Article

Fish assemblage patterns in a subtropical estuary in southern Brazil

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Abstract: In this study, the relationship between fish assemblage structure and environmental factors was analyzed in a bay in southern Brazil. Fish were collected every two months between February and December 2002 at six sampling sites using bottom trawl nets. Abiotic data (salinity, temperature, rainfall, and depth) and biotic data (number of individuals, biomass, and total length of individuals from each species) were obtained. In total, 56 fish species representing 27 families were collected. Assemblage structure varied with seasonality, as was evidenced by the variation in temperature and rainfall in each season. Catches showed a high abundance of demersal fishes, particularly *Genidens genidens, Eucinostomus gula,* and *E. argenteus.*
Keywords: Coastal area; spatio-temporal variation; fish fauna; southwest Atlantic.

Padrões da assembleia de peixes em uma baía subtropical do sul do Brasil

Resumo: Neste estudo, a relação entre a estrutura da assembleia de peixes e fatores ambientais foi analisada em uma baía no sul do Brasil. Os peixes foram coletados a cada dois meses entre fevereiro e dezembro de 2002 em seis locais de amostragem usando redes de arrasto de fundo. Dados abióticos (salinidade, temperatura, precipitação e profundidade) e dados bióticos (número de indivíduos, biomassa e comprimento total de indivíduos de cada espécie) foram obtidos. No total, 56 espécies de peixes representando 27 famílias foram coletadas. A estrutura da assembleia variou com a sazonalidade, conforme evidenciado pela variação da temperatura e precipitação em cada estação. As capturas mostraram grande abundância de peixes demersais, principalmente *Genidens genidens, Eucinostomus gula e E. argenteus.*
Palavras-chave: Área costeira; variação espaço-temporal; ictiofauna; Atlântico Sudoeste.

Introduction

Bays, estuaries, and lagoons are coastal transition environments between fresh and saltwater (Mclusky & Elliott 2004, Basset et al. 2013). These environments, in tropical and subtropical coastal areas, provide a variety of ecosystem services that have strong implications for their conservation and management, including the provision of fishing resources, protection of the coast, areas of tourism, and rich biodiversity (Lotze et al. 2006, Sheaves et al. 2014).

In coastal environments, abiotic and biotic conditions are constantly changing, with rapid variations in salinity, temperature, oxygen, and turbidity (Elliott & Hemingway 2002). In addition to these physical and chemical factors, the reproductive biology of species, recruitment and/ or migration patterns, and biological interactions, such as predation and competition, can also influence the spatial and temporal distribution of fish fauna (Mclusky & Elliott 2004, Whitfield & Elliott 2011, Potter et al. 2015).

Although they are unstable environments, coastal environments, especially estuaries, are among the most productive natural habitats, as the accumulation of sediments from the sea and adjacent rivers forms a rich source of food that supports a large number of animals (Mclusky & Elliott 2004). Knowledge of biological patterns is essential for understanding the coastal system as a whole (Barletta et al. 2010). Fish are indicators of environmental status, and it is essential to understand the dynamics and distribution of fish assemblages to formulate strategies for managing the effects of human activities on coastal environments (Whitfield & Elliott 2002, Mérigot et al. 2017).

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Thus, several studies have investigated the patterns of spatial and temporal variation in fish assemblages and their relationship with habitats and physical conditions in these environments (Azevedo et al. 2007, Favero et al. 2019, Cattani et al. 2020). Most fishes are not adapted to spend their entire life cycle in estuarine environments. These environments are usually inhabited by seasonal members or by species that use this habitat strictly as a migration route between feeding and spawning areas. This results in a fish fauna assemblage consisting mainly of species that occur on the adjacent continental shelf (Blaber et al. 1995).

In this context, the aim of this study was to quantify the spatiotemporal distribution of estuarine fish and their key abiotic associations in a subtropical bight in southern Brazil. This may improve our understanding the ecosystem functioning, which is an important consideration for adopting conservation and preservation measures.

## Material and Methods

1. Data collection

Fish were collected every two months between February and December 2002 from six sampling sites. The samplings were carried out in the Saco dos Limões cove, state of Santa Catarina, Brazil (Figure 1). The Saco dos Limões cove is located on the inner side of Santa Catarina Island, on the east of the South Bay. The cove is shallow, with depths less than 1 meter in its southern portion, and a little deeper in the northern portion. Moving away from the cove towards the center of the bay, to the west, there is a slope with a depth of more than 3 meters. To the north, in the region of the strait between the North and South bays, the depth is greater than 10 meters. Has a sandy-muddy bottom with large amount of biodetritic material, with a predominance of the fine sediments fraction in the innermost region of the cove, while the sandy fraction is found in the nearby shallows to the Rio Tavares Mangrove

(Schettini et al. 2002, Souza-Conceição & Schwingel 2011). Sites 1, 2, and 6 were furthest from the coast, with deeper water and greater marine influence than the remaining three sites, at which water was shallower, under less marine influence, and the input of continental waters was greater (Figure 1). At each sampling site, one simultaneous double trawling lasting 10 min was carried out at a speed of 2 knots, using two identical bottom trawl nets with 4.5, 7.5, and 9 m footrope, a mesh size of 14 mm in the top and bottom panels, and a mesh size of 12 mm at the cod-end. Before each trawl, depth data were collected using an echo sounder and bottom water temperature and salinity data were collected using a Horiba U-10 multi-parameter water quality meter. Rainfall data were provided by the AGRI/CIRAM meteorological station in Florianópolis (27°34′41.89″ S and 48°30′32.79″ W). The caught specimens were identified based on taxonomic keys (Figueiredo & Menezes 1978, 1980, Fischer 1978, Menezes & Figueiredo 1980, 1985, Marceniuk 2005). Taxonomic classification and nomenclature of fish species were confirmed by comparison with information by Eschmeyer (2020).

2. Data analysis

Multivariate permutational analysis of variance (PERMANOVA) was used to assess temporal and spatial differences in fish abundance (Anderson et al. 2008). In case of rejection of the null hypothesis in PERMANOVA, the factors with significant differences ($p < 0.05$) were subjected to pairwise PERMANOVA, and were visualized through the canonical analysis of principal coordinates (CAP) using Spearman's correlation at 0.5 (Anderson et al. 2008).

PERMANOVA was also used to test temporal and spatial differences in environmental variables, while distance-based linear models (DistLM), using the Akaike selection criterion (AIC), assessed the influence of environmental variables on fish data variability. For graphic visualization of the influence of predictor variables on the spatial
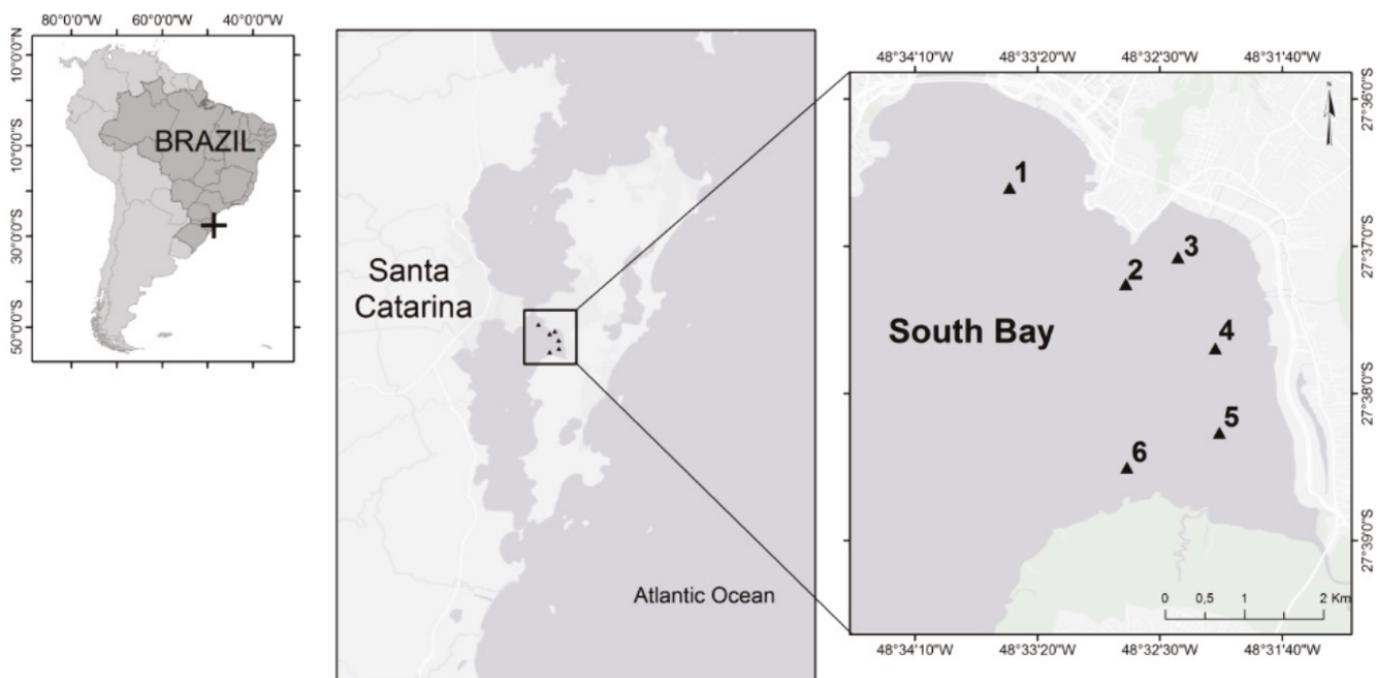
Figure 1. Map of Santa Catarina Island, with details of the collection sites.

grouping of the samples, distance-based redundancy analysis (dbRDA) was applied (Anderson et al. 2008).

To identify differences in the taxonomic structure (genuine diversity) of fishes among the seasons, the average taxonomic distinctness (Delta+ or AvTD) and variation in taxonomic distinctness (Lambda+ or VarTD) indices were calculated based on a matrix of species, gender, family, class, and order as taxonomic hierarchies. Biplots and funnel charts were used to assess whether the index values (Delta+ and Lambda+) of the seasons were within the expected ranges of variation (Clarke & Warwick 1994). Taxonomic differences between the seasons were tested using a one-way PERMANOVA in which the dependent variables were the species richness and the values of AvTD and VarTD, and the fixed factor was season (Anderson et al. 2008).

Results

1. Environmental variables

There were no significant differences in salinity among the seasons and sampling sites (Figure 2a). Mean temperature differed significantly among seasons (Pseudo-F = 12.672; p = 0.0006). Pairwise comparisons revealed differences between summer and fall (t = 2.849; p = 0.0254), fall and winter (t = 3.4821; p = 0.0122), fall and spring (t = 3.7009; p = 0.0035), and winter and spring (t = 4.8468; p = 0.0035). Mean temperatures were the highest in spring (mean ± standard deviation; 25.7 ± 2.14 °C), followed by summer (24.7 ± 1.6 °C), fall (22.1 ± 1.45 °C), and winter (18.92 ± 0.49 °C) (Figure 2b).

Depth differed significantly among sampling sites (Pseudo-F = 46.67; p = 0.0001) and seasons (Pseudo-F = 7.7778; p = 0.0038). Pairwise comparisons revealed significant differences in depth between sites 1 and 2, 1 and 3, 1 and 4, 1 and 5, 2 and 6, 3 and 6, 4 and 6, and 5 and 6 (Table 1). Depth also differed significantly between fall and winter, and between winter and spring (Table 1). The highest mean depth values were detected in fall at site 1 (6 m), in spring at sites 1 and 6 (5.5 ± 0.7 m), and in summer at sites 1 and 6 (5 m). The lowest mean depth values (2 m) were observed in winter at sites 4 and 5, fall at site 4, spring at sites 3 and 4, and in summer at sites 3, 4, and 5 (Figure 2c).

Significant differences in rainfall were detected among seasons based on values extrapolated and applied to all sampling sites (Pseudo-F = 7.5865; p = 0.001). Pairwise comparison indicated that only winter differed from other seasons (Table 1). The highest mean rainfall was observed in summer (232 mm), followed by spring (185.05 ± 29.51 mm), fall (127.25 ± 85.98 mm), and winter (113.2 mm) (Figure 2d).

2. Fish assemblage

A total of 11,327 specimens were collected, distributed across 27 families and 56 species (Table 2). The families represented by the highest richness of species in our study were Sciaenidae (11), Carangidae (7), Gerreidae and Tetraodontidae (4 each), Paralichthyidae and Epinephelidae (3 each), and Serranidae, Ariidae and Mugilidae (2 each) (Table 2). All other families were represented by only one species. The families with the highest catch numbers (five families totaling 85.04%) were Gerreidae (39.75%), Ariidae (32.87%), Paralichthyidae (7.29%), Carangidae (5.13%), and Tetraodontidae (3.87%). The families
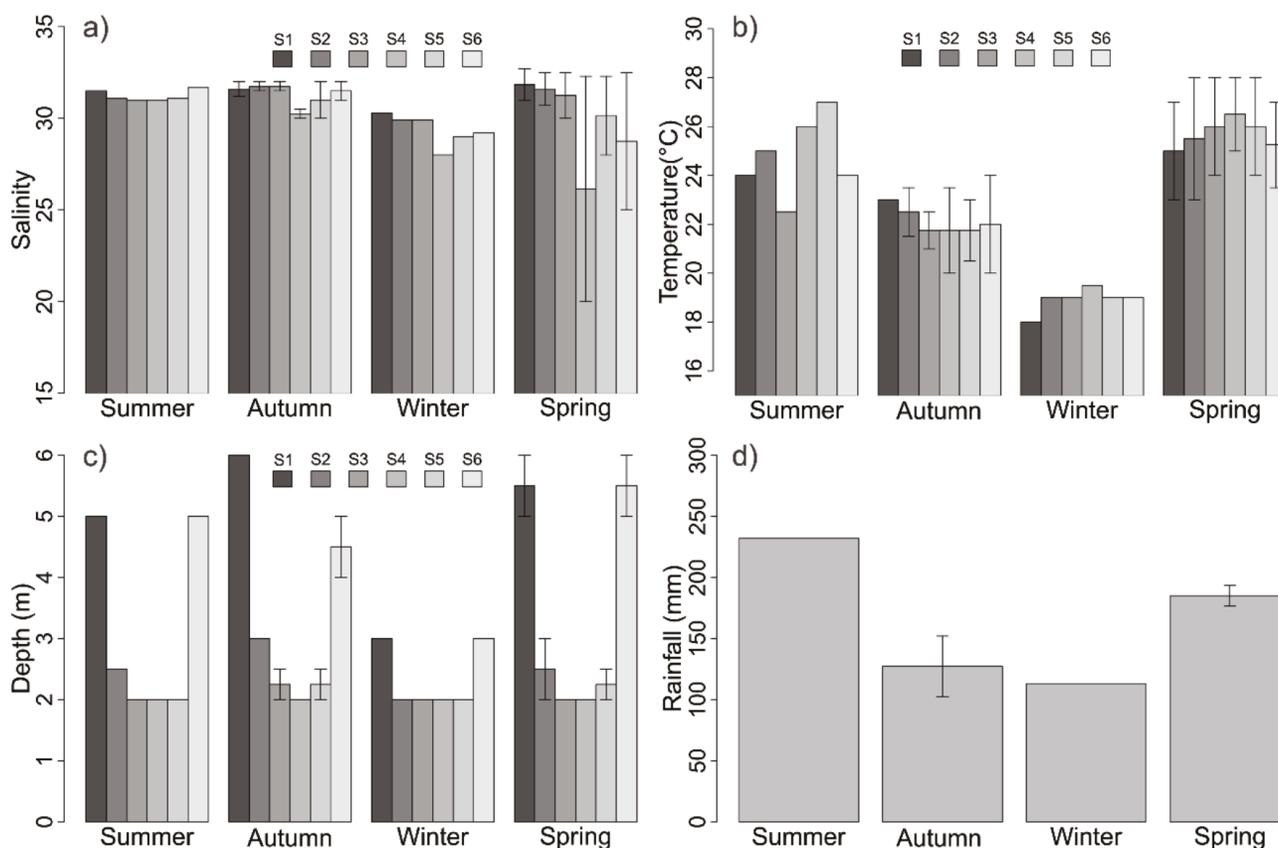

Figure 2. Average values (standard error) in the salinity (a), temperature (b), depth (c) and rainfall (d) bars, comparing the seasons of the year at the six sample sites.

Table 1. PERMANOVA pairwise based on the Euclidean distance from the depth (normalized) between the sites and the seasons, with the t-values (Student's t test) and the permutation *p*-value [p (perm)]. In bold, variables with significant *p*-value.

Groups	T	*p*(perm)
1, 2	**7.7567**	**0.0008**
1, 3	**11.619**	**0.0004**
1, 4	**13.279**	**0.0004**
1, 5	**10.371**	**0.0009**
1, 6	1	0.3576
2, 3	1.8074	0.1434
2, 4	2.3094	0.0844
2, 5	1.4142	0.2254
2, 6	**5.3333**	**0.0072**
3, 4	0.57735	0.6288
3, 5	0.33333	0.7615
3, 6	**7.5056**	**0.0025**
4, 5	0.8165	0.4541
4, 6	**8.165**	**0.0017**
5, 6	**6.9378**	**0.0028**
Summer, Autumn	1.4142	0.2339
Summer, Winter	**3.74821**	**0.0096**
Summer, Spring	0.80064	0.4519
Autumn, Winter	**5.6569**	**0.002**
Autumn, Spring	0.22942	0.8438
Winter, Spring	**3.6829**	**0.0083**

with the heaviest catch weights (five families, 84.39%) were Gerreidae (30.11%), Ariidae (28.22%), Tetraodontidae (10.55%), Sparidae (6.54%), Sciaenidae (5.05%), and Paralichthyidae (4.92%).

The most common species in this study were *Genidens genidens* (29.30%), *Eucinostomus gula* (15.50%), *E. argenteus* (15.03%), *Diapterus rhombeus* (8.88%), *Citharichthys spilopterus* (6.34%), *Chloroscombrus chrysurus* (4.10%), and *Genidens barbus* (3.58%). Together these species represented 82.73% of the individuals captured. Only one individual each was captured from the species *Elops saurus*, *Lutjanus synagris*, *Paralichthys orbignyanus*, *Scorpaena plumieri*, *Stellifer brasiliensis*, *S. rastrifer*, and *Trachinotus carolinus* (Table 2).

The total catch weight was 260,822.7 g (Table 2). The catch weights for *G. genidens* (26.33%) was the highest, followed by *E. gula* (11.99%), *D. rhombeus* (9.92%), *Sphoeroides testudineus* (9.02%), *E. argenteus* (7.64%) and *Archosargus rhomboidalis* (6.54%). Together these represented 71.44% of the total catch weight.

Thirty species occurred in all seasons and 12 species occurred in only one season. The greatest richness was observed in fall and spring (45 species each), followed by summer (38 species), and winter (31 species) (Table 2). Twenty-five species occurred at six sites, and 14 species occurred at only one site. The highest number of species occurred at site 4 (42 species), followed by sites 6 (39), 5 (37), 3 (36), 2 (35), and 1 (31) (Table 2).

Forty-two species were found during both day and night trawls. Eight species were found only during night trawls and six species were found only during day trawls (Table 2). Species richness was greater in

the nighttime (50 species) than in the daytime (48 species). Additionally, greater abundance occurred at night than at day; 7,256 fishes (64.06% of the total catch) and 4,071 fishes (35.94%) were captured in the nighttime and daytime, respectively. Twenty-six of the species occurring in both periods were more abundant at night, while 13 were more abundant during the day, and three were equally abundant in both periods (Table 2).

Mean abundance differed significantly among the seasons, periods, and sites. PERMANOVA detected significant differences ($p < 0.05$) for the three factors (Table 3). However, pairwise comparisons (PERMANOVA pairwise test), revealed that the differences were not significant between summer and winter, and fall and winter. Mean abundance also did not differ significantly between sites 1 and 2, 1 and 3, and 2 and 3 (Table 4).

Mean abundance was the highest in fall at site 4 (311.75 ± 97.83), followed by winter at site 4 (280 ± 251.73), fall at sites 5 (259.5 ± 258.59) and 6 (258.75 ± 97.8), spring at sites 5 (239.75 ± 64.86) and 4 (200.75 ± 94), winter at site 6 (194 ± 59.4), and spring at site 6 (188.5 ± 98.89). Mean abundance was the lowest in summer at site 1 (33), followed by winter at sites 1 (48.5 ± 54.45) and 2 (50.5 ± 2.12), spring at site 1 (52.33 ± 19.65), summer at sites 2 (56 ± 4.24) and 3 (74.5 ± 4.95), fall at site 1 (82.5 ± 37.22), and spring at site 3 (93.33 ± 19.65) (Figure 3a). The highest number of fish was captured at night in fall (259.92 ± 155.03) and winter (219 ± 148.97), and the lowest during the day in winter (66 ± 53.21) and summer (70.17 ± 42.49) (Figure 3b).
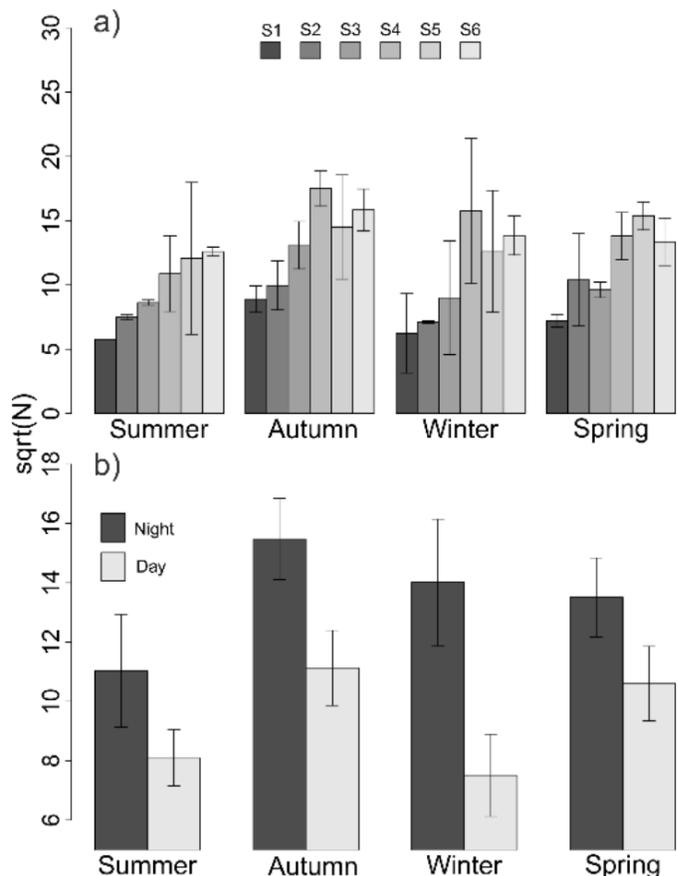
Figure 3. Mean values (standard error in the bars) of the square root of the abundance of fish caught in the seasons at sites 1, 2, 3, 4, 5 and 6 (a) and between day and night (b).

Table 2. List of species, number of individuals (n), weight (W), average, minimum and maximum of the total length (TL), season (S = spring, Su = summer, A = autumn, and W = winter), sites and period (D = day, N = night) of the fish caught (* species present in only one site). The fish classification follows Van der Laan et al. (2020).

Family/Specie	n	W(g)	Average TL (mm)	Mín-Máx TL (mm)	Season	Sites	Period
ELOPIDAE							
*Elops saurus**	1	6.38	100.00	100-100	W	5	D
OPHICHTHIDAE							
Ophichthus gomesii	6	766.46	494.33	390-610	S, Su	2, 4, 5	D, N
ARIIDAE							
Genidens barbus	405	4950.27	110.02	42-213	S, Su, A, W	1, 2, 3, 4, 5, 6	D, N
Genidens genidens	3318	68665.10	123.17	47-125	S, Su, A, W	1, 2, 3, 4, 5, 6	D, N
SYNODONTIDAE							
Synodus foetens	114	5234.00	197.13	217-469	S, Su, A, W	1, 2, 3, 4, 5, 6	D, N
BATRACHOIDIDAE							
*Porichthys porosissimus**	2	6.57	70.50	60-81	S, A	6	N
POMATOMIDAE							
Pomatomus saltatrix	22	841.25	151.05	105-253	S, Su, A	1, 2, 3, 4, 5, 6	D, N
TRICHIURIDAE							
Trichiurus lepturus	8	266.62	369.50	65-538	S, Su, A	4, 6	D, N
GOBIIDAE							
Gobionellus oceanicus	19	516.16	179.39	132-247	S, Su, A, W	1, 3, 4, 5	D, N
CENTROPOMIDAE							
*Centropomus parallelus**	6	864.02	226.67	68-346	S, Su, A, W	6	D, N
SPHYRAENIDAE							
Sphyraena guachancho	5	41.09	115.80	95-145	A	3, 4	D, N
PARALICHTHYIDAE							
Citharichthys spilopterus	718	11812.06	94.87	11-385	S, Su, A, W	1, 2, 3, 4, 5, 6	D, N
Etropus crossotus	107	726.44	85.29	41-142	S, Su, A, W	1, 2, 3, 4, 5, 6	D, N
*Paralichthys orbignyanus**	1	299.34	310.00	310-310	S	2	D
ACHIRIDAE							
Catathyridium garmani	25	328.80	80.92	35-121	S, Su, A, W	1, 2, 3, 4, 5, 6	D, N
CYNOGLOSSIDAE							
Symphurus tessellatus	84	1713.09	139.53	90-261	S, Su, A, W	1, 2, 3, 4, 5, 6	D, N
CARANGIDAE							
Caranx latus	3	56.83	102.33	91-125	W	5, 6	N
Chloroscombrus chrysurus	464	2314.65	69.84	34-171	S, Su, A, W	1, 2, 3, 4, 5, 6	D, N
Oligoplites saliens	7	154.96	143.29	107-182	S, Su, A, W	5	D, N
Oligoplites saurus	22	226.35	109.86	40-161	S, Su, A, W	1, 2, 3, 4, 5, 6	D, N
Selene setapinnis	51	941.70	108.53	56-162	S, Su, A, W	1, 2, 3, 4, 6	D, N
Selene vomer	33	1033.79	111.58	37-218	S, Su, A, W	1, 2, 3, 4, 5, 6	D, N
*Trachinotus carolinus**	1	209.21	248.00	248-248	Su	4	N
MUGILIDAE							

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Family/Specie	n	W(g)	Average TL (mm)	Mín-Máx TL (mm)	Season	Sites	Period
Mugil curema	42	4404.37	213.67	156-334	S, Su, A, W	1, 2, 3, 4, 5	D, N
Mugil platanus	16	4009.85	295.63	238-379	S, Su, A, W	1, 2, 3, 4, 5, 6	D, N
LUTJANIDAE							
Lutjanus synagris*	1	402.23	315.00	315-315	S	4	D
GERREIDAE							
Diapterus rhombeus	1006	25870.13	99.73	35-709	S, Su, A, W	1, 2, 3, 4, 5, 6	D, N
Eucinostomus argenteus	1703	19932.59	83.84	34-251	S, Su, A, W	1, 2, 3, 4, 5, 6	D, N
Eucinostomus gula	1756	31289.34	97.08	10-203	S, Su, A, W	1, 2, 3, 4, 5, 6	D, N
Eucinostomus melanopterus	37	1431.18	144.57	102-207	Su, A, W	1, 2, 3, 4, 5, 6	D, N
HAEMULIDAE							
Orthopristis ruber	40	1683.13	122.55	55-227	S, Su, A, W	1, 2, 3, 4, 5, 6	D, N
SPARIDAE							
Archosargus rhomboidalis	179	17045.82	167.12	84-279	S, Su, A, W	1, 2, 3, 4, 5, 6	D, N
SCIAENIDAE							
Bairdiella ronchus*	4	313.07	180.00	150-223	S, Su	5	N
Ctenosciaena gracilicirrhus	14	492.84	122.71	56-225	Su, A	1, 3, 6	D, N
Cynoscion leiarchus	36	1287.32	133.36	43-225	S, Su, A, W	1, 2, 3, 4, 5, 6	D, N
Cynoscion microlepidotus	2	11.08	91.00	91-91	W	1, 3	N
Isopisthus parvipinnis	41	324.10	80.71	40-204	A, W	2, 3, 4, 6	D, N
Menticirrhus americanus	3	603.13	261.33	251-278	Su, A	2, 4	D, N
Menticirrhus littoralis*	2	1275.00	369.50	334-405	A	3	N
Micropogonias furnieri	245	8815.89	133.41	25-262	S, Su, A, W	1, 2, 3, 4, 5, 6	D, N
Stellifer brasiliensis*	1	7.87	88.00	88-88	S	6	D
Stellifer rastrifer*	1	8.26	99.00	99-99	S	6	D
Stellifer sp.	2	35.26	94.00	94-94	S	6	D
SERRANIDAE							
Diplectrum radiale	64	2291.10	131.39	63-199	S, Su, A, W	1, 2, 3, 4, 5, 6	D, N
Rypticus randalli	4	211.77	153.00	119-183	S, A	2, 4	D, N
EPINEPHELIDAE							
Mycteroperca acutirostris	13	904.93	159.54	57-270	S, Su, A	2, 3, 4, 5, 6	D, N
Mycteroperca bonaci*	2	805.61	309.00	271-347	S, A	4	D, N
Mycteroperca microlepis	5	713.40	209.20	134-261	S, Su, A	4, 5	N
SCORPAENIDAE							
Scorpaena plumieri*	1	22.43	98.00	98-98	A	6	N
TRIGLIDAE							
Prionotus punctatus	156	3780.50	115.69	33-302	S, Su, A, W	1, 2, 3, 4, 5, 6	D, N
EPHIPPIDAE							
Chaetodipterus faber	81	3065.24	96.09	23-135	S, Su, A, W	1, 2, 3, 4, 5	D, N
TETRAODONTIDAE							

Family/Specie	n	W(g)	Average TL (mm)	Mín-Máx TL (mm)	Season	Sites	Period
Lagocephalus laevigatus	55	1991.12	102.73	52-273	S, Su, A, W	1, 2, 3, 4, 5, 6	D, N
Sphoeroides greeleyi	71	734.17	72.17	33-120	S, Su, A	1, 2, 3, 4, 5, 6	D, N
Sphoeroides spengleri	36	1271.93	97.44	30-223	S, Su, A	2, 3, 4, 5, 6	D, N
Sphoeroides testudineus	277	23517.30	136.41	46-274	S, Su, A, W	1, 2, 3, 4, 5, 6	D, N
MONACANTHIDAE							
Stephanolepis hispida	9	295.65	105.56	50-192	S, Su, A, W	4, 6	D, N

Table 3. PERMANOVA based on the Bray-Curtis similarity of abundance (transformed by the square root) comparing the collection points, seasons and periods (day and night). d.f = degrees of freedom; MS = sum of the mean squares; *p* (perm) = permutation p-value.

| Variation source	d.f	MS	Pseudo-F	*p*(perm)
Site	5	4359.2	3.9294	0.0001
Season	3	4695.6	4.2326	0.0001
Period	1	5506.8	4.9638	0.0002
SitexSeason	15	1282.0	1.1556	0.1746
SitexPeriod	5	1280.9	1.1546	0.2688
SeasonxPeriod	3	1478.6	1.3328	0.1593
SitexSeasonxPeriod	15	792.8	0.7146	0.9689
Residue	22	1109.4		

Table 4. PERMANOVA pairwise based on the Bray-Curtis similarity of abundance (transformed by the square root) comparing the sites, with the t-values (Student's t test) and the permutation *p*-value [*p* (perm)]. In bold, variables with significant *p*-value.

Grups	t	*p*(perm)
1, 2	1.2362	0.1886
1, 3	1.3100	0.1808
1, 4	**2.1656**	**0.0052**
1, 5	**2.6586**	**0.0015**
1, 6	**2.8788**	**0.0015**
2, 3	1.1583	0.2681
2, 4	**1.8302**	**0.0137**
2, 5	**2.0974**	0.0056
2, 6	**2.0460**	**0.0064**
3, 4	**1.6457**	**0.0370**
3, 5	**2.4455**	**0.0036**
3, 6	**2.0042**	**0.0066**
4, 5	**1.5482**	**0.0482**
4, 6	**1.7946**	**0.0122**
5, 6	**2.5396**	**0.0019**

High abundances of *M. furnieri*, *C. spilopterus*, and *G. genidens* at site 6 and *E. argenteus*, *D. rhombeus*, and *E. gula* at site 5 (Figure 4) were responsible for the spatial clusters observed in CAP. High abundances of *S. greeleyi* in the spring samples, *S. foetens*, *D. radiale,* and *E. crossotus* in the fall samples, and *C. chrysurus* in the winter samples were responsible for the seasonal clusters observed in CAP (Figure 5).

In the linear model developed by DistLM, the predictor variables that were most important were temperature (AIC = 269.91) and rainfall (AIC = 270.87). Salinity and depth did not significantly explain the variation in fish community composition (Table 5). dbRDA showed the greatest association between rainfall and summer and fall samples with axis 1, and temperature and spring samples with axis 2 (Figure 6).

PERMANOVA detected significant differences in Delta+ (average taxonomic distinctness) associated with species richness, but not in Lambda+ (variation in taxonomic distinctness) (Table 6). Pairwise PERMANOVA revealed significant differences between the spring and summer and fall and summer samples. However, despite the difference in the number of species (Figures 7a and 7b), the values of Delta+ and Lambda+ for all four seasons were very similar. The average taxonomic distinctness was greater than the simulated average for all four seasons, while the variation in distinctness was below average (Figures 7a and 7b). The biplot graph of both indices revealed a greater differentiation in Lambda+ values, with very close values of Delta+ (Figure 7c). The value of Lambda+ for the spring was especially high, and varied among samples.

Discussion

Significant differences in salinity were detected between both the seasons and the sampling sites; this is expected for an exposed area under constant influence of the continental shelf water (Veado & Resgalla 2005, Nakayama et al. 2020). Temperature also differed significantly between the seasons. However, distLM detected a significant p-value only for rainfall and temperature, such that summer and fall samples were positively associated with rainfall and spring samples were positively associated with temperature.

Based on the results of the analysis of environmental variables, our results indicate that both temperature and rainfall are important drivers of variability in fish fauna. Although salinity does not have statistical significance in explaining the variability of fish in the present study, it is an important determinant of fish assemblage structure in marine and estuarine environments (Barletta et al. 2005; 2008, Bot et al. 2018). The importance of rainfall detected by the analyses directly reflects salinity patterns. In environments with fluctuations in salinity such as coastal

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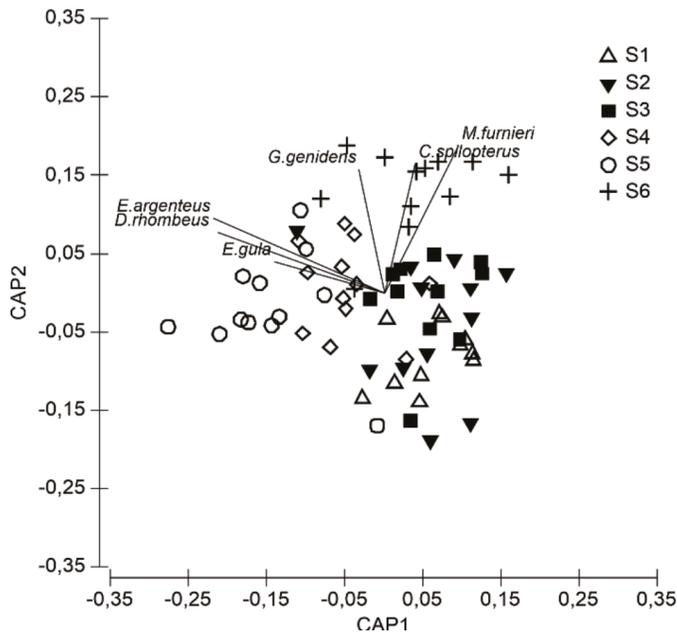
Figure 4. Result of the canonical analysis of main coordinates (CAP), with the species that contributed to the differences between the sites (1 to 6). Species vectors elaborated based on Spearman's correlation with index above 0.5 (p> 0.5). The canonical correlation of the two axes obtained by the analysis was δ1 = 0.7986 and δ =20.7452.

Figure 5. Result of the canonical analysis of main coordinates (CAP), with the species that contributed to the differences between summer (Su), autumn (A), winter (W) and spring (S). Species vectors elaborated based on the Spearman correlation with an index of 0.5 (p> 0.5). The canonical correlation of the two axes obtained by the analysis was δ1 = 0.8506 and δ2 = 0.743

and estuarine environments, fish migrate to areas that do not have high variation in salinity during times of high rainfall, which results in an influx of freshwater to the sea. For example, along the east-west axis of the Paranaguá Estuarine Complex, fish assemblages migrated to the median areas of the estuary (where salinity varies relatively little) during rainy seasons (Barletta et al. 2008).
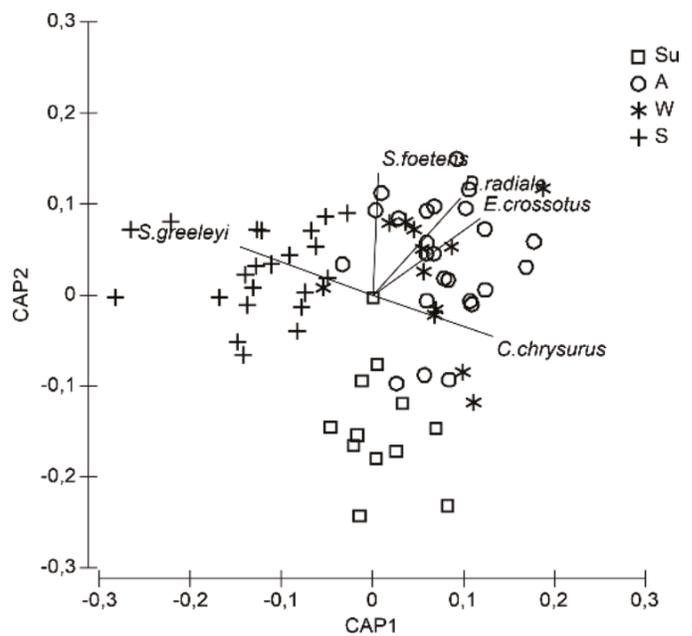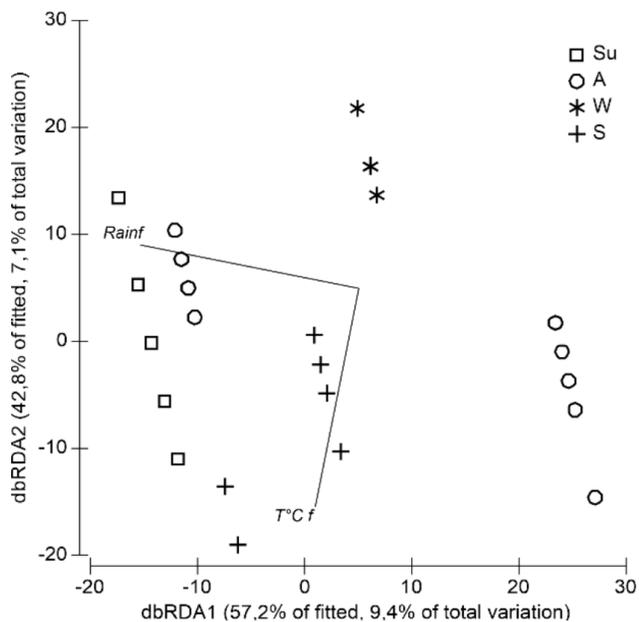
In a previous study of demersal fish fauna in a region close to the area of this study (Cattani et al. 2016b), and in studies at lower latitudes, such as in Paraná (25°S) (Schwarz Jr. et al. 2006, Barletta et al. 2008, Possato et al. 2017) and Ubatuba, São Paulo (23°S) (Rossi-Wongtschowski &

Paes 1993), a high number of species of *Sciaenidae* were observed. This predominance is common in Brazil (Reis-Filho et al. 2010, Vilar et al. 2011) and in estuaries worldwide and is due to the transition between marine/euryhaline environments throughout the evolutionary history of the family. This suggests that fishes in this adapt easily to changes in salinity, which facilitates their stay in estuarine regions (Lo et al. 2015).

The dominance of a few demersal fish species in the fish assemblages was observed in this study. Gerreidae and Ariidae were of the greatest abundance in this area. The high abundance of Ariidae in estuarine environments demonstrates the high adaptive capacity of these fish, which allows them to survive in these environments in different ontogenetic phases, despite variation in e.g. salinity, temperature, turbidity, and dissolved oxygen (Azevedo et al. 2007, Barletta et al. 2008, Cattani et al. 2016a, Possato et al. 2017). Gerreidae species are not typically more abundant than are Ariidae and Sciaenidae in estuaries (Queiroz et al. 2007, Barletta et al. 2005, Pinheiro et al. 2008).

Three species in the genus *Eucinostomus* (*E. argenteus, E. gula,* and *E. melanopterus*) were found in greater abundance in Guaratuba Bay during the period of low rainfall (May October), when salinity was nearly 35, and in lesser abundance during rainy periods, when salinity

Table 5. Result of the DistLM analysis with permutation p-value and the proportion of explanation of the variables for the selected model. In bold, variables that had a significant p-value.

Variable	P (Perm)	Proportion
Rainfall	**0.0002**	**9.3519E-02**
Temperature	**0.0018**	**7.7931E-02**
Salinity	0.4187	2.8904E-02
Depth	0.1508	4.0931E-02

Table 6. Result of PERMANOVA of richness, average taxonomic distinction (AvTD) and variation of taxonomic distinction (VarTD), considering the season. df = degrees of freedom; MS = sum of the mean squares; *p* (perm) = permutation *p*-value.

Variation source		df	MS	Pseudo-F	*p*(perm)
Richness	Season	3	122.6	2.4947	0.0634
	Residue	66	49.1460		
AvTD	Season	3	0.0429	3.6281	0.0175
	Residue	66	0.0118		
VarTD	Season	3	2.2997	0.9697	0.4140
	Residue	66	2.3714		

Figure 6. Result of the redundancy analysis based on the linear model (dbRDA), with the predictor variables that were most important for the linear model. Su = summer, A = autumn, W = winter, S = spring.
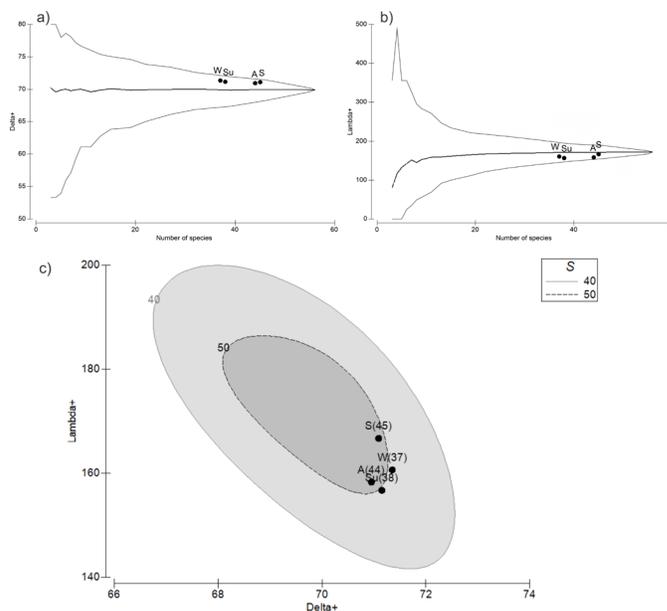

Figure 7. Average taxonomic distinction (AvTD - Delta +) (a) and variation of the taxonomic distinction (VarTD - Lambda +) (b) calculated for the Saco dos Limões by season (S = spring, Su = summer, A = autumn, and W= winter). For both indexes, the expected average is represented by the central dotted line and the limit of the 95% confidence interval by the solid line of the surroundings, in the form of a funnel. Biplot graph of Lambda + and Delta + (c). The ellipse represents the value of the 95% confidence interval of probability of finding 40 and 50 species respectively.

was nearly 5 (Chaves & Otto 1998). The high occurrence of Gerreidae in this study may have been associated with the generally high salinity values in that region; salinity values were almost always above 30, particularly in the summer and fall.

The present study indicated that catch is higher during the night. However, for shallow areas, such as beaches and tidal creeks, fish abundance seems to be greater during the day (Oliveira-Neto et al. 2010, Ignácio & Spach 2009, Ribeiro et al. 2014). The displacement of demersal species to shallower areas can interfere with abundance patterns between periods (Oliveira-Neto et al. 2010).

Although there are behavioral differences between species during the day and the night, demersal assemblages are well-adapted to low visibility conditions, with light being a secondary factor for structuring assemblages, particularly during the post-larval stages (Oliveira-Neto et al. 2010). However, in Sepetiba Bay, there were no major differences in assemblage structure between day and night (Pessanha & Araujo 2003). Possibly, for demersal fishes, differences in abundance between periods are more linked to the probability of catch, which is greater at night because it is more difficult for fish to see the net (Johnson et al. 2008). This would justify the greater abundance at night observed in the present study.

We also observed seasonal variation in fish fauna in this study. In particular, we did not observe seasonality in the taxonomic structure of the community, rather, seasonality was due mainly to different occurrence patterns for some species. The average taxonomic distinctness and variation in taxonomic distinctness indicate that taxonomic complexity did not differ among seasons.

However, the main regulatory mechanism for fish assemblages in this area is not clear. Despite seasonal differences directly reflecting the physical and chemical parameters of the water column, which in turn influence the distribution and occurrence patterns of demersal assemblages (Whitfield et al. 2012, Possato et al. 2017), the environmental gradients in the present study were not well demarcated.

It is possible that the processes of reproduction, spawning, and recruitment have a strong influence on assemblage structure because of the large abundance of small individuals belonging to a small number of species.

Considering the size (e.g. total lenth) at first maturity of the three most abundant species, 155 mm to *G. genidens* (Mishima & Tanji 2018), 120 mm to *E. argenteus* (Corrêa & Vianna 2016), and 110 mm to *E. gula* (Froese & Pauly 2021), which together account for 60% of the total abundance, its suggests that there is a predominance of young individuals in our study (see Table 2). The abundance of juveniles of these species highlights the ecosystem function of the coastal environment as a growth zone for juvenile fish (Elliott et al. 2007), due to the high biological productivity generated by the inflow of the Tavares River (Souza-Conceição & Schwingel 2011).

The essential role in the nursery function, particularly for marine fishes (Strydom et al. 2003), could be associated with the availability of food and refuge from predators (Elliot & Hemingway 2002). The importance of this study area to juvenile fishes may also indicate that juveniles are valuable for assessing ecological conditions in transitional waters.

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Author Contributions

André Pereira Cattani: Substantial contribution to the idea and design of the study, and contribution to the analysis and interpretation of data, the writing of the paper, and critical review (adding intellectual content).

Yuri Gerke: Contribution to the analysis and interpretation of data and the writing of the paper.

Helen Audrey Pichler: Contribution to the analysis and interpretation of data and the writing of the paper.

Johnatas Adelir-Alves: Contribution to the analysis and interpretation of data, the writing and preparation of the paper.

Henry Louis Spach: Contribution to the analysis and interpretation of data, the writing of the paper, and critical review (adding intellectual content).

Paulo Ricardo Schwingel: Substantial contribution to the idea and design of the work, and contribution to data collection, the analysis and interpretation of data, and the writing of the paper.

Conflicts of Interest

The authors declare no conflict of interest related to the publication of this manuscript.

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