SCIENTIA MARINA

Composition, structure and zonation of intertidal macroinfauna in relation to physical factors in microtidal sandy beaches in Rio de Janeiro state, Brazil*

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SUMMARY: The intertidal macroinfauna of fiftheen exposed sandy beaches located in Rio de Janeiro State was studied to determine species richness, density, biomass and zonation. Morphodynamic influence on biological parameters is also evaluated in this paper. Dean's morphodynamic index (Ω) ranged from reflective to intermediate values and mean grain size ranged from fine to coarse sands. A total of 17 species were identified, with the crustaceans *Emerita brasiliensis*, *Excirolana braziliensis* and *Pseudorchestoidea brasiliensis* being the most abundant species. Species richness had a significant positive linear relationship with Ω values, swash period and slope, and a negative relationship with grain size. Significant positive relationships were also observed for total density with the swash period and slope, total biomass with slope, density of *Emerita brasiliensis* with swash period and slope and biomass of *Emerita brasiliensis* with slope. Zonation analysis showed that two or three biological zones could be recognised, with the two-zone pattern being observed in most of the beaches. This pattern consisted of a lower zone characterised by *Emerita brasiliensis, Donax haleyanus* and *Hemipodus oliveri*; and an upper zone characterised by *Excirolana braziliensis*, *Pseudorchestoidea brasiliensis* and *Phaleria testacea*. The three-zone pattern as a disruption of the general two-zone pattern and its formation was attributable to the variation in the distributions of *P. brasilensis* and *E. braziliensis*. Our results suggest that beach morphodynamics is the best predictor for the variability of macroinfaunal community composition.

Key words: sandy beaches, macroinfauna, zonation, morphodynamics, Brazil.

RESUMEN: COMPOSICIÓN, ESTRUCTURA Y ZONACIÓN DE LA MACROINFAUNA INTERMAREAL EN RELACIÓN A FACTORES FÍSICOS EN PLAYAS ARENOSAS MICROMAREALES EN EL ESTADO DE RIO DE JANEIRO, BRASIL. – La macroinfauna intermareal de quince playas arenosas en el Estado de Rio de Janeiro fue estudiada con el objetivo de determinarse la riqueza de especies, la densidad, la biomasa y la zonación. La influencia de la morfodinámica en los parámetros biológicos también fue evaluada en este trabajo. El índice morfodinámico de Dean (Ω) fluctuó de reflectivo a valores intermediarios y el tamaño medio de los granos osciló entre arenas finas a gruesas. Un total de 17 especies fueron identificadas, siendo los crustáceos *Emerita brasiliensis*, *Excirolana braziliensis* y *Pseudorchestoidea brasiliensis* las especies más abundantes. La riqueza de especies tuvo correlaciones lineales positivas con los valores de Ω, con el período y la pendiente de barrido y relación negativa con el tamaño de grano. Relaciones positivas significantes también se observaron para la densidad total con el período y la pendiente de barrido, la biomasa total con la pendiente, la densidad de *Emerita brasiliensis* con el período y la pendiente de barrido y la biomasa de *Emerita brasiliensis* con la pendiente. Un análisis de la zonación mostró que 2 o 3 zonas biológicas pueden ser reconocidas, observándose un patrón de 2-zonas en la mayoría de las playas. Dicho patrón consistió de una zona inferior, caracterizada por *Emerita brasiliensis, Donax haleyanus* y *Hemipodus oliveri*; y una zona superior, caracterizada por *Excirolana braziliensis*, *Pseudorchestoidea brasiliensis* y *Phaleria testacea*. El patrón de 3-zonas fue un disturbio del patrón general de 2-zonas y su formación fue atribuida a variación en las distribuciones de *P. brasilensis* y *E. braziliensis*. Nuestros resultados sugieren que la morfodinámica de playa es el mejor pronóstico de variabilidad en composición de la comunidad macroinfaunal.

Palabras clave: playas arenosas, macroinfauna, zonación, morfodinámica, Brasil.

INTRODUCTION

Exposed sandy beaches are dynamic environments. Wave energy, tide amplitude, wind action, grain size, slope and swash climate are the most important factors in their physical characterization (McLachlan, 1990; McArdle and McLachlan, 1992; McLachlan *et al.*, 1993). Interactions among these factors generate morphodynamic gradients, with reflective beaches with coarse sand, steep slope and a narrow surf zone at one extreme, and dissipative beaches with fine sand, a gentle slope and a wide surf zone at the other (Short and Wright, 1983). Because most species of beach macroinfauna show high physiological plasticity, being able to live on different types of beaches (Dugan *et al.*, 1991, 1994; Gómez and Defeo, 1999, Defeo *et al.* 2001), it is difficult to correlate differences between populations and communities with environmental parameters. Variations in macroinfaunal structure are more easily perceived between morphodynamically extreme beaches: species richness, abundance and biomass all tend to be highest in dissipative beaches (McLachlan, 1990, 1996; Defeo *et al.*, 1992; Jaramillo and McLachlan, 1993; McLachlan *et al.*, 1993; Borzone *et al.,* 1996).

Recent population studies have shown, however, that population-level responses to variations in beach morphodynamics may differ markedly from community-level responses. Thus, the abundance and biomass of a population may increase in the more reflective beaches, that is, in the opposite direction from the expected trend for the community, as observed for *Pseudorchestoidea brasiliensis* (Gómez and Defeo, 1999). Defeo *et al.* (2001), testing the swash-exclusion hyphothesis in populations of the mole crab *Emerita brasiliensis*, found no significant differences in most parameters of population and reproductive biology between dissipative and reflective beaches.

Abiotic parameters also undergo remarkable variations along the beach topographic profile, so the interactions between these factors and the intrinsic features of each species determine biological zonation in sandy beaches. The zonation thus reflects the restriction of each species to a particular section of an environmental gradient (Raffaelli *et al.*, 1991). Several general schemes of zonation have been proposed. The most generally employed schemes are that of Dahl (1952), which divides the beach into three zones, the subterrestrial, midlittoral and sublittoral fringes, based on the distribution of crustaceans; and that of Salvat (1964), based on physical parameters, in which four zones of drying, retention, resurgence and saturation are identified. Generally, the schemes proposed so far are still the focus of controversy.

The state of Rio de Janeiro in Brazil has an extensive coastline, with sandy beaches that vary in degree of wave exposure, grain size and beach slope, but despite these differences harbour the same communities (Veloso *et al.*, 1997; Veloso and Cardoso, 2001). This apparent similarity makes this an interesting region to test for the influence of environmental parameters on the populations and communities. In this study, 15 beaches were sampled during winter and summer, aiming to (1) correlate the species richness, density and biomass of their communities with the physical parameters; (2) verify whether the most abundant species showed the same responses to environmental variations, and (3) analyse the patterns of macrofaunal zonation among the beaches.

MATERIAL AND METHODS

Sampling and laboratory procedures

A total of 15 beaches located in the state of Rio de Janeiro, Brazil, were selected for this study (Fig. 1): Restinga da Marambaia (MAR), Grumari (GRU), Barra da Tijuca (BAT), Urca (URC), Itaipu (ITA), Itaipuaçu (ACU), Jaconé (JAC), Restinga de Massambaba (MAS), Foguete (FOG), Peró (PER), Pecado (PEC), Formosa (FOR), Tucúns (TUC), Unamar (UNA) and Carapebus (CAR).

The beaches MAR, GRU, BAT, URC, ITA, ACU, JAC and MAS were sampled in winter 1996 and summer 1997. The beaches FOG, PER, PEC, FOR, TUC, UNA and CAR were sampled in winter and summer 1998, during low spring tide. On each beach, two transects were established from the lower limit of the swash zone to 10 m above the drift line, and 10 equally spaced sampling strata were marked: the first below the swash line (N1 - 30 cm water layer), the second last (N9) on the drift line, and the last (N10) 10 m above the drift line. At each stratum, 5 samples were randomly taken with a 0.04 m^2 (3 m apart) quadrat to a depth of 25 cm. The collected sediment was washed through a 0.71 mm sieve, and the retained material was taken to the laboratory, where the organisms were sorted by species, counted and fixed in 5% formaldehyde. In addition to the
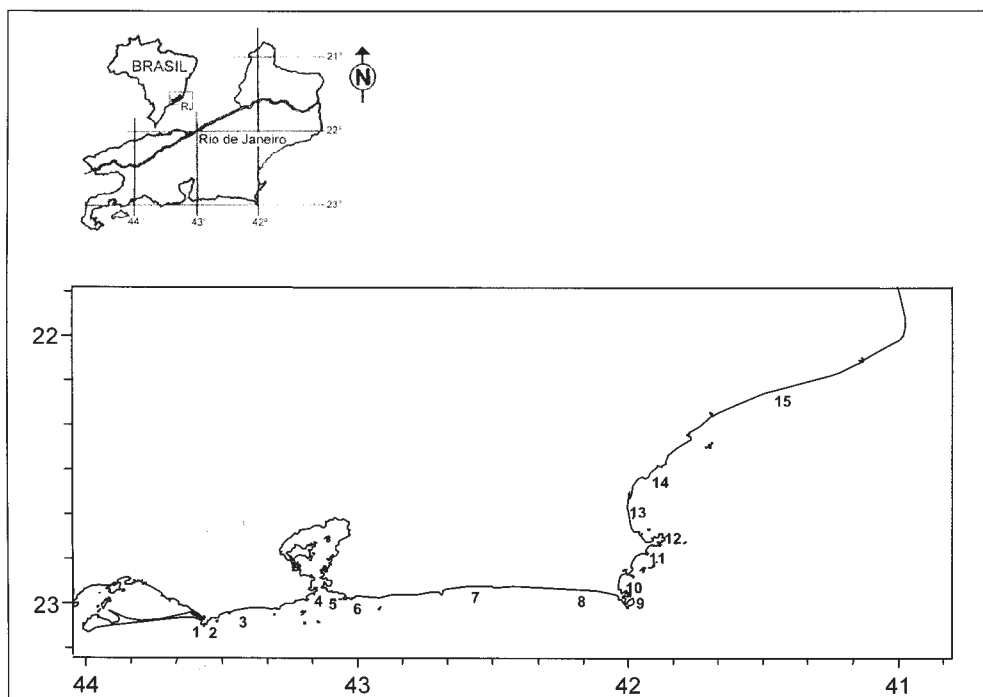
FIG. 1. – Map showing the locations of the beaches studied. (1) - MAR, (2) - GRU, (3) - BAT, (4) - URC, (5) - ITA, (6) - ACU, (7) - JAC, (8) - MAS, (9) - FOG, (10) - PER, (11) - PEC, (12) - FOR, (13) - TUC, (14) - UNA and (15) - CAR.

quadrats, qualitative samples were taken in the supralittoral zone for ghost crabs, which were usually not sufficiently abundant to appear in the quantitative samples. These qualitative data were only used to characterise the faunistic composition of the beaches and were not included in the statistical analysis. Biomass was determined by drying specimens at 70ºC for 24 h.

Physical characterization

Sediment samples for particle size analysis were taken with a plastic corer of 3.5 cm diameter to a depth of 10 cm at strata 10 (supra), 6 (middle) and 2 (waterline). Samples were oven-dried at 70°C and passed through a series of sieves of –2.5, –2.0, –1.0, 0.0, 0.5, 1.0, 1.5, 2.0, 2.5, 3.0 and 4.0 phi (phi = – log$_2$ mm) in order to determine mean particle size (Folk and Ward, 1957). Results were expressed in mm.

The beach-face slope of each transect was measured by the height difference (Emery, 1961) between the drift line and the waterline. Dean's dimensionless parameter (Ω) (Short and Wright, 1983) was calculated for each beach as a measure of its morphodynamic state: $\Omega = H_b / W_s$. T, where H_b is the breaker height in cm, W_s the sand settling velocity in cm s^{-1} (obtained from particle size and Gibbs *et al.*, 1971) and T the wave period in seconds.

Statistical analysis

Simple linear regressions were performed to investigate the relationship between the species richness, density and biomass of the entire macroinfauna community and the most abundant species, and the physical variables (mean grain size, intertidal slope, wave height and period, swash period, Dean's parameter) (Zar, 1996). The Mann-Whitney nonparametric statistic was used to test temporal variations in density and biomass of macroinfauna and in mean grain size for each beach (Zar, 1996).

The Kruskal-Wallis test was employed to examine for differences in the mean grain size and macrofauna density between beaches. Dunn's multiple comparisons test was used *a posteriori* to assess significant differences between beaches. Because of the differences in season between samples, the beach group MAR, GRU, BAT, URC, ITA, ACU, JAC and MAS was analysed separately from the beach group FOG, PER, PEC, FOR, TUC, UNA and CAR.

Cluster analysis was used to aid the interpretation of zonation patterns. Abundance values were transformed to log (x+1), and similarity values were calculated between stations using the Bray-Curtis coefficient. Dendrograms were obtained from the dissimilarity matrix by Unweighted Pair-Group Matching Analysis (UPGMA). For simplicity, only repre-

TABLE 1. – Kruskal-Wallis test. Relation between mean grain size of MAR, GRU, BAT, URC, ITA, ACU, JAC and MAS beaches and results of Dunn's test analysis undertaken as an *a posteriori* test of multiple comparisons to indicate statistical significance.

H = 57.36; p<0.0001			Dunn's multiple comparisons test				
MAR	ITA	URC	MAS	GRU	BAT	JAC	ACU
Mean ranks 7.66	25.78	29.75	48.00	49.71	49.75	66.83	78.25
Non-significance							

TABLE 2. – Kruskal-Wallis test. Relation between mean grain size of de FOG, PER, PEC, FOR, TUC, UNA and CAR beaches and results of Dunn's test analysis undertaken as an *a posteriori* test of multiple comparisons to indicate statistical significance.

H = 16.19; p<0.05		Dunn's multiple comparisons test				
PER	PEC	FOR	FOG	UNA	TUC	CAR
Mean ranks 10.83	12.33	12.83	15.66	17.00	21.60	29.33
Non-significance						

sentative dendrograms are presented. These representative dendrograms correspond to zonation patterns that are described in the following section.

RESULTS

Physical characterization

Significant differences were observed between the beaches studied (Kruskal-Wallis test; Tables 1 and 2). The sediment was composed of medium sand at URC, BAT, GRU, ITA (summer), MAS (summer), UNA (winter), PEC, FOG (summer) and PER; coarse sand was found at ACU, JAC, MAS (winter), CAR, UNA (summer), TUC and FOG (winter), and fine sand was found at MAR, ITA (summer) and FOR (see Table 3). Dean's parameter ranged from reflective values at URC, GRU, ITA,

ACU, JAC, FOG, PER, TUC, UNA and CAR to intermediate values at BAT, MAR and MAS. The beach of PEC showed intermediate values during the winter and reflective ones in summer (Table 3). The beaches did not show significant variations in mean grain size between sampling periods (Mann-Whitney test; p>0.05).

Biological characterisation

A total of 17 taxa were collected and identified during this study, with 5 to 9 species present on each beach. The highest species richness, density and biomass in both sampling periods were recorded at MAR (Table 4). Crustaceans were the most abundant and frequent animals, represented by *Emerita brasiliensis, Lepidopa richmondi*, *Ocypode quadrata* (Decapoda), *Pseudorchestoidea brasiliensis* (Amphipoda), *Excirolana armata*, *Excirolana*

TABLE 3. – Physical characterisation of beaches studied. Data are expressed as mean values: ± standard deviation.

Physical variables	URC	BAT	GRU	MAR	ITA	ACU	JAC	MAS	CAR	UNA	PEC	TUC	FOR	FOG	PER
Mean grain size (mm)	0.33	0.45	0.40	0.20	0.29	0.91	0.82	0.45	1.19	0.51	0.30	0.52	0.22	0.45	0.48
	0.02	0.05	0.04	0.01	0.06	0.06	0.11	0.13	0.13	0.06	0.04	0.01	0.04	0.18	0.03
Swash period (sec.)	17.05	8.13	10.75	22.00	9.58	10.61	9.60	8.06	10.42	12.50	17.40	6.92	8.28	27.48	12.58
	0.07	1.07	0.49	2.83	1.02	1.26	3.39	0.69	0.46	7.35	2.85	1.43	3.02	2.12	3.20
Wave period (sec.)	11.00	10.85	12.55	9.80	11.10	18.05	15.30	12.00	18.48	13.18	19.04	19.15	12.65	12.96	13.16
	0.10	3.18	1.06	0.05	2.83	0.78	3.54	3.54	1.55	0.37	5.92	0.40	2.11	0.22	2.03
Wave height (m)	0.50	1.30	0.55	0.80	0.33	1.30	1.35	0.68	1.38	0.40	0.75	0.60	0.50	0.40	0.60
	0.02	0.28	0.07	0.00	0.11	0.99	0.64	0.04	0.88	0.14	0.07	1.52	0.14	0.11	0.10
Dean's parameter	0.88	1.86	0.75	2.41	0.76	0.53	0.62	1.21	0.46	0.36	0.98	0.46	1.51	0.49	0.60
	0.01	0.70	0.04	1.00	0.17	0.45	0.36	0.19	0.06	0.08	0.32	0.11	0.01	0.26	0.01
Intertidal slope (1/m)	11.13	8.83	8.71	23.00	11.36	8.94	10.20	15.85	10.24	13.02	12.89	6.60	9.38	17.02	16.67
	3.08	3.92	4.38	2.02	2.60	0.33	0.85	1.63	3.73	1.18	4.89	0.64	2.06	0.73	0.11

TABLE 4. – Density (individual m^{-2}) and total biomass (dry weigth m^{-2}) of macroinfauna at beaches studied. *W* – winter, *S* – summer.

Species		URC	BAT	GRU	MAR	ITA	ACU	JAC	MAS	CAR	UNA	PEC	TUC	FOR	FOG	PER
Emerita brasiliensis	w	32.5	0.5	9.3	478.8	12.3	3.9	2.5	41.5	760.3	327.0	563.7	1.2	39.1	682.7	323.2
	s	462.2	12.8	193.0	6807.8	13.0	15.8	55.0	737.0	11.4	0.8	34.0	1.3		153.7	5.0
Lepidopa richmondi	w													0.6		
	s										0.2					
Excirolana armata	w	0.6														
	s	0.4														
Excirolana braziliensis	w	15.0	21.3	7.3	38.8	3.8	27.5	10.3	66.7	13.2	34.3	45.7	59.4	33.4	50.0	0.2
	s	9.8	9.0	1.0	5.3	3.3	10.8	5.5	13.5	19.5	43.5	210.0	7.5	36.3	14.0	8.5
Macrochiridotea lilianea	w	6.9														0.2
	s	4.5														
Pseudorchestoidea brasiliensis	w	19.4	14.5	28.0	18.5			6.0	35.5	5.2	1.2	9.2	10.3	10.9	18.5	
	s	61.2	159.8	26.0	58.5			8.0	72.0	17.2	5.7	14.5	16.3	13.1	5.5	2.5
Olivancillaria vesica vesica	w				0.8											0.5
	s				0.3				0.3							
Hastula cinerea	w															
	s												0.3			0.3
Donax hanleyanus	w	0.3	0.3		0.8	1.3	0.5	0.5		3.3	1.7	1.2	9.4	9.1	2.2	
	s	0.3			0.7	0.3	0.4		0.5	9.2	8.5	12.0	6.3	3.8	1.7	15.2
Hemipodus olivieri	w		2.3	1.3	1.3		0.5	0.3		5.8	1.2	12.0	2.8	6.6	2.5	2.0
	s		1.8		1.3		0.4			5.6	2.0	3.0	1.9	8.8	0.3	
Dispio sp.	w				14.3	0.5										
	s				128.3	4.5										
Euzonus furciferus	w															3.2
	s					0.8									12.8	
Scolelepis squamata	w															0.2
	s														6.8	
Polychaeta sp.	w															
	s										0.3					
Phaleria testacea	w	4.1	3.0		1.8	28.3			0.5		0.5	0.2		1.2		0.7
	s	4.8	5.3	1.8	2.1	17.5	0.4	0.3	3.8	0.3		2.3	0.6	5.0		
Diptera larvae	w							19.5								
	s															
Richness	w	8	7	5	9	6	5	7	5	6	7	7	6	8	6	9
	s	8	6	5	9	7	6	5	7	7	8	7	8	6	8	8
Total biomass	w	223.0	527.5	365.8	5409.9	1842.6	835.4	331.1	3355.1	6130.0	341.2	6715.0	239.0	134.3	753.8	5110.5
	s	793.8	1419.4	7937.5	17553.4	398.0	834.8	1745.1	13867.5	6533.6	363.6	709.6	435.9	764.7	547.6	5105.1

braziliensis and *Macrochiridotea lilianea* (Isopoda). The decapod *Ocypode quadrata* was only collected by the qualitative samples and its occurrence was registered at all beaches studied. Molluscs were represented by the gastropods *Olivancillaria vesica vesica* and *Hastula cinerea*, and by the bivalve *Donax hanleyanus*; and polychaetes by *Hemipodus olivieri*, *Scolelepis squamata*, *Euzonus furciferus* and *Dispio* sp. Insects were represented by the coleopteran *Phaleria testacea*, and dipteran larvae. The most abundant species were the crustaceans *Emerita brasiliensis*, *Pseudorchestoidea brasiliensis* and *Excirolana braziliensis*, contributing 97% of the total density. In spite of their higher frequency, *Phaleria testacea*, *Donax hanleyanus* and *Hemipodus olivieri* occurred in lower densities. No significant differences in macroinfauna density and biomass were observed between sampling periods at any of these beaches (Mann-Whitney test; p>0.05).

The Kruskal-Wallis test for beaches MAR, GRU, BAT, URC, ITA, ACU, JAC and MAS indicated the existence of significant variations in macroinfauna density between these beaches, the macroinfauna density at ITA being significantly lower than at MAR and MAS (Table 5). There were no significant differences in macroinfaunal densities between

TABLE 5. – Kruskal-Wallis test. Relation between macrofauna density of beaches studied and results of Dunn's test analysis undertaken as an *a posteriori* test of multiple comparisons to indicate statistical significance.

H = 22.54; p<0.01				Dunn's multiple comparisons test				
	ITA	ACU	JAC	BAT	GRU	URC	MAS	MAR
Mean ranks	16.25	20.12	27.00	29.75	31.75	38.87	46.87	48.50
Non-significance								

TABLE 6. – Simple linear regression equations.

Characteristic	Intercept	Slope	r	n
Species richness				
Grain size	6.89	- 1.86	- 0.37*	30
Swash period	3.94	0.15	0.62***	30
Dean's parameter	5.27	0.66	0.37*	30
Intertidal slope	4.25	0.12	0.43*	30
Total Density				
Swash period	- 832.66	100.17	0.42*	30
Intertidal slope	- 841.75	96.39	0.38*	30
Emerita brasiliensis density				
Swash period	- 858.53	97.29	0.42*	30
Intertidal slope	- 851.26	92.43	0.37*	30
Total biomass				
Intertidal slope	- 2562.20	419.58	0.46*	30
Emerita brasiliensis biomass				
Intertidal slope	- 2549.50	386.77	0.46*	30

*$p < 0.05$, ***$p < 0.001$.

FOG, PER, PEC, FOR, TUC, UNA and CAR (Kruskal-Wallis test; $p > 0.05$).

Species richness showed a significant positive linear relationship with Dean's parameter, swash period and slope, and a significant inverse linear relationship with mean grain size. Macroinfauna density was significantly and linearly related to swash period and slope, while total biomass showed a positive linear relation only with slope (Table 6).

At the population level, almost no significant relationships were observed between the physical parameters analysed and the density and biomass of the three most abundant species. The exceptions were the density of *Emerita brasiliensis*, which showed a significant positive relationship with the swash period and intertidal slope; and the biomass of *Emerita brasiliensis,* which showed a significant positive relationship with the intertidal slope.
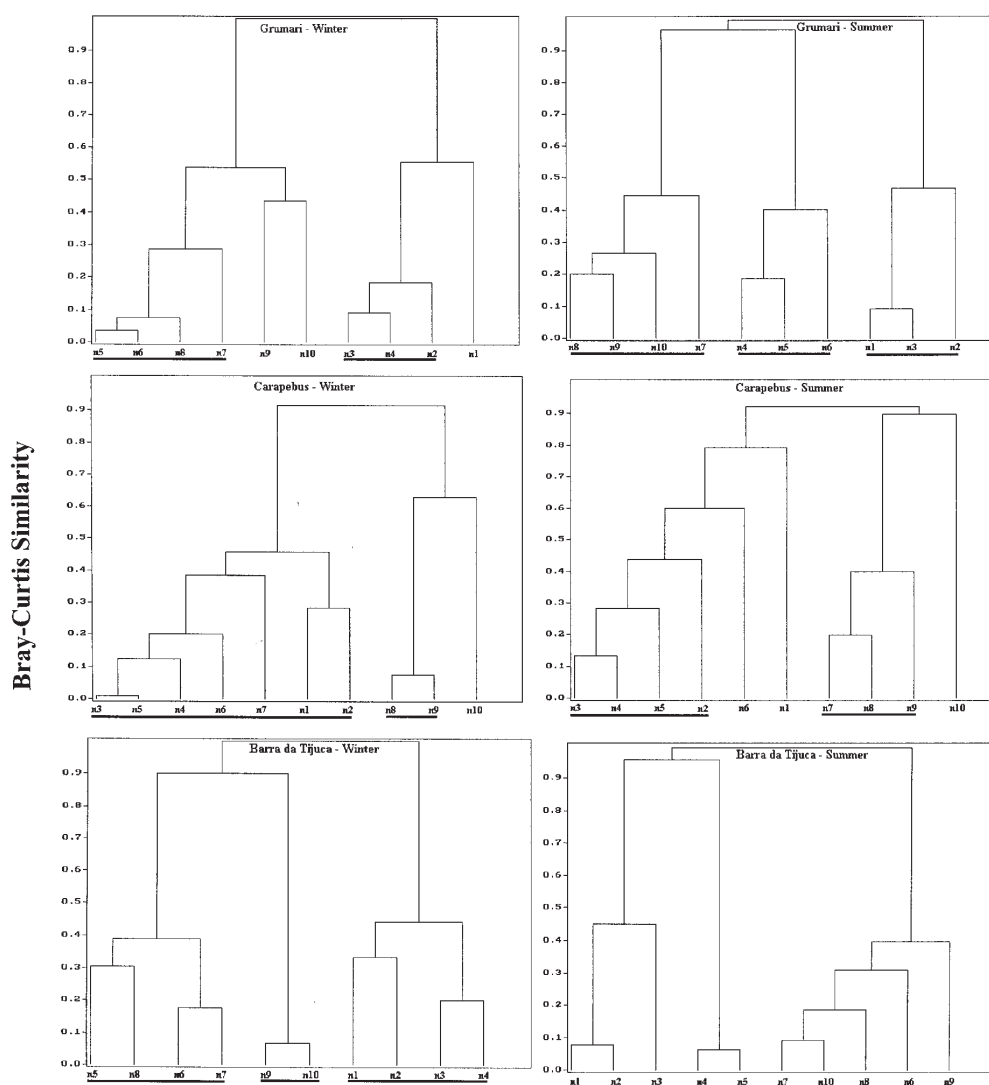

FIG. 2. – Dendrograms illustrating the zonation patterns observed at the sandy beaches studied.
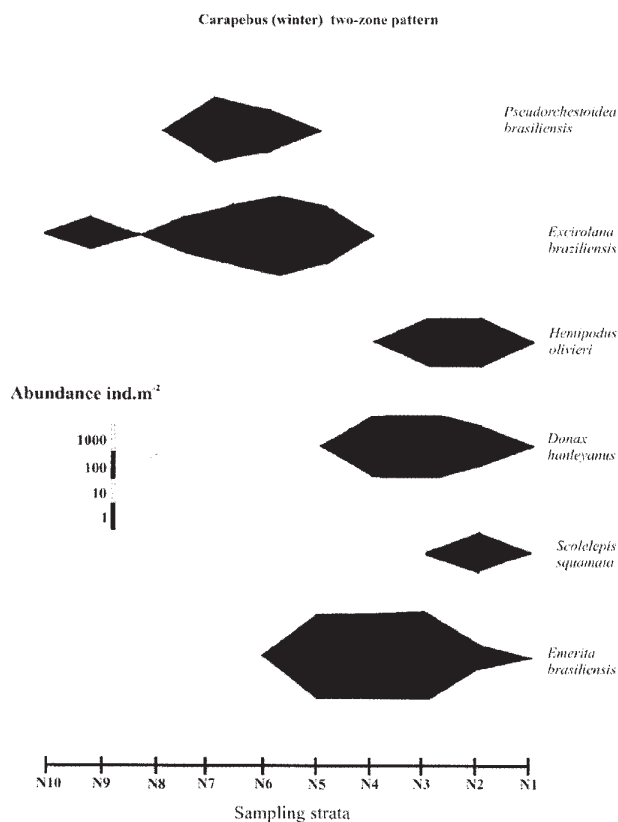
Carapebus (winter) two-zone pattern

Pecado (summer) three-zone pattern

FIG. 3. – Diagram illustrating the two-zone pattern of macroinfauna zonation.

Zonation

The analysis showed that a single pattern of zonation could not be presented for the beaches studied; rather, either two or three biological zones could be recognised (see Figs. 2, 3 and 4). The two-zone pattern consisted of a lower zone, characterised by *Emerita brasiliensis, Donax haleyanus* and *Hemipodus oliveri*; and an upper zone, characterised by *Excirolana braziliensis*, *Pseudorchestoidea brasiliensis* and *Phaleria testacea* (Fig. 3). This pattern was observed at most of the beaches (Table 7).
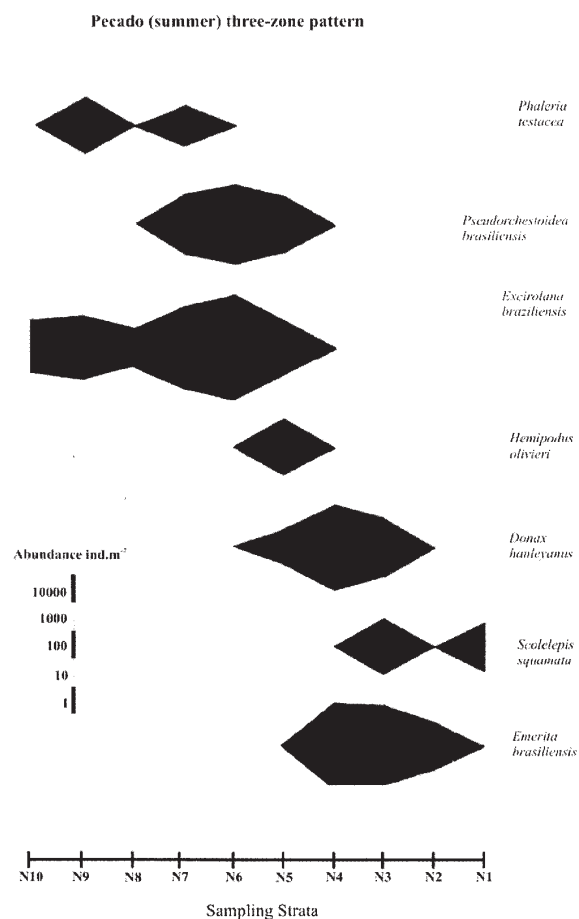
FIG. 4. – Diagram illustrating the three-zone pattern of macroinfauna zonation.

In the three-zone pattern, a lower zone, again characterised by *Emerita brasiliensis, Donax haleyanus* and *Hemipodus oliveri*; a middle zone, characterised by *Excirolana braziliensis* and *Pseudorchestoidea brasiliensis*; and an upper zone, in which the coleopteran *Phaleria testacea* was found alone or associated with *Excirolana braziliensis*, were distinguished (Fig. 4). This pattern was observed at the beaches BAT (winter and summer), MAR (winter

TABLE 7. – Number of zones formed in beaches studied in relation to grain size and intertidal slope. Beach slope – values < 1/10m are considered steep while those > 1/10m are considered gentle. w – winter, s – summer.

Type of sediment	Intertidal slope	Number of zones	Beaches
Coarse	steep	2	CAR (s); JAC (w); ACU (w, s); TUC (w; s)
	gentle	2	JAC (s); UNA (s); MAS (w); CAR (w); FOG (w)
Medium	steep	2	GRU (w); PEC (w); URC (w)
		3	BAT (w)
	gentle	2	FOG (s); URC (s); ITA (s); PER (s); PER (w); UNA (w)
		3	BAT (s); GRU (s); MAS (s); PEC (s);
Fine	steep	2	ITA (w); FOR (w, s)
	gentle	3	MAR (w, s)

and summer), GRU (summer), MAS (summer) and PEC (summer).

The beaches GRU, MAS and PEC varied in the number of zones formed between sampling periods. At these beaches, two zones in winter and three zones in summer were recognisable. When we associated these variations with the variations in grain size and intertidal slope, we observed that an increase in the number of zones at GRU and PEC was related to the gentler slope in summer at these beaches; while at MAS, grain size seemed to be the source of this variation. Also, coarse-sand beaches always showed two zones, independently of changes in beach slope (Table 7).

DISCUSSION

Grain size and wave/swash processes have been widely reported as physical features controlling the structure of macroinfauna communities (McLachlan, 1990; Defeo *et al.*, 1992; McArdle and McLachlan, 1992; Borzone *et al.*, 1996). Reflective beaches, typically with coarse sand and a steeper slope, have impoverished communities dominated by crustaceans, because crustaceans bear the wave impact better and possess greater mobility and ability to bury themselves. On the other hand, the proportion of polychaetes and molluscs increases towards the dissipative extreme (Eleftheriou and Nicholson, 1975; McLachlan *et al.*, 1981; Dexter, 1984).

In our study, species richness seemed to respond directly to morphodynamic changes, being correlated with the majority of environmental parameters analysed (mean grain size, swash period, Dean's parameter and intertidal slope). Total density was only correlated with beach slope and swash period. McLachlan (1990), relating spatial variation in abundance of benthic macroinfauna to physical parameters, found a better correlation of total abundance with Dean's parameter. In contrast, Jaramillo and McLachlan (1993) found that grain size was the best predictor of variability in the abundance and biomass of macroinfauna communities at Chilean beaches. Borzone *et al.* (1996) also suggested that sediment particle size is closely related to density. However, in spite of the granulometric differences observed between the beaches in our study, there were no significant correlations between grain size and density. The lack of a relationship between Dean's parameter and density may be explained by the narrow morphodynamic spectrum of the beaches studied. On the other hand, these results (density *vs.* intertidal slope and swash period) may be a consequence of the fact that *Emerita brasiliensis* alone accounted for most of the macrofaunal abundance. According to Bowman and Dolan (1985), beaches with relatively flat slopes and longer swash periods may provide more favourable conditions for filter-feeders. This proposal was supported by the finding of significant correlations between density and biomass of *E. brasiliensis*, and these parameters. The densities of *Pseudorchestoidea brasiliensis* and *Excirolana braziliensis* showed no significant correlations with the parameters tested. Therefore, beach morphodynamics seemed to influence community composition more than the abundance and density of the component populations.

Recently, certain investigators have pointed out the difficulties in establishing major biological zones of the intertidal zone (Raffaelli *et al.*, 1991; Defeo *et al.*, 1992), and have suggested that the only applicable zonation scheme might be that of Brown and McLachlan (1990). This scheme recognises two zones: a higher shore assemblage of air-breathers, below which all species are water-breathers. According to Gimenéz and Yannicelli (1997), two or three zones could be distinguished on exposed microtidal sandy beaches. Jaramillo *et al.* (1993) found an increase in the number of zones on more dissipative beaches. However, the beach MAR, characterised as an intermediate morphodynamic type (gentle slope and fine sand), showed three zones during both sampling periods, that is, the same pattern found on reflective medium-sand beaches such GRU (summer) and PEC (summer) . Gimenéz and Yannicelli (1997) also observed no increase in the number of zones on dissipative beaches, but nevertheless suggested that beach width and slope are the most important factors affecting the zonation pattern. The only apparent relationship observed for the beaches in our study was that coarse-sand beaches always showed two zones, independently of variations in slope (Table 7). This is probably related to the low water-retention capacity of coarse sediments, which limits the movements of their inhabitants to the wetter areas. The CAR beach, for example, changed in slope from 1/7.60 m in winter to 1/12.87 m in summer, and still continued to show the formation of two zones. Medium- and fine-sand beaches showed more variability, with three zones being more frequent on low-slope, medium-sand beaches. Thus, reflective microtidal beaches appear to show a more stable pattern of two zones, one characterised by the water-

breathing animals of the swash zone, and the other characterised by the air-breathers, as proposed by Brown and McLachlan (1990). In the subaereal zone there was constant dislocation of the organisms, probably related to their search for wetter areas.

In this study, the formation of three zones was attributable to the variation in the distributions of *P. brasilensis* and *E. braziliensis*, which appeared together in an intermediate zone, located between the swash zone and the upper part of the beach, and together with the coleopteran *P. testacea*. Defeo *et al.* (1992) observed that *P. brasiliensis* and *E. braziliensis* occupied not only the supralittoral zone but also the upper part of the midlittoral zone of Uruguayan beaches, in contrast to the observations of Dahl (1952) and Escofet *et al.* (1979), in which the talitrid amphipods dominated in the supralittoral zone and cirolanid isopods were found just below, in the midlittoral zone. The detritivores *Excirolana braziliensis*, *Pseudorchestoidea brasiliensis* and *Phaleria testacea* appear to migrate continually along the entire midlittoral zone, occurring on some beaches at the same levels (and thus only two zones were recognised, one lower and one upper) and on other beaches at separate levels (which resulted in the recognition of an intermediate zone). According to Brazeiro and Defeo (1996) and Giménez and Yannicelli (1997), species alter their distributions in response to changes in the environment (mainly the slope, position of the swash zone and width of the beach), besides other factors such as competition and availability of food, whose effects are still poorly studied. In the absence of *P. brasiliensis* and *E. braziliensis*, the coleopteran *P. testacea* enlarges its distribution along the entire midlittoral zone, as observed by Veloso (*pers. comm.*) at two other beaches of Rio de Janeiro, Ipanema and São Conrado. These results suggest that interspecies competition is occurring, and that this competition affects the distribution pattern. Defeo *et al.* (1997) studied the distribution of *Excirolana armata* and *Excirolana braziliensis*, and observed that at beaches where these species cohabit, *E. braziliensis* occurs in lower densities and in the upper part of the midlittoral zone, above *E. armata*.

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