SEASONAL DYNAMICS OF BENTHIC COMMUNITIES IN A SHALLOW SUBLITORAL SITE OF THE LAGUNA ESTUARINE SYSTEM (SOUTH, BRAZIL)

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ABSTRACT

The temporal variability of benthic communities in a shallow sub-litoral site in the Laguna Estuarine System, an enclosed lagoon in south Brazil, was analyzed. Monthly replicate samples of the microphytobenthos, meiofauna and macrofauna were undertaken from October 2003 to October 2004. Temporal asynchronism in the microphytobenthos, meiofauna – both temporary and permanent –and macrofauna was clearly evident from the analysis of univariate measurements of the increase and decline in the various benthic components. Sediment chlorophyll *a* and phaeopigments followed a similar seasonal trend, with low biomass in the winter, higher in the summer and intermediate in both spring and autumn. Seasonal oscillation, but with a mutually contrary pattern of variation, was also clearly apparent among benthic fauna components. Whereas the number of species and abundance of the macrofauna were significantly higher in the spring and summer, in the meiofauna, these were significantly higher during the winter and autumn. The correlations between benthic fauna and environmental variables (meiofauna and nematodes positively correlated with salinity and macrofauna positively so with temperature) were similar to those revealed between univariate descriptors of the two faunal components (the number of nematode genera negatively correlated with macrofauna density). These results implied that divergent seasonal variations in both the meiofauna and macrofauna might be linked to their different life strategies, and that possible biological interactions between meiofauna and macrofauna might also play a significant role in structuring these associations.

Keywords: Temporal variability, Microphytobenthos, Meiofauna, Macro-fauna, Laguna Estuarine System, Brazil.

INTRODUCTION

Benthic communities play a crucial role in the functioning of estuaries. Microphytobenthos and benthic consumers are essential components in coastal ecosystems (22) by influencing sediment biogeochemistry via the uptake and release of nutrients (29), as well as sediment erosion through their production of exopolymers (15). Microphytobenthos, more nutritious and labile than other vascular plants, are a major source of nutrition that fuels secondary production (7 and 35). The invertebrate benthic species – meiofauna and macrofauna - provide key linkages between primary producers and higher trophic levels in estuarine food chains (14 and 23).

World-wide, estuaries are among the most modified and threatened of aquatic environments. Almost all have been affected by human beings in some way or the other, the degree of degradation varying, to the point that, in some estuaries, the very shape, hydrology, and functioning of the system itself have been completely altered. Relatively few remain in anywhere near their natural state (5). Benthic invertebrates are extensively used as indicators of estuarine environmental status and trends, since numerous studies have demonstrated that benthos respond predictably to many kinds of natural and anthropic disturbances (e.g. 16 and 38). Contaminants often accumulate in sediments and, therefore, relative immobility is advantageous in environmental assessments, since, unlike most pelagic fauna, benthic assemblages reflect local environmental conditions. Nevertheless, a major limitation in the methology for determining the status of estuarial environments is the lack of knowledge regarding temporal variability of benthic fauna, thus making it difficult to distinguish between man-made and natural variability (25).

Meiobenthos and macrobenthos, apart from the difference in size, have a series of distinctive ecological and evolutionary characteristics which suggest different mechanisms for the maintenance of diversity (39). The dynamics of each component of the benthos may also differ, depending on environmental and trophic conditions (19 and 9). Surprisingly, data on simultaneous seasonal comparisons between macro-fauna and meiofauna in estuaries or coastal lagoons are scarce (6, 12 and 24). The aim is to describe and compare the temporal variability of benthic communities – microphytobenthos, meiofauna, macro-fauna – in a shallow sublitoral site of the Laguna Estuarine System, a coastal lagoon in south Brazil.

MATERIAL AND METHODS

Study area

The Laguna Estuarine System, located in the State of Santa Catarina, on the south coast of Brazil (S 28°12' E 48°38'; Figure 1), is an enclosed lagoon with an area of 184 km². The estuarine system is bounded by salt marshes, and is composed of three main lagoons orientated parallel to the shore line and mutually connected and to the adjacent ocean by narrow courses. To the north, the system itself is separated from the ocean by a sand barrier with large dunes, whereas to the south, most of the dunes have already been destroyed by human occupation. The western portion of the estuarine system is characterized by highlands, the Serra do Tabuleiro. Although the system experiences tides that co-oscillate together with those along the south Brazilian coast (mean of 0.47 m; 10), the narrow entrance channel serves as a dynamic filter which largely eliminates tidal currents and water-level fluctuations inside the lagoon itself. Here, the average depth is only around 2 m, and thus the wind can play a significant role in water circulation. NE winds are the most frequent, but during the winter, those from the S-SE are common. Average air temperatures in the winter are around 13º C and in the summer ca. 22º C. The average total annual rainfall is 1,260 mm, with no marked differences throughout the year (11). Studies on the Laguna Estuarine System are few. Data on the composition and distribution of the meiofauna and macro-fauna from sublitoral areas along the lagoon are to be found in Fonseca & Netto (2006)

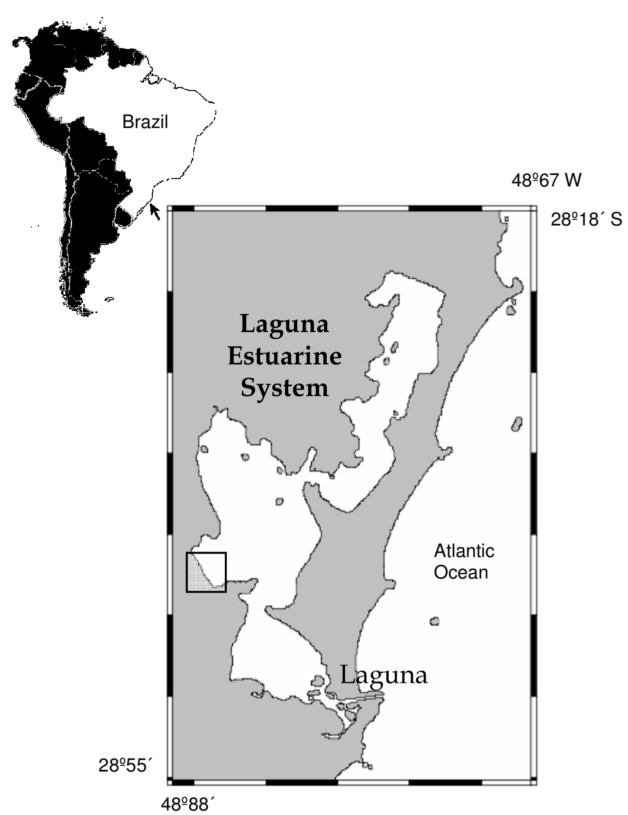


Figure 1 - Location of the sampling site in the Laguna Estuarine System, south Brazil.

Sampling and sample processing

Monthly sampling was carried out in a shallow sublitoral area (ca. 1 m deep) from October 2003 to October 2004 (Figure 1). Four samples were taken of each component of the benthic community – microphytobenthos (a 2 cm-diameter core pushed to a depth of 1 cm), meiofauna (2 cm diameter x 10 cm) and macrofauna (15 cm diameter x 10 cm). In addition, four sediment samples for defining organic matter and grain size were taken with a 10 cm diameter PVC core pushed to a depth of 5 cm. Values referring to depth, water salinity and temperature were recorded with a YSI 600 multiparameter system. Samples of Microphytobenthos were stored in dark plastic pots and frozen (-12ºC), and those of the fauna were fixed in 10% formalin before processing.

Sediment chlorophyll *a* and phaeopigments biomass were extracted with 90% v/v acetone and analysed according to Strikland and Parsons (1972). Chl *a* and phaeopigment concentration were estimated using the Lorenzen (1967) equation. Meiofauna samples were sieved through a 63 µm mesh and extracted by flotation with Ludox TM 50 (specific gravity of 1.15). Samples were then evaporated to anhydrous glycerol, whereupon permanent slides were made (33). Fixed macro-faunal samples were sieved through a 0.5 mm mesh and preserved in 70% alcohol. All the invertebrates were identified to the lowest possible taxonomic level, and then counted. Total sediment organic content was determined by combustion at 550ºC for 60 minutes. Granulometry was done by the sieve and pipette methods (17).

Data analysis

Data were analyzed by means of univariate and multivariate statistical techniques. The number of species and total density constituted faunal univariate descriptors. Data from monthly samplings were nested into seasons. 1-way ANOVA (32) was employed for testing differences in environmental variables (total organic content, percentage of sand and silt, mean grain-size, sorting, salinity and temperatures), besides the number of species and density of macrofauna, meiofauna, nematodes and microphytobenthos (chlorophyll *a* and phaeopigments biomass) between periods (spring, summer, autumn and winter). Cochran C tests were applied and, where necessary, data were log (x+1) transformed, in order to test the assumption of variance homogeneity. Post-hoc HSD-Tukey tests were employed when differences were significant ($p<0.05$; 32). Ranked lower triangular similarity matrices derived from macrofauna, meiofauna and nematode abundance were constructed using the Bray-Curtis similarity measure on log (x+1) transformed data. Ordinations were undertaken using non-metric multidimensional scaling (MDS). Formal significance tests for differences in the multivariate structure of benthic communities between periods were carried out using the 1-way ANOSIM permutation test (8). The relationships between environmental variables and biological data were analyzed through correlation based principal component analysis (PCA). Furthermore, Pearson product-moment correlations for all abiotic and biotic univariate data were executed.

RESULTS

Environmental variables

Mean values, and the results from ANOVA testing for differences in environmental variables, are shown on Table 1. Water temperature was significantly higher in summer, whereas salinity was so in autumn and winter (Table 1). Sediments were characterized as medium silt and moderately sorted, with total organic content values between 4% and 12%. Fine percentages (silt and clay) were significantly higher in spring (mean of 94.1%) than in the other seasons. Total sediment organic content, with a mean around 8%, did not vary significantly by season (Table 1). Ordination by correlation-based principal component analysis of average environmental data (Figure 2) revealed a distinction between the spring-summer and autumn-winter periods. Components 1 and 2 were responsible for 63.3% of total variability (PC 41.2 %; PC 22.1%). Spring and summer were associated with temperature and total organic content, whereas autumn and winter were related to salinity.

	Period				
	Spring	Summer	Autumn	Winter	Comparison
Temperature (ºC)	25 (4.5)	25.5 (1.5)	22 (4.5)	20.5 (2.5)	Su>W
Salinity	13 (3)	12 (2)	19 (4)	19 (4)	W,A>Su, S
Mean grain size (mm)	0.02 (0.002)	0.02 (0.002)	0.02 (0.002)	0.02 (0.002)	ns
Sorting	0.9 (0.15)	1.1 (0.16)	1.0 (0.22)	1.0 (0.06)	ns
Sand (%)	5.7 (2.5)	10.0 (3.3)	9.2 (1.9)	8.4 (2.2)	S<Su, A, W
Silt-clay content (%)	94.1 (3.5)	90.0 (3.3)	90.8 (1.9)	91.6 (3.2)	S<Su, A, W
Organic content (%)	7.8 (1.3)	6.8 (2.8)	8.0 (2.8)	8.5 (1.5)	ns

TABLE 1 - Mean, standard deviation (in parenthesis) and the results from 1-way ANOVA tests evaluating changes in environmental variables during sampling periods in a shallow site of the Laguna Estuarine System (S Brazil). Comparisons among these were defined by the Tukey post hoc test. Su – summer; S – spring; W – winter; A autumn; ns - no significant differences.

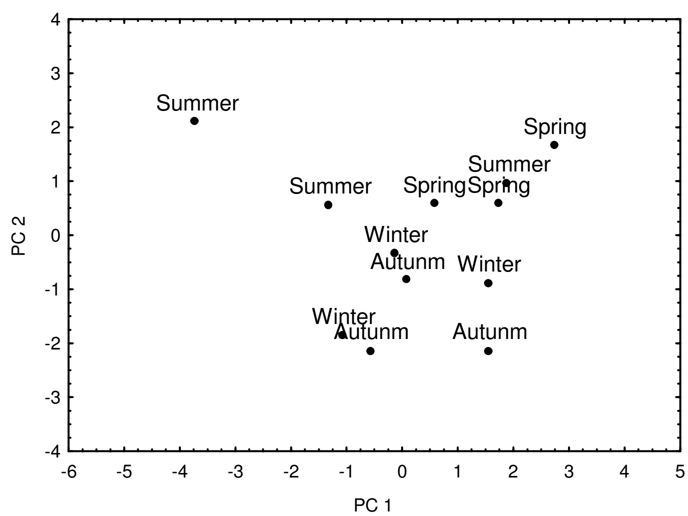


Figure 2 - Ordination of sampling seasons by correlation-based principal component analysis of environmental variables.

Microphytobentos

Total microphytobenthos biomass varied significantly throughout the year, ranging from 0.11 $mg.cm^{-3}$ at the end of winter to 57,350 $mg.cm^{-3}$ in the summer. Surface sediment Chl *a* biomass ranged between 0.007 and 24.489 $mg.cm^{-3}$, being significantly lower in the winter (Figure 3). Differences in chl *a* biomass in other periods were not significant ($p<0.05$), ranging from 0.1 to 33,443 $mg.cm^{-3}$. Phaeopigment biomass was significantly higher in the summer and autumn and lower in the winter and spring (Figure 3). Mean values of chlorophyll *a* biomass (9,523 $mg.cm^{-3}$) were lower than phaeopigments (16,366 $mg.cm^{-3}$), although differences were not significant ($p<0.05$).

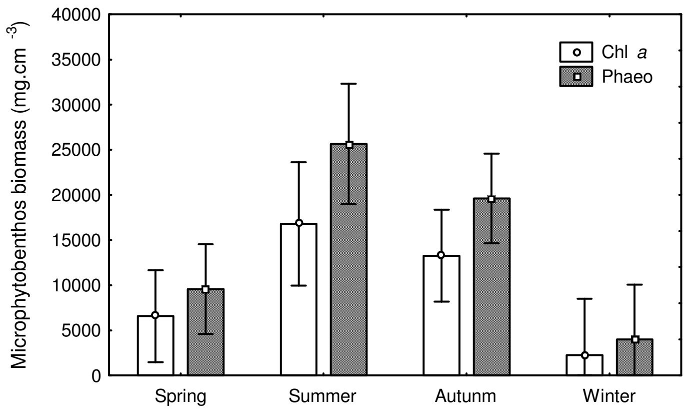


Figure 3 – Cooncentrations of sediment chlorophyll *a* and phaeopigment (mean ± SE).

Benthic fauna

Univariate descriptors

A total of 15 macro-faunal species were recorded in this study, with densities ranging from 176 to 49.235 inds. m^2. The polychaete *Heteromastus similis* (45% of the total macrofauna collected), unidentified species of oligochaetes (18% of the total fauna) and ostracods (15% of the total macro-fauna) were the most abundant species. Apart from *H. similis*, the polychaetes *Laeoneris acuta* and *Nephtys fluviatilis,* and the gastropod *Heleobia australis*, were the most frequent throughout the sampling period, occurring in more than 70% of the samples.

Regarding macrofauna, the number of species and total density were significantly higher in spring and summer, and lower in winter and autumn (Figure 4). *H. similis* was the only macrobenthic species with insignificant variation throughout sampling periods. Densities of all other macrobenthic taxa followed the same tendency of univariate descriptors; significantly higher in spring and summer, and lower in winter and autumn.

The meiofauna, composed of 8 higher taxa, was numerically dominated by nematodes (more than 80 % of the total meiofauna collected). Copepods and temporary meiofauna (polychaetes and oligochaetes) were also abundant, accounting for 9% and 2% of the total, respectively. Meiofauna density, strongly influenced by the nematodes, ranged between 165 and 4,550 inds.10 cm^{-2}.

Forty nematode genera were recorded in this study, the most abundant being *Leptolaimus*, *Terchellingia*, *Parodontophora*, *Theristus* and *Sabatieria*, which together represented 62% of total nematodes, besides occurring in more than 80% of the samples. *Theristus* and *Sabatieria* were recorded in all the meiofauna samples. From ANOVA tests, it was shown that seasonal oscillations of both the meiofauna and nematode descriptors were contrary to those of the macrofauna. Numbers representing meiofauna higher taxa, nematode genera and total density of both meiofauna and nematodes, were significantly higher in autumn and winter (Figure 4).

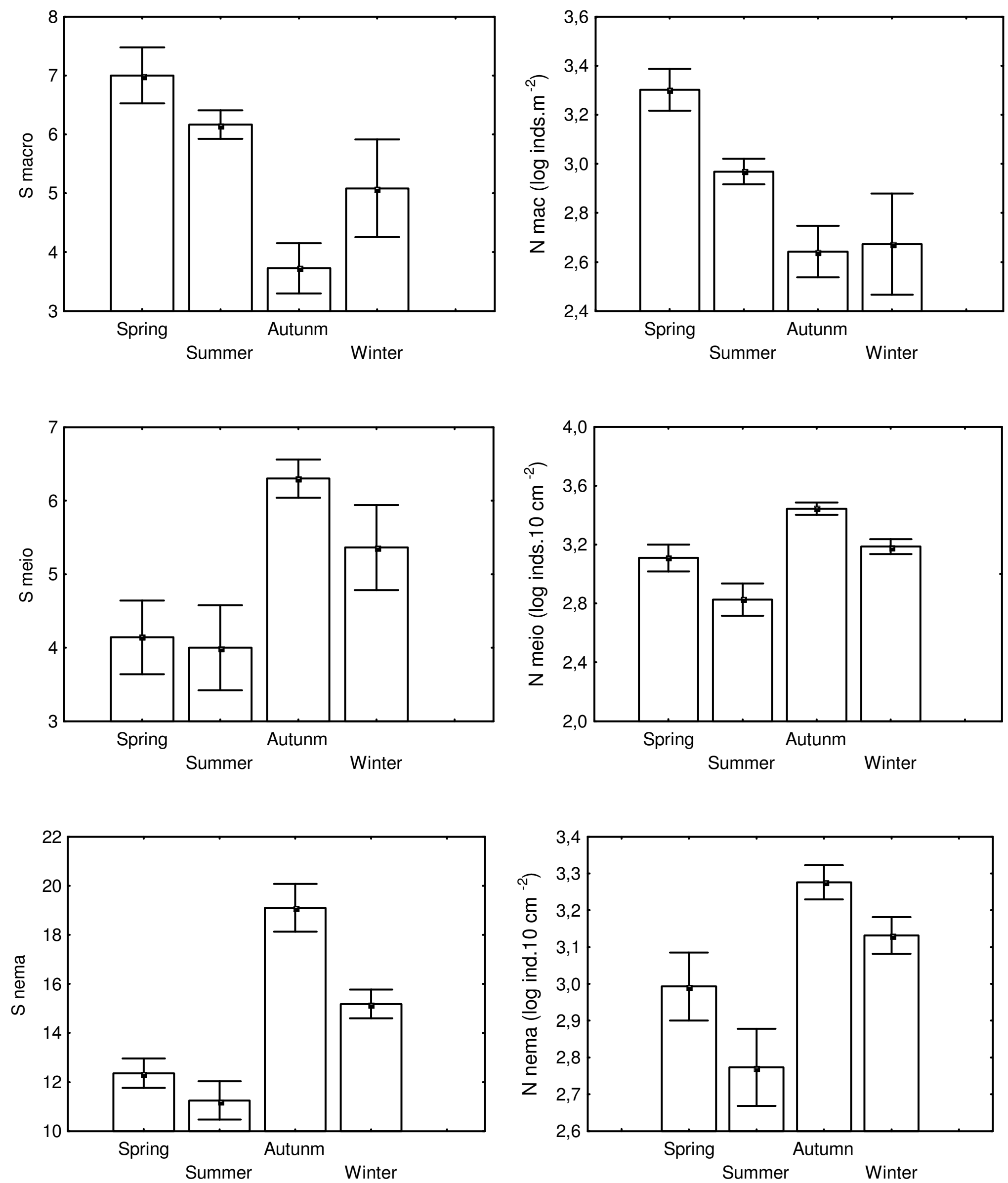


Figure 4 - Univariate measurements (mean ± SE) of macrofauna (S mac –number of species; N mac –density), meiofauna (S meio – number of higher taxa; N meio - density) and nematodes (S nema –number of genera; N nema – density). Data are mean ± SE.

The relative abundance of permanent and temporary meiofauna organisms throughout the sampling period is shown on Figure 5. It can be observed that temporary meiofauna followed the same seasonal trend of the macrofauna, thereby indicating recruitment episodes. Temporary meiofauna abundance was significantly higher in the summer and spring (Figure 5).

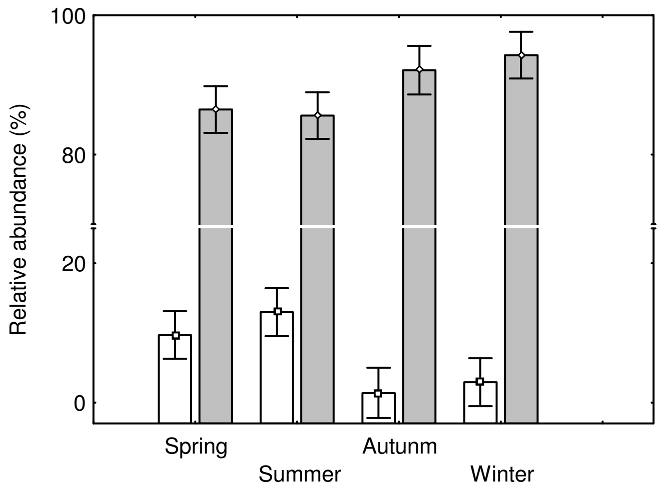
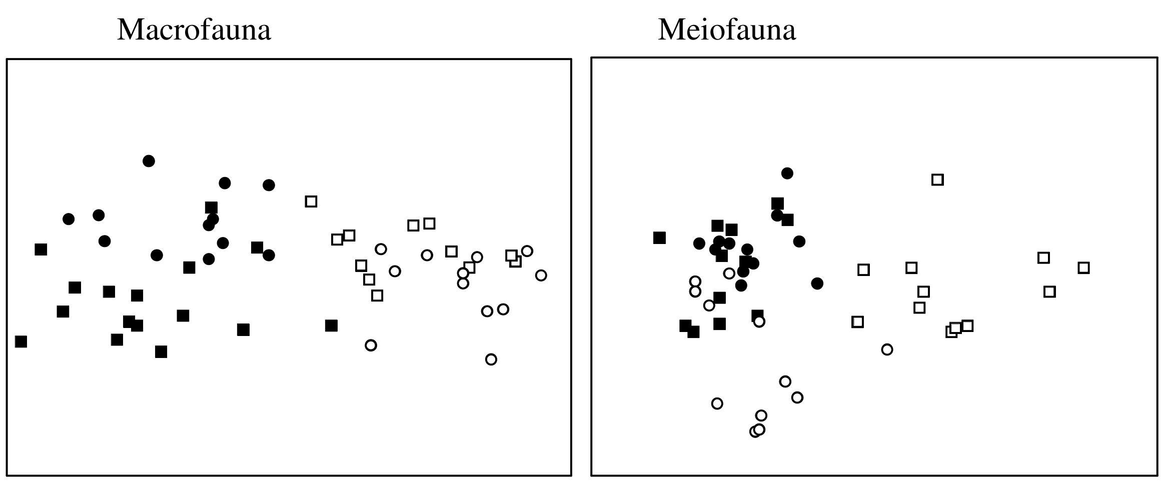


Figure 5 - Relative abundance of temporary (white bars) and permanent meiofauna (grey bars). Data are mean ± SE.

Multivariate community structure

MDS ordination derived from macrofauna, meiofauna and nematode transformed data are shown in Figure 6. Temporal oscillation in all benthic fauna components was clearly apparent, although seasonal variation was more pronounced, in the case of nematodes (Figure 6). ANOSIM tests confirmed the significance of differences ($p<0.05$), but pairwise comparison between seasons showed that, from meiofauna data, there was no significant variation in spring and summer ($p>0.05$). Based on macrofauna and nematode data, ANOSIM pairwise comparison showed that the multivariate community structure differed significantly in all the four seasons.



Nematoda

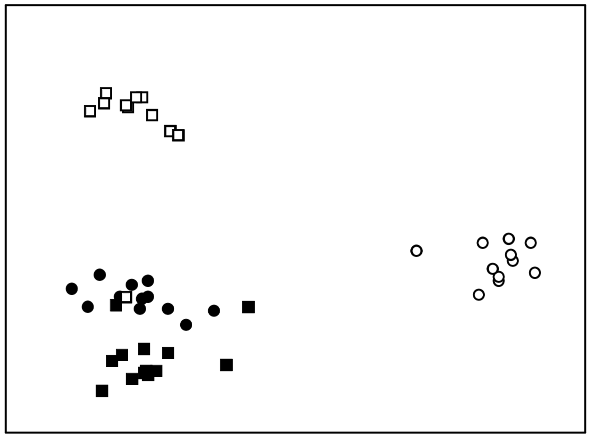


Figure 6 - MDS ordination for transformed macrofauna, meiofauna and nematode abundance. ■ - summer; ● - spring; □ - winter ; ○ -autumn.

Interactions between benthic components and environmental variables

The relationships between abiotic and biological data were investigated by means of standard product-moment correlation analysis. Meiofauna richness was negatively correlated with macrofauna abundance (-0.45), whereas meiofauna density was positive as regards salinity (0.5). As to nematodes, significant correlations were detected for the number of genera, positively so with salinity (0.5) and negatively with temperature (-0.4). Both macrofauna abundance and richness were negatively correlated with phaeopigment biomass (0.5 and 0.6 respectively).

On applying principal component analysis (PCA) to data on benthic fauna, microphytobenthos biomass, sediment, salinity and temperatures, a clear distinction between sampling seasons became apparent (Figure 7). Components 1 and 2 were responsible for 51.1% of total variability (PC1 - 28.5; PC 2 - 22.6). The projection of variables onto components 1 and 2 revealed that winter and autumn samples were related to meiofauna and nematode descriptors, as well as salinity and phaeopigment biomass. Spring and summer samples were mainly associated to macrofauna taxa, both number and abundance, as well as temperature and total organic content.

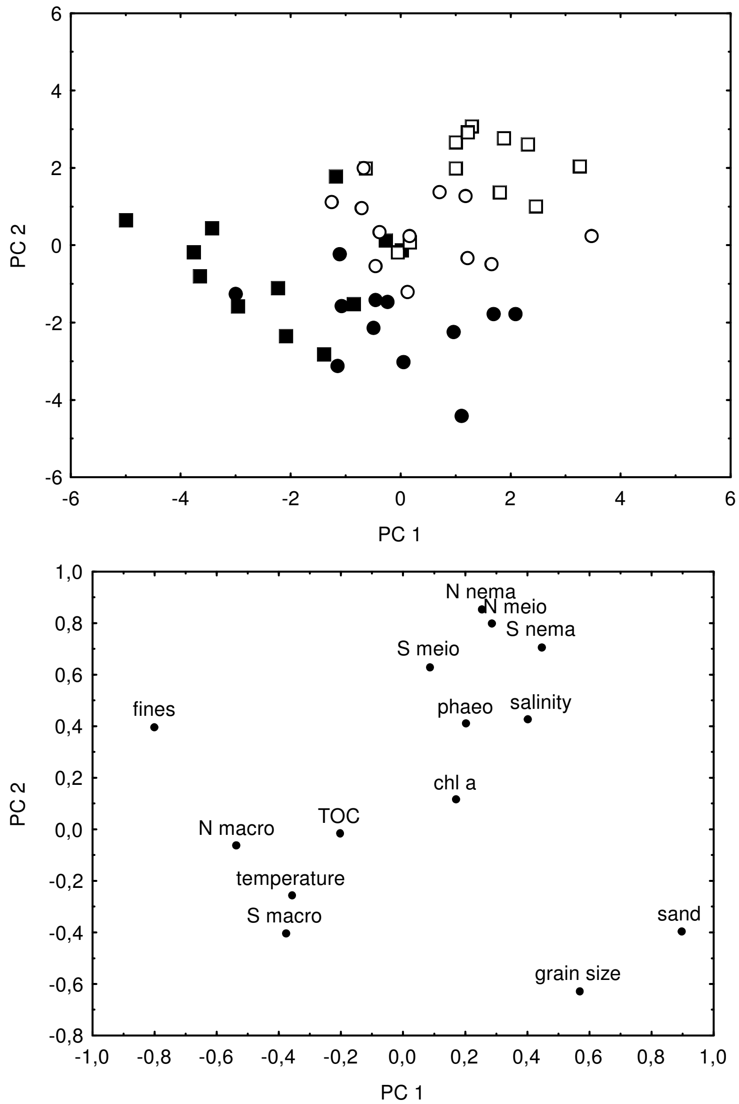


Figure 7 - Ordination of sampling seasons by correlation-based principal component analysis of environmental variables and univariate measures derived from macrofauna, meiofauna and nematode data (A) and projection of the variables onto components 1 and 2 (B). ■ - summer; ● - spring; □ - winter ; ○ -autumn; S mac –number of macrofauna species; N mac –macrofauna density; S meio – number of meiofauna higher taxa; N meio – meiofauna density; S nema – number of nematode genera; N nema – nematode density; TOC – total organic content; Chl a – sediment chlorophyll *a* biomass ; phaeo - sediment phaeopigments biomass.

DISCUSSION

At the study site, marked seasonal variability was prevalent among benthic communities. From the analysis of univariate measures associated to various components thereof, clear temporal asynchrony in microphytobenthal biomass, meiofauna - both temporary and permanent - and macrofauna was observed. Apart from water temperature and salinity, no sediment parameter changes were related to fauna seasonal variability.

The most important variables controlling oscillations in sublitoral benthic organisms, estuarinewise, are salinity and sediment characteristics, which, in turn, are largely defined by estuarine hydrodynamic conditions (3, 20 and 42). Water circulation in enclosed lagoons, such as the Laguna Estuarine System, is mainly wind-driven (18). Local micro-tidal regimes, together with the absence of marked differences in rainfall throughout the year, indicate the key role that the wind plays in local hydrodynamic conditions. During the summer and spring months, when winds blow mainly from the NE, lagoon water-masses are consequently being pushed towards the southern margins, thus resulting in decreased salinity thereat. In contrast, during the autumn and winter, strong S-SE winds favor marine water intrusion into the lagoon, with the consequential higher salinity. Although, short-term oscillations are also frequent, these results, on a within-site scale, are similar to those previously observed for the region by Fonseca and Netto (2006).

Throughout the study, sediment properties at the site were relatively stable. There was no significant variation in seasonal mean grain-size, with only an increase of fine percentages during springtime. Apart from oscillations due to river discharge, according to Fonseca and Netto (2006) sediment transport from sand dunes, and mainly during spring and summer, may increase the percentage of sand in the eastern-part bottom of the estuarine system. However, the study-site was located on the western margin of the lagoon, probably too far from the dunes to be susceptible to this kind of influence. As sublitoral areas of coastal lagoons are generally shallow, they are easily remodeled by wind-waves (13 and 26). Rosa and Bemvenuti (2006) showed that in the Patos Lagoon (south Brazil), the wind, through an increase in intensity, changes local hydrodynamics, thereby favoring the resuspension, transport and disposal of sediment. The study site is exposed to NE winds, which are the strongest during spring (11). Thus, it is possible that the increase in fine sediments during this season could result in wind-driven sediment resuspension and disposal on the bottom, as also suggested by Shideler (1984).

The seasonal trend in sediment chlorophyll *a* and phaeopigments was similar, with low biomass in the winter, higher in the summer and intermediate in spring and autumn. Pronounced seasonality is a typical feature of microphytobenthic communities in estuarine areas, and from several studies, it has been shown that seasonal variation is mainly guided by temperature and irradiance (1 and 36). On shallow sublitoral bottoms, biomass peaks for benthic microalgae usually coincide with alterations in the water column, expressed by increases in sediment, surface temperature and disposal of pelagic algae. At the study site, the incidence of phaeopigment biomass composed of photosynthetic pigment degradation products, was generally higher than chlorophyll *a*. Although the benthic fauna may contribute significantly to degrading chl *a* into phaeopigments, as shown from correlation and principal component analysis, this most probably reflects the predominant local sedimentation process the area is passing through, whereupon chlorophyll *a* decomposition rates are high (28).

Benthic fauna components revealed clear, though contrary, seasonal variation. While macrofauna species number and abundance were significantly higher in spring and summer, in the meiofauna, these were significantly so during the winter and autumn. Moreover, the correlationships between benthic fauna and environmental variables (meiofauna and nematodes positively correlated with salinity and macrofauna positively correlated with temperature) were similar to those between univariate descriptors of the two faunal components (number of nematode genera negatively correlated with macrofauna density). Thus, it can be surmised that probably divergent seasonal variations in the meiofauna and macrofauna might be linked to their different life strategies, and that possible biological interactions between meiofauna and macrofauna may also play a significant role in structuring these associations.

Although it is known that the mechanisms involved in maintaining diversity in meiofauna and macrofauna are different (39), very few studies have dealt with comparing simultaneous seasonal variation between estuarine meiofauna and macrofauna (6, 12 and 24). Both Fonseca and Netto (2006) and Montagna & Kalke (1992) demonstrated the different trends in variation of meiofauna and macrofauna. Besides being conservatively separated on the basis of size, meiofauna and macrofauna each have a series of distinctive biological traits, as a result of evolutionary adaptation to the spatial and temporal structure of the marine environment, rather than to ecological constraints imposed by the physical nature of particular habitats (41). Reproduction, growth and feeding strategies differ between meiofauna and macrofauna. In addition, the response of the meiobenthos to the constant and unpredictable disturbances perpetrated on shallow bottoms is not always the same as that of the macrobenthos (13 and 4).

Apart from differences in life-strategies, biological interactions between meiofauna and macrofauna could possibly contribute to the contrary seasonal variation observed in benthic faunal components. Warwick (1989) suggested that the imperative need for evolving planktonic larvae in larger animals (macrofauna) was a way of avoiding competition with and predation by elements of the permanent meiobenthos, a highly efficient consumer unit. In the Laguna Estuarine System, the increased reproductive activity of macrofaunal species during spring and summer, as shown by the higher densities in temporary meiofauna, coincided with the lower level in the meiofauna. Moreover, the highest peak in the meiofauna during the autumn and winter months corresponded with the collapse of macrobenthos recruits. Indeed, Danovaro et al (1995) showed that selective predation by the meiofauna on the dominant polychaete families in the temporary meiofauna may take a hand in structuring macrofaunal communities, by both altering density and acting selectively on a few families of macrofaunal juveniles.

The results of experimental studies regarding the overall impact on the macrofauna from processes such as predation, bioturbation and the competition for food, also indicate like effects on meiobenthos (27). For example, Alongi and Tenore (1985) showed that *Capitella capitata*-meiofauna interactions led to a reduced abundance of all nematode species due to the competition for food. Tita et al. (2000) demonstrated that high densities of a species of nereididae polychaete affected the meiofauna both by predation and disturbance of the intricate nematode sedimental tube system, thereby reducing feeding opportunities.

CONCLUSIONS

Marked seasonal variability was noted in meiofauna and macrofauna communities from a sublittoral muddy site in the Laguna Estuarine System, south Brazil. Richness and population densities of macrobenthic invertebrates were significantly higher during the spring and summer months, whereas, in the meiofauna, these densities were significantly so during the autumn and winter. A complex array of variables may influence the relative significance of the two different-sized benthic groups. Diversity in life-strategies, competition for food, predatory pressure and environmental disturbances, may be of have different importance. However, if the behavior of each component of the benthos and the interactions between them are to be understood, simultaneous observations on the different components of the benthic community should be make.

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RESUMO

A variabilidade temporal das comunidades bênticas foi analisada em uma área sublitoral rasa do Sistema Estuarino de Laguna, uma lagoa costeira do tipo estrangulada do sul do Brasil. Amostragens mensais replicadas para o microfitobentos, meiofauna e macrofauna foram realizadas de outubro de 2003 a outubro de 2004. A análise dos diferentes componentes do bentos permitiu mostrar uma clara assincronia temporal entre a biomassa microfitobêntica, meiofauna – tanto temporária quanto permanente – e macrofauna. A clorofila *a* e feopigmentos seguiram uma tendência sazonal similar, com menores valores de biomassa no inverno, maiores no verão e intermediários na primavera e outono. Os componentes da fauna bêntica do Sistema Estuarino de Laguna também mostraram uma clara oscilação sazonal, mas com padrões de variação opostos. Enquanto o número de espécies e a densidade da macrofauna foram significativamente maiores na primavera e verão, para a meiofauna, tanto o número de taxa quanto a densidade foram significativamente maiores durante o inverno e outono. Valores de correlação entre a fauna bêntica e variáveis ambientais (meiofauna e Nematoda positivamente correlacionados com salinidade; macrofauna positivamente correlacionada com temperatura) foram similares aos exibidos entre os descritores da fauna (número de gêneros de Nematoda negativamente correlacionado com a densidade da macrofauna). Estes resultados sugerem que as variações sazonais divergentes da meiofauna ae macrofauna podem estar ligadas a diferentes estratégias de vida, e que possíveis interações entre a meiofauna e macrofauna podem também ter um papel significativo na estruturação destas associações.

Palavras-chave: Variabilidade temporal, Microfitobentos, Meiofauna, Macrofauna, Sistema Estuarino de Laguna, Brasil.