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Morphodynamic influence on the structure of inter and subtidal macrofaunal communities of subtropical sandy beaches

Influencia de la morfodinámica sobre la estructura de las comunidades intermareales y submareales de la macrofauna de playas arenosas subtropicales

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ABSTRACT

Benthic macrofauna communities of ten beaches were studied during a survey in February 1993, in Paraná State, southern Brazil. Sampling stations were distributed along a transect from the limit of vegetation on the upper sub-aerial beach, to nearly 2 m deep on the sub-aqueous beach. Biological and sedimentological samples, slope of the beach and wave height and period were recorded for each beach. Subtidal samples were collected by scuba diving. Dimensionless fall velocity (Ω) and surf scaling (Σ) parameter modal values ranged from reflective to dissipative extremes. Sedimentological parameters varied little among beaches, with average grain size from 2.57 to 2.88 ϕ. Only one intermediate beach had an average grain size of medium sand (1.84 ϕ). Intertidal species richness and total abundance had significant correlations with Ω values, increasing from reflective to dissipative beaches. The trend for the subtidal was the reverse, with species richness negatively correlated with Σ. Species richness of each station increased along the transect towards offshore stations. This increase was more accentuated at the reflective extreme. Intertidal species composition and dominance were similar on all beaches, varying little throughout the morphodynamic spectrum. The subtidal communities had more variable species composition and dominance than the intertidal communities. Zonation patterns obtained from classification and ordination analyses were similar for all beaches, with at least four faunistic zones recognized. Biological zonation in the subaerial portion of dissipative beaches was fitted to Salvat's physical zones, with saturation and subtidal zones sharing species. The homogeneity of sand composition buffered the possible morphodynamic influence on the intertidal dominance and density patterns, suggesting that these parameters are controlled by sedimentological characteristics. Subtidal communities seem to be controlled by water and sediment movement, which is higher in dissipative beaches.

Key words: sandy beaches, subtropical macrofauna, morphodynamic influence.

RESUMEN

Las comunidades bentónicas macrofaunales de diez playas fueron estudiadas a partir de un muestreo realizado en febrero de 1993, en el estado de Paraná, sur del Brasil. Las estaciones de muestreo estuvieron distribuidas a lo largo de un transecto desde el límite de la vegetación, en la parte superior de la playa subaérea, hasta aproximadamente 2 m de profundidad, en la porción subacuosa de la playa. Para cada playa se obtuvieron muestras biológicas y sedimentológicas, perfil topográfico, altura y período de las olas. Las muestras infralitorales se colectaron por medio de buceo autónomo. Valores modales de los parámetros de Ω ("dimensionless fall velocity") y Σ ("surf scaling") variaron del extremo reflectivo al disipativo. Los parámetros sedimentológicos mostraron una pequeña variación entre playas, con valores medios del tamaño de partículas entre 2,57 y 2,88 ϕ. Solamente una playa intermedia presentó un valor medio correspondiente a arena media (1,84 ϕ). La riqueza de especies y la abundancia total del intermareal estuvo correlacionada significativamente con los valores de Ω, aumentando de playas reflectivas a disipativas. La tendencia en el infralitoral fue inversa, estando la riqueza negativamente correlacionada con el parámetro de Σ. La riqueza de especies de cada estación aumentó a lo largo del transecto en dirección a las estaciones infralitorales. Este aumento fue más acentuado en el extremo reflectivo. La composición y la dominancia de especies del intermareal fue similar en todas las playas, variando poco a través del espectro morfodinámico. El patrón de zonación, obtenido de los análisis de clasificación y de ordenación, resultó similar en todas las playas, con el reconocimiento de por lo menos cuatro zonas faunísticas. En la porción subaérea de playas disipativas, la zonación biológica sigue el esquema de zonas físicas de Salvat, con la zona de saturación compartiendo especies con la zona infralitoral. La homogeneidad de los sedimentos ocultó alguna influencia morfodinámica en los patrones de dominancia y densidad, sugiriendo que las características sedimentológicas estarían controlando estos parámetros. Las comunidades infralitorales estarían controladas por el movimiento de agua y sedimento, que sería mayor en las playas disipativas.

Palabras clave: playas arenosas, macrofauna subtropical, influencia morfodinámica.

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INTRODUCTION

Most of the studies dealing with beach communities have been restricted to the subaerial portion of the beach. Generalizations about trends and patterns of beach community structure have been inferred from surveying that narrow portion, in spite of the fact that a beach is that area which can be actively reworked by wave action and extended, across the nearshore, from depths at the wave base to the upper limit of swash action (Swart 1983, Short & Wright 1983). In fact, sampling the benthos in the subaquous portion of a beach is not a simple task, requiring intensive and special sampling effort. The first attempts were undertaken by Day et al. (1971) and Field (1971), who used van Veen grab in an extensive sampling throughout the entire continental shelf. More accurate subtidal sampling was done with by scuba diving and the development of suction samplers (for a brief review of the different suction samplers used in benthic studies, see also Borzone et al. 1990). Masse (1972), Oliver et al. (1980), Christie (1976), McLachlan et al. (1984), Morin et al. (1985), Fleischack & Freitas (1989) and Soares (1992) sampled the subtidal of different sandy beaches using this new approach. However, few studies included the intertidal and the subtidal of a beach. Hill & Hunter (1976), Leber (1982) and Knott et al. (1983) did an extensive sampling extending from intertidal to subtidal. Some general trends were evident from these studies: species composition of the intertidal was different from the subtidal, and species richness increased offshore with diminishing water movement.

Over the last ten years, the new morphodynamic concept of beach classification developed by Short & Wright (1983) was extensively used by beach ecologists for the description of the sandy beach environment. Studies searching for patterns of macrobenthic communities structure along the reflective-dissipative beach spectrum are numerous, but restricted to the intertidal environment. The present contribution is the first attempt to analyze the influence of morphodynamics on the structure of inter and subtidal macrobenthic communities of different beaches spread over the entire morphodynamic spectrum.

MATERIAL AND METHODS

The Paraná Coast stretches for 100 km in a NE-SW direction and include several Atlantic open beaches. Mel Island separates the Paranaguá Bay estuarine system access to the open sea. It has many beaches exposed to the sea, delimited by rocky shore headlands. Leste Coastal Plain is 30 km long and comprises only one beach. This beach presents a heterogeneous morphology and sediment characteristics throughout its extent. The tides are characterized by diurnal inequality and attain maximum and minimum amplitudes of approximately 2 and 0.5 m respectively (Knoppers et al. 1987). Salinity and temperature of the surf zone water varied from 26 to 33‰ and 26 to 30 °C, respectively. These differences were more related to climatic variation during the sampling survey than to the different beach locations.

Ten beaches of Paraná State, southern Brazil (Lat. 25° 30-50' S; Long. 48° 15-30' W) were studied during a survey in February and March 1993. Six beaches were located on Mel Island, namely Ponta do Bicho (PPB), Fortaleza (PFZ), Farol (PFL), Fora Norte (PFN), Grande (PG) and Fora Sul (PFS). Four other beaches were located south of the island, on the Leste Coastal Plain, namely Centro (CBM), Atami (ATA), Leste (PLST) and Gaivotas (GAI) (Fig. 1). Nine to twelve sampling stations were distributed along a transect, from the limit of the vegetation to nearly 2 m depth, in the subidal. Triplicate macrofaunal samples were collected at each station with an iron core of 0.05 m^2 surface area, taken to a depth of 20 cm. Sand was sieved through a 0.5 mm mesh and organisms fixed in 10% formalin, these were identified to the lowest taxonomic level possible. One sand sample was collected at each station for standard mechanical-sieving grain size analysis. Mean and standard deviation were computed according to Folk & Ward (1957) and results expressed as ϕ values ($\phi = -\log_2$ diameter in mm). Slope of the beach, water table profile, water salinity and temperature in the surf zone, wave height and

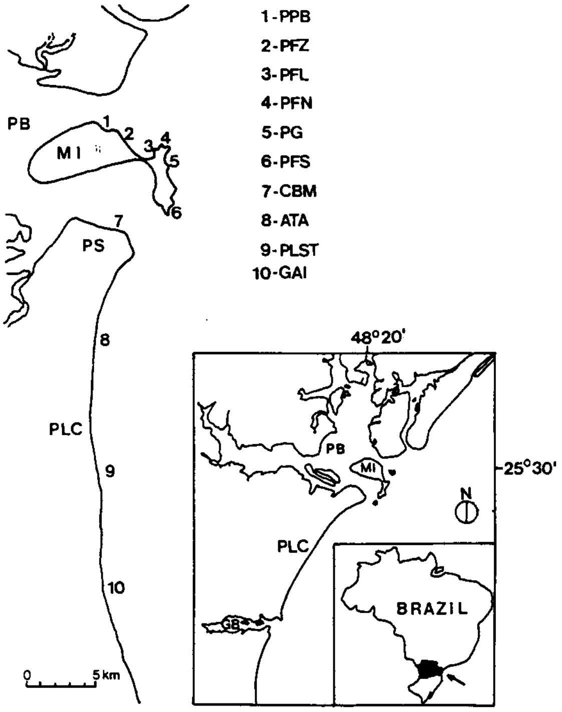

Fig. 1: Paraná coast, Brazil, showing the location of the beaches. GB: Guaratuba Bay, MI: Mel Island, PB: Paranaguá Bay, PLC: Praia de Leste Coastal Plain, PS: Pontal do Sul.

Costa de Paraná, Brasil, mostrando la localización de las playas. GB: Bahía de Guaratuba, MI: Ilha do Mel, PB: Bahía de Paranaguá, PLC: Planicie costera de Praia de Leste, PS: Pontal do Sul.

period were measured for each beach. Subtidal samples were collected by scuba diving.

Modal morphodynamic states were computed employing the dimensionless fall velocity parameter $\Omega = H_b/W_s\ T$ (Dean 1973), where H_b is the breaker height, W_s is the mean fall velocity of the intertidal sand and T the wave period (see also Short & Wright 1983); and the surf-scaling parameter $\Sigma = a_b\ ^2/g\ \tan^2$ (Guza & Inman 1975), where ab is the breaker amplitude, is incident wave radian frequency ($2\pi/T$), g is acceleration of gravity and is the intertidal / surfzone gradient (see also Wright et al. 1982). Mean values of H_b and T were obtained from field observations over one year.

A series of linear regression analyses were performed between biological and physical variables to assess the relationships between community structure and morphodynamics. For the analysis of species zonation patterns, abundance data of samples at each station were pooled and a cluster analysis of the root-root transformed matrix performed, using the Bray-Curtis coefficient and the Unweigthed Mean Arithmetic clustering method (Clifford & Stephenson 1975). A Nonmetric Multidimensional Scaling ordination technique was carried out with the same matrix, in order to verify the relationship between groups. A "mega" cluster analysis was finally performed with all ten beaches (106 samples), in order to test the robustness of the biological zonation over the morphodynamic spectrum.

RESULTS

The beaches

The profiles, sediment and morphodynamics characteristic of PFN, PG, and PFS represented the dissipative extreme. These beaches had gentle slopes, 1/40 - 1/59, fine sand, 2.80-2.75 ϕ, good sorting, 0.23-0.31, intertidal beach widths from 90 to 116 m, and high values of Ω and Σ parameters (Table 1). PG presented a ridge and runnel morphology on the lower shore during the sampling period. A value of $\Omega = 3.8$, corresponding to an intermediate state, was presented by ATA, but in combination with a high value of $\Sigma = 46$, corresponding to a dissipative surf zone. This beach, with similar sedimentological and morphological features to the former beaches, streched to the south in an uninterrupted typical bar-trough system that characterizes PLST and GAI. On these beaches the intertidal sand grain size increased, reaching a medium sand value of 1.89 ϕ on GAI. The intertidal slope ranged from 1/30 to 1/25, and Ω values from 2.9 to 1.5. The subtidal bar of these beaches was well developed, and the inclusion of these features in the profile resulted in gentle slopes.

As a result, Σ reached values greater than 20, allowing some dissipativeness. CBM and PFL beaches had very similar sedimentological and morphological characteristics, e.g. fine and well sorted sands and subaerial slopes ranging from 1/30 to 1/39. Because of their geographical position, these beaches are impacted by low energy refracted waves.

TABLE I

Physical characteristic of the beaches. IT: intertidal, ST: subtidal

Características físicas de las playas. IT: intermareal, ST: submareal

		Sediment grain characteristic						Beach profile		Morphodynamics		
Beach	Width (m)	Mean IT (ϕ)	Mean ST (ϕ)	Mean IT (mm)	Mean ST (mm)	δ IT (ϕ)	δ ST (ϕ)	Slope IT	Slope ST	Hb (cm)	W	S
PG	116	2.80	2.77	0.144	0.147	0.24	0.31	49.8	59.2	111	5.6	55
PFS	105	2.78	2.75	0.146	0.149	0.27	0.31	40.9	43.4	108	5.3	28
PFN	90	2.80	2.78	0.144	0.145	0.24	0.23	40.3	47.7	134	6.7	50
ATA	105	2.88	2.94	0.136	0.130	0.34	0.37	49.4	69	69	3.8	46
PLST	75	2.57	2.49	0.168	0.178	0.40	0.60	30	50.3	72.5	2.9	26
GAI	54	1.89	2.19	0.270	0.219	0.72	0.68	25.1	49.8	70	1.5	24
PFZ	50	2.81	2.66	0.143	0.158	0.28	0.40	22.5	20	80	4.1	4
CBM	60	2.79	2.85	0.145	0.139	0.24	0.32	32.5	20.9	15	0.7	1
PFL	60	2.79	2.76	0.145	0.147	0.23	0.28	39.2	30	25	1.2	3
PPB	54	2.65	2.68	0.159	0.156	0.41	0.56	25	13.7	39	1.7	3

PFZ and PPB beaches had a steep intertidal and subtidal profile without a bar system. The former, with finer sediments, received stronger wave action, resulting in an intermediate value of Ω. On this beach longshore currents associated with the north tidal channel determined a very steep subtidal profile (1/20). PPB beach, at the reflective extreme, showed a small increase in average particle size and standard deviation, a steep profile and low values of Ω and Σ due to weak wave action.

Species composition, richness and abundance

Species composition, richness and abundance were analyzed separately for intertidal and subtidal portions of the beach, in order to allow comparison with the previous literature.

Species composition and dominance of the intertidal stations were similar on all the beaches, varying little throughout the morphodynamic spectrum (Table 2). Eight beaches were dominated by the polychaete *Scolelepis squamata*. Two isopods, *Excirolana armata* and *Tholozodium rombofrontalis*, and the bivalve *Donax gemmula*, showed high abundances on at least six beaches. The insects *Bledius bonaerensis* and *B. microcephalus* appeared on the dissipative beaches. Other common components of the Atlantic beach macrofaunal communities, such as *Emerita brasiliensis* and *Excirolana braziliensis* occurred occasionally, the former only on GAI and the latter on the beaches PLST, GAI, and CBM.

The subtidal stations had a more variable species composition. However, the clypeasteroid *Mellita quinquiesperforata* and again the bivalve *Donax gemmula* dominated in numbers and were constant on all of the beaches. *D. gemmula* is one of several species that extended its distribution from subtidal to intertidal stations. The mysids *Metamysidopsis neritica* and *Bowmaniella brasiliensis*, and the polychaete *Dispio remanei*, occurred on most of the beaches, with lower abundance (Table 2). CBM beach presented two exclusive species with highest abundance, one unidentified tanaidacean and the polychaete *Goniada multidens*.

Significant correlations between species richness, mean beach density (number of individuals m^{-2}) and total abundance (number of individuals m^{-1}) with physical parameters were only obtained when dealing separately with the intertidal and subtidal (Table 3). Intertidal species richness had the best correlation with dimensionless fall velocity ($r = 0.75$, $p < 0.012$) and surf scaling ($r = 0.79$, $p < 0.007$), increasing from reflective to dissipative beaches. In contrast, subtidal richness was negatively correlated with the slope and surf scaling ($r = -0.67$, $p < 0.03$ and $r = -0.78$, $p < 0.01$, respectively): species richness decreased with increasing surf

TABLE 2

Species composition and abundances (individual m^{-2}). A: amphipod, B: bivalve, C: coleopteran, D: decapod, E: echinoid, G: gastropod, I: isopod, M: mysidacean, P: polychaete,

Composición específica y abundancias (individuos m^{-2}). A: anfípodo, B: bivalvo, C: coleptero, D: decapodo, E: equinoideo, G: gasterópodo, I: isópodo, M: miscidáceo, P: poliqueto.

INTERTIDAL	BEACHES									
Species	PG	PFS	PFN	ATA	PLST	GAI	PFZ	CBM	PFL	PPB
Scolelepis squamata (P)	877	1372	1426	865	1574	79	2146	4212	291	839
Puelche sp.G (A)	496	45	282	10	0	0	265	0	7	139
Emerita brasiliensis (D)	0	0	0	0	0	41	0	0	0	0
Excirolana armata (I)	231	244	376	358	37	14	107	140	371	170
Excirolana braziliensis (I)	0	0	0	0	27	102	0	34	0	0
Tholozodium rombofrontalis (I)	100	7	428	194	0	0	111	20	598	336
Donax gemmula (B)	66	154	104	250	71	1	92	37	27	54
Donax hanleyanus (B)	7	0	0	4	7	1	41	0	0	0
Euzonus furciferus (P)	27	51	0	36	48	0	24	41	44	0
Hemipodus olivieri (P)	14	7	7	20	0	0	16	0	14	32
Macrochiridothea giambiagi (I)	0	0	27	0	0	0	20	0	0	7
Lepidopa richmondi (D)	20	11	7	7	7	0	20	20	7	0
Mellita quinquiesperforata (E)	14	0	0	0	0	0	0	0	0	0
Dispio remanei (P)	0	10	54	17	0	0	20	0	0	0
Orbinidae (P)	0	0	0	0	0	0	0	0	0	54
Bathyporeiapus ruffoi (A)	14	0	41	7	0	0	20	0	7	14
Bowmaniella brasiliensis (M)	7	12	7	7	0	0	7	0	14	7
Bledius bonaerensis (C)	78	61	20	41	7	0	0	7	14	0
Sipuncula	0	0	0	0	0	0	0	0	14	0
Bledius microcephalus (C)	14	285	0	0	0	0	0	0	0	0
Puelche sp.P (A)	14	0	0	23	27	0	0	0	0	0
Tivela sp. (B)	0	0	0	0	20	0	0	0	0	0
Crasinella sp. (B)	0	0	7	7	7	0	0	0	0	0
Pinnixa patagoniensis (D)	7	0	0	31	0	0	0	0	0	0
Richness (no. spp.)	21	13	16	15	13	7	14	10	13	10
Mean Density (x 1000 m^{-2})	1.16	1.38	1.46	1.05	1.33	0.09	2.16	2.26	0.57	1.13
Abundance (x 1000 m^{-1})	119.3	140.9	150.7	121.2	100.7	3.56	92.4	125.7	32.2	37.3
Donax gemmula (B)	0	34	186	265	276	239	439	56	48	120
Puelche sp.P (A)	14	16	54	27	0	0	139	0	36	17
Metamysidopsis neritica (M)	7	0	7	34	7	0	109	14	7	14
Macrochiridotea giambiagi (I)	0	7	14	0	7	0	42	0	0	0
Mellita quinquiesperforata (E)	156	240	34	113	66	24	75	51	10	54
Dispio remanei (P)	0	0	31	20	18	27	27	19	16	27
Orbiniidae (P)	0	7	10	0	7	7	43	14	25	41
Scolelepis squamata (P)	24	0	0	0	17	0	102	14	68	0
Cumacea	0	0	7	7	0	0	31	14	58	20
Sipuncula	0	0	0	0	0	0	20	34	7	0
Paranoidae (P)	0	41	0	20	0	0	0	88	29	0
Bowmaniella brasiliensis (M)	7	50	7	0	11	17	14	12	27	10
Hemipodus olivieri (P)	0	0	0	0	27	32	7	10	7	9
Nemertinea	0	0	0	0	0	0	7	70	9	14
Bathyporeiapus ruffoi (A)	10	0	0	0	0	0	14	0	7	14
Spionidae indet. (P)	0	0	0	0	7	0	0	68	14	27
Nephtys simoni (P)	7	0	7	7	0	0	17	25	41	10
Olivancillaria vesica (G)	0	0	7	0	0	0	0	0	7	
Ancinus braziliensis (I)	0	0	7	0	17	7	0	0	0	0
Tanaidacea	0	0	0	0	0	0	0	2427	14	0
Ogyrides hayi (D)	7	7	0	0	0	0	11	7	14	10
Armandia sp. (P)	0	0	0	0	0	7	0	81	10	14
Synidothea marplatensis (I)	7	7	0	0	0	0	0	0	0	0
Phoxocephalopsis sp. (A)	7	0	0	0	0	0	0	0	14	0
Pinnixa patagoniensis (D)	7	0	0	0	0	7	10	0	7	0
Dissodactylus crinitichelis (D)	10	10	0	0	7	0	0	0	0	0
Psionidens indica (P)	0	7	0	0	29	7	0	0	7	0
Ophiuroidea	0	34	0	0	7	34	7	0	20	0
Onuphis emereti (P)	0	0	0	0	0	0	0	0	20	0

TABLA 2 (CONTINUED)

INTERTIDAL	BEACHES									
Species	PG	PFS	PFN	ATA	PLST	GAI	PFZ	CBM	PFL	PPB
Caridea	0	14	0	0	0	0	0	0	0	0
Felaniella vilardeboana (B)	0	0	0	0	17	0	0	0	0	0
Crasinella sp. (B)	0	0	0	0	37	0	14	0	0	0
Goniada multidens (P)	0	0	0	0	0	0	0	229	0	0
Strigilla carnaria (B)	0	0	0	14	0	0	7	44	7	0
Tivela ventricosa (B)	0	0	0	0	27	0	7	7	0	0
Lepidopa richmondi (D)	7	7	7	0	7	7	14	7	0	0
Sthenelais limicola (P)	0	0	0	14	0	0	17	7	0	7
Olivella minuta (G)	0	0	0	0	0	0	0	17	7	0
Sigalium cirriferum (P)	0	0	0	7	7	7	0	7	7	0
Richness (no. spp)	13	16	14	15	22	14	30	33	30	17
Mean Density (x 1000 m^{-2})	0.22	0.4	0.32	0.44	0.43	0.32	0.84	2.58	0.34	0.29
Abundance (x 1000 m^{-1})	8.71	22.51	14.1	44.47	49.35	35.4	46.62	147.37	8.76	5.72
INTER + SUBTIDAL										
Richness (no. spp)	26	25	25	25	25	20	35	38	36	22
Mean Density (x 1000 m^2)	0.88	1.09	1.12	0.84	0.88	0.19	1.61	2.39	0.49	0.88
Abundance (x 1000 m^{-1})	128.0	163.4	164.8	165.7	150.1	38.9	139.0	273.1	40.9	43.1

TABLE 3

Correlations between physical and community parameters (n =10). RIT: intertidal species richness, RST: subtidal species richness, RT: total species richness, D: density , A: linear abundances, Underlined values = $p < 0.05$

Correlaciones entre parámetros físicos y de la comunidad (n = 10). RIT: riqueza específica del intermareal, RST: riqueza específica del submareal, RT: riqueza específica total, D: densidad, A: abundancia lineal, Valores subrayados = $p < 0.05$

	RIT	RST	RT	DIT	DST	DT	AIT	AST	AT
Width	0.74 (0.014)	-0.61 (0.063)	-0.32 (0.365)	-0.02 (0.948)	-0.32 (0.372)	-0.11 (0.758)	0.68 (0.031)	-0.28 (0.419)	0.31 (0.375)
Slope IT	0.72 (0.019)	-0.39 (0.270)	-0.05 (0.887)	-0.12 (0.748)	-0.20 (0.571)	-0.12 (0.739)	0.54 (0.104)	-0.23 (0.521)	0.25 (0.472)
Slope ST	0.46 (0.180)	-0.66 (0.037)	-0.50 (0.139)	-0.40 (0.245)	-0.44 (0.206)	-0.46 (0.185)	0.31 (0.383)	-0.26 (0.459)	0.08 (0.828)
W	0.75 (0.012)	-0.54 (0.105)	-0.29 (0.421)	0.20 (0.579)	-0.42 (0.223)	-0.14 (0.969)	0.70 (0.025)	-0.44 (0.207)	0.23 (0.516)
S	0.66 (0.035)	-0.78 (0.007)	-0.54 (0.104)	-0.21 (0.557)	-0.47 (0.170)	-0.31 (0.380)	0.51 (0.135)	-0.38 (0.275)	0.14 (0.695)

zone dissipativeness. Density was not correlated with any of the physical parameters, and only intertidal abundance (m^{-1}) was significantly correlated with the beach width ($r = 0.68$, $p < 0.031$) and dimensionless fall velocity ($r = 0.69$, $p < 0.025$). No significant relationship was obtained with sedimentological parameters, as they varied little over the morphodynamic spectrum.

Species richness and density of each station along the transect showed characteristic trends on all beaches. Species richness increased towards offshore stations (Fig. 2). This increase was more accentuated at the reflective extreme (PFZ, CBM and PFL), with an abrupt change around low water level (Fig. 2a). Dissipative beaches (PFS, PFN, PG and ATA) had a smaller rate of increase offshore (Fig. 2c). Variation of density was very similar on these beaches and in PPB and PLST, with a maximum value of 3,000 individuals m^{-2} in the intertidal, around station 4-2 above low water level. Seaward from that point there was a very pronounced decrease, down to 200 individuals m^{-2}, that was maintained offshore along the transect (Fig. 3a, b). PFZ and CBM showed higher intertidal values (5,000 and 7,000 individuals m^{-2} respectively), decreasing around low water level and increasing subtidally again (Fig. 3c). The lowest density occurred on GAI and PFL (Fig. 3d). The first had a maximum of 1,700 individuals m^{-2} intertidally, decreasing around low water level

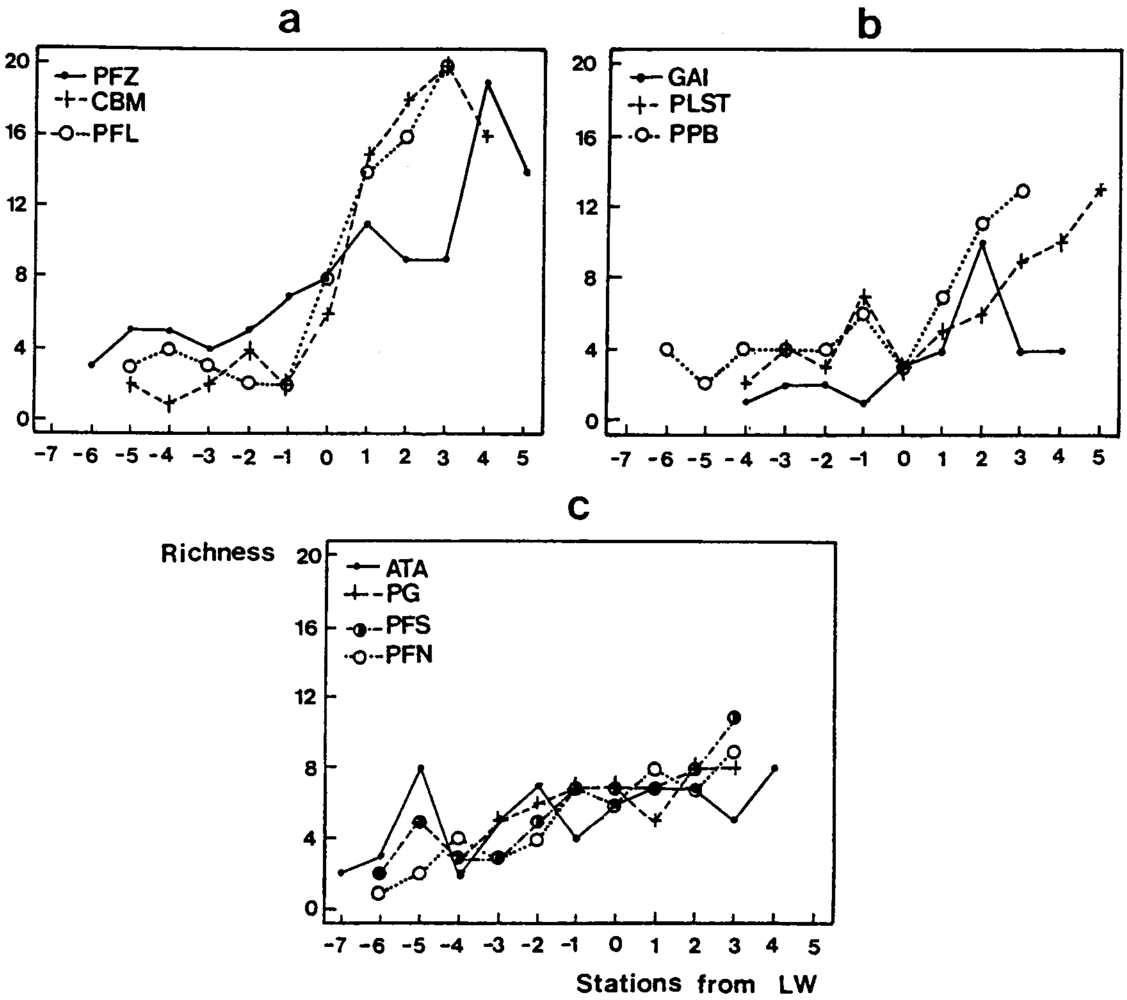

Fig. 2: Variation of the species richness along the transect. Stations are numbered from the low tide water level (0).

Variación de la riqueza de especies a lo largo del transecto. Las estaciones están enumeradas desde el nivel de marea baja (0).

and the second had lower intertidal density values, increasing up to 500 individuals m^{-2} subtidally (Fig. 3d).

Zonation

Zonation patterns obtained from classification and ordination analyses were similar for all beaches, with at least four faunistic zones discriminated along the whole transect (Fig 4). These biological zones were named (in part) according to Salvat's physical scheme (Salvat 1964). An upper drying zone was present on all the beaches of the coastal plain and on two beaches of Mel Island, PG and PFS. The presence of two staphylinids, *Bledius bonaerensis* and *B. microcephalus*, characterized that zone. At CBM, GAI and PLST the isopod *Excirolana brasiliensis* was restricted to this upper zone, showing more adaptation to drying than *Excirolana armata*. The latter species characterized the retention zone, where the sand remains wet during low tide, on all the beaches. The isopod *Tholozodium rhombofrontalis* occurred in this zone on all Mel Island beaches and on ATA, showing no relationship between its distribution and morphodynamic characteristics. The deposit feeder polychaete *Euzonus furciferus* had an occasional presence in the retention zone, but extended its distribution across other zones on ATA. The resurgence zone had the greatest abundance of *Scolelepis*

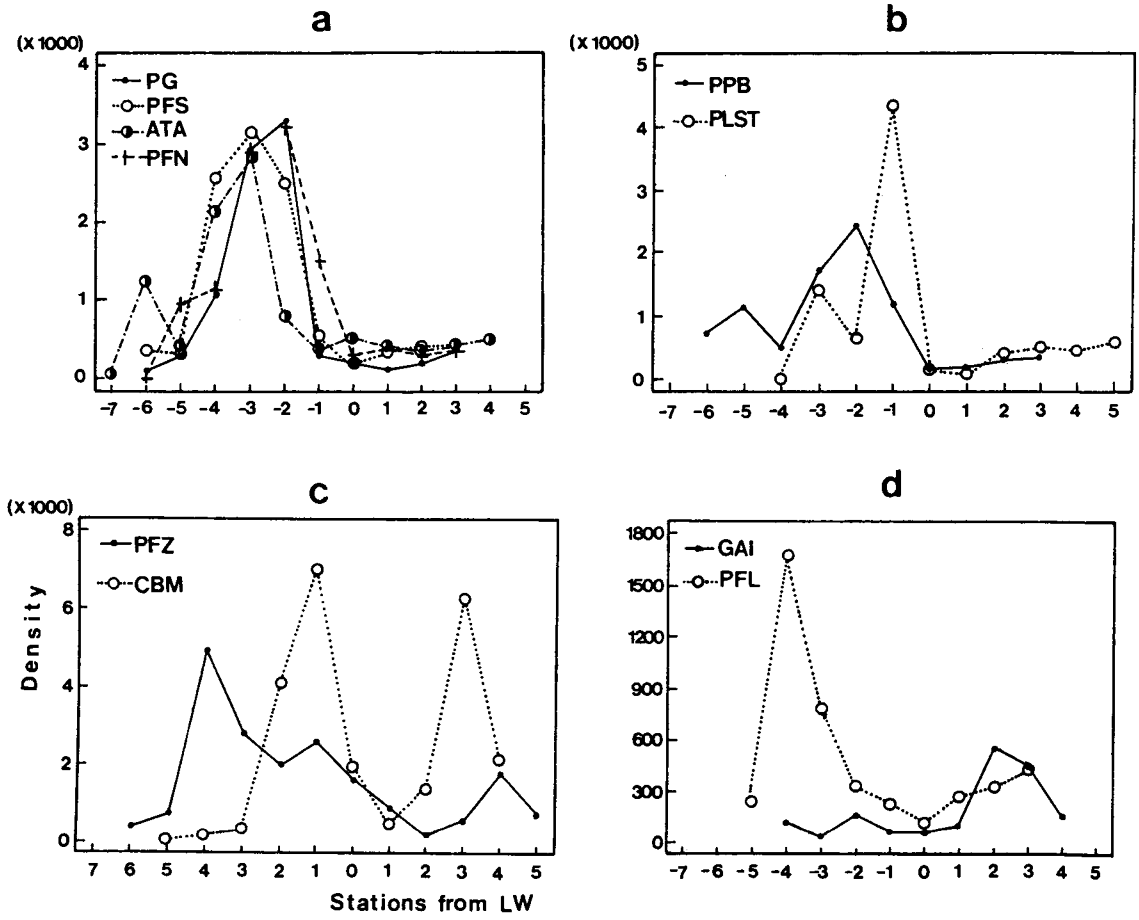

Fig. 3: Variation in density (individuals m^{-2}) along the transect. Stations are numbered from the low tide water level (0).

Variación de la densidad (individuos m^{-2}) a lo largo del transecto. Las estaciones están numeradas desde el nivel de marea baja (0).

squamata on all beaches. This suspension feeder spread its distribution towards offshore zones, especially at the dissipative extreme. Only on PLST did it spread onshore, overlapping with *E. armata* in the retention zone. Together with *S. squamata*, the amphipod *Puelche* sp. G characterized the resurgence zone of all Mel Island beaches and ATA. Except for PFN, stations included in the retention and resurgence zones clustered together on all the beaches. Two other groups of stations on beaches PFZ, PFS, PG and ATA were formed. The first group, saturation zone, included stations at the low water level This zone represented a transition between the two main environments (intertidal and subtidal). It was characterized by the overlapping distributions of *S. squamata* with subtidal species, e.g. *Donax gemmula*, *Macrochiridothe giambiagi*, *Puelche sp. P*, *Hemipodus olivieri*, and *Lepidopa richmondi*. The other group of stations, named infralitoral, corresponded to the surfzone on these beaches. The scutellid *Mellita quinquiesperforata* and the polychaete *Dispio remanei* are the most representative species of this zone.

A similar zonation pattern was formed when all the stations of the ten beaches were analyzed together (Fig. 5). Drying, retention and resurgence zones were very robust, with 90 to 100% of the stations clustering together. Saturation zone stations were similar to those of the resurgence zone (28%) and especially with the infralitoral zone (72%). Finally, all the infralitoral stations clustered together (100%), although with the highest dissimilarity values.

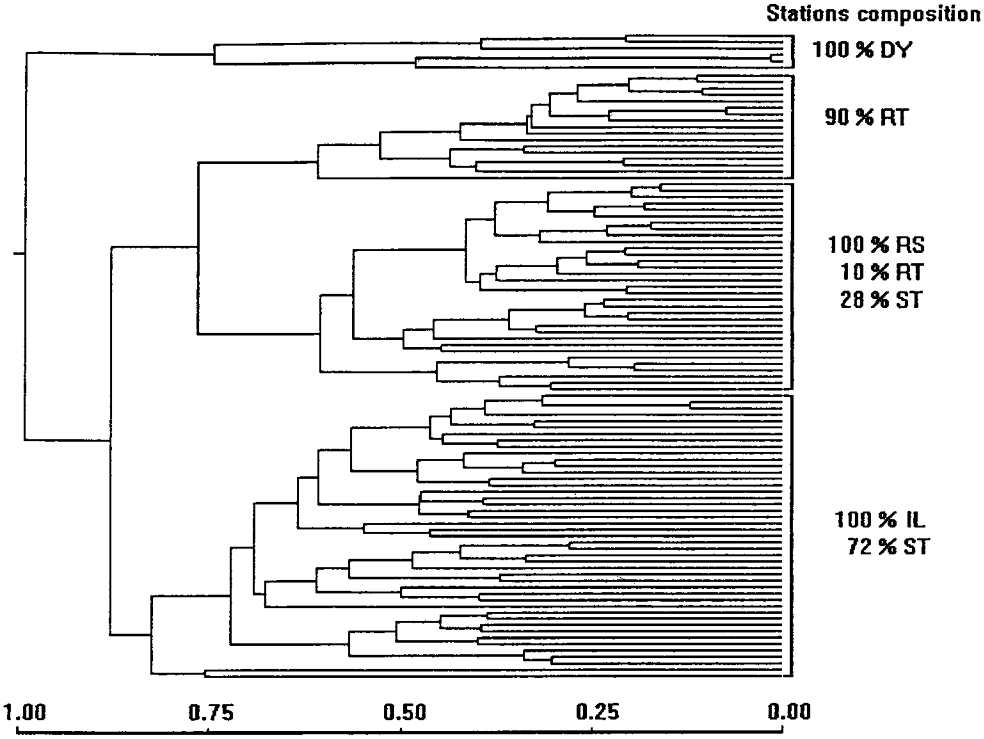

Fig. 4: Cluster analysis and ordination of stations (MDS) of the beaches. Groups identified in the dendrogram are encircled in the MDS. Scale represents dissimilarity.

Análisis de agrupamientos y ordenación de las estaciones (MDS) de las playas. Los grupos identificados en el dendrograma están circunscriptos en el MDS. La escala representa disimilitudes.

DISCUSSION

The definition of the morphodynamic state of any beach using the "dimensioness fall velocity" formulation is a function of three parameters: grain size, wave height and wave period. The combination of different values of these parameters will determine the position of a beach on the reflective-dissipative morphodynamic spectrum. When the geological history of a region determines the existence of a sediment source of great volumes of fine sands, as is the case with the Paranaguá Bay area, the morphodynamic evolution of the beaches of this area will be an exclusive function of wave action. The particular geographic positions of the Mel Island beaches resulted in beaches with the same sedimentological characteristics, but receiving varied wave action and dispersed throughout the morphodynamic spectrum. Guaratuba Bay is the sediment source of medium sand that occurs at GAI, the only medium sand intermediate beach.

This great sedimentary homogeneity is responsible for the similar species composition and abundance of the intertidal macrofauna on all the beaches, with the exception of GAI, with a coarser intertidal grain size, resulting in a significant reduction of the species abundance. In spite of this homogeneity, the intertidal species richness and the linear abundance were positively correlated with morphodynamic parameters and increased from reflective to dissipative conditions, showing the independence of this relationship with sediment grain characteristics. A correlation between beach face slope and linear abundance and diversity of the macrofauna was first found by McLachlan et al. (1981). Subsequent studies (McLachlan 1990, McLachlan et al. 1993), included in these positive correlations "omega" values and grain size and found this correlation for different zoogeographical areas.

Studying the intertidal of Uruguay's beaches (South Atlantic), Defeo et al. (1992) stated that grain size and slope are among the

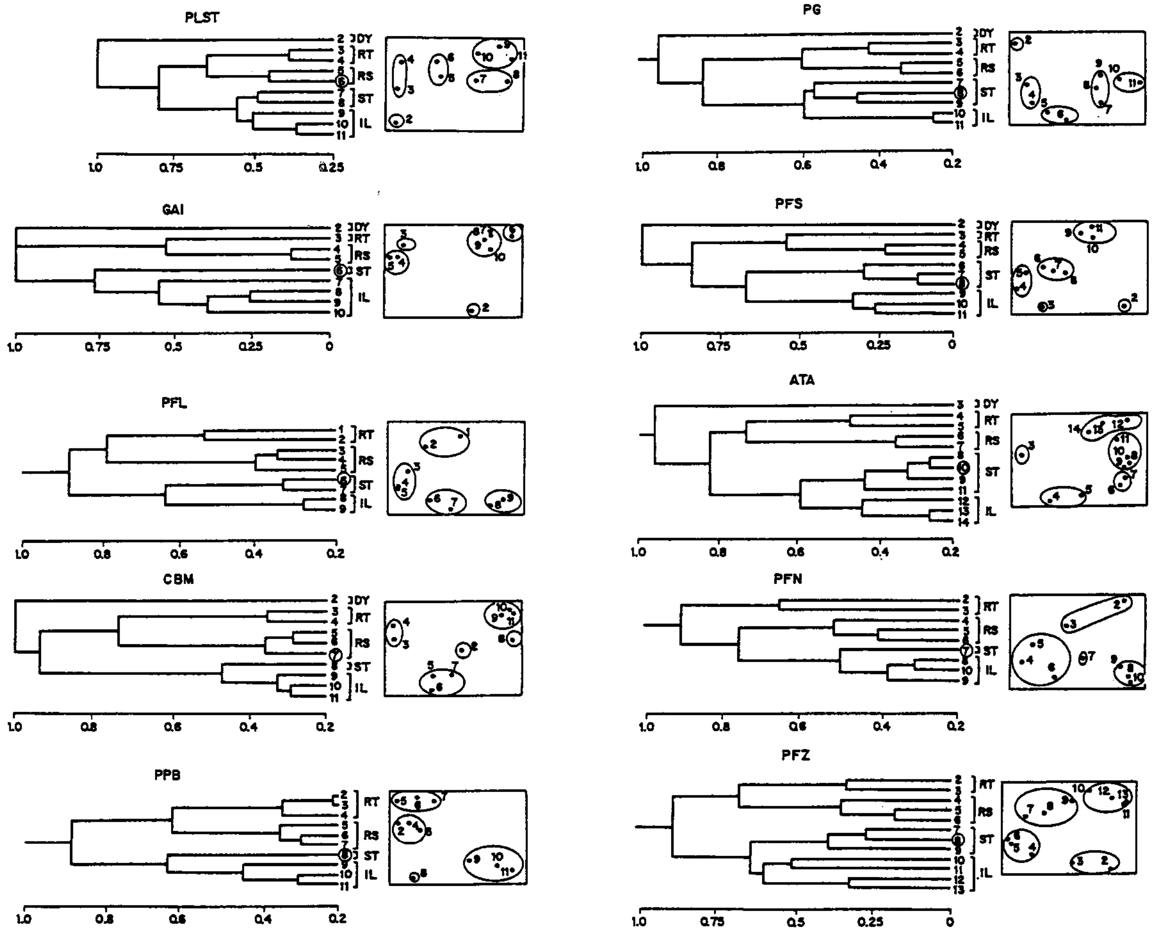

Fig. 5: Results of cluster analysis of all the stations sampled. Scale represents dissimilarity.

Resultados del análisis de agrupamiento de todas las estaciones muestreadas. La escala representa disimilitudes.

dominant factors controlling sandy beach community structure. They found an increase in number of species and total abundance (density) from reflective to dissipative beaches, and a negative and exponential correlation between grain size and slope with density.

No correlation was found in the present study between intertidal density and any physical parameters. However, only one beach had a larger grain size sediment in comparison to the others, with a remarkable reduction in macrofauna density. This result could suggest that density is independent of the morphodynamic state of the beach but closely related to the sediment particle size.

Significant correlations in subtidal species richness were found with the surf scaling parameter and the subtidal slope, showing that the number of subtidal species increases with decreasing dissipativeness of a beach, but also with increasing beach-surf zone profile. No significant correlation was found between physical parameters and macrofaunal community parameters when the intertidal and subtidal data were combined.

The trend of richness along whole transects exhibited an offshore increase, as has been shown by numerous authors (e.g. McLachlan et al. 1984). This increase was different within the morphodynamic spectrum, being gentle on dissipative beaches, and very accentuated at the reflective extreme. This is a direct consequence of a morphodynamic difference in wave energy dissipation, that is limited at the reflective extreme to a narrow zone of strong breaker action on the beach face. Density patterns were very similar at the dissipative extreme, as a result of the distribution of the dominant species *Scolelepis squamata.* Similar high density values were subtidally found on CBM, probably due to a more estuarine influence on the macrofauna. GAI was the only beach that showed higher subtidal than intertidal density values.

Zonation patterns of the ten beaches were very similar, with three intertidal zones that maintained their identity throughout the morphodynamic spectrum. Each of these zones, named as drying, retention and resurgence zone, have at least one species with the peak of its distribution centered in one of them. This scheme of biological zonation, that fits Salvat's physical one, was extensively studied over a year by Souza & Gianuca (1995) near ATA beach, showing its persistence over any seasonal fluctuation. The saturation zone, identified by several authors as a unique biological zone (Bally 1983, Wendt & McLachlan 1985) presented great variation between the beaches, and lost its identity when analyzed by "mega" clustering of all stations. This confirms previous observations (Day et al. 1971, Field 1971, Christie 1976, McLachlan et al. 1984, McLachlan 1990) that species occupying the saturation zone also extend into the sublittoral and may more appropriately be called surfzone species whose upper limits of distribution are on the lower shore. Therefore, the saturation zone represents an area that links intertidal and subtidal compartments, allowing biological interaction amongst their members. For instance, in this zone occur the polychaetes *Hemipodus olivieri* and *Nephtys simoni* which are predators of juvenile and adult intertidal macrofauna (McDermott 1987).

McLachlan et al. (1993) remarked that it is not the type of beach state that is important to the fauna, but the swash climate associated with it. Swash climate is highly correlated with morphodynamics, an increase of swash periods and swash lengths existing from reflective to dissipative beaches (McArdle & McLachlan 1992). If the existence and width of the saturation zone are related to swash climate, this zone will be better developed at the dissipative extreme, allowing more widespread occurrence of subtidal species in intertidal stations. In this case, the increase in species richness from reflective to dissipative on beaches with the same granulometric characteristics, reflects the inclusion of subtidal species in the intertidal environment. The list of species (Table 2), that was "a priori" divided in intertidal and subtidal, shows this pattern.

It is generally accepted that sandy beaches constitute a unique environment where sand and water are in continuous movement, and that macrofauna is controlled primarily by physical conditions. The physical environment has discontinuities and zones, not only in the intertidal (Salvat 1964, Pollock & Hummon 1971), but also in the subtidal (Riedl 1964, Riedl & McMaham 1974, Hiscok 1983, Short 1983). The existence of physical zones indicates that a beach may be divided into different physical subenvironments that will vary in width and general characteristics throughout the morphodynamic spectrum. If macrobenthic communities are dominated by the physical environment, then their structure may be influenced by physical zonation. The variation of the width of subtidal biological zones in relation to change in morphodynamic state was indirectly shown by Knott et al. (1984), Fleischack & Freitas (1989) and Borzone & Gianuca (1990), working on beaches in the proximity of jetties. In the present work, the name of infralitoral zone included two different subenvironments, surfzone and nearshore. On dissipative beaches, the subtidal sampling included only the surfzone, well developed on these beaches. On reflective beaches, a narrow surfzone was represented by only one station, and the rest of the subtidal stations represented the nearshore zone.

The three intertidal biological zones found on these beaches were persistent throughout the morphodynamic spectrum. Nevertheless, some authors have recently remarked on the difficulties in establishing major intertidal biological zones (Raffaelli et al. 1991, Defeo et al. 1992), suggesting that the only valid zonation scheme might be division into a high shore assemblage of air-breather and a lower shore zone of water-breathers (Brown & McLachlan 1990). This is an oversimplification of both the physical and ecological environment, and not in agreement with many studies that have been showing complex adaptations of species to this dynamic environment (Ansell 1983, Brown 1983).

It is obvious that beach zonation, considering both the intertidal and the subtidal environment, is highly influenced by morphodynamic state and faunal composition. Biological zones are more evident on dissipative than on reflective beaches, since some physical zones (e.g. resurgence and saturation) tend to diminish in width or disappear towards the reflective extreme. Biological zones will also be more evident in the presence of less motile and sedentary species, e.g. polychaetes or tube builder thalassinid crustaceans, than in the presence of tidal migratory species.

In this study we have shown the importance, when analyzing the structure of beach communities, of considering the entire beach ecosystem boundaries and morphodynamic spectrum. The homogeneity of sand composition buffered the possible morphodynamic influence on the intertidal dominance and density patterns, suggesting that these parameters are not controlled only by morphodynamics but also by sedimentological characteristics. This alternative hypothesis awaits further testing.

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