# Effect of morphodynamics on the spatial and temporal variation of macrofauna on three sandy beaches, Rio de Janeiro State, Brazil

Valéria Gomes Veloso\* and Ricardo Silva Cardoso<sup>†</sup>

Laboratório de Dinâmica de Populações Marinhas, Departamento de Ciências Naturais, Universidade do Rio de Janeiro (UNI-RIO) Rio de Janeiro, RJ, Brazil. E-mails: \*vgveloso@osite.com.br; †rcardoso@br.homeshopping.com.br

Three exposed sandy beaches were selected to compare fluctuations in density of the most abundant species, and to verify the influence of spatial and temporal variations on the community structure. Sampling was carried out every three months, from June 1993 to May 1995, on Fora, Prainha, and Boqueirão Beaches. The first two beaches were classified by Dean's morphodynamic index ( $\Omega$ ) as intermediate, and the last as reflective. Slope, beach width and median grain size were significantly different among the beaches. Two-way analysis of variance revealed significant differences in species richness only among the beaches. No significant differences in density of the macrofauna between beaches and season were observed. However, Prainha Beach showed a higher temporal variation of the density of the macrofauna (and higher standard deviation) than the other two beaches. *Emerita brasiliensis* (Crustacea: Decapoda), *Excirolana braziliensis* (Crustacea: Isopoda), and *Pseudorchestoidea brasiliensis* (Crustacea: Amphipoda) were the most abundant species. Canonical correspondence analysis calculated the influence of the temporal variation as 27.5%; the influence of the environmental variation on community structure was 20.9%. The results suggest that in spite of the long-term fluctuations in species density, the beaches did not have temporal differences in the species richness and total density macrofauna during the study period.

#### INTRODUCTION

Variation in distribution, composition and structure of sandy beaches communities have been related to changes in environmental parameters, e.g. precipitation and temperature (Ansell et al., 1972; Croker, 1977; Dexter, 1979; Leber, 1982) and to the beach morphodynamics, e.g. slope, grain size, waves (Dexter, 1992; McLachlan, 1990,1996; McArdle & McLachlan, 1992; McLachlan et al., 1993; Jaramillo et al., 1993; McLachlan & Jaramillo, 1995). These studies have shown that there is an increase in species richness, abundance, and biomass of the macrobenthos from reflective (coarser sand, stepper slope) to dissipative beaches (finer sands, flatter slope), and also from micro/mesotidal to macrotidal beaches. McLachlan et al. (1993, 1995) have shown that the sediment parameters, wave height, and beach slope regulate the intertidal macrofauna of the sandy beaches.

Many studies about physical influences on the community structure do not consider temporal variations (Borzone et al., 1996; Defeo et al., 1992; Jaramillo et al., 1993; McLachlan et al., 1993; McLachlan, 1996). These studies cannot be used to form generalizations because they are easily misinterpreted (Brazeiro & Defeo, 1996). Moreover, studies using monthly samples have sampled only at one beach and only point which does not allow appropriate temporal comparison between communities (Santos, 1994; Souza & Gianuca, 1995; Brazeiro & Defeo, 1996; Giménez & Yannicelli, 1997; Veloso et al., 1997).

Seasonal changes in community density have been related too with the population biology of dominant species more than the physical parameter (Boesh, 1973;

Dexter, 1976, 1984, 1990; Holland & Polgar, 1976; Gianuca, 1983; Shimizu, 1991; Bamber, 1993; Veloso et al., 1993, 1997; Stecher & Dorjes, 1993; Souza & Gianuca, 1995; Cardoso & Veloso, 1996; Borzone & Souza, 1997; Veloso & Cardoso, 1999; Fonseca et al., 2000).

Studies about macrofauna life histories suggested that the beach morphodynamics might affect abundance, biomass, and maximum length (Jaramillo & McLachlan, 1993; Dugan & Hubbard, 1996). Besides, Gomez & Defeo (1999) evaluated the effect of the morphodynamics on the population biology of *Pseudorchestoidea brasiliensis* (Dana, 1853) and observed more abundance in reflective beaches. This observation contrasts with what has been verified for sandy beach communities, i.e. the dissipative beaches are more abundant (McLachlan 1990, 1996; McLachlan et al., 1993; Jaramillo et al., 1993; McLachlan & Jaramillo, 1995).

Even after several studies describing communities (cf McLachlan, 1990; Defeo et al., 1992; McLachlan et al., 1993; Jaramillo et al., 1993; McLachlan & Jaramillo, 1995), many questions are still unclear. For instance, how does the morphodynamic parameter affect the structure of communities; whether communities and populations do show different responses to physical characteristics, and whether communities which have the same species composition do have the same temporal variations.

Exposed beaches on the coast of the state of Rio de Janeiro have same communities, in which *Emerita brasiliensis* Schmitt, 1935, *P. brasiliensis* and *Excirolana braziliensis* Richardson, 1912 are the dominant species (Veloso et al., 1997; Veloso et al., unpublished data). This common occurrence provides the opportunity to compare

Journal of the Marine Biological Association of the United Kingdom (2001)

Table 1. Geographical location and physical characteristics of the beaches. Overall means values calculated from each stratum at each beach. Standard deviation in parentheses.

Beaches characteristics	Fora Beach	Prainha Beach	Boqueirão Beach
Longitude	43°11′W	43°25′W	42°29′W
Latitude	$22^{\circ}57'S$	$23^{\circ}05'S$	$22^{\circ}56'S$
Length (m)	800	500	4000
Tidal regime	Microtidal	microtidal	Microtidal
Dean parameter $(\Omega)^a$	1.87 (intermediate)	1.13 (intermediate)	0.87 (reflective)
Exposure <sup>b</sup>	sheltered	exposed	very exposed
Textural group <sup>c</sup>	medium	medium	medium to coarse
Width (m)	37.80 (5.07)	57.16 (8.16)	63.23 (13.18)
Grain size (mm)	$0.36 \ (0.06)$	0.43 (0.04)	0.58 (0.10)
Sorting (mm)	0.69 (0.06)	$0.40\ (0.03)$	$0.50\ (0.08)$
Sloped	1/12.43 (0.02)	1/7.86 (0.02)	1/6.55 (0.03)

a, Ω = breaker height/sand fall velocity×wave period; b, after McLachlan (1980); c, type of sand after Folk & Ward (1957); d, slope=1 mean gradient from above the drift line to the low tide swash region after McLachlan et al. (1993).

the communities and populations of these species on distinct type of beaches with temporal variations.

The rationale for the present work was that, if community and population have the same pattern temporal variation in density, beaches with the same species composition will show the same pattern of variation regardless of the different morphodynamic states. Three exposed sandy beaches were studied. The composition of the communities and differences in abundance of the dominant species were compared and discussed. Two null hypotheses were tested. The first was that the physical parameters (grain size, width and beach face slope) do not affect community structure and population density in the sandy beaches studied. The second was that time (represented as samples taken in different seasons) does not affect community structure and population density.

## MATERIALS AND METHODS

Sampling design

Prainha Beach, Fora Beach, and Boqueirão Beach are microtidal beaches located in the state of Rio de Janeiro, on the south-eastern coast of Brazil. The beaches were

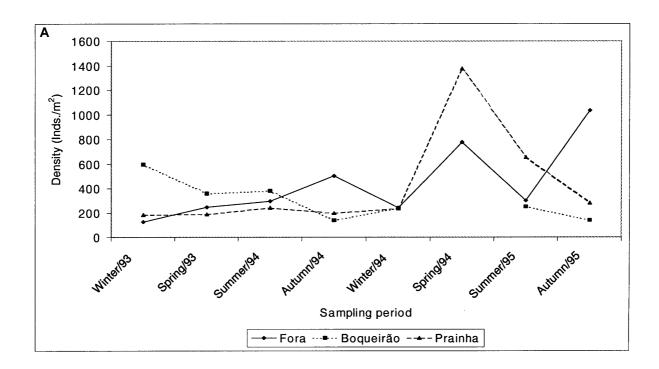
sampled during the spring low tides, every three months from July 1993 to May 1995 (Table 1). The sampling area (1.6 m<sup>2</sup>) was determined through a species-area curve. According to Cardoso & Veloso (1997), this sample area is sufficient to capture at least 90% of the intertidal macrofauna present on exposed sandy beaches.

Two transects (20-m length each) were extended from above the drift line to below the swash line, and five sampling strata parallel to the water line were sampled according to a stratified random design, defined: (i) the supralittoral zone, which corresponds to the subterrestrial fringe described by Dahl (1952) and to the zone of drying or dry sand (Salvat, 1964) above the normal high tide mark (stratum 5); (ii) the intertidal zone, which corresponds to Dahl's midshore, located between the drift line and the water line—this zone was divided into upper intertidal (stratum 4), middle intertidal (stratum 3), and lower intertidal (stratum 2)—; and (iii) the upper sublittoral zone, which corresponds to Dahl's sublittoral, where the sand is permanently saturated with water (stratum 1) (30-cm water layer). The distance between strata varied with the beach's width.

From each stratum, four replicates were randomly taken with a 0.04 m<sup>2</sup> quadrat sampler to a depth of 25 cm. The collected sediment was washed through a 0.71-mm sieve

**Table 2.** Species richness and overall mean density of species (ind  $m^{-2}$ ). Standard deviation in parentheses (Fora Beach,  $\mathcal{N}=8$ ; Prainha Beach,  $\mathcal{N}=8$ ; Boqueirão Beach,  $\mathcal{N}=7$ ).

Species	Fora Beach	Prainha Beach	Boqueirão Beach
Macrofauna species	6.75 (0.89)	5.25 (0.89)	5.00 (0.58)
Macrofauna density	440.38 (313.17)	421.85 (415.53)	301.31 (161.90)
Emerita brasiliensis Schmitt, 1935	240.95(272.30)	263.27(443.20)	35.58(24.77)
Pseudorchestoidea brasiliensis Dana, 1853	130.31(99.97)	85.53(49.78)	114.94(57.68)
Excirolana braziliensis Richardson, 1912	46.71(26.67)	63.43(36.30)	223.19(215.20)
Phaleria testacea Say, 1824	10.17(6.94)	7.33(7.61)	1.86(1.94)
Donax hanleyanus Phillipi, 1847	5.35(4.66)		0.09(0.24)
Hemipodus olivieri Orenzans & Gianuca, 1974	0.10(0.28)	2.11(2.05)	13.66(16.45)
Pisionidens indica Aiyar & Alikunhi, 1940		0.29(0.66)	0.92(1.95)
Excirolana armata Dana, 1853	1.07(1.38)	_ ′	_ ` '
Lepidopa richmondi Benedict, 1903	0.27(0.38)	0.16(0.44)	_
Macrochiridothea lilianae Moreira, 1973	4.17(4.30)	_ ` '	_



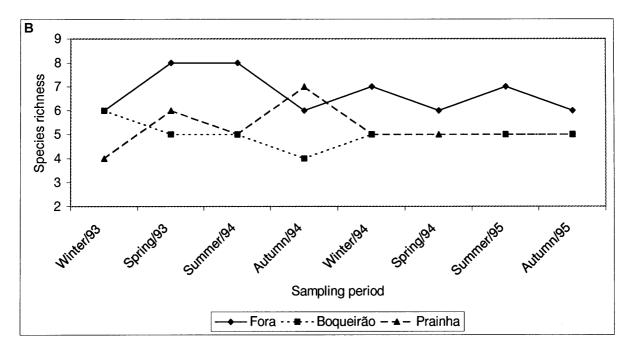


Figure 1. Macrofauna community during the study period at Fora, Prainha, and Boqueirão beaches.(A) Total density (ind m<sup>-2</sup>); (B) species richness (number).

and the retained material was taken to the laboratory, where the organisms were sorted by species, counted, and fixed in 5% formaldehyde. Density values per square metre were calculated at each beach by averaging all replicates. Species richness was also calculated pooling all replicates at each beach.

# 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 5 (supra), 3 (middle), and 1 (water line). Samples were dried in the oven at 70°C and sieved through graded screens in order to determine mean particle size and sorting parameters for each stratum (Folk & Ward, 1957). Afterwards it was calculated the mean particle size between these three strata. The beach face slope of each transect was measured by the height difference (Emery, 1961) between drift line and water line. The rating system proposed by McLachlan (1980) was used to categorize the three sandy beaches in relation to exposure. The morphodynamic state was described by Dean's  $\Omega$  parameter (Wright & Short, 1984), which was previously estimated for these beaches by Cardoso & Veloso (1997).

Journal of the Marine Biological Association of the United Kingdom (2001)

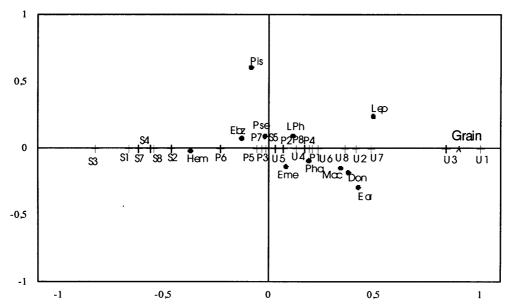


Figure 2. Diagram of the first factorial plan of the partial canonical correspondence analysis of the biological matrix conditioned by the spatial matrix, using the temporal matrix as the covariables matrix. S, Boqueirão Beach; U, Fora Beach; and P, Prainha Beach. 1–8 are the eight successive samplings. Eme, Emerita brasiliensis; Pse, Pseudorchestoidea brasiliensis; Ebz, Excirolana braziliensis; Ear, Excirolana armata; Pha, Phaleria testacea; LPh, larva de Phaleria testacea; Don, Donax hanleyanus; Pis, Pisionidens indica; Hem, Hemipodus olivieri; Lep, Lepidopa richmondi; Mac, Macrochiridothea lilianae.

#### Statistical analysis

Two way analysis of variance (ANOVA) (beach× season) was used to test for temporal and spatial differences in the physical parameters (grain mean size and beach slope) and biological parameters (total abundance, species richness, and in the density of *Excirolana braziliensis*, *Pseudorchestoidea brasiliensis*, and *Emerita brasiliensis*). Tukey's test was used *a posteriori* to assess significant differences between beaches and/or seasons. The significance level adopted was 5% (Zar, 1984).

Canonical correspondence analysis (CCA) was used to explore the structural variation of the macrofaunal community. Three matrices were constructed. The temporal matrix was composed of eight binary variables, which represent the eight sampling periods, three months apart. The spatial matrix was composed of two physical variables (grain mean size and beach slope). The biological matrix was composed of 23 seasons (sampling periods) and eight species. The multivariate analysis was performed on square-root transformed data. The variables were selected by Monte Carlo permutation.

# RESULTS

#### Habitat characterization

In Table 1 are shown the physical characteristics of the beaches. Physical parameters between the beaches were markedly different; Boqueirão was the longest beach. Significant differences among the beaches in grain size  $(F_{\rm beach}=16.93;\ df=2/11;\ P<0.05)$ , width  $(F_{\rm beach}=13.07;\ df=2/11;\ P<0.05)$  and beach slope  $(F_{\rm beach}=6.26;\ df=2/11;\ P<0.05)$  were observed. Tukey test showed significant differences in mean grain size and width of beach between the three beaches. Boqueirão Beach was significantly the wider beach which also had the coarser sediment (Table 1). Slope of the Fora Beach was significantly

lower than the slopes of the Boquerão and the Prainha beaches. However, there were no significant temporal differences in mean grain size ( $F_{\rm season}$ =0.83; df=3/11; P>0.05), width ( $F_{\rm season}$ =1.47; df=3/11; P>0.05) and in beach slope ( $F_{\rm season}$ =0.38; df=3/11; P>0.05). Physical parameters did not show significant interaction effects (season×beach).

# Community composition

The main species were *Emerita brasiliensis* (Decapoda: Hippidae), *Excirolana braziliensis* (Isopoda: Cirolanidae), and *Pseudorchestoidea brasiliensis* (Amphipoda: Talitridae), which together represented 92.6% of the Fora Beach community, 97.2% of the Prainha Beach community, and 95.3% of the Boqueirão Beach community (Table 2).

Two-way ANOVA revealed significant differences in species richness only among the beaches ( $F_{\rm beach}$ =10.66; df=2/11; P<0.05). No significant differences in density of the macrofauna between beaches and season ( $F_{\text{beach}}$ =0.25, df=2/11, P>0.05;  $F_{season}0.83$ , df=3/11, P>0.05) were observed. Also, density of Emerita brasiliensis ( $F_{\text{beach}}$ =0.95, df=2/11, P>0.05;  $F_{season}=0.69$ , df=3/11, P>0.05), P. brasiliensis ( $F_{\text{beach}} = 0.81$ , df=2/11, P > 0.05;  $F_{\text{season}} = 0.1.77$ , df=3/11, P>0.05) and Excirolana braziliensis ( $F_{\text{beach}}=2.57$ , df=2/11, P>0.05;  $F_{season}=0.73$ , df=3/11, P>0.05) did not show significant differences. However, Prainha Beach showed a higher temporal variation of the density of the macrofauna (and higher standard deviation) than the other two beaches (Figure 1A, Table 1). Species richness was usually higher at Fora Beach than and at Boqueirão Beach (Figure 1B).

The physical parameters (slope and width beaches) were not related to total density and species richness. However, there was a significant inverse linear relationship (r=-0.53; F=8.42; P<0.05; N=23) between grain size and number of species. Grain size was not significantly

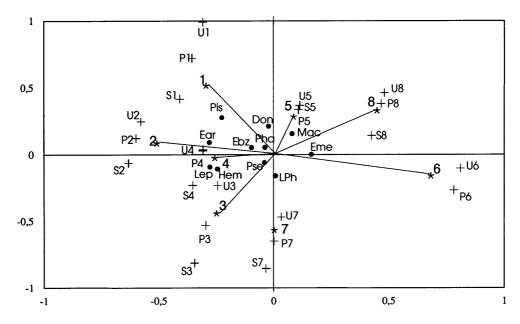


Figure 3. Diagram of the first factorial plan of the partial canonical correspondence analysis of the biological matrix, conditioned by the temporal matrix, using the spatial matrix as the matrix of covariables. Temporal variables 1, 2, 3, 4, 5, and 7 were plotted, although there was no significant relationship between them and the biological matrix. S, Boqueirão Beach; U, Fora Beach; and P, Prainha Beach. 1–8 are the eight successive samplings. Eme, Emerita brasiliensis; Pse, Pseudorchestoidea brasiliensis; Ebz, Excirolana braziliensis; Ear, Excirolana armata; Pha, Phaleria testacea; LPh, larva de Phaleria testacea; Don, Donax hanleyanus; Pis, Pisionidens indica; Hem, Hemipodus olivieri; Lep, Lepidopa richmondi; Mac, Macrochiridothea lilianae.

linearly related to the density of *Emerita brasiliensis* (F=0.44; P>0.05; N=23), or to the density of *P. brasiliensis* (F=0.92; P>0.05; N=23). However, the density of *Excirolana braziliensis* was positively and linearly related to grain size (r=0.65; F=15.64; P<0.05; N=23).

## Multivariate analysis

The three beaches were discriminated by CCA. Of the two physical variables analysed (beach slope and mean grain size), only the mean grain size contributed significantly to explain the structural variation of the community (20.9%), regardless of the temporal variation. The three beaches were discriminated along the principal axis by grain size. In Figure 2, the Boqueirão Beach samples (the coarsest grain) lie to the left of the main axis, whereas Prainha Beach samples are near the origin, and Fora Beach samples (the finest grain) lie to the right.

Temporal variation, regardless of physical variation, explained 27.5% of the structural variation of the community. Two of the eight temporal variables (samples from periods six and eight) were significantly related to the biological matrix (Monte Carlo permutation). The beaches were grouped by sampling period (season). The distances between groups increased with the time interval between the samples. In Figure 3, the values of the first year of sampling are to the left of the main axis, whereas the values of the second year of sampling are to the right of the origin.

## DISCUSSION

Studies about communities have shown that species richness, density, and biomass are inversely related to grain size and slope (Dexter, 1979,1983; McLachlan

et al., 1981, 1993, 1995; Jaramillo, 1987; Defeo et al., 1992). In the present study, grain size and beach slope were significantly different among the beaches and no significant temporal differences were observed. The grain size was correlated with richness. Fora Beach, which has finer sand and flatter slope, has the highest number of species. No correlation between total abundance and grain size was observed. Grain size seems to affect species richness to a greater extent. However, width and slope of beach did not show correlation with richness nor with total abundance. The physical influence on community structure (20.9%) showed that sediment parameters and beach slope might not be considered as the main factors affecting the dynamic of the macrofaunal communities.

Canonical analysis showed that beaches of the same sampling period formed clusters, which became separated as the time between samples increased. This suggests that density varies more between months, than between beaches at the same period. However, no statistical differences in total abundance between the beaches and sampling period (season) were found.

Physical variables were not the main factor affecting fluctuations in the densities of *Emerita brasiliensis* and *Pseudorchestoidea brasiliensis*. Dugan & Hubbard (1996), on the coast of California, did not observe any relationship between the abundance of *Emerita brasiliensis* and beach morphodynamic states but this study did not consider the temporal variation. Gomez & Defeo (1999), evaluating the effect of the morphodynamics on life history of *P. brasiliensis*, did not find correlation between abundance and beach morphodynamics. However, the density of *Excirolana braziliensis* was positively related to grain size. Defeo et al. (1997) previously reported higher abundances of *E. braziliensis* on reflective beaches than on dissipative beaches. According to Defeo et al. (1997), *E. braziliensis* 

Journal of the Marine Biological Association of the United Kingdom (2001)

374

has the highest densities on reflective beaches because of the absence of competition with *E. armata* Dana, 1853, which is a related species observed on dissipative (finergrained) beaches. This is a possible explanation, given that the lowest abundance of *E. braziliensis* was observed on Fora Beach, the only beach where *E. armata* occurred.

The results show that the abundance of the communities was not related with grain size, beach width and slope, but the number of beaches sampled may have affected the analysis. Moreover, the abundance of a population may result from the interaction between many factors (which were not assessed in this work) such as, food source, recruitment, predation, and competition which cause large variability between beaches. Thus, variation of the abundance is probably related to these interactions and few isolated factors are not enough to describe it. Therefore, population studies are needed to clarify the effect of beach morphodynamics on species biology and communities.

We wish to thank Dr D.B. Fonseca and two anonymous referees for English language revision and for critically reading the manuscript. Thanks to all participants in the field work.

## REFERENCES

- Ansell, A.D., Sivadas, P., Naraynan, B. & Trevallion, A., 1972.
  The ecology of two sandy beaches in south west India. II.
  Notes on *Emerita houthuisis*. *Marine Biology*, 17, 311–317.
- Bamber, R.N., 1993. Changes in the infauna of a sandy beach. Journal of Experimental Marine Biology and Ecology, 172, 93-107.
- Boesch, D.F., 1973. Classification and community structure of macrobenthos in Hampton Roads Area. Virginia. *Marine Biology*, 21, 226–244.
- Borzone, C.A. & Souza, J.R.B., 1997. Estrutura da macrofauna bentônica no supra, meso e infralitoral de uma praia arenosa do sul do Brasil. *Oecologia Brasiliensis*, **3**, 197–212.
- Borzone, C.A., Souza, J.R.B. & Soares, A.G., 1996. Morphodynamic influence on the structure of inter and subtidal macrofaunal communities of subtropical sandy beaches. Revista Chilena de Historia Natural, 69, 565–577.
- Brazeiro, A. & Defeo, O., 1996. Macroinfauna zonation in microtidal sandy beaches: is it possible to identify patterns in such variable environments? *Estuarine, Coastal and Shelf Science*, 42, 523–536.
- Cardoso, R.S. & Veloso, V.G., 1996. Population biology and secondary production of the sandhopper *Pseudorchestoidea brasiliensis* (Amphipoda: Talitridae) at Prainha Beach, Brazil. *Marine Ecology Progress Series*, **142**, 111–119.
- Cardoso, R.S. & Veloso, V.G., 1997. Estratégia amostral para caracterização da macrofauna da região entre-marés em três praias arenosas expostas do Estado do Rio de Janeiro, Brasil. *Oecologia Brasiliensis*, 3, 171–182.
- Croker, R.A., 1977. Macroinfauna of northern New England marine sand: long-term intertidal community structure. In *Ecology of marine benthos* (ed. B.C. Coull), pp. 439–450. Columbia: University of South Carolina Press.
- Dahl, E., 1952. Some aspects of the ecology and zonation of the fauna on sandy beaches. *Oikos*, **4**, 1–27.
- Defeo, O., Brazeiro, A., Alava, A. de & Riestra, G., 1997. Is sandy beaches macroinfauna only physically controlled? Role of substrate and competition in isopods. *Estuarine, Coastal and Shelf Science*, 45, 453–462.
- Defeo, O., Jaramillo, E. & Lyonnet, A., 1992. Community structure and intertidal zonation of the macroinfauna on the Atlantic coasts of Uruguay. *Journal of Coastal Research*, 8, 830–839.

- Dexter, D.M., 1976. The sandy beach fauna of Mexico. Southwestern Naturalist, 20, 479–485.
- Dexter, D.M., 1979. Community structure and seasonal variation in intertidal Panamanian sandy beaches. *Estuarine, Coastal and Marine Science*, **9**, 543–558.
- Dexter, D.M., 1983. Community structure of intertidal sandy beaches in New South Wales, Australia. In *Sandy beaches as ecosystems* (ed. A. McLachlan and T. Erasmus), pp. 461–472. The Hague: Dr W. Junk Publishers.
- Dexter, D.M., 1984. Temporal and spatial variability in the community structure of the fauna for four sandy beaches in southeastern New South Wales. *Australian Journal of Marine and Freshwater Research*, **35**, 663–672.
- Dexter, D.M., 1990. The effect of exposure and seasonality on sandy beach community structure in Portugal. *Ciéncia Biologia Ecologia e Systemática*, **10**, 31–50.
- Dexter, D.M., 1992. Sandy beach community structure: the role of exposure and latitude. *Journal of Biogeography*, **19**, 59–66.
- Dugan, J.E. & Hubbard, D.M., 1996. Local variation in populations of the sand crab *Emerita analoga* on sandy beaches in Southern California. *Revista Chilena de História Natural*, 69, 579–588
- Emery, K.O., 1961. A simple method of measuring beaches profiles. *Limnology and Oceanography*, **6**, 695–710.
- Folk, R.L. & Ward, W.C., 1957. Brazos River Bar: a study in the significance of grain size parameters. *Journal of Sedimentary Petroly*, **27**, 3–26.
- Fonseca, D.B., Veloso, V.G. & Cardoso, R.S., 2000. Growth, mortality, and reproduction of *Excirolana braziliensis* Richardson, 1912 (Isopoda: Cirolanidae) on the Prainha Beach, Rio de Janeiro, Brazil. *Crustaceana*, **73**, 535–545.
- Gianuca, N., 1983. A preliminary account of the ecology of sandy beaches in southern Brazil. In *Sandy beaches as ecosystems* (ed. A. McLachlan and T. Erasmus), pp. 413–420. The Hague: Dr W. Junk Publishers.
- Gimenez, L. & Yannicelli, B., 1997. Variability of zonation patterns in temperate microtidal Uruguayan beaches with different morphodynamic types. *Marine Ecology Progress Series*, **160**, 197–207.
- Gomez, J. & Defeo, O., 1999. Life history of the sandhopper Pseudorchestoidea brasiliensis (Amphipoda) in sandy beaches with contrasting morphodynamics. Marine Ecology Progress Series, 182, 209–220.
- Holland, A.F. & Polgar, T.T., 1976. Seasonal changes in the structure of an intertidal community. *Marine Biology*, **37**, 341–348.
- Jaramillo, E., 1987. Community ecology of Chilean sandy beaches. PhD thesis, University of New Hampshire, Durham, USA.
- Jaramillo, E. & McLachlan, A., 1993. Community and population responses of the macroinfauna to physical factors over a range of exposed sandy beaches in south-central Chile. *Estuarine, Coastal and Shelf Science*, 37, 615–624.
- Jaramillo, E., McLachlan, A. & Coetzee, P., 1993. Intertidal zonation patterns of macroinfauna over a range of exposed sandy beaches in south-central Chile. *Marine Ecology Progress* Series, 101, 105–118.
- Leber, K.M., 1982. Seasonality of macroinvertebrates on a temperature, high wave, energy sandy beach. *Bulletin of Marine Science*, 32, 86–98.
- McArdle, S. & McLachlan, A., 1992. Sand beach ecology: swash factors relevant to the macrofauna. *Journal of Coastal Research*, **8**, 398–407.
- McLachlan, A., 1980. The definition of sand beaches in relation to exposure: a simple rating system. *South African Journal of Science*, **76**, 137–138.
- McLachlan, A., 1990. Dissipative beaches and macrofauna communities on exposed intertidal sands. *Journal of Coastal Research*, **6**, 57–71.
- McLachlan, A., 1996. Physical factors in benthic ecology: effects of changing sand particle size on beach fauna. *Marine Ecology Progress Series*, 131, 205–211.

- McLachlan, A. & Jaramillo, E., 1995. Zonation on sandy beaches. Oceanography and Marine Biology. Annual Review, 33, 305–335
- McLachlan, A., Jaramillo, E., Defeo, O., Dugan, J., Ruyck, A. de & Coetzee, P., 1995. Adaptations of bivalves to different beach types. Journal Experimental Marine Biology and Ecology, 187, 147–160.
- McLachlan, A., Jaramillo, E., Donn, T.E. & Wessels, F., 1993. Sandy beach macrofauna communities and their control by the physical environment: a geographical comparison. *Journal of Coastal Research*, **15**, 27–38. [Special Issue.]
- McLachlan, A., Wooldrige, T. & Dye, A.H., 1981. The ecology of sandy beaches in southern Africa. South African Journal of Zoology, 16, 219–231.
- Salvat, B., 1964. Les conditions hydrodynamiques interstitielles des sédiments meubles intertidaux et la répartition verticale de la jemme endogée. Cahiers de Recherche de l'Académie des Sciences de Paris, 259, 1576–1579.
- Santos, P.J.P.S., 1994. Environmental characterization of sandy beaches in southern Brazil. *Neritica*, 8, 31–45.
- Shimizu, R.M., 1991. A comunidade de macroinvertebrados da região entre-marés da praia de Barequeçaba, São Sebastião, SP. Dissertação de Mestrado. Universidade de São Paulo, Brazil.

- Souza, J.R.B. & Gianuca, N.M., 1995. Zonation and seasonal variation of the intertidal macrofauna on a sandy beach of Paraná State, Brazil. Scientia Marina, 59, 103–111.
- Stecher, J. & Dörjes, J., 1993. Das makrozoobenthos im vorfeld der inesel spiekerooj i. saisonale fiedungsftrukturen im foreshore-bereich. Fenckenbergiana Maritima, 23, 49–66.
- Veloso, V.G. & Cardoso, R.S., 1999. Population biology of the mole crab *Emerita brasiliensis* (Decapoda: Hippidae) at Fora Beach, Brazil. *Journal of Crustacean Biology*, 19, 147–153.
- Veloso, V.G., Cardoso, R.S. & Fonseca, D.B., 1997. Spatio-temporal characterization of the intertidal macrofauna community at Prainha Beach (Recreio dos Bandeirantes), State of Rio de Janeiro. Oecologia Brasiliensis, 3, 213–225.
- Veloso, V.G. & Valentin, J.L., 1993. Larval distribution and seasonal abundance of *Emerita brasiliensis* Schmitt, 1935 (Decapoda: Hippidae) in southern Brazil. *Revista Brasileira de Biologia*, 53, 131–141.
- Wright, L.D. & Short, A.D., 1984. Morphodynamic variability of surf zones and beaches: a synthesis. *Marine Geology*, 48, 259–284
- Zar, J.H., 1984. Biostatistical analysis. New Jersey: Prentice-Hall.

Submitted 12 June 2000. Accepted 30 January 2001.