Meiofauna structure in Tramandaí-Armazém estuary (South of Brazil).

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ABSTRACT: Meiofauna structure in Tramandaí-Armazém estuary (South of Brazil). The meiofauna spatial and temporal distribution at Tramandaí-Armazém estuary was investigated through 4 seasons (summer, autumn, winter, spring), in 2000, in three environments: Tramandaí lagoon, with constant fresh water inflow; Armazém lagoon, where saline wedge is more frequent; the channel between the lagoons and the Atlantic Ocean. Nematoda was the dominant taxonomic group in the samples, but there was a differentiation in the second most abundant group, being Copepoda co-dominat in Armazém lagoon, Ostracoda and Copepoda in Tramandaí lagoon, and juveniles of Gastropoda (Heleobia australis) in the channel. The meiofauna structure in Armazém, characterized by higher densities (mean 916 ind/10cm²), was different from the other environments, in all seasons. The meiofauna collected samples from Tramandaí (mean 259 ind/10cm²) and channel (mean 373 ind/10cm²) were similar in almost every station, except in spring. Density peaks were evidenced in the summer. The results suggest that the environmental variables considered important in a meso-scale, such as salinity, hydrodynamic, stability of the sediment and temperature are the main conditioners of variability found in the sampled environments.

Key-words: meiofauna, Nematoda, estuary, spatial-temporal distribution.

RESUMO: Estrutura da meiofauna no estuário Tramandaí-Armazém (Sul do Brasil). A distribuição espacial e temporal da meiofauna, no estuário Tramandaí-Armazém, foi analisada em coletas sazonais (verão outono, inverno e primavera), no ano de 2000, em três ambientes: laguna Tramandaí, com aporte constante de água doce, laguna Armazém, onde ocorre a entrada mais freqüente da cunha salina e no Canal de ligação entre as lagunas e o Oceano Atlântico. Nematoda foi o grupo taxonômico que dominou amplamente nas amostras, no entanto, percebe-se uma diferenciação no segundo grupo mais abundante, sendo Copepoda o grupo co-dominante na laguna Armazém, Ostracoda na laguna Tramandaí e juvenis de Gastropoda (Heleobia australis) no Canal. A estrutura da meiofauna na laguna Armazém, caracterizada pelas densidades mais elevadas (916 ind/10cm²), é diferenciada da estrutura encontrada nos demais ambientes analisados, em todas as estações de coleta. As amostras coletadas na laguna Tramandaí (259 ind/10cm²) e no Canal (373 ind/10cm²) foram similares em quase todas as estações, com exceção da primavera. Picos de densidade da meiofauna foram evidenciados no verão. Os resultados sugerem que as variáveis ambientais, citadas como importantes numa meso-escala, como salinidade, hidrodinâmica, estabilidade do sedimento e temperatura, são as principais condicionantes da variabilidade encontrada nos ambientes amostrados.

Palavras-chaves: meiofauna, nematoda, estuário, distribuição espaço-temporal.

Introduction

Meiofauna organisms are found abundantly in estuarine environments (Coull, 1999) where their spatial distribution is associated to an aggregated behaviour. This

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standard can be explained by several related factors depending on the analysed scale (Li et al., 1997; Ozorio et al., 1999).

In meso-scale, abiotic factors such as sediment granulometry, salinity and hydrodynamics, are generally mentioned as the most important factors structuring the meiofauna (Heip et al, 1985; Alongi, 1987; Sarma & Wilsanand, 1996; Li & Vincx, 1993; Smol et al., 1994; Soetaert et al., 1994). In a micro-scale, however, biological factors such as inter and intra-specific relationships, the presence of biogenic structures, food availability (Santos et al., 1996; Moens et al., 1999; Pinto & Bemvenuti, 2003) have the principal role.

In estuarie regions, the gradients of abiotic variables occur either spatial or temporally (Soetaert et al., 1994). Salinity is the most relevant variable and its alterations are generally followed by changes in the sedimentary habitat characteristics, current flow, oxygen concentrations, food sources supply, among others (Little, 2000). In general, the abundance and the number of species tend to decrease as one moves from the sea to freshwater (Coull, 1988).

Associated with the salinity, sedimentary characteristics also influence meiofauna composition and abundance (Wieser, 1959; Coull, 1988). Grain characteristics (size, selection rate), are influenced by environmental factors such as active hydrodynamics and determine other variables such as porosity, permeability, oxygen content (Giere et al., 1988). Finer substrates characterized by low permeability and oxygen level can reduce meiofaunal populations (Dye & Furstenberg, 1978). In these places, burrowing organisms are principally found in the superior centimeters of the substract and their density is significatively reduced with depth (Ansari & Parulekar, 1993; Cruz & Vargas, 1987). In coarse sediments, where pore spaces are larger, meiofauna is mostly interstitial and can be found in depths of about one meter in the substract (Fenchel & Riedl, 1970).

In Brazil, studies on meiofauna distribution in estuary environments are scarce and recent. In the Rio Grande do Sul State, Ozorio et al. (1999) and Pinto & Bemvenuti (2003) studied the Lagoa dos Patos estuarine area, while Kapusta et al. (2002, 2004) carried out works in the Tramandaí-Armazém estuarine system. Fonseca (2003) studied the Laguna estuary and Netto & Gallucci (2003) the mangrove of the Ratones River estuary (both in Santa Catarina State). In the southeast region, Dalto & Albuquerque (2000) examined the meiofauna in the Jacuacanga Bay (Rio de Janeiro), whereas in the northeast of Brazil, Somerfield et al. (2003) studied the meiofauna in the Baía de Pina estuary, Pernambuco State.

In Tramandaí-Armazém estuary, a stable gradient of abiotic variables is absent, but exist a wide variation of these variables in a short period of time (Würdig, 1987). This intense dynamics is regulated mainly by wind direction and intensity, rainfall and the entry of saline water (Würdig, 1987). In this estuary, Kapusta et al. (2002, 2004) studied the horizontal and vertical distribution of meiofauna in winter and summer.

The present study aimed to analyze the spatial variability of meiofauna structure in Tramandaí-Armazém estuary and to describe the seasonal variation of this community.

Material and methods

Tramandaí-Armazém estuary is located in the northern coast of Rio Grande do Sul (Fig.1), between the coordinates of 29° 55′ 49″S and 30° 00′56″S and 50° 06′ 21″ W and 50° 11′ 20″ W (Tommazeli, 1990).

In this estuary, the connexion with the Atlantic Ocean is accomplished through a narrow and short channel. In Tramandaí Iagoon, the water and fine sediments inflow take place through the Tramandaí river (Tommazeli, 1990), while in Armazém there is a higher tendency for a saline wedge inflow. The amplitude of the astronomical tide in this region is low, oscillating around 0.3m and meterological effects such as wind and precipitation are therefore dominant over astronomical ones (Lira et al., 1976).



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To analyse the meiofauna community, three areas located in Armazém lagoon (R, 1 and 2), three areas in Tramandaí lagoon (4, 5 and 6), and one area in the connecting channel with the Atlantic Ocean (3) were sampled in summer, autumn, winter and spring in 2000 (Fig.1). The sampled area "R" was located in a bank of Ruppia maritima.





At each area, six samples were collected for the meiofauna, to a depth of 5cm with a corer which was 2.7cm in diameter. The material collected was fixed in the field with 10% formaldehyde, having previously been buffered with Borax and coloured with Rose Bengala. Sediment samples were collected, with a corer with a diameter of 10cm, in order to analyse granulometry and organic material.

Water column depth (obtained with measuring tape), water transparency (with Secchi disc), pH (with WTW potentiometer pH 197 model), bottom water temperature (with a thermometer in $^{\circ}$ C), salinity (with a refractometer) and dissolved oxygen (with a oximeter YSI-54) were the variables measured in the field.

In the laboratory, LUDOX TM, (1.15) (Somerfiel & Warwick, 1996) was used to extract the organisms from the sediment. The supernatant was passed through sieves with a 0.500 and 0.063mm mesh and only the organisms retained by the sieve with the smallest opening were considered. The biological material was analysed under estereomicroscope. The organisms belonging to meiofauna were counted and identified.

Granulometry analysis was done according to Suguio (1973), while the organic matter was determined by drying the sediment at 60° C for 24 hours and burning it for 5 hours in an oven at 550° C.

Data analyses

Data were analysed using univariate and multivariate techniques. The significance of differences in density between the environments and seasons was tested using one-way and two-way ANOVA, with the Statistica[®] 5.0 program. In order to test the

assumption of homogeneity of variances, Cochran's tests were applied and data were square root transformed. Tukey's multiple comparison tests were used when significant differences were detected (p<0.05).

Similarity matrices were constructed using the Bray-Curtis similarity measure on square root transformed data. Ordination was done by non-metric multidimensional scaling (MDS). The 1-way and 2-way ANOSIM permutation test was used to confirm the differences between the environments and seasons. For these analyses, the PRIMER^â program, version 5.2.4, was used.

In order to detect the abiotic variables correlated to the structure of the meiofauna, BIO-ENV analysis was carried out using the $\textsc{PRIMER}^{\hat{a}}$ program, 5.2.4 version, with the matrix of abiotic data created from the euclidian distance and the biological similarity matrix as described for the ordination analysis MDS.

Results

Fourteen taxonomic groups were identified (Tab.I). Nematoda were the most abundant group of the population numerically, contributing between 35.7% (channel) and 78.8% (Armazém lagoon) of the total density. The next most representative groups were Copepoda (11.1%) in Armazém lagoon, juvenile of Heleobia australis (34.6%) in channel and Ostracoda (13.9%) and Copepoda (13.3%) in Tramandaí lagoon.

Table I: Mean density (ind/IOcm²), standard deviation (SD) and relative abundance (%) of taxonomic groups collected in Armazém and Tramandaí lagoons, and in the Channel. MP - permanent meiofauna, MT - temporary meiofauna.

	Armazém		Channel		Tramandaí	
	Ind/10cm $^2\pm$ SD	%	Ind/10cm $^2\pm$ SD	%	Ind/10cm $^2\pm$ SD	%
Turbellaria	4.9 ± 12.5	0.5	22.3 ± 25.8	6.0	6.1±11	2.3
Nematoda	719.2 ± 642	78.8	133.1± 193.9	35.7	154.4 ± 227	59.7
Ostracoda	41.4 ± 54.4	4.5	54.7 ± 66.3	14.7	36.0 ± 53.9	13.9
Copepoda	103.4 ± 154.1	11.1	15.0 ± 25.5	4.0	34.4 ± 81	13.3
Nauplii	22.8 ± 49	2.4	7.9 ± 12.7	2.1	16.8 ± 46.2	6.5
Acari	2.9 ± 4.9	0.3	0.4 ± 1.2	0.1	2.7 ± 5.7	1.1
Tardigrada	0.0± 0.2	0.0	-	0.0	0.3±1.3	0.1
MP	895 ± 349	98.0	233.5± 95.3	63.0	250.7 ± 107.1	97.0
Gastropoda	10.3±22	1.1	128.8±143.6	34.6	4.6 ± 6.7	1.8
Bivalvia	1.5 ± 3.6	0.2	6.6 ± 10.2	1.8	-	0.0
Oligochaeta	2.8 ± 4.7	0.3	2.3 ± 4.6	0.6	2.0± 7.1	0.8
Polychaeta	6.4 ± 8.1	0.7	1.1 ± 1.7	0.3	0.8 ± 1.7	0.3
Isopoda	0.2 ± 0.8	0.0	-	0.0	0.1 ± 0.4	0.0
Chironomidae	0.4 ± 1.4	0.0	-	0.0	0.3 ± 1.2	0.1
Cumacea	0.0 ± 0.2	0.0	0.3 ± 1.1	0.1	0.2 ± 0.8	0.1
MT	21.6 ± 9.8	2.0	139.9 ± 65.4	37.0	8.8 ± 4	3.0
Total density	916.2±254.6	100.0	373.4±77.7	100.0	259.5 ± 75.2	100.0

The MDS ordination showed that the meiofauna structure is different in the three sampled environments and among seasons, and that meiofauna structure in the channel and Tramandaí lagoon tends to be similar (Fig.2). The 2-way ANOSIM permutation test confirm these results.

The results of the two-way ANOVA tests derived from meiofauna data are shown on Tab.II. They showed that the densities of meiofauna, Nematoda and Copepoda were significantly higher in the Armazém lagoon than in the channel and Tramandaí lagoon. Temporary meiofauna densities were significantly higher in the channel. Density peaks were evidenced in the summer.



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Figure 2: Multi-dimensional scaling ordination (MDS) for square-root transformed meiofauna density (stress=0.19) from Armazém lagoon (A), Channel (C), and Tramandaí lagoon (T).

Table II: Results of 2-way ANOVAs (p<0.05) considering density of taxonomic group more representative, among environments (A - Armazém lagoon, T - Tramandaí lagoon, C - Channel) and among seasons (S - summer, A - autumn, W - winter, P - spring). NS non significant difference. Significant difference recorded by the Tukey analysis.

	Among evironments	Among seasons
Total density	A>C, T	S Y A , W , P
	(p=0.000)	(p=0.000)
Nematoda	A>C, T	S > A , W , P
	(p=0.000)	(p=0.000)
Ostracoda	N S	S > A ,W
	(p=0.069)	(p=0.008)
Copepoda	A ightarrow C , T	S>A,W,P
	(p=0.000)	(p=0.000)
Temporary	$C \rightarrow A \rightarrow T$	S>A,W
	(p=0.000)	(p=0.000)

Meiofauna structure in Armazém lagoon is different from the other sampled environment in all season, when the seasons are analysed separately. The meiofauna structure found in the channel and the Tramandaí lagoon were similar in almost every season, except in spring (Fig. 3, Tab. III).



Figure 3: Multi-dimensional scaling ordination (MDS) analysis performed with meiofauna density data, considering Armazém lagoon (A), Channel (C), and Tramandaí lagoon (T) in summer, autumn, winter and spring of the year 2000.

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	Armazém	Armazém - Channel		- Tramandaí	Channel - Tramandaí		
	R	р	R	р	R	р	
Summer	0.405	0.008	0.299	0.001	0.129	0.172	
Autumn	0.930	0.001	0.392	0.001	0.018	0.361	
Winter Spring	0.891 0.845	0.001 0.001	0.589 0.233	0.001 0.001	0.132 0.331	0.112 0.014	

Table III: ANOSIM (p<0.05) result in Tramandaí-Armazém lagoons and in Channel in the summer, autumn, winter, and spring of the year 2000.

In summer, total average density and Nematoda were significatively higher in Armazém lagoon, when compared to other environments. Ostracoda densities were higher in Armazém lagoon and channel. However, there was no significative difference for Copepoda (Fig.4, Tab.IV).

During autumn and winter, total average density, Nematoda and Copepoda were significatively higher in Armazém lagoon. Ostracoda, however, was similar among the lagoons (Fig.4, Tab.IV).

In spring, the highest densities occurred in Armazém lagoon and channel. In Armazém lagoon, Nematoda accounted for 85% of the organisms, while in the channel, Heleobia australis was the prevailing taxon (63%). Copepoda densities in Armazém and Tramandaí lagoons were similar, but higher than in channel. There was no significative difference among Ostracoda densities (Fig.4, Tab.IV).

The shallowest depths were registered in the Armazém lagoon in all sampling periods, and there was total transparency in almost all seasons. Higher salinity, oxygen and pH levels were also found here, when compared with Tramandaí lagoon.



Figure 4: Mean density (ind/IOCm²) and standard deviation of total meiofauna samplings and most representative groups in each environment, collected in summer, autumn, winter, and spring in the year 2000.

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Summer	F	р	Environment	Autumn	F	р	Environment
Total	11.03	0.000*	A>T	Total	12.83	0.000*	A>C, T
Nematoda	14.39	0.000*	A>C, T	Nematoda	20.89	0.000*	A>C, T
Ostracoda	6.95	0.003*	$A,C \to T$	Ostracoda	2.05	0.142	-
Copepoda	0.88	0.422	-	Copepoda	37.69	0.000*	A>C, T
Winter	F	р	Environment	Spring	F	р	Environment
Total	22.68	0.000*	A>C, T	Total	8.73	0.001*	A,C>T
Nematoda	20.49	0.000*	A>C, T	Nematoda	11.43	0.000*	A>C,T
Ostracoda	5.77	0.006*	A) T	Ostracoda	1.32	0.280	-
Copepoda	43.78	0.000*	A>C, T	Copepoda	14.93	0.000*	A,T>C

Table IV: ANOVA and Tukey test result in Armazém (A) and Tramandaí (T) lagoons and in Channel (C), considering meiofauna density (total) and most abundant groups density. * Significance level $p \in 0.05$.

The mean percentage of fine sediments was relatively low in all the environments, although it tended to show a greater variation in the percentage of silt and clay in the Tramandaí lagoon and the channel throughout the whole year. The level of organic matter was generally higher in the Armazém lagoon due to the presence of submerged vegetation. The data of the abiotic variables measured in the sampled environments can be seen in Tab.V.

Through the analysis of the biological matrix and that of the abiotic data using BIO-ENV analysis, it could be seen that transparency, depth and pH variables had the highest Spearman correlation coefficient (0.314).

Table V: Mean values and standard deviation of temperature, salinity, dissolved oxygen and pH recorded for the bottom water, transparency and depth, sand, silt/clay and organic matter (OM) percentuals in the Armazém lagoon and Tramandaí lagoon and the Channel for summer, autumn, winter and spring 2000.

	Temp. (°C)	Transp. (cm)	Water depth (cm)	Salinity	O₂ (mg/L)	pН	% sand	%silt/clay	% OM
summer									
Armazém	29.2 ± 0.8	32.0 ± 17.6	40.0 ± 10.0	3.3 ± 0.6	8.2 ± 0.7	8.3 ± 0.5	93.5 ± 6.6	6.5 ± 6.6	$O.3 \pm O.1$
Channel	27.5	20	110	0.0	6.2	7.5	95.0	4.8	0.3
Tramandaí	25.7 ± 1.0	32.0 ± 14.4	57.0 ± 15.3	0.0 ± 0.0	7.3 ± 0.5	7.1 ± 0.5	93.7 ± 4.9	6.3 ± 4.9	0.4 ± 0.1
autumn									
Armazém	20.4 ± 0.7	23.3 ± 16.1	35.0 ± 5.0	6.8 ± 0.3	6 ± 1.3	8.3 ± 0.2	98.1 ± 3.2	1.9 ± 3.2	1.1 ± 1.5
Channel	20.0	50.0	105.0	11.5	5.5	7.2	99.8	0.0	0.3
Tramandaí	19.1 ± 0.3	48.3 ± 53.9	93.3 ± 42.5	5 ± 4.6	4.7 ± 0.2	6.3 ± 1.0	84.1 ± 19.5	15.9 ± 19.5	0.5 ± 0.4
winter									
Armazém	16.2 ± 1.4	28.3 ± 7.6	28.3 ± 7.6	4.0 ± 5.2	8.0 ± 0.7	7.9 ± 0.2	93.1 ± 7.9	6.9 ± 7.9	1.1 ± 1.5
Channel	17.0	40.0	80.0	8.0	7.3	7.9	86.8	12.6	0.4
Tramandaí	18.6 ± 1.2	28.3 ± 36.9	64 ± 23.5	3.2 ± 3.0	7.2 ± 1.2	7.7 ± 0.5	96.6 ± 1.8	3.4 ± 1.8	0.7 ± 0.6
spring									
Armazém	23.4 ± 0.3	38.3 ± 7.6	38.3 ± 7.6	0.2 ± 0.3	8.9 ± 4.5	7.6 ± 0.1	91.3 ± 6.7	8.7 ± 6.7	2.3 ± 3.2
Channel	24.3	35.0	90.0	0.5	7.6	7.4	86.5	12.8	0.4
Tramandaí	22.6 ± 0.1	36.7 ± 12.6	68.3 ± 20.2	0.3 ± 0.6	8.4 ± 3.0	7.4 ± 0.4	96.1 ± 4.6	3.9 ± 4.6	0.3 ± 0.1

Discussion

The composition of meiofauna found in Tramandaí-Armazém estuary was similar to the one recorded by Kapusta et al. (2002, 2004) in this same environment in the

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winter and summer, by Ozorio et al. (1999) and by Pinto & Bemvenuti (2003) in Lagoa dos Patos estuary (RS), and by Fonseca (2003) in Laguna Estuarine System (SC).

Nematoda was the dominating group. However, there was a differentiation concerning the second most representative group according to environment collected. Nematoda and Copepoda have been largely cited in literature as the most abundant in several environments (Coull, 1988; Ansari & Parulekar, 1993; Ingole & Parulekar, 1998; Ozorio et al., 1999; Dalto & Albuquerque, 2000). Nevertheless, there are works that mention other co-dominat groups such as Ostracoda (Ozorio et al., 1999; Pinto & Bemvenuti, 2003) and Acarina (Nozais et al., 2004). This result is mainly due to the different habitats found in the environment (Castel, 1992).

The meiofauna highest densities in Tramandaí-Armazém estuary occurred in summer. Increase in meiofauna density in reponse to high temperature and food source availability has also been reported from other estuaries (Alongi, 1987; Ansari & Parulekar, 1993; Smol et al., 1994).

The MDS and ANOSIM showed a clear distinction of the environments sampled. Meiofauna densities were higher in Armazém lagoon (mean 916.2 ind/10cm²) than in Tramandaí lagoon (mean 259.5 ind/10cm²) and channel (mean 373.4 ind/10cm²). In general, in estuaries, a decrease in meiofauna density, mainly of Nematoda, occurs due the high instability of sediments (Soetaert et al., 1994). In the present study, the lowest meiofauna density was found in Tramandaí lagoon and channel. In these environments, the effect of freshwater inflow by River Tramandaí and the unpredictable entry of saline water lead to wide variations in salinity throughout the day, regardless of the time of year (Chomenko & Schäfer, 1984). Associated with the variations in salinity, occur an unstable sediment due the presence of bidirectional currents and the constant fine material in suspension (Tabajara & Dillenburg, 1997; Nelson Machado, Ecology Center, UFRGS).

The sediment physical instability developed by the currents or by wave action, apart from fine sediments resuspension, may cause the passive transport of organisms, once the currents are responsible for meiofauna entrance in the water column in places without vegetation (Palmer, 1986; see revision Palmer, 1988). In areas with high hydrodynamic, such as the channels, meiofauna density diminishes and suitable conditions for groups that can adapt themselves better to this situation in detriment of nematodes (Soetaert et al.,1994). Similar results were registered in this study, the lowest meiofauna densities in the channel, favoring other groups such as Helobia australis. This species can migrate under unfavorable conditions becoming able to occupy environments physically perturbated where it can benefit from the reduced number of competitors (Chomenko & Schäfer 1984; Bemvenuti et al. 1992).

A distinct situation is found in Armazém lagoon where a tendency for a saline wedge inflow exists, influenced by the northeast wind, typical of the region (Hasenack & Ferraro, 1989; Fausto & Fontoura, 1999), by Coriolis force, by the freshwater inflow from Tramandaí, and by Camarão river low influence (Würdig, 1987, 1988; Scharzbold & Schäfer, 1984). Probably the time of low salinity waters permanence in this lagoon is quite larger than in both Tramandaí lagoon and channel.

Although sediment in Armazém lagoon is formed by fine sand, the currents are mainly unidirectional (Nelson Machado, Ecology Center, UFRGS, personal communication), different from Tramandaí lagoon and channel. The presence of the macrophyte Ruppia maritima in this lagoon is another important aspect. Studies of beds of submersed macrophytes have shown that there is a decrease in current speed in these areas, causing fine particles to deposite (Madsen et al., 2001), thus reducing turbidity and increasing water transparency. Another important function of the seagrass beds, according to aforementioned authors, is the decrease of the meiofauna potencial for ressuspension (see review by Madsen et al., 2001). These beds offer micro-habitats, protection and food for the organisms, supporting higher densities (Garcia et al., 1996; Kapusta & Bemvenuti, 1998), and a larger species diversity (De Troch et al, 2003).

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Rosa-Filho & Bemvenuti (1998), based on the method of Abundance/Biomass comparision curves for macrozoobenthos (Warwick, 1986), classified the area vegetated by R. maritima in Armazém lagoon as non-perturbed, and the adjacent non-vegetated area as slightly perturbed. Due to its proximity, the non-vegetated area can also benefit from vegetation by hydrodynamic diminution or debris inflow. Saco do Ratão, located in the southeastern bank of Armazém lagoon, is another area that presents saltmarsh in its overturn containing large debris concentration.

Finally, a larger meiofauna density in Armazém lagoon in almost every sampling station is probably due to a low hydrodynamics, larger amount of fine sediments and organic matter, higher oxygen and pH values, and total transparency associated to a small depth. There was a positive correlation of organisms density with water transparency and pH and a negative correlation with depth. On the other hand, the unstable conditions of salinity and hydrodynamic in channel and Tramandaí lagoon are probably the causes of the smallest densities found in these environments.

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