



SPATIOTEMPORAL CO-OCCURRENCE PATTERNS OF DEMERSAL FISHES IN A SUBTROPICAL MARINE AND ESTUARINE ENVIRONMENT

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Abstract: In order to investigate spatiotemporal co-occurrence patterns of demersal fishes from the Paranaguá Estuarine Complex (PEC) and the adjacent continental shelf, state of Paraná, Southern Brazil, fish from nine sampling sites within the estuary and three additional sites in open sea (N = 12 sampling sites) were sampled at quarterly intervals between 2014 and 2016. The assemblage structure was evaluated by the C-Score index and null models developed through 5,000 randomizations. Species co-occurred as expected, but a general pattern in both temporal and spatial matrices was only detected in the Upper sector, which showed a random co-occurrence pattern. In contrast, fish species from the other sectors co-occurred less than expected by chance in some circumstances. According to the concepts related to the organization of communities on temporal scales, many communities tend to become disorganized after disturbances and then present a progressive increase in organization, that is, they display a random co-occurrence pattern, similar to initial response, and over time the species in the community segregate or aggregate in response to system stability restoration. Therefore, understanding how fish assemblages are structured at different spatial and temporal scales, and especially what processes drive such conformations, including assembly rules for communities, is crucial for ecosystem maintenance and understanding, as well as providing baselines for conservation and management policies, interventions, and practices in these environments.

Keywords: C-score; Community ecology; Demersal fish fauna; Null models.

INTRODUCTION

Estuaries are environments subjected to a wide array of hydrological, oceanographic, and anthropogenic processes, resulting in habitats

with thermal and salinity gradients, as well as varying nutrient and pollutant concentrations (Wolanski 2007). Changes in water temperature, salinity, turbidity, dissolved oxygen, sediment composition, and depth can all have an impact

on the diversity of fish assemblages in shelf regions and estuaries (Jung & Houde 2003, Oliveira Neto *et al.* 2004, Falcão *et al.* 2006, Passos *et al.* 2013, Possato *et al.* 2016). As a result, even slight variations in the water column can readily amplify the high environmental stress that occurs naturally in these areas.

The study of the multiple and complex possible interactions between species and their environment aids in understanding these processes by revealing potential factors influencing the richness and composition of communities over time (Begon *et al.* 2006). Therefore, community ecology aims at filling knowledge gaps regarding the co-occurrence of species, or even why certain species are never found in a community, to explore the patterns of occurrence and distribution of species in space and time (Gotelli 2000, Both 2009).

Distinct mechanisms have been shown to shape the organization of communities, including deterministic (Gotelli & McCabe 2002) and stochastic (Ulrich 2004) processes, as well as the combination of these two mechanisms (Ruhí *et al.* 2014). Any process contributing to the organization of communities leads to distinct patterns of species occurrence. For instance, communities structured by stochastic mechanisms can present patterns of random co-occurrence, in which one species occurs independently of the occurrence of the other, whereas communities structured by deterministic processes can present patterns of species aggregation, or even patterns of species segregation (Presley 2011, Heino & Grönroos 2013).

Predicting how environmental, biological and anthropogenic factors and their interactions determine the organization patterns of communities on estuaries and continental shelves remains a challenging task (Muto *et al.* 2000, Azevedo *et al.* 2007, Contente *et al.* 2011, Barletta & Dantas 2016). In this regard, several investigations on fish co-occurrence (Andrade-Turbino *et al.* 2008, Froeschke *et al.* 2010, Matchh *et al.* 2017) suggested that a variety of factors, such as salinity, water temperature, and even depth, have an impact on catch rates. Hence, such studies are of great importance as they provide baselines for developing and testing hypotheses about the variables that can influence the occurrence of species.

Besides the extrinsic mentioned factors, intrinsic biotic processes such as abundance cycles, which are regulated by fish entering and exiting the estuary for feeding and reproduction in different seasons (Araújo *et al.* 2002, Azevedo *et al.* 2006), may also influence the structure and development of fish assemblages in these environments. Thus, the study of species co-occurrence is important for understanding how communities are organized to further identify changes in their abundance, distribution, and behavior at small spatial scales (Matich *et al.* 2017). Species co-occurrence data also assists in understanding how each community relates to the environment in a particular spatiotemporal context, making it possible to address both natural (Sanders *et al.* 2007, Boschilia *et al.* 2012) and anthropogenic (Sanders *et al.* 2003) disturbances. The use of this method is essential not only for assessing the structure and development of fish assemblages but also for understanding the ecosystem and attempting to forecast future changes based on knowledge of the processes governing these changes over time and space.

In order to identify the existence of interactions between demersal fish communities from the Paranaguá Estuarine Complex (PEC henceforth) and the adjacent continental shelf, patterns of species co-occurrence were tested through null models to determine whether these communities are structured randomly or determined by any factor (environmental or biological). The null-model-based hypothesis states that if biotic interactions predominate as the main driving force in structuring fish assemblages, then the observed pattern of co-occurrence differs from what would be expected by chance.

MATERIAL AND METHODS

Study area

The Subtropical PEC is a 612 km² water system located in the northern area of the state of Paraná, South Brazil (Angulo 1992). It is divided into two main orientation axes, the east-west axis (about 56-km long) and the north-south axis (about 30-km long) (Andriguetto Filho *et al.* 2006; Figure 1). This estuarine area is home to a large number of fishermen who rely on fishing for their livelihood and survival (Mendonça *et al.* 2017) and harbors

two important Brazilian ports (Ports of Paranaguá and Antonina). Therefore, the PEC has great economic relevance in the fishing, industrial, and tourism.

This study focused on the PEC’s east-west axis, which is more than 50 km long and 7 km wide and comprises the bays of Antonina and Paranaguá, as well as the channel of waterways that lead ships to the Ports of Paranaguá and Antonina.

Data collection

Between 2014 and 2016, 144 demersal trawls were used to capture fish at twelve quarterly sampling locations. Nine sampling sites (one to nine) are

located along the east-west axis of the PEC and three (10 to 12) in the open sea (Figure 1).

For fish sampling, a motorized wooden boat with a 60-hp engine and two bottom-trawling nets (“round-sleeve” nets) for duplicate sampling was utilized. Nets were deployed and withdrawn from the water after a 5 minute. The nets had mesh size of 3 cm between opposite knots on the body and 2 cm between opposite knots on the bagger, which were controlled by two wooden doors (one at each end) weighing roughly 30 kg each to maintain a mouth openness of 10m.

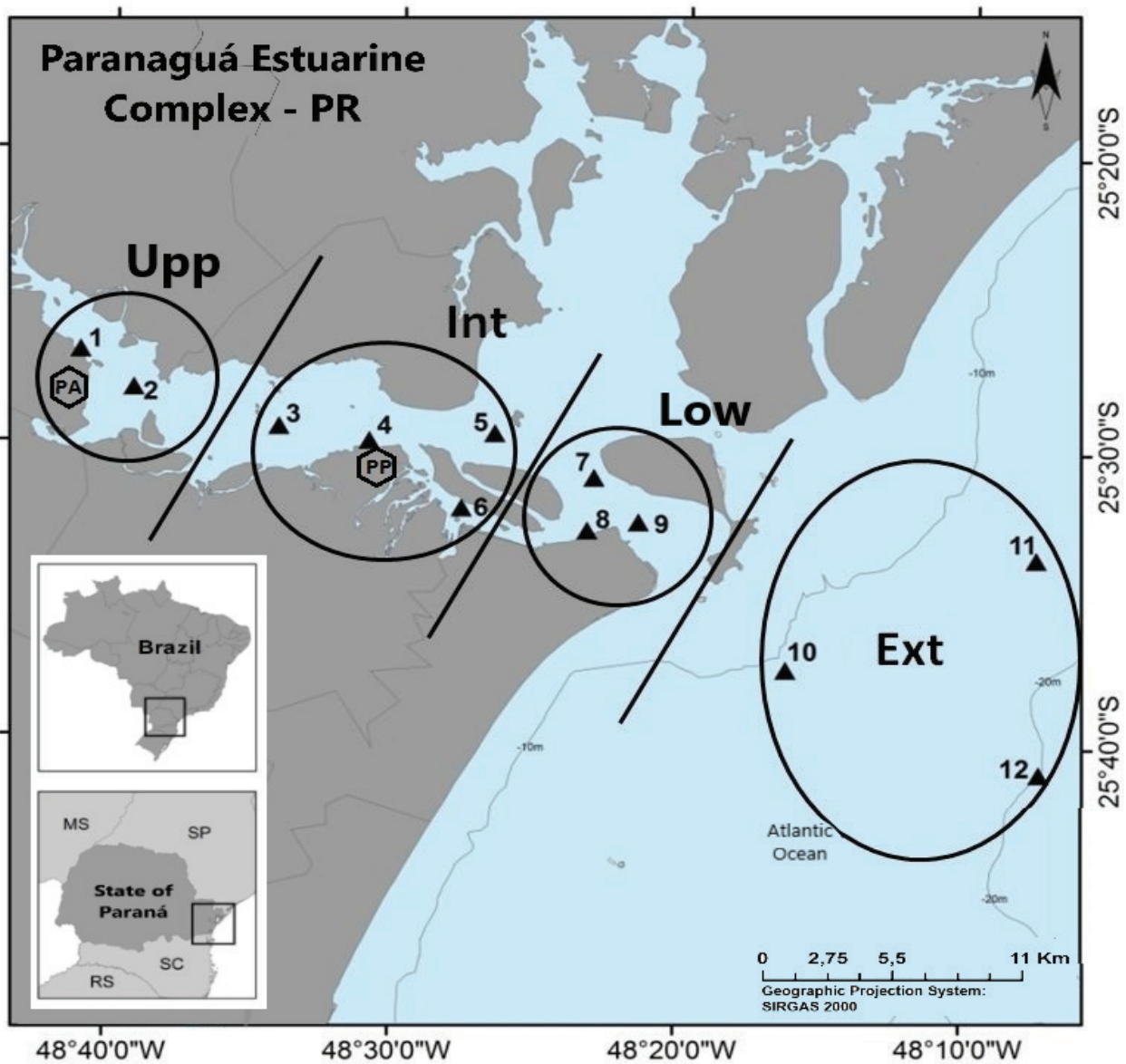


Figure 1. Location of the twelve sampling sites on the coast of the state of Paraná and the adjacent continental shelf, southern Brazil. Highlights include the Ports of Antonina (PA) and Paranaguá (PP), as well as the four (4) sectors of the east-west axis: External (Ext), Lower (Low), Intermediate (Int), and Upp (Upp).

Data analysis

All individuals were sorted and identified to the lowest possible taxonomic level, according to the specialized literature (Barletta & Corrêa 1992, Figueiredo 1978, Figueiredo & Menezes 1978, 1980a, 1980b, 2000). Occurrence matrices were built, with the rows representing the sampling species and the columns representing the sampling sites and periods. Other matrices distinguishing temporal and geographical scales to be investigated were obtained from a generic matrix containing the sampling locations for each month and year of collection arranged in the columns. Geographic scales (PEC, PEC Upper sector, PEC Intermediate sector, PEC Lower sector, and External sector) were examined by distinguishing and combining the three sampling years (2014, 2015, and 2016). For temporal-scale models, seasonal matrices were generated for each year of collection. It is important to note that in these co-occurrence analyses, the influence of each type of scale (spatial or temporal) is not independent of the other; thus, in each analysis of temporal scale co-occurrence, the effect of spatial scale is still present, and vice versa.

According to Stone & Roberts (1990), the C-Score co-occurrence index can assist researchers to estimate the spatiotemporal organization pattern of an assemblage. This index calculates the average occurrence of pairs of species using the checkerboard model.

Null models were used to simulate randomly generated patterns to assess the observed patterns of organization of fish assemblages and their co-occurrences (Gotelli & McCabe 2002). According to Gotelli & McGill (2006), null models are statistical models that, through randomization, allow inferences about a certain pattern or process observed with respect to what would be predicted by chance. Thus, such models enable one to make inferences about a certain pattern or process observed in comparison to what would be expected by chance.

A total of 5000 simulations were performed for each matrix, and the simulated C-Score was calculated and compared to the observed C-Score. Values larger than those expected by chance indicate that the assemblage presents a segregation pattern, whereas values smaller than those expected by chance suggest an aggregation pattern (Gotelli 2000, Gotelli & McCabe 2002,

Krasnov *et al.* 2014). A random distribution of species over time and space emerges when the simulated values are equal to the observed values, resulting in a pattern of co-occurrence similar to that expected by chance. Null models are based on the null hypothesis principle, which states that patterns do not represent biological interactions but rather random variations in colonization and extinction, rather than any biological process (Azevedo *et al.* 2006).

Statistical analyses were performed using the computational environment R (R Development Core Team 2017), using the 'vegan' package (Oksanen *et al.* 2013) to calculate the C-Score. A significance level of 5% was applied.

RESULTS

Fish assemblage

A total of 15,040 demersal fish specimens were caught, distributed in 21 orders, 33 families, and 67 species. The families with the highest number of taxa were Sciaenidae (16 species), Paralichthyidae (6 species), Haemulidae and Tetraodontidae (5 species) and Achiridae (4 species). The External sector contained 52 of the 67 species sampled, eight of which were only found in this sector. Within the PEC sectors, the Lower sector had 51 species, four of which were exclusive; the Intermediate sector had 44 species, one of which were unique; and the Upper sector had 29 species, two of which were exclusive to this sector (Table 1).

Co-occurrence Patterns

In general, matrices exhibited co-occurrences similar to those expected by chance, suggesting a random distribution pattern. This pattern was especially seen in matrices from the Upper sector of the PEC. Deepening the results at the spatial scale, eight of the 20 models showed lower co-occurrences than would be expected by chance, indicating an aggregation pattern of species. Being them:

- 2016: Lower and External sectors;
- 2015: External sector;
- 2014: PEC and the External sector;
- Three years combined: PEC, Lower, and External sectors (Table 2).

Table 1. Taxonomic classification of the ichthyofauna caught quarterly between 2014 and 2016. In bold, species that were exclusive to a given sector. Sectors: External (Ext), Lower (Low), Intermediate (Int), and Upper (Upp).

Species	Upp	Int	Low	Ext
Actinopterygii				
Acanthuriformes				
Sciaenidae				
<i>Bairdiella ronchus</i> (Cuvier, 1830)			X	X
<i>Ctenosciaena gracilicirrhus</i> (Metzelaar, 1919)		X	X	X
<i>Cynoscion acoupa</i> (Lacepède, 1801)	X			
<i>Cynoscion jamaicensis</i> (Vaillant & Bocourt, 1883)	X		X	X
<i>Cynoscion leiarchus</i> (Cuvier, 1830)	X	X	X	X
<i>Cynoscion microlepidotus</i> (Cuvier, 1830)	X	X	X	X
<i>Isopisthus parvipinnis</i> (Cuvier, 1830)	X	X	X	X
<i>Larimus breviceps</i> Cuvier, 1830			X	X
<i>Macrodon atricauda</i> (Günther, 1880)	X	X	X	X
<i>Menticirrhus americanus</i> (Linnaeus, 1758)	X	X	X	X
<i>Menticirrhus littoralis</i> (Holbrook, 1847)	X	X	X	X
<i>Micropogonias furnieri</i> (Desmarest, 1823)	X	X	X	X
<i>Paralonchurus brasiliensis</i> (Steindachner, 1875)			X	X
<i>Stellifer brasiliensis</i> (Schultz, 1945)		X	X	X
<i>Stellifer rastrifer</i> (Jordan, 1889)	X	X	X	X
<i>Umbrina coroides</i> Cuvier, 1830				X
Aulopiformes				
Synodontidae				
<i>Synodus foetens</i> (Linnaeus, 1766)		X	X	X
Batrachoidiformes				
Batrachoididae				
<i>Porichthys porosissimus</i> (Cuvier, 1829)		X		X
Carangiformes				
Carangidae				
<i>Selene vomer</i> (Linnaeus, 1758)		X	X	
Clupeiformes				
Engraulidae				
<i>Lycengraulis grossidens</i> (Spix & Agassiz, 1829)	X	X		
Pristigasteridae				
<i>Pellona harroweri</i> (Fowler, 1917)		X	X	X
Gadiformes				
Phycidae				
<i>Urophycis brasiliensis</i> (Kaup, 1858)			X	X
Gobiiformes				
Gobiidae				
<i>Bathygobius soporator</i> (Valenciennes, 1837)	X			
<i>Ctenogobius shufeldti</i> (Jordan & Eigenmann, 1887)		X	X	
Moroniformes				
Ephippidae				

Table 1. Continues on next page...

Table 1. ...continued

Species	Upp	Int	Low	Ext
<i>Chaetodipterus faber</i> (Broussonet, 1782)	x	x	x	x
Mulliformes				
Mullidae				
<i>Mullus argentinus</i> Hubbs & Marini, 1933				x
Ophidiiformes				
Ophidiidae				
<i>Ophidion holbrookii</i> Putnam, 1874				x
Perciformes				
Gerreidae				
<i>Diapterus rhombeus</i> (Cuvier, 1829)		x	x	x
<i>Eucinostomus argenteus</i> Baird & Girard, 1855		x	x	x
<i>Eucinostomus gula</i> (Quoy & Gaimard, 1824)	x	x	x	x
Haemulidae				
<i>Conodon nobilis</i> (Linnaeus, 1758)				x
<i>Genyatremus luteus</i> (Bloch, 1790)	x	x		x
<i>Haemulon aurolineatum</i> Cuvier, 1830				x
<i>Orthopristis ruber</i> (Cuvier, 1830)			x	x
<i>Pomadasys corvinaeformis</i> (Steindachner, 1868)	x		x	x
Lutjanidae				
<i>Lutjanus synagris</i> (Linnaeus, 1758)			x	
Priacanthidae				
<i>Heteropriacanthus cruentatus</i> (Lacepède, 1801)			x	x
Serranidae				
<i>Diplectrum formosum</i> (Linnaeus, 1766)				x
<i>Diplectrum radiale</i> (Quoy & Gaimard, 1824)		x	x	x
Triglidae				
<i>Prionotus punctatus</i> (Bloch, 1793)	x	x	x	x
Pleuronectiformes				
Achiridae				
<i>Achirus declivis</i> Chabanaud, 1940	x	x	x	
<i>Achirus lineatus</i> (Linnaeus, 1758)	x	x	x	x
<i>Catathyridium garmani</i> (Jordan, 1889)	x	x		
<i>Trinectes microphthalmus</i> (Chabanaud, 1928)				x
Cynoglossidae				
<i>Symphurus tessellatus</i> (Quoy & Gaimard, 1824)	x	x	x	x
Paralichthyidae				
<i>Citharichthys arenaceus</i> Evermann & Marsh, 1900		x	x	x
<i>Citharichthys macrops</i> Dresel, 1885			x	x
<i>Citharichthys spilopterus</i> Günther, 1862	x	x	x	x
<i>Etropus crossotus</i> Jordan & Gilbert, 1882		x	x	x
<i>Paralichthys patagonicus</i> Jordan, 1889			x	
Siluriformes				
Ariidae				
<i>Cathorops spixii</i> (Agassiz, 1829)	x	x	x	x

Table 1. Continues on next page...

Table 1. ...continued

Species	Upp	Int	Low	Ext
<i>Genidens barbatus</i> (Lacepède, 1803)	x	x	x	
<i>Genidens genidens</i> (Cuvier, 1829)	x	x	x	
Syngnathiformes				
Dactylopteridae				
<i>Dactylopterus volitans</i> (Linnaeus, 1758)		x		x
Syngnathidae				
<i>Hippocampus reidi</i> Ginsburg, 1933			x	
Tetraodontiformes				
Balistidae				
<i>Balistes capricus</i> Gmelin, 1789			x	
<i>Chilomycterus spinosus spinosus</i> (Linnaeus, 1758)	x	x	x	x
Monacanthidae				
<i>Stephanolepis hispidus</i> (Linnaeus, 1766)		x	x	
Tetraodontidae				
<i>Lagocephalus laevigatus</i> (Linnaeus, 1766)		x		
<i>Sphoeroides greeleyi</i> Gilbert, 1900		x	x	x
<i>Sphoeroides spengleri</i> (Bloch, 1785)		x	x	x
<i>Sphoeroides testudineus</i> (Linnaeus, 1758)	x	x	x	x
<i>Sphoeroides tyleri</i> Shipp, 1972		x	x	x
Chondrichthyes				
Myliobatiformes				
Dasyatidae				
<i>Dasyatis guttata</i> (Bloch & Schneider, 1801)	x	x	x	x
Pristiformes				
Rhinobatidae				
<i>Pseudobatos percellens</i> (Walbaum, 1792)		x	x	x
<i>Zapteryx brevirostris</i> (Müller & Henle, 1841)				x
Torpediniformes				
Narcinidae				
<i>Narcine brasiliensis</i> (Olfers, 1831)	x	x	x	x

Similar to our findings from spatial models, temporal models have likewise evidenced the presence of only one pattern, aggregation, which arises when the observed C-scores are lower than the expected value. For the year 2014, only seven of the 20 models revealed patterns of co-occurrence that were smaller than those expected by chance. In 2015, only six of the 20 models indicated patterns of co-occurrence smaller than the ones expected by chance, while in 2016, 50% of the models (N = 10) displayed patterns of co-occurrence smaller than the ones expected by chance (Table 3).

The Upper sector was the only one that displayed a general pattern of random co-

occurrence in all matrices (observed C-Scores equal to the simulated values) for both temporal and spatial models (Table 3), whereas the other sectors displayed co-occurrence values lower than those expected by chance at some point in the spatial and temporal models, indicating aggregation patterns.

DISCUSSION

Our study revealed that in all sectors with patterns different from the patterns simulated by the null model, aggregation patterns were found in the communities. Thus, 40% of the model results

Table 2. Observed, simulated C-Score, standard deviation (sd), and significance level (p) in each model for the spatial matrices elaborated for the External (Ext), Lower (Low), Intermediate (Int), and Upper (Upp) sectors and the Paranaguá Estuarine Complex (PEC).

Calculated Models		C-Score		sd	p
		Observed	Simulated		
Three years combined	PEC	34.9595	34.9600	0.1972	<0.001
	Upp	9.8043	9.8043	0.1575	0.8300
	Int	33.5390	33.5390	0.1954	<0.001
	Low	40.6032	40.6032	0.1670	0.3261
	Ext	31.6349	31.6350	0.2461	<0.001
2014	PEC	36.6666	36.6670	0.2494	0.0005
	Upp	7.5357	7.5357	0.2644	0.3125
	Int	34.0250	34.0250	0.3129	<0.001
	Low	38.3182	38.3182	0.4282	0.0841
	Ext	37.7727	37.7732	0.4155	<0.001
2015	PEC	23.7063	23.7063	0.2710	<0.001
	Upp	5.3214	5.3214	0.3078	0.7277
	Int	22.9333	22.9333	0.4502	0.6205
	Low	34.3484	34.3484	0.4709	0.2865
	Ext	30.0909	30.0910	0.5515	0.2254
2016	PEC	39.5650	39.5650	0.2180	<0.001
	Upp	11.6071	11.6071	0.3138	0.6957
	Int	39.3500	39.3500	0.3420	<0.001
	Low	38.5606	38.5610	0.4386	0.6021
	Ext	26.4697	26.4700	0.3389	0.3901

indicate the presence of aggregation patterns among the species throughout the samples, that is, when the simulated values are greater than the observed values. Non-random patterns of species co-occurrence were also evidenced to a lesser extent in the Intermediate, Lower, and External sectors. This type of pattern does not necessarily imply biotic interactions directly influencing the ichthyofauna, but it may be related to other factors, such as similarities or differences in the species' dispersion capacities or environmental

requirements (Peres-Neto *et al.* 2001, Azevedo *et al.* 2006). On the other hand, Queiroz *et al.* (2007) argue that the presence of numerous fish aggregates at different stages of development causes changes in dominance relationships that appear to be biological nature and cannot be interpreted as a fish response to changes in environmental integrity level.

There is still considerable controversy surrounding the co-occurrence of fish groups (Ortega 2014) as some authors suggest that fish

Table 3. Observed, simulated C-Score, standard deviation (sd), and significance level (p) in each model for the temporal matrices elaborated for the External (Ext), Lower (Low), Intermediate (Int), and Upper (Upp) sectors, as well as the Paranaguá Estuarine Complex (PEC).

Calculated Models		C-Score				
		Observed	Simulated	sd	p	
2014	Summer	PEC	25.3330	25.3330	0.4749	0.3497
		Upp	15.0000	15.0000	0.0000	1.0000
		Int	11.6667	11.1670	0.4414	0.7824
		Low	27.0000	27.0000	0.8241	1.0000
		Ext	20.6666	20.6670	0.6617	1.0000
	Fall	PEC	31.5277	31.5280	0.3718	<0.001
		Upp	12.0000	12.0000	0.0000	1.0000
		Int	33.5000	33.5000	0.6930	0.3185
		Low	25.6667	25.6670	0.7969	0.9468
		Ext	48.3333	48.3333	0.6394	1.0000
	Winter	PEC	46.2778	46.2780	0.6587	0.0957
		Upp	4.0000	4.0000	0.0000	1.0000
		Int	35.6666	35.6670	0.7468	0.1210
		Low	48.3333	48.3333	0.9332	0.8992
		Ext	35.6666	35.6670	0.6571	<0.001
	Spring	PEC	30.6111	30.6111	0.3592	<0.001
		Upp	6.0000	6.0000	0.0000	1.0000
		Int	40.3330	40.3330	0.7844	0.9908
		Low	10.6666	10.6670	0.5792	0.4785
		Ext	17.3333	17.3333	0.4732	0.2601
2015	Summer	PEC	28.8055	28.8060	0.5808	0.0686
		Upp	5.0000	5.0000	0.0000	1.0000
		Int	24.3333	24.3333	1.1750	0.4153
		Low	18.3333	18.3333	0.4457	0.3405
		Ext	22.3333	22.3333	1.0089	0.8980
	Fall	PEC	13.4166	13.4170	0.4197	<0.001
		Upp	1.0000	1.0000	0.0000	1.0000
		Int	17.0000	17.0000	0.6145	0.6405
		Low	17.0000	17.0000	1.1128	0.5461
		Ext	29.0000	29.0000	1.0093	0.2282
	PEC	30.5277	30.5280	0.6225	0.3389	

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Calculated Models		C-Score				
		Observed	Simulated	sd	p	
2016	Winter	Upp	16.0000	16.0000	0.0000	1.0000
		Int	30.1666	30.1670	0.7709	0.3669
		Low	46.6660	46.6670	1.5842	0.1014
		Ext	14.6660	14.6670	0.7134	1.0000
		PEC	18.7222	18.7222	0.5931	0.3873
	Spring	Upp	2.0000	2.0000	0.0000	1.0000
		Int	18.3330	18.3330	0.8577	0.5673
		Low	9.0000	9.0000	1.1096	0.9796
		Ext	24.0000	24.0000	1.0521	0.6641
	Summer	PEC	31.1388	31.1390	0.5913	<0.001
		Upp	3.0000	3.0000	0.0000	1.0000
		Int	30.5000	30.5000	1.0872	<0.001
Low		55.6660	55.6670	1.0311	<0.001	
Ext		16.3333	16.3333	0.1508	0.5753	
Fall	PEC	32.6388	32.6390	0.5347	0.1182	
	Upp	21.0000	21.0000	0.0000	1.0000	
	Int	17.5000	17.5000	1.0172	0.6865	
	Low	17.6660	17.6670	0.6494	0.3913	
Winter	Ext	17.6666	17.6670	0.7279	0.9492	
	PEC	38.0556	38.0560	0.4350	<0.001	
	Upp	10.0000	10.0000	0.0000	1.0000	
	Int	40.1666	40.1670	0.9001	0.1490	
	Low	29.6666	29.6670	0.8163	0.6905	
	Ext	27.0000	27.0000	1.1208	<0.001	
	PEC	37.3333	37.3333	0.5934	<0.001	
	Upp	12.0000	12.0000	0.0000	1.0000	
	Int	45.1666	45.1670	0.8743	<0.001	
	Low	18.0000	18.0000	1.2086	1.0000	
Spring	Ext	54.6666	54.6670	0.5935	0.5581	

assemblages have random patterns of distribution, whereas others propose that they have segregation and even aggregation patterns (Gotelli & McCabe 2002, Azevedo *et al.* 2006, Bhat & Magurran 2007).

Even though values of aggregation patterns were only slightly different from the simulated values, this pattern was found in at least 40% of our temporal and spatial models. In this regard,

species co-occurrence may have arisen as a result of similar responses from species that share the same niche and use the resource in a similar manner (Simberloff & Dayan 1991, Presley 2011), or even due to the characteristics of this group, which explores a wide range of environments (Matthews 1998).

According to Mouchet *et al.* (2013), temporal analysis allows for more accurate inferences about the mechanisms influencing the patterns of organization of fish communities, particularly when environmental constraints can drive the composition of species in local assemblages. Based on the results of our three-year-long study, we can infer possible short-term fish community responses to the processes that may be affecting the ecosystem of the PEC and the adjacent continental shelf. However, the Upper sector displayed patterns similar to observed co-occurrence values in all simulated models, revealing random patterns, which emerge when one species occurs independently of the occurrence of the other.

In contrast to the other sectors, we were able to identify potential alterations in the ecosystems of the Intermediate, Lower, and External sectors that may be linked to anthropogenic stressors. This outcome may be attributed to an increase in port activities as well as their maintenance (by dredging), which modifies the geomorphology, hydrography, and physiography of these sectors. Such modifications are likely to have an impact on fish community dynamics, perhaps leading to a rapid decline in biodiversity and the disappearance of Sciaenidae species (Barletta & Dantas 2016, Cattani *et al.* 2016).

Since the Intermediate and Lower sectors are the most impacted by the channel of waterways that lead ships to the berths of the Ports of Paranaguá and Antonina, which are sources of disturbance, some response from the fish communities was previously expected. According to the concepts related to the organization of communities in temporal scales, many communities tend to become disorganized following disturbances and subsequently display a progressive rise in the organization. The communities exhibit a pattern of random co-occurrence, similar to initial response, and over time, the species in the community segregate

or aggregate in response to system stability restoration (Arrington *et al.* 2005, Fernandes *et al.* 2009, Boschilia *et al.* 2012).

A more thorough consideration of the possible effects of anthropogenic activities performed within the study area is recommended for future strategic planning focusing on the conservation and maintenance of these water bodies, particularly concerning the intermediate, lower, and external sectors, which were shown to be the most vulnerable to human activities.

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