.8
Temperature	1	8.1	0.0001	38.1	6.2
Depth	1	3.4	0.0012	39.7	6.3
Lagoons (L)	2	5.2	0.0001	331.7	18.2
Season (S)	1	2.9	0.0011	72.3	8.5
Sites (nested in L)	27	6.3	0.0001	424.7	20.6
L × S	2	1.1	0.4090	2.3	1.5
S × sites (L)	25	2.9	0.0001	287.6	16.9
Residual	268			803.9	28.3
Biomass	df	Pseudo-*F*	*P* (perm)	ECV	
				Estimate	Square root
Salinity	1	6.7	0.0001	102.4	10.1
Turbidity	1	4.9	0.0001	36.6	6.1
Temperature	1	6.5	0.0001	46.5	6.8
Depth	1	4.5	0.0001	42.7	6.5
Lagoons (L)	2	5.1	0.0001	336.1	18.3
Season (S)	1	4.2	0.0001	173.7	13.2
Sites (nested in L)	27	5.0	0.0001	439.0	20.9
L × S	2	1.2	0.2550	13.7	3.7
S × sites (L)	25	2.8	0.0001	380.1	19.4
Residual	268			1086.7	32.9

df degrees of freedom, *ECV* percentage of estimated components of variation

summer ($t = 1.7$, $P = 0.007$), whereas no change was detected for the euhaline ($t = 0.9$, $P = 0.45$) or hyperhaline ($t = 1.2$, $P = 0.14$) lagoons.

Two species (*A. januaria* and *A. brasiliensis*) contributed the most to within-group similarity for all lagoons, being dominant in number and biomass, according to SIMPER (Table 4). Other species also contributed significantly to the within-group similarity, such as *J. multidentata*, *M. meeki* and *P. vivipara* for the mesohaline lagoons, *E. argenteus* and *Micropogonias furnieri* (Desmarest, 1823) for the euhaline lagoon and *B. aurea* and *Elops saurus* Linnaeus, 1766 for the hyperhaline lagoon (Table 4).

Seasonally, in addition to the two most abundant species, *A. januaria* and *A. brasiliensis*, *E. argenteus*, *J. multidentata* and *E. saurus* substantially contributed to the within-group similarity in terms of number during both seasons, with *Achirus lineatus* (Linnaeus, 1758) and *M. meeki* in the winter and *M. curema* in summer. In relation to biomass, *E. argenteus* contributed significantly to within-group similarity in both seasons, *J. multidentata* in the winter, and *M. curema* in the summer (Table 4).

Environmental influences on fish assemblages

The four explanatory environmental variables explained a significant proportion of the variance in the species data (pseudo-F ranged from 6.2 to 9.7 in number and from 6.1 to 10.1 in biomass). Salinity had the most significant effect on fish community structure (ECV = 9.75 in number and 10.1 in biomass) (Table 3).

We found a significant relationship between fish assemblages and covariates, especially salinity and depth and to a lesser extent turbidity and temperature (Figs. 4 and 5). The first distance-based redundancy analysis (dbRDA) axis accounted for 10.5% of the total variation in the fish assemblages in terms of number and 5.6% of the total variation in the fish assemblages in terms of biomass and distinguished among samples from the hyperhaline lagoon that has a higher salinity and depth and generally a lower temperature and turbidity and the samples from the mesohaline and euhaline lagoons with the inverse of this pattern of variables. The second dbRDA axis accounted for only 2.2% in terms of number and 3.2% in terms of biomass. A better seasonal pattern was found for the fish assemblages expressed as biomass

data compared with the numerical abundance that had no clear seasonal pattern according to the dbRDA plots, suggesting that the examined variables did not change significantly in terms of number between the two examined seasons.

The distance-based multivariate linear model (DistLM) analysis indicated significant relationships between the fish assemblages and environmental predictors (14.3% of the explained variance in number and 12.2% in biomass). Salinity (6.4% of the variance in number and 5.2% in biomass), followed by the depth (3.2% variance in number versus 2.7% variance in biomass) and turbidity (3.8% variance in number versus 2.2% variance in biomass) were the most significant predictors of assemblage structures, whereas the temperature explained only 1.9% in terms of number and 2.0% in terms of biomass of the data variance.

The results of the DistLM for the relationship between the selected discriminant species (determined by the SIMPER analysis) and the environmental variables revealed that salinity was the most important environmental variable for predicting the occurrence of the species, followed by turbidity and depth (Table 5). Most of those species have either positive (*B. aurea* and *A. lineatus*) or negative (*A. brasiliensis*, *E. argenteus*, *J. multidentata*, *M. meeki* and *P. vivipara*) correlations with salinity (Table 5).

High turbidity favoured the high numerical abundance of *J. multidentata*, *M. meeki* and *B. aurea* and the high biomass of *A. lineatus, B. aurea* and *M. furnieri*. Low depths favoured the numerical abundance and biomass of *A. lineatus*, *M. furnieri* and *M. meeki* and the high biomass of *E. argenteus* (Table 5). Temperature had a significant positive correlation with the biomass of *E. argenteus*. Other relationships explained parts of the species variation that were irrelevant to this study.

Size structure for the selected species

Size structure was assessed for the two dominant species that were common in the three systems, namely, *A. januaria* and *A. brasiliensis.* No significant differences were found between all combinations of pairs of comparisons among the lagoons and seasons. However, some trends were detected by examining the length frequency of the distribution plots.

Table 4 Species that most contributed to within-average similarity (%) for each lagoon and season, according to SIMPER analyses

Lagoons—individuals	Mesohaline (45.01)		Euhaline (44.85)		Hyperhaline (52.24)	
	Av. abund.	Av. sim.	Av. abund.	Av. sim.	Av. abund.	Av. sim.
Anchoa januaria	2.12	10.04	2.46	11.61	2.71	21.51
Atherinella brasiliensis	3.08	22.19	2.58	15.58	2.45	21.21
Brevortia aurea					0.72	1.54
Elops saurus					0.71	3.44
Achirus lineatus			0.47	1.06		
Eucinostomus argenteus			1.40	6.36		
Micropogonias furnieri			0.53	1.15		
Jenynsia multidentata	1.14	4.10	0.56	1.26		
Microgobius meeki	0.59	1.36	0.78	2.06		
Mugil curema	0.75	1.84	0.53	1.00		
Poecilia vivipara	0.82	1.84				
Seasons—individuals	Winter (44.88)			Summer (43.40)		
Anchoa januaria	2.65		16.40	2.23		12.02
Atherinella brasiliensis	2.69		17.97	2.69		20.53
Elops saurus	0.45		1.11	0.50		1.79
Achirus lineatus	0.38		0.84			
Eucinostomus argenteus	0.71		1.52	0.79		2.47
Jenynsia multidentata	0.84		2.33	0.54		1.18
Microgobius meeki	0.48		0.85			
Mugil curema				0.55		1.34
Lagoons—biomass	Mesohaline (40.21)		Euhaline (35.51)		Hyperhaline (48.5)	
	Av. abund.	Av. sim.	Av. abund.	Av. sim.	Av. abund.	Av. sim.
Anchoa januaria	4.96	7.41	4.13	8.59	5.35	16.65
Atherinella brasiliensis	13.24	25.64	7.00	14.47	7.84	27.09
Brevortia aurea					1.74	1.37
Eucinostomus argenteus			3.92	5.71		
Micropogonias furnieri			1.14	1.44		
Jenynsia multidentata	2.18	2.06				
Microgobius meeki			0.65	0.88		
Mugil curema	1.98	1.80	1.93	1.23		
Seasons—biomass	Winter (40.37)			Summer (37.67)		
Anchoa januaria	5.15		14.29	4.54		7.81
Atherinella brasiliensis	7.92		20.22	10.58		22.99
Eucinostomus argenteus	1.30		1.07	2.42		2.25
Jenynsia multidentata	1.42		1.19			
Mugil curema				1.63		1.29

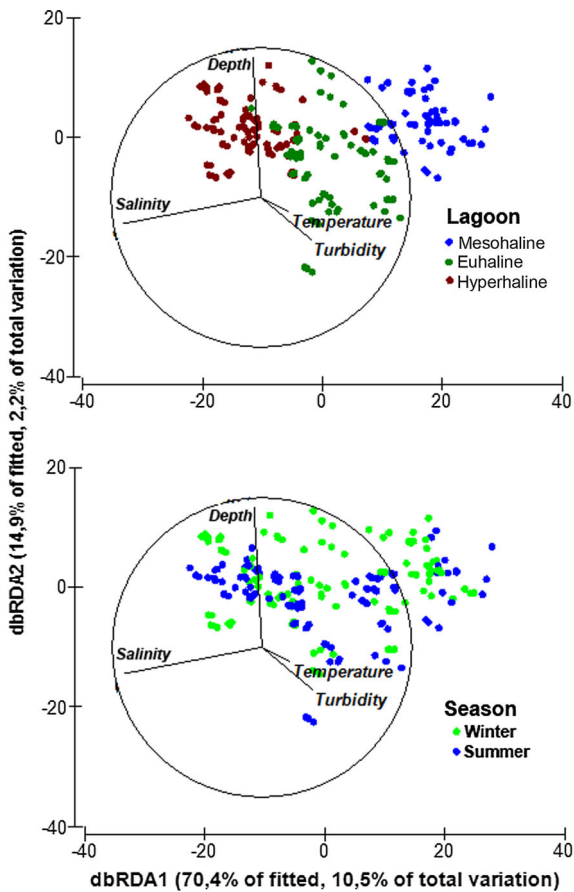*Av. Abund.* average abundance, *Av. Sim.* average similarity

Fig. 4 Distance-based redundancy analysis (dbRDA) demonstrating the relationships between fish assemblage structures in terms of number of individuals and the covariates for the three lagoons and two seasons. Sampling sites coded by lagoons (above) and seasons (below)

Fig. 5 Distance-based redundancy analysis (dbRDA) demonstrating the relationships between fish assemblage structures in terms of biomass and the covariates for the three lagoons and two seasons. Sampling sites coded by lagoons (above) and seasons (below)

Anchoa januaria The smallest size classes (< 2.5 cm TL) were better represented (> 20%) in the mesohaline lagoon in the summer (Fig. 6). The intermediate size classes (2.5–5.4 cm TL) dominated the population structures of all the lagoons and seasons, whereas the largest individuals (> 5.5 cm TL) were better represented (> 10%) in the hyperhaline lagoon in both seasons.

Atherinella brasiliensis The new recruits that form the smallest size class (CT < 2.5 cm TL) were better represented in the euhaline lagoon in both seasons (> 20%) and in the mesohaline lagoon in the summer (Fig. 7). Intermediate-higher size classes (3.5–7.4 cm) dominated the size structure in the mesohaline and hyperhaline lagoons in the winter and in the hyperhaline lagoon in the summer. The
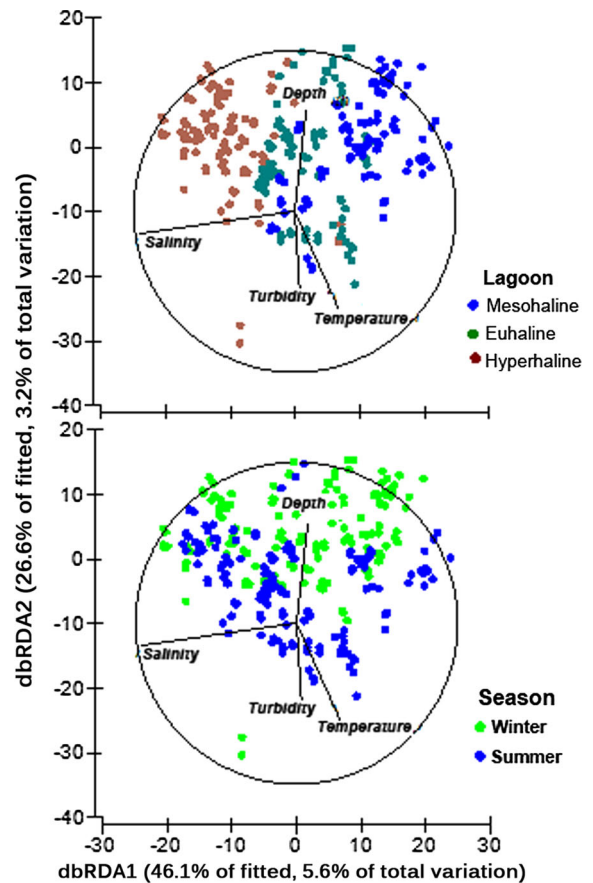
largest individuals were better represented in the mesohaline lagoon in the summer (> 15%). In only the euhaline lagoon, we observed a well-balanced size structure, with a higher abundance of the smallest individuals, followed by a successive decrease in number as they reached larger sizes.

Discussion

Different fish assemblages were detected in the coastal lagoons (approximately 18% of the explained variance), a probable effect of their different salinity ranges (approximately 10% of the explained variance) and associated with other environmental variables to a lesser extent. The wider range of salinity in the

Table 5 Significant Pseudo-F values from the DistLM marginal test for abundance (in number and biomass) of the selected fish species (response variable) and the predictors environmental variables of salinity, temperature, turbidity and depth

Species—number	Salinity	Temperature	Turbidity	Depth	R^2
Achirus lineatus		8.5(+)	6.5(+)	**39.6(−)**	**0.13**
Anchoa januaria		13.5(−)		9.6(−)	0.08
Atrerinella brasiliensis	**49.2(−)**				**0.14**
Brevortia aurea	**27.4(+)**		**17.4(+)**		**0.12**
Elops saurus	24.3(+)				0.08
Eucinostomus argenteus	**22.1(−)**	8.4(+)	2.6(−)	6.0(−)	**0.11**
Jenynsia multidentata	**47.6(−)**		**10.1(+)**		**0.15**
Micropogonias furnieri			5.5(+)	**26.2(−)**	0.10
Microgobius meeki	**48.6(−)**	7.7(+)	**11.8(+)**	12.2(−)	**0.15**
Mugil curema				7.8(−)	0.04
Poecilia vivipara	33.5(−)		3.8(+)		0.09
Species—biomass	Salinity	Temperature	Turbidity	Depth	R^2
Achirus lineatus	**13.3(+)**		**13.9(+)**	15.8(−)	**0.12**
Anchoa januaria		16.0(−)	8.9(−)		0.08
Atrerinella brasiliensis	**22.3(−)**	7.5(+)	8.0(−)	10.5(+)	**0.13**
Brevortia aurea	**15.2(+)**		**40.2(+)**		**0.16**
Elops saurus	11.3(+)	12.7			0.08
Eucinostomus argenteus		**17.7(+)**	7.5(−)	18.6(−)	**0.13**
Jenynsia multidentata	**74.7(−)**		7.5(+)		**0.21**
Micropogonias furnieri	9.6(+)		**15.6(+)**	18.4(−)	0.13
Microgobius meeki	**55.6(−)**	7.7(+)	4.5(+)	**15.5(−)**	**0.20**
Mugil curema				27.0(−)	0.09
Poecilia vivipara	**53.0(−)**				**0.15**

The determination coefficient (R^2) also indicated. The highest significant relationship ($R^2 > 10\%$) and their highest pseudo-F values marked in bold. Positive (+) or negative (−) relationship between species and environmental variables indicated in brackets

Fig. 6 Size structures (% abundance by size class, measured in cm) of *Anchoa januaria* sampled in different lagoons and seasons
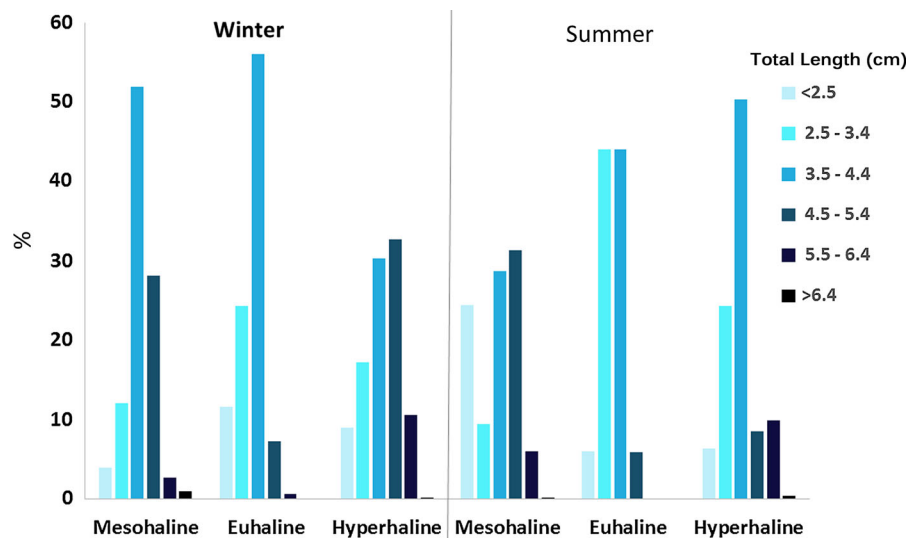
mesohaline lagoon, associated with the comparatively higher turbidity, appears to favour a community with

higher number of individuals and biomass compared to the hyperhaline lagoon that had a lower number of
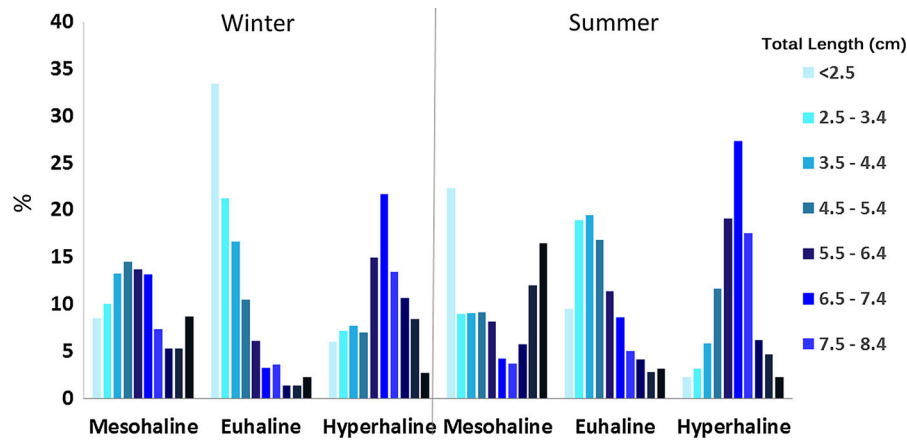
Fig. 7 Size structures (% abundance by size class, measured in cm) of *Atherinella brasiliensis* sampled in different lagoons and seasons

individuals and biomass. The highest numerical abundance and biomass in the mesohaline lagoon was likely associated with the large freshwater inputs that increase the range of salinity from estuarine to marine conditions and increase the organic loads, thus resulting in more food resources for fish species. On the other hand, the euhaline lagoon, which had salinity levels similar to the adjacent marine coast, supported a comparatively higher number of species than the other lagoons. In addition, characteristics intrinsic to each lagoon that were not measured in this study, such as hydrological and morphometric parameters of the lagoons, and biotic variables, may be part of the unexplained variation in the differences in the fish communities among the three systems.

Salinity fluctuation has been proposed as an important determinant of estuarine fish distribution (Khlebovich, 1990; Moser & Gerry, 1989; Barletta et al., 2005) and, in this study, it was the most important variable to influence the structure of the assemblages in the three lagoons. Elsewhere, salinity has been reported as a major factor structuring estuarine fish assemblages (Mariani, 2001; Martino & Able, 2003; Barletta et al., 2005; Harrison & Whitfield, 2006, Telesh et al., 2013). Small changes in salinity have been shown to influence the structure of fish assemblages and estuarine fish in general, with particular species being often more prevalent in waters with different salinity ranges (Potter & Hyndes, 1999; Harrison & Whitfield, 2006). This seems to be the case of the three studied coastal lagoons.

Although most species of fish, especially those that are typically estuarine, were caught more frequently, in larger numbers and with higher biomass in the mesohaline lagoon (e.g. *A. brasiliensis*, *J. multidentata* and *P. vivipara*), some other species were caught more frequently, in larger numbers and with higher biomass in the euhaline lagoon (e.g. the gerreids *E. argenteus* and *Eucinostomus melanopterus* and the goby *Ctenogobius boleosoma*) and in the hyperhaline lagoon (*B. aurea* and *E. saurus*). Differential fish distributions along the salinity gradient in transitional waters, such as estuaries and coastal lagoons, have been reported for both tropical (Barletta et al., 2005; Neves et al., 2013) and temperate areas (e.g. Martino & Able, 2003; Bruno et al., 2013). This species-specific preference of lagoons with different salinity ranges was detected in this study. Moreover, the lowest species richness recorded in both the mesohaline and hyperhaline lagoons, where the salinity levels are far from marine conditions, reflected stress conditions with fewer species tolerating these extremes. On the other hand, in the euhaline lagoon, only a few freshwater species that use the estuary are not present, with all species of the hyperhaline lagoon occurring there. In the hyperhaline lagoon, freshwater and stenohaline species that do not tolerate high salinity are not present; thus, this lagoon had the lowest species richness despite its larger area compared with the other two lagoons. In addition, the highest renewal time in the hyperhaline lagoon favour evaporation and the maintenance of hyperhaline conditions that contribute to the low species richness.

Although differing in structure, these permanently open coastal lagoons do not therefore have a unique ichthyofauna that differs in bays and estuaries in southeastern Brazil (see also Araújo & Azevedo, 2001; Araújo et al., 2016; Da Silva et al., 2016). Notably, however, lagoons that are only intermittently open generally contain depauperate assemblages of ichthyofauna (Sheaves, 2009; Petry et al., 2016) compared to those that are permanently open (e.g. Araújo & Azevedo, 2001; Franco et al., 2014; Azevedo et al., 2017). These studied coastal lagoons have a more limited ichthyofauna (30–33 species) when compared with regional bays that have larger areas and wider sea connections, such as the Sepetiba Bay (Araújo et al., 2016), Guanabara Bay (Da Silva et al., 2016) and Ilha Grande Bay (Neves et al., 2013, 2016) that have more than 100 fish species in each bay. Although cautions should be taken when comparing species richness between studies with different methodologies, the great differences in richness between coastal lagoons and bays, which have larger areas and wider sea connection, are compelling evidence that these two factors are important to influence the highest species richness in bays. Similarly, a coastal lagoon in the Adriatic Sea (Lesina Lagoon) had a smaller number of species than the European and Mediterranean averages (Franco et al., 2008; Manzo et al., 2016) with these difference in richness being attributable to the limited colonization by marine species, reflected especially in the failure to find marine stragglers. The three studied lagoons are connected to the sea by a single narrow canal (< 80 m in width), which may restring marine fish colonization. We hypothesize that the narrow and shallow channel connecting the lagoons to the sea and the microtidal characteristics of the area limit the connectivity between the lagoon and sea, reducing the marine influence and making colonization by marine fish difficult.

The dominant species caught in all the lagoons (*A. brasiliensis* and *A. januaria*) are generally considered residents in bays and estuarine areas in southeastern Brazil. They are small-sized species with short life spans that have adapted well to the estuarine environment. Similarly, in the coastal lagoons, these species generally dominate the ichthyofauna in the lower marine-dominated sections of estuaries and bays (Pereira et al., 2015; Araújo et al., 2016). Atherinids and engraulids are particularly prevalent components of the ichthyofaunal assemblages in coastal areas throughout the tropical Brazilian coast. Coastal lagoon fish populations consist mainly of juveniles (Beck et al., 2001). Juveniles prefer shallow and calm waters, where they are likely to find food and where there are fewer predators (Blaber & Blaber, 1980), and the water in all the studied lagoons was calm and shallow.

The most abundant and common species were generally present year round, and consequently, there were few consistent seasonal differences among the assemblages in any lagoon. Only the mesohaline lagoon had changes in its ichthyofauna between the summer and winter, a probable effect of the freshwater inputs that are more important for this lagoon compared with the other two lagoons that had more stable salinity levels. In the summer, the mesohaline lagoon has comparatively more saline and turbid waters and a lower depth compared with the winter. Depth is a kind of proxy for "seasonal changes" and for the "water level" since higher depths were found for all the three lagoons in winter. Moreover, species richness and abundance were greater in the shallower lagoons (mesohaline and euhaline). The summer conditions may favour high numbers and biomass of *M. curema*, whereas the winter conditions favour high numbers of *A. lineatus and M. meeki* and a high biomass of *J. multidentata*. These conditions very likely correspond to the reproductive peaks of these species in tropical regions (Mendonça & Andreata, 2001; Favaro et al., 2003; Albieri et al., 2010; Reis-Filho and Giarrizzo, 2016). A temporal and spatial analysis of fish assemblages also showed weak temporal and spatial patterns of variation in a Mediterranean coastal lagoon that, similar to our findings, also had a resident atherinid (*Atherina boyeri* Risso, 1810) as a numerically prevalent species (Manzo et al., 2016). The weak seasonal changes in species occurrence in the present study may be related to the fact that most species were either residents with few marine migrants or marine stragglers.

Although the PCA of the environmental variables revealed a clear separation among the lagoons, the two first dbRDA axes indicated that the examined environmental variables explained 12.7% of the variation in the species data. Therefore, there are other unmeasured variables that may be responsible for the species variation as indicated by the residual variation of 28.3% in the numerical data and 32.9% in the biomass data. Both the dbRDA and PERMANOVA analyses

were consistent with the discrimination of the assemblages among the lagoons, in that three heterogeneous systems differed mainly in salinity (from mesohaline to hyperhaline conditions), among other differences. There was also a significant variation in some of the examined sites, mainly between the mesohaline and euhaline lagoons that overlapped in the dbRDA plots. Moreover, differences in the habitat conditions of some unmeasured variables, such as the type of substrate, renewal time, width of the sea connection, marginal cover along the lagoon shoreline and area of each lagoon, could also influence species distribution. In addition, winds that promote circulation and mixing and water exchange with the coastal ocean in choked lagoons that largely depend on the hydrological cycle are other important factors (Kjerfve, 1994).

Slight differences in fish body sizes in the two dominant species were also detected among the lagoons and seasons. Catches from the intermediate size class (2.5–5.4 cm TL for *A. januaria* and 3.5–7.4 cm TL for *A. brasiliensis*) were dominant in the mesohaline and hyperhaline lagoons. However, for *A. brasiliensis* in the euhaline lagoon during both seasons, we detected a fish size structure skewed towards smaller size classes. This result could suggest a very well-balanced size structure with the larger size classes being represented in small numbers compared with the small size class. Moreover, a trend in the smallest size classes (new recruits) of these two species in the mesohaline lagoon indicated that low salinity is not a constraint for the early juveniles. No differences in size composition between two coastal lagoons in New South Wales, Australia, were found for several species, demonstrating the structural complexity of estuarine fish assemblages (Gray et al., 2011). Low habitat quality in coastal lagoons may increase fish growth rates (by the mean of a cascading effect), but it may reduce juvenile abundance in lagoons by increasing larval mortality; however, this hypothesis needs to be validated (Brehmer et al., 2013). More detailed studies on size structure focusing on the type of habitat and location within each lagoon are necessary to assess specific habitats within the lagoons that are nursery grounds for the main fish species.

We specifically identified some consistent differences in fish assemblages among the lagoons. These differences were primarily due to the larger abundances and relative occurrences of certain species.

These results reinforce previous hypotheses that there are some intrinsic dissimilarities in the ichthyofaunal assemblages in these lagoons and most likely among other transitional waters throughout southeastern Brazil. Similar results were obtained for assemblages of fish in coastal lagoons in Europe, where different ichthyofauna often characterize different lagoons and other water bodies (Jones & West, 2005; Franco et al., 2008).

Anthropogenic activities are a real threat for coastal lagoons. The modification of shorelines and the introduction of large amounts of physical materials and man-made structures adversely change the functioning of the system (Amorim et al., 2017). In addition, most coastal ecosystems are facing increasing human pressures through fishing, recreational activities, population increases and consequences of global change (Crooks and Turner, 1999; Karakassis & Hatziyanni, 2000; Harley et al., 2006). Thus, the processes that determine the distribution of fish biodiversity in coastal ecosystems deserve attention. Historical information on these coastal lagoons suggests that salinities in these lagoons decreased over the past few decades (e.g. the hyperhaline lagoon was recorded as having a mean salinity of 75 in the early 1950s (Kjerfve et al., 1990, 1996) and a mean salinity of 52 in the nineties (Knoppers et al., 1991; Kjerfve et al., 1996), and in this study, the salinity had a range of 36–54. This decreasing trend may influence the structure of fish assemblages. Moreover, human pressure from urbanization is increasingly affecting the natural habitat of lagoons, especially the mesohaline lagoon (Knoppers et al., 1991). At first, this could increase the abundance of fish, but in the long run could deteriorate water quality, putting at risk the occurrence of more sensitive species. In Ria de Aveiro, an estuarine area in Portugal, the structure and function of fish assemblages changed over time, which was attributed to human activities that ensured the lagoon was operational and that resulted in a gradual increase in salinity in the lagoon (García-Seoane et al., 2016).

The ichthyofauna of the three coastal lagoons is predominated by small-sized short-lived species, which could suggest previous stress conditions in the past. Other factors, such as the shallow characteristics of the lagoons, narrow connection with the sea and habitat limitations cannot be discarded as having an important role on the fish size structure in these

systems. Future research should investigate the patterns and processes from a conservation perspective. This requires knowledge on the relationships between taxonomic and functional diversity, and their links with ecosystem function and resilience. Understanding the function of each habitat and the relation between them in a heterogeneous environment, specially their effects on abundance, movement and growth of the associated fish fauna, is crucial for a rational management of these systems.

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