

Influence of a tropical lagoon discharge and depth on the structure of adjacent shelf macroinfauna (Southern Caribbean)

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Abstract: At the outlet of rivers and coastal lagoons, the distribution of benthic organisms is affected by depth, variations in sediment composition and salinity. This relationship was assessed in the area influenced by the discharge from a tropical coastal lagoon (Ciénaga Grande de Santa Marta, Colombia) analyzing the taxonomic and trophic structure of the associations. The abundance, biomass and trophic guilds of the macroinfauna were related to physical and chemical variables (turbid-water conditions, salinity, dissolved oxygen, temperature, silt and organic contents in sediment) using univariate tests and multivariate analysis. Assemblages differing in density, richness, abundance-biomass relation and trophic groups were found; these differences were all related to the distance from the lagoon and to depth. Taxonomic and trophic structure of assemblages did not change seasonally. Biological variability was high, correlated with the distance from the lagoon outlet and the depth affecting the grain size and the organic content in the sediment. This suggested that taxonomic and trophic structure was more affected by spatial variation than by temporal variation, which was determined by the sediment heterogeneity related to the discharge from the lagoon and to depth.

Résumé : *Influence des écoulements issus d'une lagune tropicale sur la structure de la macrofaune endogée adjacente (Sud Caraïbe).* A l'embouchure des fleuves et des lagunes côtières, la distribution et l'abondance des organismes benthiques sont affectées par la profondeur, la variation de la composition du sédiment et la salinité. Ce type de relation a fait l'objet de recherches dans la zone d'influence du panache turbide d'une lagune côtière tropicale (Ciénaga Grande de Santa Marta, Colombie), en étudiant la structure taxinomique et trophique de la macrofaune endogée. Ceci, l'abondance, la biomasse et les mécanismes trophiques de la macrofaune endogée ont été mis en relation avec les variables physico-chimiques (turbidité, salinité, oxygène dissous, matière organique et concentration en particules fines), au moyen d'analyses multivariées. Des associations différentes en densité, richesse, relation abondance-biomasse et groupes trophiques, ont été comparées en fonction de la distance à la lagune et de la profondeur. La structure taxinomique et trophique des associations ne varie pas saisonnièrement. La variabilité biologique est fortement corrélée à la distance à l'embouchure de la lagune et à la profondeur, qui conditionne la granulométrie et le contenu en matière organique du sédiment. Ceci suggère que la variabilité de la structure taxinomique et trophique est davantage touchée par la variation spatiale (hétérogénéité du sédiment) que par la variation temporelle, en fonction des écoulements issus de la lagune et de la profondeur.

Keywords: Tropical macroinfauna, Abundance, Biomass, Shelf, Tropical lagoon, Caribbean Sea.

Introduction

There are many studies on the structure of sedimentary soft-bottom communities of coastal areas in temperate zones, and theory relating to assemblage structure is largely based on these studies; by contrast, quantitative data from tropical areas are quite scarce (Gray, 2002; Alongi, 1990). The lack of information and the fast deterioration of tropical coastal zones make difficult to understand and evaluate the natural- and anthropogenic- originated impact on the structure and function of this ecosystem.

The distribution of benthic fauna widely varies over time and space due to the heterogeneous distributions of benthic habitats (Mistri et al., 2000). In temperate zones at a small scale ($< 1^\circ$ latitude), it was found that the assemblage structure, rather than the richness, varies with small depth changes (Gray, 2002). The distribution and abundance of benthic organisms are also affected by spatial variations in salinity and sediment composition that are produced in the area of influence of discharge from rivers and coastal lagoons (Zajac & Whitlatch, 1982; Mannino & Montagna, 1997; Gray, 2002). At an annual time scale, in temperate regions, seasonal and hydrodynamic conditions are strongly influencing the patterns of organic matter sedimentation and benthic community. In the tropics, the magnitude of seasonal fluctuations is dependent upon distance from the equator; habitats bordering the equator exhibit less seasonal variability than tropical assemblages under higher latitudes, reflecting the fact that climate and its effects on shallow benthos vary greatly within the tropics (Alongi, 1990). For instance, in India, the richness of tropical assemblages and benthic density is heavily influenced by seasonal changes in rainfall and run-off (Longhurst & Pauly, 1987; Alongi, 1990). In some areas in the Caribbean as Jamaica, Venezuela, Colombia, species richness and density do not change significantly with the season (Jackson, 1972; Bone & Klein, 2000; Guzman-Alvis et al., 2001).

The community organization may be assessed by considering any convenient component unit, e.g. taxa, trophic groups, etc.; as community structure changes along any environment gradient, so does its organization (Pearson & Rosenberg, 1978). Trophic relationships are particularly influenced by the gradient of organic input, and changes in trophic structure may, therefore, be considered as fundamental to any analysis of community change in relation to such inputs to the benthos.

We hypothesize that the depth and discharge from the lagoon gradually changes the physico-chemical characteristics of the water column and sediment affecting the infaunal assemblages, then that these changes will be reflected in the taxonomic and trophic structure. The discharge from coastal lagoon being related to the regional climate, it would then be expected that the structure of the

infaunal assemblages would change with the seasonal variation in the discharge from the lagoon.

The purpose of this study is to determine structural changes in the infaunal assemblages in relation to the depth, to the distance from the outlet and to temporal changes in the discharge from the coastal lagoon. These structural changes were evaluated according to taxa composition and trophic groups. The discharge was evaluated indirectly through the environmental variables in the sediment (grain size, carbon, nitrogen, and organic phosphorus content) and water column (salinity, transparency, dissolved oxygen content) measured in both dry and wet seasons and distance from the outlet of the lagoon.

Materials and methods

Study site

The study was carried out in area adjacent to Ciénaga Grande de Santa Marta (Fig. 1). This is a 425 square kilometer lagoon, which is part of the delta of the Magdalena River, the largest river in the Caribbean basin (Alongi, 1990). It is a shallow body of water (mean depth 1.5 m), with a very high net primary productivity ($1.40\text{--}5.76 \text{ gC m}^{-2} \text{ day}^{-1}$) and resuspension of particles that are carried out to adjacent marine areas (Gocke et al., 2003). In the marine part, the superficial distribution of water masses is influenced by circulating winds, currents and the topography. During the dry season, the northeastern trade winds are strong and persistent while the Caribbean current moves towards West. In the Gulf of Salamanca, a cyclonic cell is formed due to the vicinity of Sierra Nevada de Santa Marta (SNMS) that blocks the wind, and the outflow from Ciénaga Grande is distributed in the eastern sector of the Gulf, without passing beyond Punta Gloria (Fig. 1a). During the wet season, the trade winds are replaced by weaker southeastern winds and the Panama-Colombia countercurrent flowing from the Northeast gets stronger. An anti-cyclonic cell is formed in the Gulf of Salamanca and the water discharged from the Ciénaga may flow out beyond Punta Gloria (Blanco 1988; Andrade 2000; Criales et al., 2002) (Fig. 1b).

Sampling and methods

Nine stations (Fig. 1) were sampled every three months during two years (Dec-1994 to Nov-1996). Macrobenthic organisms were collected using a van Veen grab (0.05 m^2), with three replicates per station, and the sediment was sieved through a 0.5 mm mesh screen. Samples were identified to genus level because of the scarce taxonomic description to species level existing for this area. According different authors, the identification of organisms to species

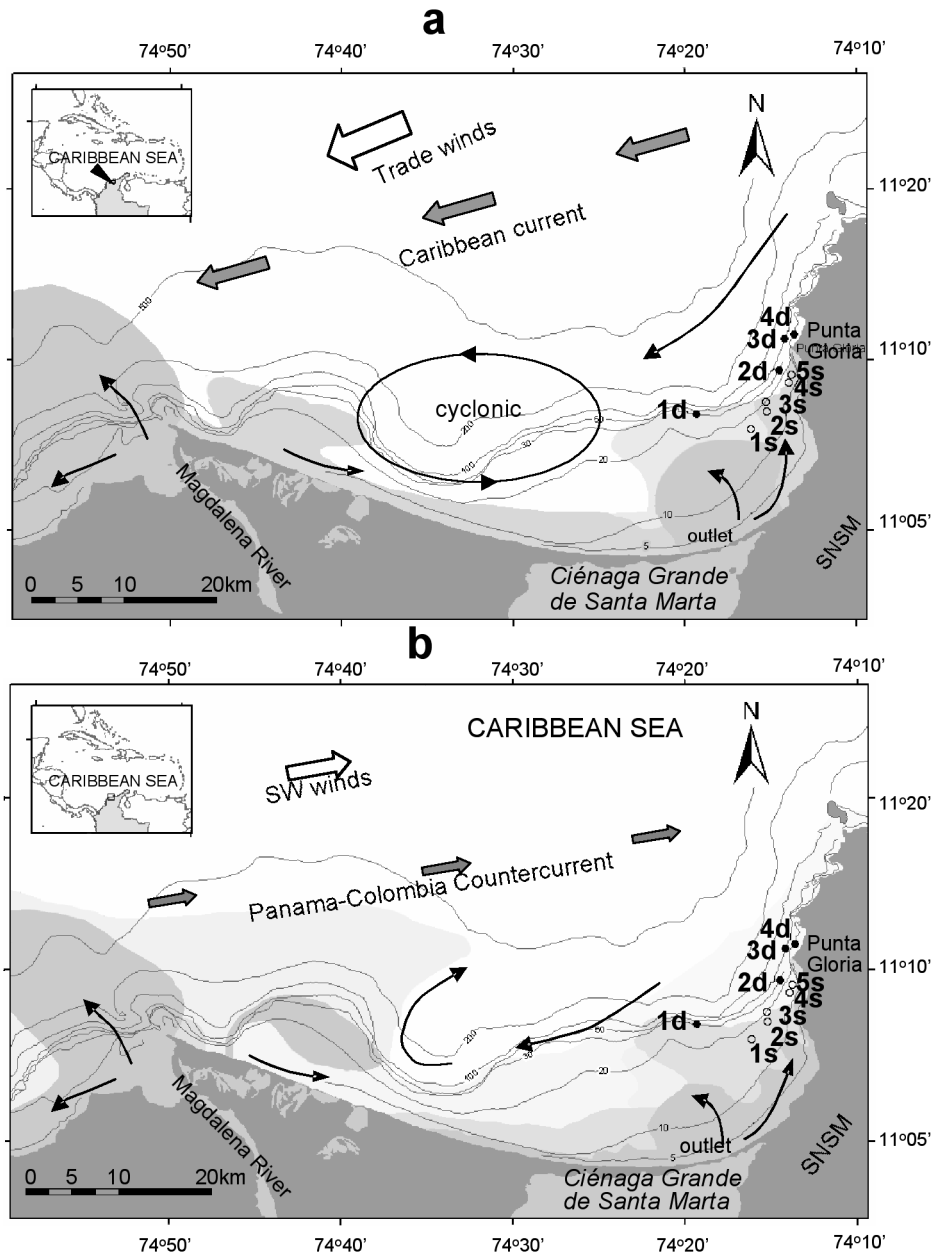


Figure 1. Direction of main winds, circulation of surface water masses in Golfo de Salamanca and turbidity plume of the Ciénaga Grande de Santa Marta during the two annual climate seasons: dry (a) and wet (b). Gray shades correspond to turbidity intensity of the lagoon's and the Magdalena River's plume. Location of sampling stations: shallow (s) and deep (d) stations. SNSM: Sierra Nevada de Santa Marta. Turbidity plume from the Landsat image TM79052 jan-2001 (a) and dec-1999 (b).

Figure 1. Direction des vents dominants, circulation des masses d'eau superficielles dans le golfe de Salamanque et panache turbide de la Ciénaga Grande de Santa Marta au cours des deux périodes climatiques annuelles: sèche (a) et humide (b). Les tons de gris correspondent à l'intensité de la turbidité du panache de la lagune et du fleuve Magdalena. Localisation des stations d'échantillonnage: stations peu profondes (s) et profondes (d). SNSM: Sierra Nevada de Santa Marta. Les panaches turbides sont extraits des images Landsat TM9052 janvier 2001 (a) et décembre 1999 (b).

level is not always necessary to describe spatial patterns; data at higher taxonomic levels assess much of community structure variations (Warwick, 1988; Somerfield & Clarke, 1995; Guzmán & García, 1996; Olsgard et al., 1998). Biomass was estimated as wet weight.

In the aim to determine the spatial and temporal distribution of assemblages, non-metric multidimensional scaling (NMDS) analyses were performed. Samplings were averaged by season (dry and wet) at each station. Abundance data were square root transformed and similarity matrices between stations were generated using the Bay-Curtis similarity index (Clarke & Warwick, 2001). Rare genera with < 2% total abundance were excluded from the analyses.

Biological variables, number of genera, number of individuals, Shannon's index (H') (natural logarithm), Simpson's dominance index (SI), and Pielou's evenness index (J') were used to determine the differences in these variables in relation to the distance from the lagoon outlet (Clarke & Warwick, 2001), for which Wilcoxon's non-parametric rank sum test was employed (Zar, 1999). According to ordination results, stations less than 15 km from the outlet were chosen as "near stations" and stations over 18 km from the outlet were chosen as "far stations". In Wilcoxon's test, sample sizes at shallow stations were $n = 24$ and 16 for near and far stations, respectively, and at deep stations they were $n = 8$ and 24 , respectively. For each variable, null hypothesis was: variable mean for near stations is equal to that for far stations (n.s.). Alternative hypothesis was: variable mean for near stations is higher than that for far stations ($>$) or variable mean for near stations is lower than for far stations ($<$).

Likewise, abundance and biomass comparison curves (ABC) were used to explore the macroinfaunal response to the discharge of the Ciénaga (Warwick et al., 1987; Clarke & Warwick, 2001). Additionally, Student t tests with W statistics using the above criteria of far and near stations were conducted. The W statistics was the result of the summation of subtracting the abundance (A_i) from the biomass (B_i) value for each genera rank (i) in an ABC curve; with an appropriately standardized sum to a common scale, so that comparisons can be made between samples with differing numbers of genera (Clarke, 1990).

Patterns of genera abundances and composition in relation to discharge from lagoon and depth were analysed using redundancy analysis (RDA, Ter Braack & Milauer, 1998). The discharge is evaluated indirectly through the environmental variables in sediment (carbon, nitrogen, and organic phosphor

and silt percentage), water column (transparency, salinity, and dissolved oxygen) and the distance of stations from the lagoon outlet. Abundance data were root square transformed, and the environmental data were standardized before statistical analyses to homogenize variances.

Each genus in the study was assigned to eight trophic guilds (suspension feeders, carnivores, herbivores, omnivores, surface deposit feeders selective and no selective and subsurface deposit feeders selective and no selective), based on information retrieved from literature sources. Abundances values were summed for each trophic group at each and station at each season. This resulted in a station-season by trophic group table that was assessed in the same way as the taxonomic data, using NMDS and RDA.

Results

NMDS analyses of genera abundance and trophic group showed a similar distribution pattern (Fig. 2). NMDS ordinations grouped dry and wet season samples at each station. Inter-sample relationships showed a distribution per depth on the horizontal axis, with shallow stations on the left and deep ones on the right (Fig. 2), and a distribution according to the distance from the outlet of the lagoon on the vertical axes. In the shallows, two subgroups were formed: the stations nearest to the Ciénaga (1s-3s) and those farthest away (4s-5s) (Fig. 2). In the deep stations, inter-samples distances were longer than in the shallows ones; the nearest station (1d) was at the bottom and the farthest away (4d) at the top (Fig. 2a). However, this pattern was not clear in the trophic structure. The plots had low stress values (0.09 and 0.03), reflecting that the NMDS preserved inter-sample relationships in a two-dimensional plot.

The abundance and number of genera for the shallow stations close to the lagoon were higher than for those far-

Table 1. Comparison of total genera (G), total individuals (I), dominance (SI), evenness (J), and diversity (H') in relation with the distance from the lagoon outlet at each depth. The statistics Wilcoxon's rank sum was used. Mean of the variable (G, I, SI, J or H') for near stations is not different (n.s.), significantly higher ($>$) or lower ($<$) than that far stations (*, $p < 0.05$).

Tableau 1. Comparaison entre la somme totale des genres (G), des individus (I), la dominance (SI), l'équitabilité (J) et la diversité (H') en relation avec la distance à l'embouchure de la lagune et pour chaque profondeur. Le test utilisé est celui de la somme des rangs de Wilcoxon. La moyenne de la variable (G, I, SI, J ou H') pour les stations proches n'est pas différente (n.s.), significativement plus grande ($>$) ou plus petite ($<$) que la moyenne de la variable des stations lointaines (*, $p < 0.05$).

Distance from the lagoon outlet	G	I	SI	J	H'
Near shallow stations (1s-3s) vs. far shallow stations (4s-5s).	0.03* ($>$)	0.01* ($>$)	0.16 (n.s.)	0.03* ($<$)	0.63 (n.s.)
Near deep stations (1p) vs. far deep stations (2p-4p).	0.68 (n.s.)	0.41 (n.s.)	0.02* ($<$)	0.03* ($<$)	0.33 (n.s.)

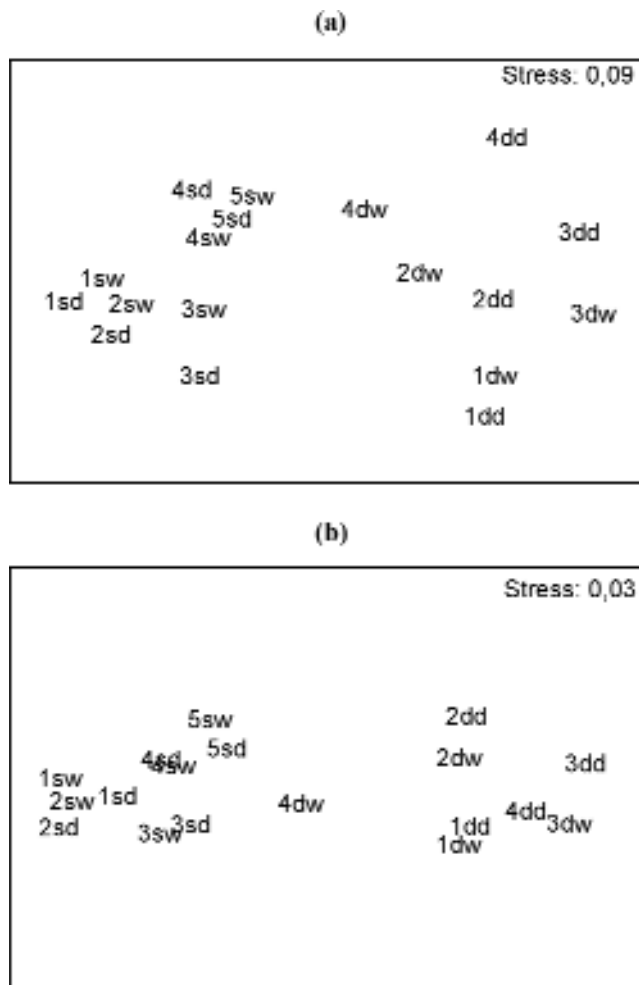


Figure 2. NMDS ordinations at the different stations sampled between Dec-1994 and Nov-1996. (a) NMDS ordination of genera abundances; (b) NMDS ordination of trophic group abundances. Labels names: numbers correspond in ascending order to the relative distance from lagoon outlet, first letter is shallow (s) or deep (d) station and the second letter is dry (d) or wet (w) season.

Figure 2. NMDS des différentes stations d'échantillonnage entre décembre 1994 et novembre 1996. (a) NMDS sur les abondances des genres ; (b) NMDS sur les abondances des groupes trophiques. Noms des marques : les chiffres correspondent à la distance relative à l'embouchure de la lagune, la première lettre désigne la profondeur (peu profonde : s ou profonde : d) et la seconde lettre désigne la saison (sèche : d ou humide : w).

thet away, showing significant differences (Table 1). In the deep stations, the abundance and number of genera were similar in stations both near to and far from the lagoon outlet (Table 1). These differences contribute to explain the groups formed in the NMDS based on genera composition.

Significant differences in relation with distance were found in evenness at the shallow stations and in dominance and evenness at the deep stations (Table 1). No significant

differences were found for the Shannon's diversity. Variations found may be due to the dominant genera in the community. As such, their distribution is analyzed below.

In the shallow stations, the abundance of *Apionsoma*, *Ampelisca*, *Aricidea*, *Chone*, *Tharyx*, *Notomastus*, *Scoloplos* and *Onuphis* individuals showed variations as a function of the distance from the lagoon (Table 2). While the abundance of the sipunculid *Apionsoma* and the polychaete *Scoloplos* was lower in the stations located nearer to the Ciénaga than in those farthest away, the other genera showed a reverse pattern. These eight genera showed significant differences in abundance in relation with the distance from the lagoon ($p < 0.05$) (Table 2). On the other hand, the abundance of *Prionospio* and *Lumbrineris* was similar at all stations ($p < 0.05$).

In the deep stations, abundances of the ten genera were lower than in the shallow ones. Their spatial distribution was similar with the exception of the polychaetes *Notomastus* and *Scoloplos* which showed significant differences in abundance in relation with distance from the lagoon (Table 2). These two polychaetes may be the main reason for the differences in dominance and evenness found in the deep stations (Table 1).

In the shallow stations, the ABC curves were closely coincident and may cross each other (Fig. 3); in stations 1s and 2s, the position of the ABC curves was inverted, indicating a disturbance. Since this method mainly depended on the genera that were the most dominant in abundance and biomass, when removing the three most dominant genera and representing the partial dominance, a pattern without alteration was obtained (Fig. 4). Consequently, the inversion was due to the differential distribution of the dominant genera that were associated with the distance from the lagoon. On the other hand, significant differences were found when comparing W statistics for near stations with those farthest away of the shallow stations (Table 3); the difference between abundance and biomass curve was lower in the stations near Ciénaga.

In deep stations, the distance between abundance and biomass curves was higher than in the shallow stations, which showed no disturbance (Fig. 3). Significant differences were found in W statistics between both depths, but not in relation with the distance from the lagoon (Table 3).

In the redundancy analyses (RDA) of genera abundance data, the sum of all canonical eigenvalues was 0.80 (total variance). The environmental variables explaining the greater proportion of the total variance were distance from the outlet (0.22), depth (0.19) and organic matter (0.10); the other variables accounted for 0.29. Eigenvalues for the first two axes explained a high proportion of the total variance (Table 4). The variation in the genera composition showed a high correlation with environmental variables. The ordination plot of RDA in the Figure 5 represented 48.1% of the

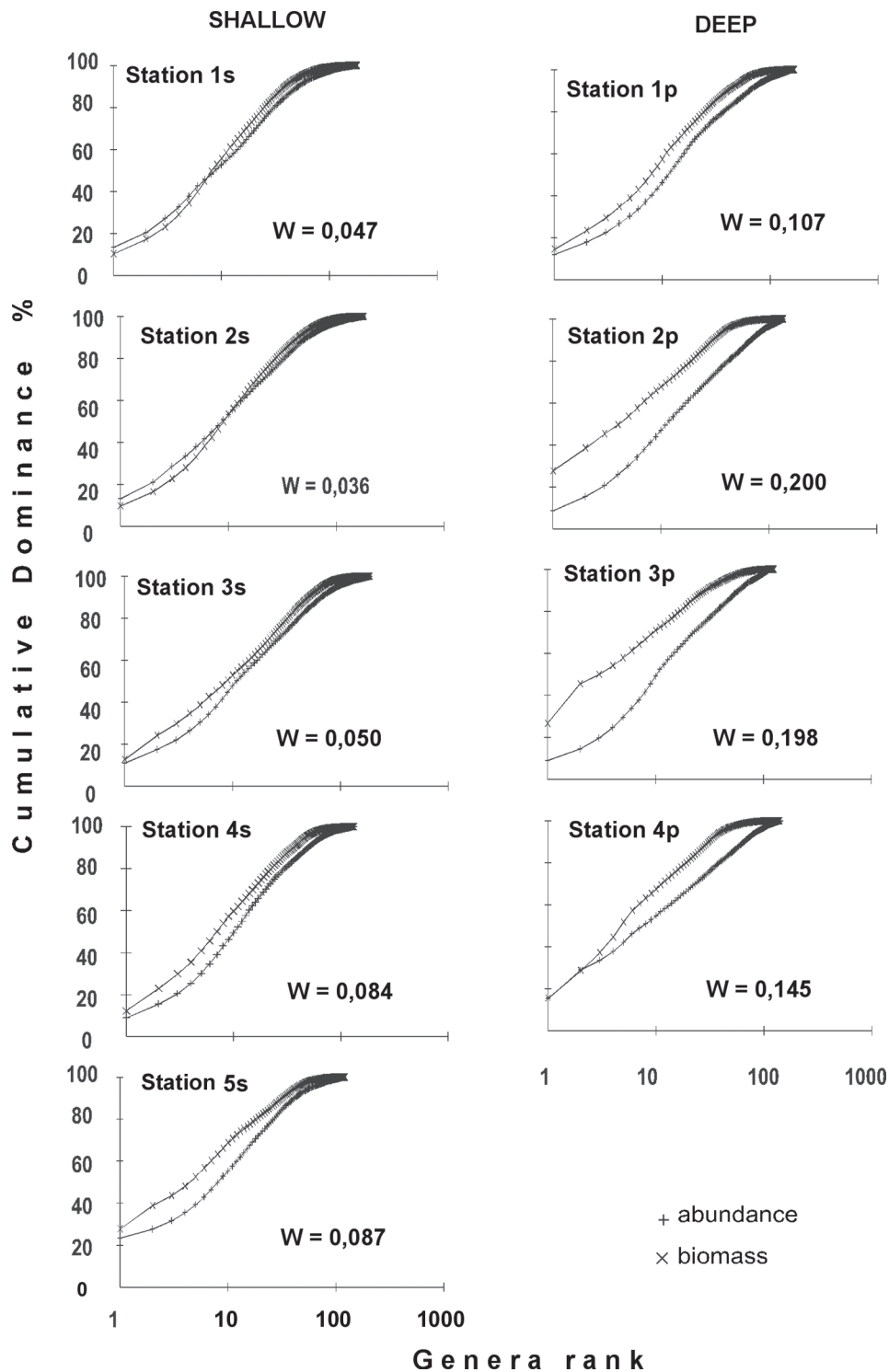


Figure 3. Comparison of distributions of genera average abundance and biomass in sampled stations (ABC). From top to bottom, stations are ordered according to their relative distance from lagoon outlet, and from left to right, according to depth.

Figure 3. Comparaison de la distribution d'abondance et de biomasse moyennes des genres (ABC). De haut en bas, stations classées en fonction de la distance de l'embouchure de la lagune et de gauche à droite en fonction de la profondeur.

Table 2. Comparison of mean abundance of the ten most dominant and frequent genera at two depths, using Wilcoxon's rank sum for statistics. Mean abundance for stations near the lagoon is not different (n.s.), significantly higher (>) or lower (<) than mean abundance for far stations (*, significant values $p < 0.05$). These 10 genera make up 48% of total infaunal abundance. si : sipunculid, po : polychaete; am : amphipod.

Tableau 2. Comparaison de l'abondance moyenne des dix genres dominants et fréquents pour deux profondeurs eu utilisant comme test la somme des rangs de Wilcoxon. L'abondance moyenne des stations proches de la lagune n'est pas différente (n.s.), est significativement supérieure (>) ou inférieure (<) à l'abondance moyenne des stations lointaines (* Valeurs significatives, $p < 0.05$). Les 10 genres constituent 48% de l'abondance totale de l'endofaune. Si: sipunculides, po: polychètes, am: amphipodes.

GENERA	SHALLOW Near shallow stations (1s-3s) vs. far shallow stations (4s-5s).	DEEP Near deep stations (1p) vs. far deep stations (2p-4p).
<i>Apionsoma</i> (si)	(<) *	(n.s.)
<i>Tharyx</i> (po)	(>) *	(n.s.)
<i>Chone</i> (po)	(>) *	(n.s.)
<i>Prionospio</i> (po)	(n.s.)	(n.s.)
<i>Aricidea</i> (po)	(>) *	(n.s.)
<i>Ampelisca</i> (am)	(>) *	(n.s.)
<i>Notomastus</i> (po)	(>) *	(>) *
<i>Lumbrineris</i> (po)	(n.s.)	(n.s.)
<i>Scoloplos</i> (po)	(<) *	(<) *
<i>Onuphis</i> (po)	(>) *	(n.s.)

Table 3. Comparison of W statistics for ABCs between the two depths and with the distance from lagoon outlet using t test (*; significant values $p < 0.05$).

Tableau 3. Comparaison du test W des courbes d'abondance et de biomasse pour les deux profondeurs et la distance à l'embouchure de la lagune au moyen du test t (* valeurs significatives $p < 0,05$).

Depth-distance	W
Shallow vs. deep	0.004*
Near-shallow (1s-3s) vs. far-shallow (4s-5s)	0.012*
Near-deep (1p) vs. far-deep (2p-4p)	0.245

variance in the genera abundance data and 60.5% of the variance in the genera-environment correlation (Table 4). The first axis was defined by distance from the lagoon outlet (dCG), silt percentage, organic nitrogen (ON), depth (D) and transparency (Se); the second by depth and transparency (see correlation coefficients in Table 4). Distance was highly correlated with silt content and organic nitrogen in

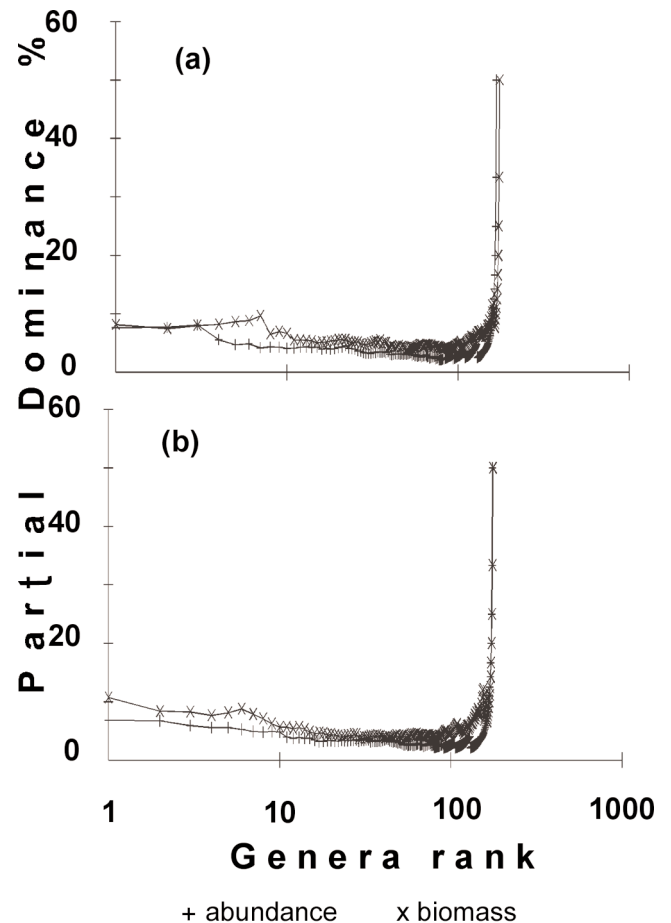


Figure 4. Partial dominance curves of shallow stations that showed inversion in ABC curves of figure 3. The three most dominant genera in station 1s (a) *Ampelisca*, *Aricidea* and *Prionospio*, and in station 2s (b) *Ampelisca*, *Apionsoma* and *Tharyx*, are not considered.

Figure 4. Courbes de dominance partielle des stations peu profondes montrant une inversion des courbes A et B de la figure 3. Les trois genres *Ampelisca*, *Aricidea* et *Prionospio* de la station 1s (a) et *Ampelisca*, *Apionsoma* et *Tharyx* de la station 2s (b) n'ont pas été pris en compte.

the sediment; and depth with transparency of the water column (arrows roughly pointing out the same direction) (Fig. 5). RDA also showed that dry and wet season samplings were grouped per station.

In the RDA plots, genera abundance and environmental variables represented by long arrows are the most important in the analysis. The greatest abundances of the polychaetes *Scoloplos* (*Scol*), *Leitoscoloplos* (*Leit*), *Maldane* (*Mal*) and *Poecilochaetus* (*Poe*), of the crustacean *Upogebia* (*Upo*) and of the sipunculid *Apionsoma* (*Apio*) were found in shallow sites, far from the lagoon outlet, with low water column transparency and lower silt and nitrogen content in the se-

In the RDA of trophic structure (Fig. 6), the sum of all canonical eigenvalues was 0.88 (total variance). Variables that contributed to explain the higher part of this total vari-

Suspension-feeders (sf), subsurface deposit-feeders

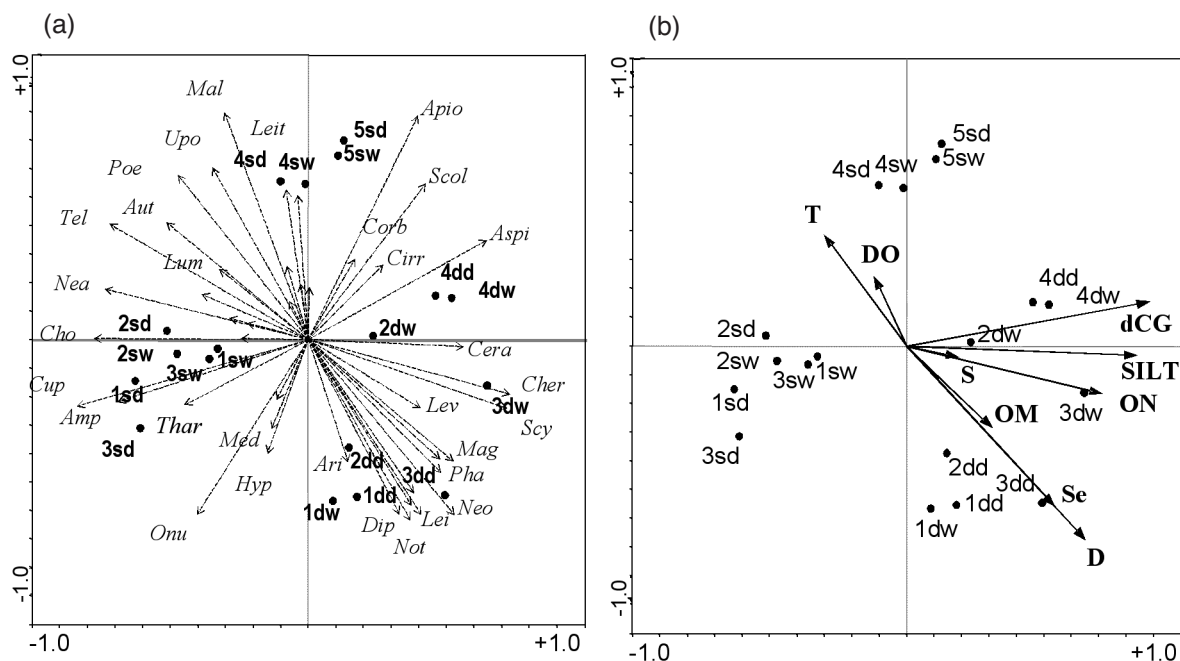


Figure 5. Ordination des stations d'après l'analyse de redondance (RDA) pour 45 genres de macrofaune endogée; les cercles pleins représentent les moyennes de 18 échantillons. (a) RDA représentant les genres (flèches) et les échantillons (cercles pleins). Seuls les genres les plus importants sont indiqués (les noms complets sont donnés dans le texte). La longueur des flèches est proportionnelle à la variance des genres expliquée sur les deux axes. (b) La même RDA montrant les variables environnementales (flèches) et les échantillons (cercles pleins). La longueur des flèches correspond à la force de l'association entre variables et ordination. Les noms des variables sont expliqués dans le tableau 4, ceux des échantillons sur la figure 2.

Table 4. Redundancy analysis (RDA) of genera abundance data (see figure 5). Eigenvalues, cumulative percentage of explained variance and correlations coefficients for the first four axes. The Sum of all canonical eigenvalues is 0.796 (total variance). Bold characters are the most important correlations coefficients for the first two axes.

Tableau 4. Analyse de redondance (RDA) de l'abondance des genres (voir figure 5). Valeurs propres, pourcentage cumulé de variance expliquée et coefficients de corrélation pour les quatre premiers axes. La somme des valeurs propres canoniques est 0,796 (variance totale). Les valeurs en gras sont les coefficients de corrélation les plus importants pour les deux premiers axes.

	1	2	3	4
Eigenvalues	0.264	0.217	0.079	0.067
genera-environment correlations	0.97	0.98	0.94	0.89
Cumulative percentage variance of genera	26.4	48.1	56.0	62.7
Cum % var. of genera-environment relation	33.2	60.5	70.4	78.8
	correlations coefficients			
Distance from the lagoon outlet (dCG)	0.860	0.150	0.274	-0.213
Depth (D)	0.632	-0.661	-0.051	0.112
Organic nitrogen (ON)	0.694	-0.159	0.255	-0.311
Organic matter (OM)	0.302	-0.279	0.705	-0.039
Silt percentage (Silt)	0.815	-0.031	0.088	-0.353
Transparency (Se)	0.524	-0.546	-0.077	0.061
Dissolved oxygen (DO)	-0.114	0.238	-0.356	-0.298
Temperature (T)	-0.291	0.379	-0.281	-0.498
Salinity (S)	0.184	-0.037	0.436	-0.046

(ssdfs and ssdfn), carnivores (ca), herbivores (h), suspension-feeders/surface deposit-feeders (sf-sdf) and surface deposit-feeders (sdf), were the most important in the analysis (Fig. 6). The abundance of suspension-feeders was opposite to subsurface deposit-feeders (ssdfs and ssdfn),

the former being highly negatively correlated with depth, transparency of the water column, silt content, organic nitrogen and distance from the outlet of the lagoon (Fig. 6). The abundance of carnivores was positively correlated with distribution of the selective subsurface deposit-feeders

Table 5. Redundancy analysis (RDA) of trophic group abundances (see figure 6). Eigenvalues, cumulative percentage of explained variance and correlations coefficients for the first four axes. The sum of all canonical eigenvalues is 0.88 (total variance). Bold characters are the most important correlations coefficients for the first two axes.

Tableau 5. Analyse de redondance (RDA) de l'abondance des groupes trophiques (voir figure 6). Valeurs propres, pourcentage cumulé de variance expliquée et coefficients de corrélation pour les quatre premiers axes. La somme des valeurs propres canoniques est 0,88 (variance totale). Les valeurs en gras sont les coefficients de corrélation les plus importants pour les deux premiers axes.

	1	2	3	4
Eigenvalues	0.464	0.173	0.126	0.084
Trophic group-environment correlations	0.97	0.98	0.90	0.84
Cumulative percentage variance of trophic group	46.4	63.7	76.3	84.8
Cum % var. of trophic group-environment relation	52.7	72.4	86.7	96.3
	correlations coefficients			
Distance from the Ciénaga Grande outlet (dCG)	0.431	-0.624	0.145	0.332
Depth (D)	0.863	0.181	-0.052	0.039
Organic Nitrogen (ON)	0.554	-0.235	0.277	0.349
Organic Matter (OM)	0.020	-0.031	0.154	0.471
Silt percentage (Silt)	0.618	-0.439	0.274	0.290
Transparency (Se)	0.776	0.102	0.069	-0.090
Dissolved Oxygen (DO)	0.097	-0.128	-0.029	0.007
Temperature (T)	-0.335	-0.302	0.240	-0.014
Salinity (S)	0.034	0.111	0.231	0.138
Organic Phosphor (OP)	-0.112	0.333	-0.259	0.169
Organic Carbon (C)	0.024	-0.032	0.084	0.545

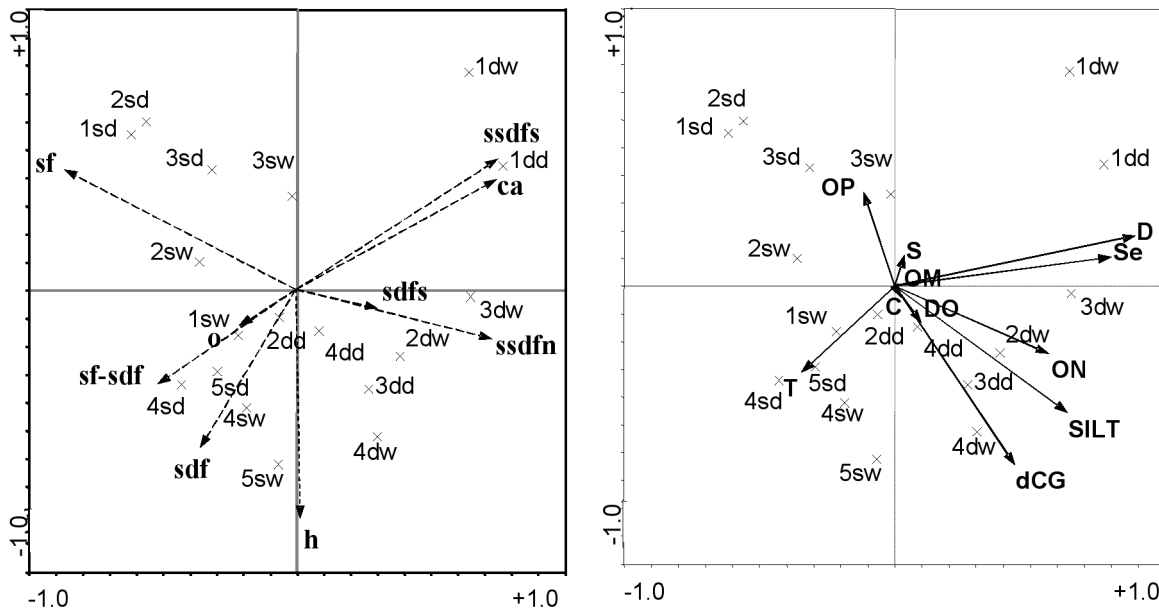


Figure 6. Redundancy analysis (RDA) ordination of trophic group abundances. x-marks; represent averages of 18 samples. (a) RDA plotting trophic groups (arrows) and sample averages (x-marks). Carnivores (ca), omnivores (o), herbivores (h), suspension-feeders (sf), surface deposit-feeders selective (sdfs) and no selective (sdfn), subsurface deposit-feeders selective (ssdfs) and no selective (ssdfn) and suspension-feeders/surface deposit-feeders (sf-sdf). Lengths of arrows proportional to the part of variance of the trophic group explained by the 2 axes. (b) Same RDA showing environmental variables (arrows) and sample averages (x-marks). Lengths of arrows proportional to the strength of association between variable and ordination. Variables names as explained in Table 5. Sample labels as explained in Figure 2.

Figure 6. L'analyse de redondance (RDA) des groupes trophiques. Les marques x représentent les moyennes de 18 échantillons. (a) RDA des groupes trophiques (flèches) et des moyennes d'échantillons (marques x). Carnivores (ca), omnivores (o), herbivores (h), suspensivores (sf), dépositivores de surface sélectifs (sdfs) et non sélectifs (sdfn), dépositivores de subsurface sélectifs (ssdfs) et non sélectifs (ssdfn), et suspensivores/dépositivores de surface mixtes (sf-sdf). La longueur des flèches est proportionnelle à la variance des genres expliquée sur les deux axes. (b) La même RDA montrant les variables environnementales (flèches) et les moyennes des échantillons (marques x). La longueur des flèches correspond à la force de l'association entre variables et ordination. Les noms des variables sont expliqués dans la tableau 5, ceux des échantillons sur la figure 2.

(ssdfs). The herbivores made a small angle with the arrow "distance from the outlet" (dCG), this trophic group was inferred to be positively correlated with distance. The suspension feeders/surface deposit feeders (sf-sdf) and surface deposit feeders (sdf) are negatively correlated with carnivores and selective subsurface deposit feeders (ssdfs).

The taxonomic and trophic structure showed a high relationship with variables measured in the water column and sediment. Among these, distance from the lagoon and depth explain the greater part of variability in genera and trophic abundances. The silt, organic matter and organic nitrogen contents in sediments increased with the distance from the lagoon, and showed a positive relationship with depth, transparency and a negative one with temperature. Phosphorous nutrient does not appear to be important in the distribution of these assemblages.

Discussion

ABC curves have been used in temperate regions to evaluate the effect of pollution on macrobenthic communities (Warwick et al., 1987; Gray et al., 1988; McManus & Pauly, 1990; Warwick & Clarke, 1991; Warwick & Clarke, 1994). However, Beukema (1988) pointed out that these curves could not be used to evaluate the pollution state of a benthic community without long-term sampling, or in areas where the number of species heavily fluctuated. Nevertheless, in this study those curves are considered as a useful tool when analyzing natural alterations in tropical benthic communities. These findings are in agreement with McManus & Pauly (1990) who considered that ABC curves better showed differences than Shannon's index did. The position of the abundance curve over the biomass

curve indicated a disturbance; this alteration being due to *Ampelisca*, *Aricidea*, *Prionospio*, *Tharyx* and *Apionsoma* abundance. They were numerically important but no dominant in terms of biomass. The abundance of these genera was related to the distance from the lagoon; after having removed them and plotting the abundance and biomass again, no pattern alteration was obtained. We assume that disturbance was natural, since there was no source of pollution nearby but an obvious turbidity. In the same sense, plots of the shallow stations were similar to the ABC curves found in the Indonesia communities at similar depth (Warwick & Ruswahyuni, 1987). These authors argued that the physical disturbance resulting from resuspension of the fine sediment due to tidal and wave action was the most likely factor maintaining the communities in an intermediate successional stage with the abundance and biomass curves crossing. On the other hand, small biomasses were favoured in the tropics because high temperatures (in the shallow stations, temperature at the water column bottom may reach 30°C) favoured the respiration on the production, thus impeding biomass formation (Rowe, 1997).

Groups formed in the NMDS ordination based on genera composition were due to significant differences in the abundance of dominant genera, total abundance of individuals, richness, evenness and in the distribution of the abundance-biomass between shallow, near and far away from the outlet stations. In deep stations, the abundance of several genera, especially capitellids, was positively correlated with the distance from the lagoon. These results agreed with those of Gray (2002) for temperate zones and small spatial scales, where richness changed with sediment grain size and small changes in depth. In the present study, the structure, richness and other biological variables of the assemblages significantly changed at a small spatial scale (< 1° latitude). That could be due to the spatial heterogeneity of the sediments (reflected here as silt content, organic nitrogen and organic matter) that increased with the distance from the outlet of the lagoon.

Salinity and sediment composition affected distribution and abundance of benthic organisms in areas where estuarine discharge occurred (Zajac & Witlatch, 1982; Mannino & Montagna, 1997; Gray, 2002). In the redundancy analysis, the salinity explained a small percentage of the biological variability; at the outlet of the Ciénaga, salinity values between 0 and 38 occurred, but for the most part of the year it showed values above 30. As such, salinity did not significantly change in the area.

Assemblage did not change seasonally. Seasonal fluctuations in the discharge from the lagoon seemed to have a lower effect on the assemblage structure than spatial variations. This suggested that most of the observed biological variability is spatial rather than temporal, and that it is determined by spatial heterogeneity. Several studies in

tropical soft-bottom and rocky shore communities showed that neither number of taxa nor their abundances significantly changed during the year (Jackson, 1972; McCarthy et al., 2000). Jackson (1972) concluded that taxa assemblages in high stress and low diversity environments may be more stable than those in lower stress, high diversity environments. Alongi (1990) suggested that in dry tropics where rainfall is sporadic and there are high temperatures and desiccation (as the study area), densities of most groups could significantly fluctuate over time without following seasons; infaunal assemblages are characterized to display small, opportunistic and surface deposit-feeder organisms.

It has been recognized that food supply may be important in determining benthic assemblage structure (Pearson & Rosenberg, 1978; Desrosiers et al., 2000). Benthic-pelagic coupling has been postulated to play a key role in structuring benthic communities. The suspension-feeders capture phytoplankton/organic particles from the water column (Josefson & Rasmussen, 2000). They dominated benthic assemblages at the shallow and nearest from the lagoon outlet stations, where turbid water conditions were high, content of organic nitrogen in the sediment low and the sand very fine. Suspension-feeders were abundant where the deposit-feeders (surface and subsurface) decreased; this could be partly explained by the activities of deposit-feeders which created and maintained an instability level in superficial sediments that excluded to some extent the settlement and development of suspension-feeders (Pearson & Rosenberg, 1978).

The dominance of surface deposit-feeders as consumers of newly deposited food is related to the production in the water column (Gaston, 1987; Gaston et al., 1988; Josefson & Rasmussen, 2000). In the study area, these organisms dominated the benthic assemblages at the shallow and far away from the lagoon stations, where the sand was very fine and organic nitrogen content was high.

Decrease in supplementary food might favour the subsurface deposit-feeders (selective and non-selective), adapted to exploit organic matter buried in the sediments by physical sediment transport and/or bioturbation processes (Desrosiers et al., 2000). The deeper assemblages received less particulate organic matter (high transparency in water column) compared to the shallow assemblages, but had high content of nutrients (nitrogen) in the sediments, which favoured the subsurface deposit-feeders. Furthermore, the high silt contents made it easier for them to bury themselves rapidly. The higher abundances of non-selective subsurface deposit-feeders related to the high contents of organic nitrogen may be explained by the fact that selective subsurface deposit-feeders are generally excluded when there is enough food available in the sediment (Pearson & Rosenberg, 1978). Deposit-feeders (surface and subsurface) made up 65.8 % of the total community reflecting the importance of detritus and benthic-pelagic coupling in

these ecosystems.

Summarizing at the spatial scale here assessed, variations in the taxonomic and trophic structure found were explained by the distance from the lagoon outlet, depth, silt content, organic matter and nitrogen in sediments. Together with the distance from the outlet, silt and nitrogen contents varied positively and significantly, and water transparency was correlated to depth. Much of the observed biological variability was rather spatial than temporal and it was mainly determined by sediment heterogeneity. Depth was more important in explaining the variations in the trophic structure and the distance from the outlet than those in the taxonomic structure. As such, assemblages settled in shallow and nearer from the outlet sites showed higher abundances and number of genera, but lower evenness and abundance-biomass ratio than assemblages farther away from the outlet. The highest silt, organic matter and organic nitrogen contents in the sediment were related to surface and subsurface deposit-feeders abundance, while suspension-feeders were distributed in sediments with very fine sand and lower content of organic matter and nitrogen.

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