Macrofaunal zonation and sediment properties on a low-energy, mesotidal sandy beach (Ria de Aveiro) (northwestern Portugal)

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ABSTRACT

We present the results of a study on faunal zonation and sediment properties on a low-energy, mesotidal sandy beach located on Ria de Aveiro (northwestern Portugal). The topography of the sampling area was mapped and five strata were defined in situ according to their macroscopic characteristics. A stratified random design was used to sample the fauna and environmental parameters. Anova (for environmental parameters) and multivariate analysis (for faunal data) showed that significant differences occurred across the shoreline. The beach is of an intermediate morphodynamic type, with a reflective, more physically controlled upper shore, and a dissipative, more chemically controlled lower shore. Although our multivariate analysis of the fauna fits in with the classical tripartite zonation of sandy beaches, the variation we found in faunal distribution makes it possible to further subdivide the two lower areas, resulting in a total of five valid faunal zones, matching the strata defined a priori.

Keywords: Beach, zonation, macroinvertebrates, estuaries, Portugal.

RESUMEN

Estructura de la macrofauna y propiedades sedimentarias en una playa arenosa mesotidal de baja energía de la ría de Aveiro (noroeste de Portugal)

Se han investigado la zonación faunística y las propiedades del sedimento en una playa arenosa, mesotidal y de baja energía, situada en la ría de Aveiro (noroeste de Portugal). Se determinó la topografía de la playa y se definieron cinco estratos en relación a sus características macroscópicas. La significatividad de las diferencias entre las subáreas fue evaluada utilizando un muestreo estratificado aleatorio, que abarcaba las características faunísticas y ambientales, y aplicando a los datos obtenidos los análisis anova y multivariante. La playa estudiada es de tipo morfodinámica intermedia, más reflectiva en la zona alta, donde se efectuó un control preferentemente de tipo físico, y más disipativa en la zona baja, más controlada químicamente. El análisis multivariante de la fauna concuerda con la clásica zonación tripartita de las playas arenosas. No obstante, la variación en la distribución de la fauna permite hacer otra subdivisión de las dos áreas más bajas, resultando, en total, cinco zonas faunísticas válidas, coincidientes con los estratos de muestreo definidos a priori.

Palabras clave: Playa, zonación, macroinvertebrados, estuarios, Portugal.

INTRODUCTION

In estuarine environments, the vertical gradient from sea to land and the marine-freshwater salinity gradient interacting with local conditions of exposure, hydrology and sediment environment may originate a complex array of shore types. In intertidal areas, osmotic problems due to groundwater runoff, rainfall or increased evaporation, and emersion factors, such as greater light intensity, temperature variation and desiccation, are limiting physico-chemical factors for macrofaunal communities (Raffaelli and Hawkins, 1996).

Primary production on most fine-particle shores is limited to diatoms and other microalgae (Reise, 1992), and most energy enters the system from plankton or as organic detritus from the land and adjacent tidal marshes. Under such conditions, drifting seaweeds left on the shore by the receding tides and the presence of seagrass beds provide an important additional source of organic matter, protection from desiccation or predation, and a nutrient-rich habitat for small organisms (Orth, 1992; Vadas and Elner, 1992). Small crustaceans are common inhabitants of these shores, and their distribution patterns have been used to characterise zonation schemes for fine-particle shores (Dahl, 1952; John and Lawson 1991; Santelices, 1991). On estuarine beaches, these arthropods, together with other macroinvertebrates, such as polychaetes and molluscs, often establish dense assemblages which are subjected to predation by waders during ebb, and foraging fishes during flood. Food availability, competition and predation are dynamic biological processes which, together with the physico-chemical factors, shape the ecology of sandy shores (Raffaelli and Hawkins, 1996). However, competition for space is of much lesser importance than on rocky shores (McLachlan and Jaramillo, 1995).

Zonation schemes proposed by several authors have been discussed in more detail by McLachlan and Jaramillo (1995) in their comprehensive review of intertidal sandy beaches on open coasts. These authors conclude that zonation on sandy beaches is dynamic, and varies according to the beach type, season, and rhythmic behaviour or mobility of their inhabitants. On rocky shores, zonation is particularly distinctive, and zones are usually defined biologically, but on sandy beaches, with their inconspicuous and rather mobile inhabitants, the definition of zones is not so evident, and only applies during low tide.

In the present study, the vertical zonation on a low-energy, mesotidal sandy beach on Ria de Aveiro is described, and discussed in relation to its sediment properties. By using a statistical approach, we intended to demonstrate that a thorough observation of the shore makes it possible to demarcate zones having biological significance. Different sub-areas across the beach were established a priori, based on a number of in situ macroscopic observations (e.g., changes in slope, colour and grain size of the sediment, presence of macroalgae, biogenic materials and bioturbation). A stratified random sampling of both faunal and environmental characteristics, followed by anova (applied to environmental parameters) and multivariate analyses (applied to faunal data) were then used to assess the significance of the differences found among the sub-areas or strata.

MATERIALS AND METHODS

Study area

The Ria de Aveiro (northwest Portugal) is a shallow coastal ecosystem with a surface area of about 45 km². The narrow sandbar that separated the lagoon from the sea a few centuries ago favoured the development of a diversity of habitats along its network of channels and islands. The nature of the sediment in intertidal areas reflects in part their exposure to water circulation, as well as the geological history of the area, which determines the availability of sediment sizes. The major input of freshwater and sediment particles of continental origin occurs in the ria's central area. In the northern areas, sheltered conditions and the extensive seagrass meadows favour the deposition of fine particles, whereas the more dynamic conditions near the mouth originate mixed and sand flats characterised by small-scale topographic formations. In the southern areas, the dominance of sandy sediments is closely related to the high-flow tidal regime, and the low input of solids from freshwater sources.

The sampling site (figure 1) is adjacent to a small patch of salt marsh, located on the western bank of the lower reaches of Mira Channel, which runs southwards from the mouth of the ria. The distance from the mouth is approximately 1.5 km, and the tidal range varies between 1.3 and 2.7 m at neap and spring tides, respectively.

Figure 1. Location of the study site on Ria de Aveiro
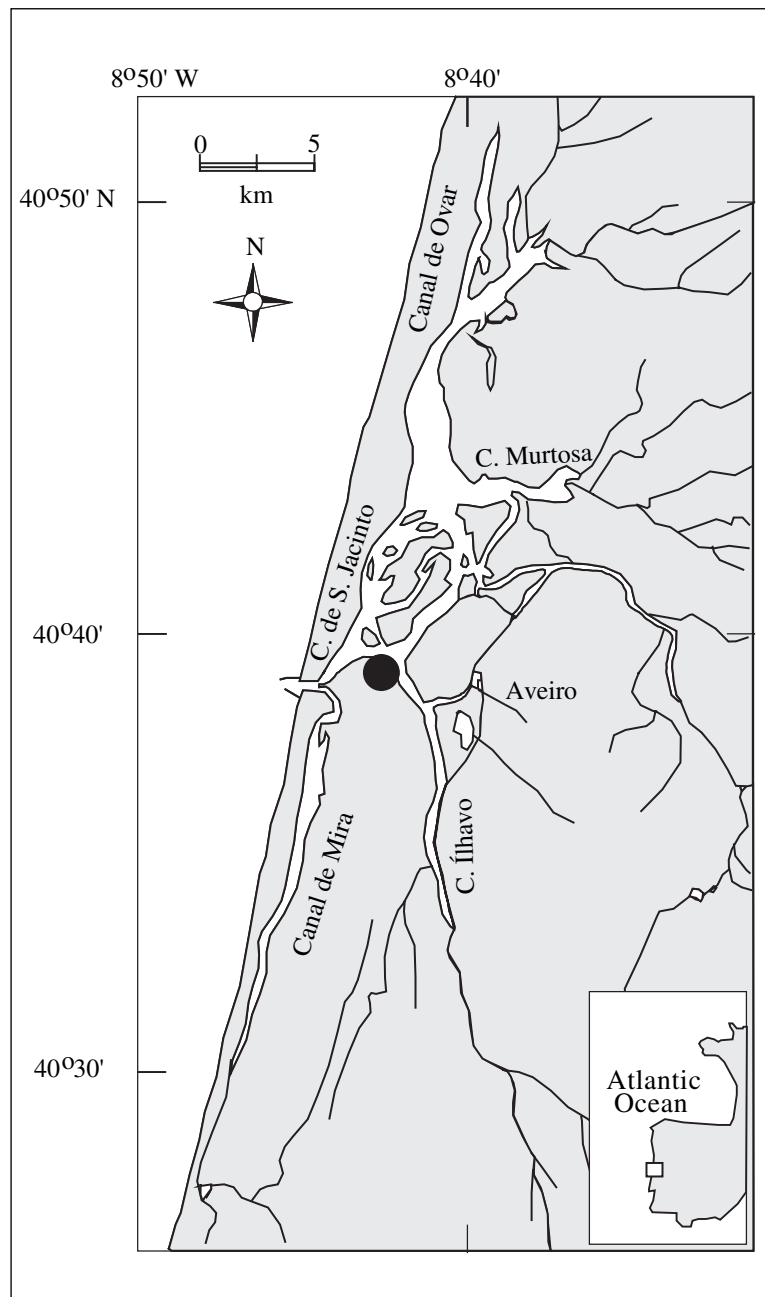
Sampling and laboratory procedures

Sampling was carried out in June 2000 at low water of a full-moon spring tide. The topography of the area was mapped according to height differences measured along two transects, at 8 m intervals, from the strandline down to the waterline and up to the beginning of marsh vegetation. The sampling area (25 m × 160 m) was divided into five sub-areas according to their macroscopic characteristics: 1) fine sand, bright and dry, above the strandline, with abundant detritus and beached algae; 2) bright sand with some broken shells, marked by numerous microripples; 3) cream-coloured sand with a few macroalgae (*Ulva* sp.); 4) light-brown sandy sediment covered by a thin layer of mud, with a few macroalgae (*Ulva* sp. and *Enteromorpha* sp.), *Cerastoderma edule* empty shells and small polychaete tubes; 5) dark-brown sediment with some macroalgae (*Gracilaria* sp., *Ulva* sp. and *Enteromorpha* sp.), and conspicuous *Diopatra neapolitana* and other polychaete tubes. Noticeable changes in the slope of the beach were also used to establish the boundaries of the sub-areas which were later compared with high- and low-wa-

ter levels at spring and neap tides (figure 2). Subsequently, the sub-areas were named as: 1) supralittoral fringe (SF); 2) upper eulittoral (UE); 3) middle eulittoral (ME); 4) lower eulittoral (LE); 5) infralittoral fringe (IF).

A stratified random design was used, and five replicates were allocated to each sub-area (or stratum). The macrofauna replicates were collected using a corer. The sampling area of each stratum (5×0.01 m²) is sufficient to obtain average densities of most species, with a standard error inferior to 20 % of the mean. The samples were washed in the field through a 0.5 mm sieve, and preserved in 10 % formalin. The organisms were later sorted, identified and counted. The biomass of each species, expressed as ash-free dry weight (AFDW), was obtained after ignition of the dried specimens (60 °C) in a muffle oven for 5 h at 450 °C. The AFDW was determined to the nearest 0.1 mg.

The temperature of the sediment, redox potential at the surface, and 2, 5 and 10 cm depths and salinity of interstitial water (when available) were recorded in the field at the exact location of each macrofauna replicate. Corresponding smaller core replicates were also taken for sediment analyses. The water content (moisture) was determined as the weight difference between the wet and dried (60 °C) sediment, and organic content was determined as the weight difference between the dried and incinerated (450 °C) sediment. Grain size was described using the Wentworth scale in phi (Φ) units (Buchanan and Kain, 1971; McLachlan and Turner, 1994). The granulometric mean was estimated as the average of the 10, 30, 50, 70 and 90 % Φ, determined graphically using the cumulative curve derived from the sieving analysis of the replicates. Sediment sorting was assessed using the quartile deviation: $QD\Phi = (Q_3\Phi - Q_1\Phi)/2$.

The sampling also included the collection of surficial sediment (area: 6.07 cm²; depth: 1 cm) for chlorophyll *a* analysis. The photosynthetic pigments were extracted with 30 ml of 90 % acetone, in the dark at 4 °C, during 24 h (Talling, 1974; Wetzel and Likens, 1991). The concentration (mg l⁻¹) in the extract was determined fluorimetrically (Yentsch and Menzel, 1963), using a Jasco FP-777 spectrofluorimeter calibrated with a known solution of chlorophyll *a*. The concentration in the sediment (mg m⁻²) was calculated by the equation:

Chlorophyll $a = $ [Chlorophyll a (mg l⁻¹) $\times$ V]/A

where V is the volume of the extract (in l) and A is the sampled area (in m²).

Statistical analysis

One-way anova was used to test the significance of the differences between strata for each measured environmental parameter. The homogeneity of variances was assessed by the Levene test. Unplanned paired comparisons of the mean values using the Tukey test were performed whenever applicable (Zar, 1996).

The nonparametric Kendall's rank correlation coefficient was used to determine the association of faunal parameters (density and biomass) with sediment properties.

Multivariate analysis of the faunal data was performed using the primer statistical package (Clarke and Warwick, 2001). The abundance data were first organised into a sample/species matrix. UPGMA classification and non-metric MDS ordination were performed using the Bray-Curtis similarity measure after fourth root transformation of the data (Field,
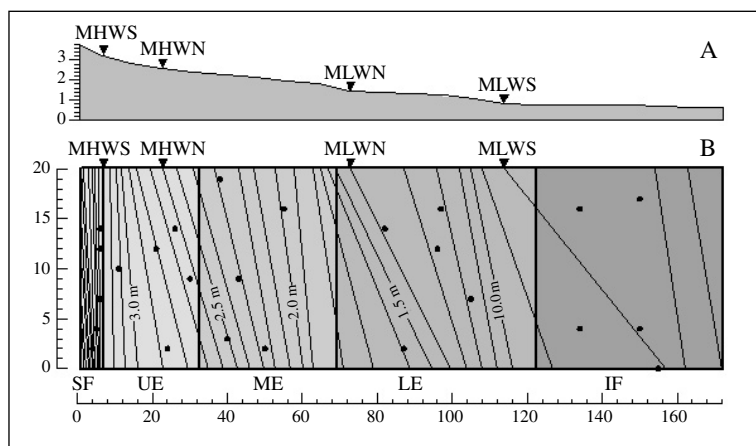

Figure 2. (A): bathymetry. (B): a priori zonation and location of the replicates. (SF): supralittoral fringe; (UA): upper eulittoral; (ME): middle eulittoral; (LE): lower eulittoral; (IF): infralittoral fringe; (MHWS): mean high-water level at spring tide; (MHWN): mean high-water level at neap tide; (MLWN): mean low-water level at neap tide; (MLWS): mean low-water level at spring tide

Clarke and Warwick, 1982). An analysis of similarities (anosim) by randomization/permutation tests was performed on the MDS results (Clarke, 1993) to assess the significance of spatial differences across the beach. Five a priori groups of replicates corresponding to the different sub-areas were used. Finally, ABC curves (abundance/biomass comparison method) were drawn to illustrate differences in the community structure of the five strata, and to detect eventual effects of natural environmental stress (Lambshead, Platt and Shaw, 1983; Warwick, 1986; Meire and Dereu, 1990).

RESULTS

This estuarine beach clearly falls within the dissipative morphodynamic type. However, it has a characteristic concave shape, with slightly more reflective conditions on the upper shore. Wave action is negligible, except for stormy conditions. Tidal currents are the most important hydrodynamic factor, and maximum velocity is attained at mid-ebb. A lower peak is observed at mid-flood, and minimum values occur at high water and low water (unpublished results).

Sediment properties

One-way anova performed on the environmental data demonstrated significant differences across the shore but the results of the subsequent Tukey tests (figure 3) showed that the strata are not grouped consistently for all variables.

The temperature varied from 25-27 °C in the upper shore (SF, UE), 22-24 °C in the midshore (ME, LE) and 18-20 °C in the lower shore (IF). Moisture increased downshore from dry sand in the SF (less than 8 % wet weight), to moist sand in the eulittoral (10-20 %) and saturated sand in the IF (more than 35 %). The zone of groundwater discharge or resurgence was located near the lower boundary of LE. Salinity could only be measured in the IF (30-33). Organic content also varied from very low values (less than 0.5 % dry weight) in the upper shore (SF, UE and ME) to increasingly important values in the LE (1.0-1.5 %) and IF (3.0-4.0 %). The organic content was positively correlated to the amount of finer particles in the sediments ($\tau = 0.593$; $P < 0.01$) and redox potential was negatively correlated to the variation of organic content ($\tau = -0.467$; $P < 0.01$). The thickness of the oxygenated layer decreased down shore and reducing conditions occurred at 5 cm depth in the LE and at the surface in the IF. Sediment sorting was poorer down shore (LE and IF) and the mean grain size ranged from very fine sand in the IF, fine sand in the SF, UE and LE and coarse sand in the ME. Chlorophyll concentration was maximal in the LE (55-75 mg m^{-2}), intermediate in the IF and ME (35-45 mg m^{-2}) and minimal in the upper shore (less than 25 mg m^{-2} in the SF and UE).

Faunal data

The variation of general faunal descriptors is illustrated in figure 4. The lowest values of species richness, density and biomass were observed at the
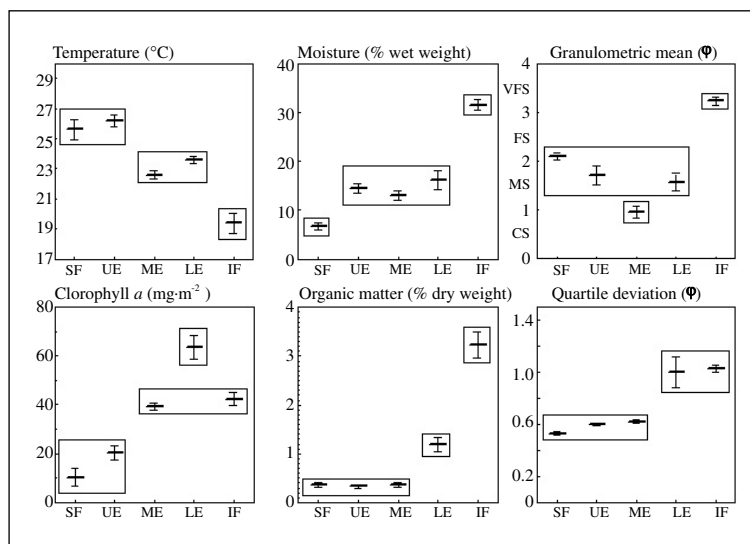

Figure 3. Environmental parameters and results of the Tukey tests. Boxes indicate nonsignificant differences. Other abbreviations as in figure 2
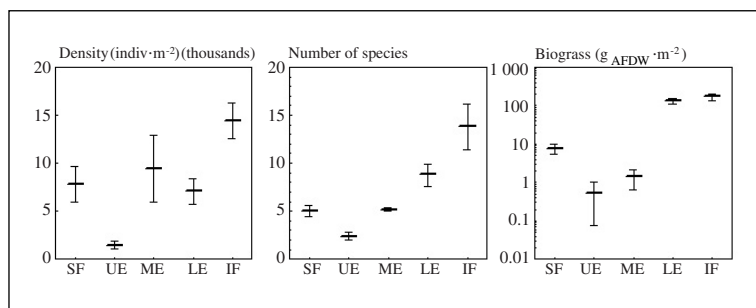
Figure 4. Faunistic indicators. Average and standard error bars. Other abbreviations as in figure 2

UE (6 species, 1 480 indiv m^{-2}, and 0.5 g m^{-2}, respectively), and the highest values were observed at the IF (28 species, 14 480 indiv m^{-2} density, and 171.1 g m^{-2} biomass). Biomass variation across the beach showed significant correlations to all sediment properties, whereas density was only significantly correlated to redox potential, organic content and temperature (table I).

The collected specimens were ascribed to a total of 41 different taxa, many of which showed restricted vertical distributions (figure 5, table II). Only one undetermined species of small-sized oligochaetes and the gastropod *Hydrobia ulvae* occurred in all the sampling strata. The bivalve *C. edule* occurred in all strata except for the SF, and it showed a clear differential zonation of size classes with the smallest individuals upper and the larger individuals lower in the shore.

The results of the UPGMA show a tripartite zonation of the beach into upper, mid, and lower shore (figure 6A-C, respectively). These three groups are formed at a 45 % similarity level, but the mid and lower shore are further divided in two groups corresponding to the UE and ME on the mid shore and to the LE and IF in the lower shore. This partition is further substantiated by the MDS ordination (figure 6), showing a clear aggregation of

the replicates of each stratum, with the five strata forming discrete groups, and a certain proximity between the UE and ME replicates and between the LE and IF replicates, which are better separated along the yy axis. The anosim tests indicated that differences between the five strata are statistically significant (R = 0.852, p < 0.1 %).

The faunal assemblages were interpreted according to the results of the multivariate analyses. The upper shore that included only the replicates from the SF was characterised by the presence of several insect species and was numerically dominated by the amphipod *Talitrus saltator*. Talitrid amphipods (*T. saltator, Talorchestia deshayesii*) and the isopod *Tylos europaeus* were the major contributors to biomass (figure 5).

The mid shore (UE and ME) was mainly typified by the presence of the cirolanid isopod *Eurydice pulchra* and by the dominance of small-sized oligochaetes (figure 5). The UE showed a very poor faunal assemblage, with only a few species present, and the lowest density and biomass values. In the ME, biomass was also very low, but the density was largely increased due to the number of oligochaetes and gastropods (*H. ulvae*). Some polychaetes began to occur at this level of the beach, which was also typified by the presence of *Scoloplos armiger*.

The lower shore (LE and IF) was characterised by high species richness and by the dominance of polychaete species. Bivalves were the major contributors to biomass, which attained its maximum value at this level of the beach. The LE was dominated by the polychaete *Pygospio elegans*, and also had the highest density of bivalves (*C. edule* and *Scrobicularia plana*). The highest value of mean individual weight (total biomass divided by total abundance) was recorded for the assemblage of this stratum. The IF was characterised by the increasing densities of many polychaetes, especially *Heteromastus filiformis* and *Mediomastus fragilis*, and by the occurrence of ty-

Table I. Kendall's rank correlation coefficients between faunal parameters (abundance and biomass) and sediment properties; n = 25; (*): p < 0.05; (**): p < 0.01; (ns): non-significant

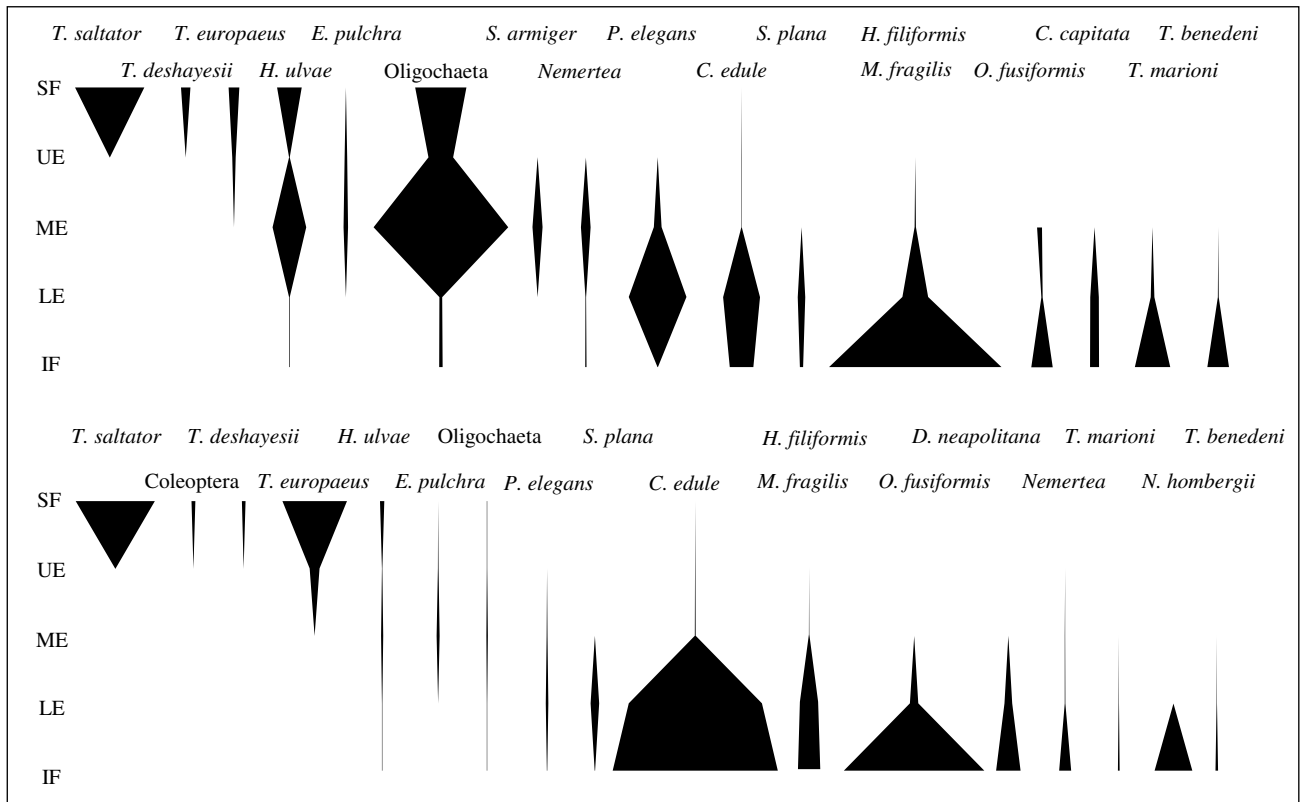| Variable	Abundance		Biomass	
Temperature	−0.500	**	−0.313	*
Redox potencial	−0.413	**	−0.467	**
Moisture	+0.193	ns	+0.380	**
Organic content	−0.413	**	+0.647	**
Clorophyll *a*	+0.227	ns	+0.353	*
Grain size	+0.160	ns	+0.340	*
Sorting	+0.217	ns	+0.357	*

Figure 5. Spatial distribution of the main macroinvertebrate taxa. Upper graph: abundance. Lower graph: biomass. Other abbreviations as in figure 2

pically sublittoral species (e.g. *Aonides oxycephala*, *Nephtys hombergii* and *Nereis longissima* and *Tharix marioni*). *Owenia fusiformis* was the second major contributor to biomass (after the bivalve *C. edule*).

The ABC curves applied to the assemblages of the five strata indicated unstressed conditions, except for the ME, where large species were absent and the assemblage was numerically dominated by very small-sized species. The curves for the lower shore (LE and IF), with the line for abundance po-

sitioned well below the line for biomass, are typical of assemblages approaching equilibrium (figure 7).

DISCUSSION

The physico-chemical environment

Our results from the beach showed decreasing temperature and increasing moisture of the sedi-
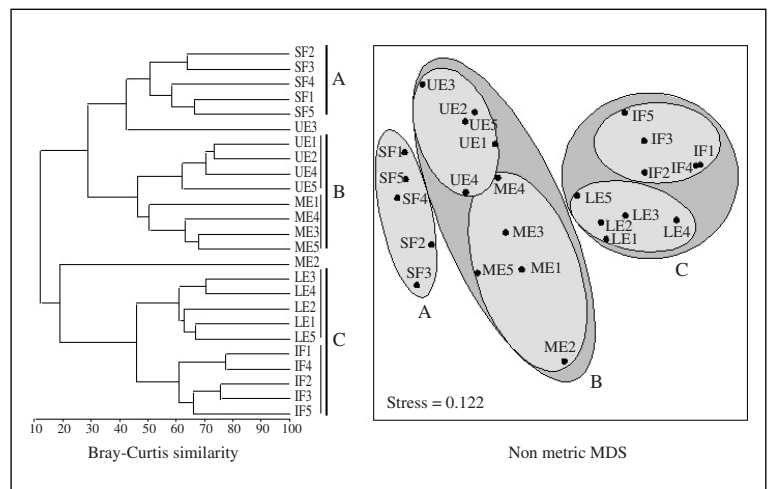

Figure 6. Results of the cluster and MDS analyses. Other abbreviations as in figure 2

Table II. Distribution of the species across the beach. Average values ($\pm$ standard error) in number of individuals per m². (SF): supralittoral fringe; (UE): upper eulittoral; (ME): middle eulittoral; (LE): lower eulittoral; (IF): infralittoral fringe

	Species	SF	UE	ME	LE	IF
Nemertea	Nemertea undet.			4.6 ± 2.89	0.4 ± 0.40	0.6 ± 0.40
Annelida	Oligochaeta undet.	23.8 ± 8.02	11.4 ± 3.99	62.6 ± 34.82	1.2 ± 0.49	1.6 ± 0.68
	Tubificoides benedeni				0.4 ± 0.24	10.2 ± 3.10
	Aonides oxycephala					0.2 ± 0.20
	Capitella cf. *capitata*				4.0 ± 2.17	4.2 ± 1.46
	Cossura sp.					0.2 ± 0.20
	Diopatra neapolitana				0.2 ± 0.20	1.6 ± 0.51
	Eteone foliosa			0.2 ± 0.20		
	Eteone picta				0.2 ± 0.20	
	Eumida bahusiensis				0.4 ± 0.24	0.6 ± 0.40
	Glycera tridactyla				0.2 ± 0.20	
	Gyptis sp. 1					0.2 ± 0.20
	Harmothoe fraserthomsoni					0.2 ± 0.20
	Heteromastus filiformis			0.6 ± 0.40	12 ± 2.92	46.0 ± 21.15
	Lanice conchilega					0.4 ± 0.40
	Mediomastus fragilis					34.2 ± 15.82
	Nephthys hombergii					0.8 ± 0.20
	Nereis sp.					0.2 ± 0.20
	Owenia fusiformis				0.6 ± 0.40	10.0 ± 2.77
	Polydora ligni					0.2 ± 0.20
	Psammathe fusca					0.4 ± 0.40
	Pygospio elegans			3.6 ± 2.23	26.8 ± 11.58	0.2 ± 0.20
	Scoloplos armiger			4.6 ± 4.35		
	Spio sp. 1				0.6 ± 0.60	
	Streblospio shrubsolii				1.0 ± 0.55	1.8 ± 0.80
	Tharyx cf. *marioni*				1.6 ± 1.03	16.6 ± 4.93
Arthropoda	*Gammarus* cf. *locusta*					0.6 ± 0.60
	Melita palmata					0.6 ± 0.40
	Talorchestia deshayesii	4.4 ± 3.44				
	Talitrus saltator	32.2 ± 19.50				
	Eurydice pulchra		1.2 ± 0.73	2.2 ± 0.66		
	Tylos europaeus	5.0 ± 2.10	1.6 ± 1.60			
	Coleoptera nid. sp. 1	0.2 ± 0.20				
	Coleoptera nid. sp. 2	0.2 ± 0.20				
	Diptera nid. sp. 1	0.4 ± 0.24				
	Diptera nid. sp. 2	0.6 ± 0.40	0.2 ± 0.20	0.2 ± 0.20		
	Chironomidae					0.2 ± 0.20
Mollusca	*Hydrobia ulvae*	11.4 ± 9.74	0.2 ± 0.20	15.6 ± 7.46	0.2 ± 0.20	0.2 ± 0.20
	Abra sp.					0.2 ± 0.20
	Cerastoderma edule		0.2 ± 0.20	0.2 ± 0.20	17.2 ± 3.12	11.0 ± 2.02
	Scrobicularia plana				3.6 ± 1.63	1.6 ± 0.93

ment downshore. Both parameters presented statistically significant differences across the beach which reflected the vertical intertidal gradient with longer emersion periods, leading to a typical pattern of mo-re variable and extreme conditions in the upper shore. These emersion factors, mainly causing physical stress, determine the upper distribution limit of many aquatic species (Raffaelli and Hawkins 1996).

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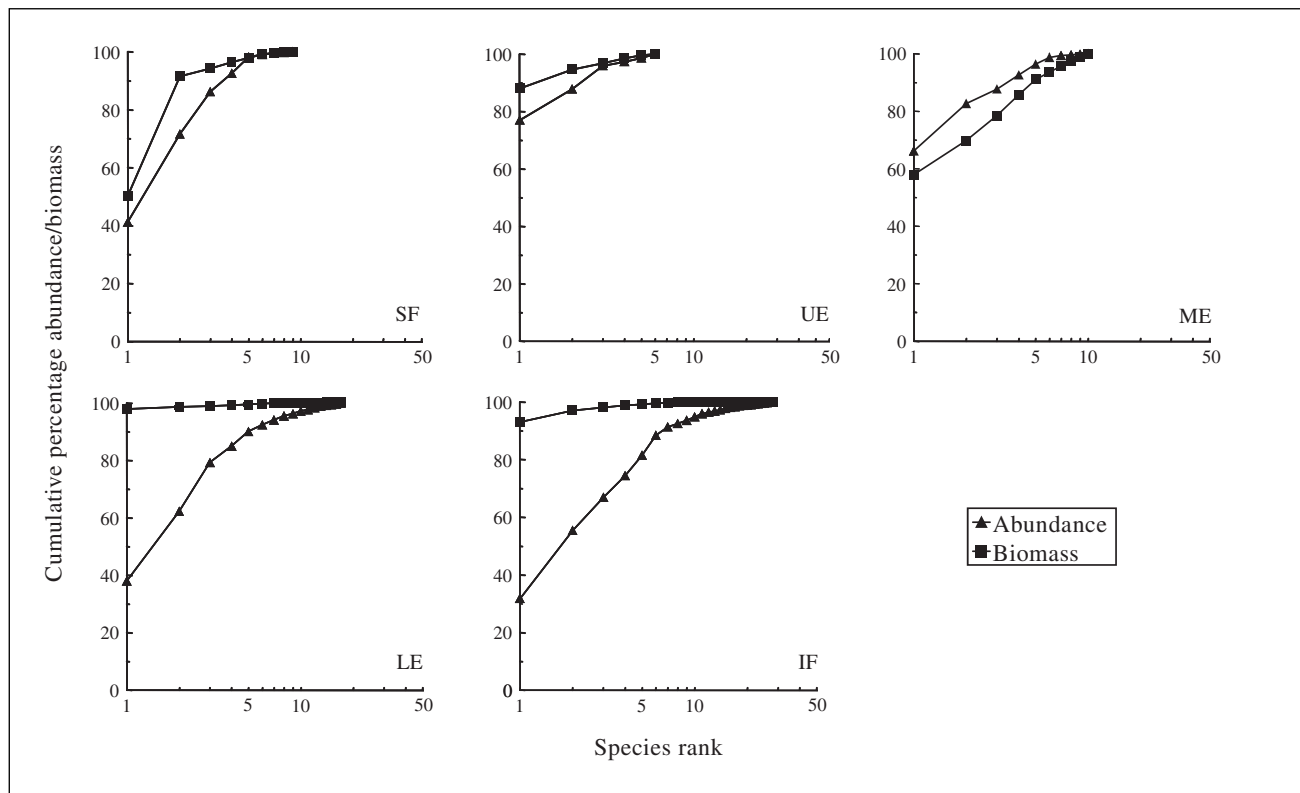*Bol. Inst. Esp. Oceanogr. 19 (1-4). 2003: 235-246*

Figure 7. ABC curves for the five strata. Other abbreviations as in figure 2

The hydrodynamic conditions shaped the slope of the beach, and appeared to be particularly important in the spatial segregation of the different grain sizes available. Grain size increased from fine sand on the supralittoral to coarse sand on the mid shore, the level that is most affected by the maximal velocity of tidal currents, and decreased again to very fine sand on the lower shore terrace. The component of fine particles played an especially important role in determining the chemical conditions of the interstitial environment. A larger proportion of silt and clay on the lower shore terrace resulted in higher porosity and lower permeability. These characteristics increased the waterlogging capacity, but decreased water and oxygen circulation, which combined with the higher organic loading results in reducing conditions, even near the surface of the sediments. The depth of reduced layers depends on the balance between organic and oxygen inputs. The absence or low availability of oxygen just below the surface is common in low-energy fine-sand beaches; low water flux through the sediments also favours the retention of organic loading. The availability of oxygen and the vertical zonation of redox conditions in the interstitial sys-

tem are crucial in determining the redox status of nutrients and levels of microbiological activity (Fenchel and Riedl, 1970; Brown and McLachlan, 1990).

The study site may be described as an intermediate morphodynamic type, with the upper shore being more reflective, tending to be more physically controlled, with increased water circulation through the loose sediments, and poor organic retention; on the other hand, the lower shore is more chemically controlled, with low water circulation, high organic loading, and reducing conditions occurring near the surface. The anova performed on our environmental data showed that the differences across the shore were statistically significant. The results of the subsequent Tukey tests suggest the existence of an environmental gradient rather than a sharp division between the upper and the lower shore.

Food sources

The different conditions on the upper and the lower shore determine the importance of the trop-

Table III. Biomass of the species across the beach. Average values (± standard error) in g of ash-free dry weight per m². (SF): supralittoral fringe; (UE): upper eulittoral; (ME): middle eulittoral; (LE): lower eulittoral; (IF): infralittoral fringe

	Species	SF	UE	ME	LE	IF
Nemertea	Nemertea undet.			0.018 ± 0.0113	0.044 ± 0.0440	0.586 ± 0.5736
Annelida	Oligochaeta undet.	0.015 ± 0.0049	0.009 ± 0.0035	0.074 ± 0.0277	0.016 ± 0.0117	0.010 ± 0.0046
	Tubificoides benedeni				0.008 ± 0.0058	0.128 ± 0.0337
	Aonides oxycephala					< 0.001
	Capitella cf. *capitata*				0.016 ± 0.0117	0.008 ± 0.0058
	Cossura sp.					< 0.001
	Diopatra neapolitana				0.376 ± 0.3760	1.198 ± 0.0058
	Eteone foliosa			0.018 ± 0.0180		
	Eteone picta				0.014 ± 0.0140	
	Eumida bahusiensis				0.006 ± 0.0060	< 0.001
	Glycera tridactyla				0.368 ± 0.3680	
	Gyptis sp. 1					0.008 ± 0.0080
	Harmothoe fraserthomsoni					< 0.001
	Heteromastus filiformis			0.024 ± 0.0150	0.884 ± 0.3233	0.688 ± 0.3208
	Lanice conchilega					0.012 ± 0.0120
	Mediomastus fragilis					0.396 ± 0.1841
	Nephthys hombergii					1.818 ± 1.0770
	Nereis sp.					0.002 ± 0.0020
	Owenia fusiformis				0.398 ± 0.3524	6.786 ± 2.4816
	Polydora ligni					0.002 ± 0.0020
	Psammathe fusca					0.078 ± 0.0780
	Pygospio elegans			0.036 ± 0.0147	0.130 ± 0.0915	0.130 ± 0.0915
	Scoloplos armiger			0.030 ± 0.0184		
	Spio sp. 1				0.020 ± 0.0200	
	Streblospio shrubsolii				0.006 ± 0.0040	0.008 ± 0.0037
	Tharyx cf. *marioni*				0.004 ± 0.0040	0.084 ± 0.0225
Arthropoda	*Gammarus* cf. *locusta*					0.004 ± 0.0040
	Melita palmata					0.004 ± 0.0027
	Talorchestia deshayesii	0.170 ± 0.1154				
	Talitrus saltator	3.790 ± 2.0969				
	Eurydice pulchra		0.036 ± 0.0150	0.166 ± 0.1029		
	Tylos europaeus	3.112 ± 1.0355	0.478 ± 0.4780			
	Coleoptera nid. sp. 1	0.088 ± 0.0880				
	Coleoptera nid. sp.	2 0.112 ± 0.1120				
	Diptera nid. sp. 1	0.042 ± 0.0257				
	Diptera nid. sp. 2	0.014 ± 0.0093	0.006 ± 0.0060	0.122 ± 0.1220		
	Chironomidae					0.002 ± 0.0020
Mollusca	*Hydrobia ulvae*	0.204 ± 0.1942	0.012 ± 0.0120	0.102 ± 0.0418	0.006 ± 0.0060	0.006 ± 0.0060
	Abra sp.					0.006 ± 0.0060
	Cerastoderma edule		0.002 ± 0.0020	0.812 ± 0.8120	128.47 ± 19.279	159.27 ± 35.380
	Scrobicularia plana				0.406 ± 0.3763	0.004 ± 0.0019

hic relationships. According to Brown and McLachlan (1990), beach ecosystems fit mainly into two types: the interface, and the self-sustained ecosystem. The first type is characteristic of reflec-

tive beaches, and depends mainly on water circulation through the sediment that provides nutrients and activates the interstitial system. Its biomass is low and the interstitial food chain is more

important than the macroscopic one. The second type is characteristic of dissipative beaches. Its low water circulation favours the retention of organic materials and primary production. The microbial loop plays a major role in the mineralization of organic matter, and in recycling the nutrients. Biomass is high, and there is more interaction between the interstitial and macroscopic food chains. Our study site in Ria de Aveiro showed a mixing of these two types. In such intermediate situations, the upper shore will tend to have more physical control by flushing (more reflective towards high tide), whereas the lower shore will be more chemically controlled, with truly reducing conditions occurring in the most sheltered and organically loaded situations. The study site showed an upper shore approaching the interface type, and depending mainly on external food sources like the stranded detritus and organic material originating in the salt marsh; its lower shore approached the self-sustained type, with high biomass, high primary production by benthic algae, and probably high bacterial activity in the organic loaded sediments, as well. Discharge of groundwater high in nutrients may have contributed to elevated productivity near the resurgence zone. This sub-area (LE) was the one that showed the highest value of chlorophyll*a* concentration, and where the organisms had the highest value of mean individual weight. Higher food availability and diversity of food resources are essential for the productivity of downshore areas.

Faunal assemblages and zonation

Species richness, abundance, and biomass were lowest at the UE, and increased downshore. High values of these faunal indicators at the LE and IF probably enhanced the importance of biological interactions in these areas. The significant Kendall correlation values between biomass and all sediment properties suggest that it might be physically controlled. Abundance was significantly correlated only to redox potential, organic matter and temperature. Redox potential and organic matter are responsible for the apparent colour of the sediment, which was one of the macroscopic properties used in the a priori definition of the strata. This may explain the good match between faunal zonation and sampling strata.

ABC curves indicated unstressed conditions, except for the ME. This area is exposed to tidal currents during mid-ebb and mid-flood, when maximal velocities are attained. These conditions may explain some physical instability, also denoted by the occurrence of coarser sediment, with possible negative effects on the faunal assemblage.

The upper shore was populated mainly by small peracarid crustaceans and oligochaetes, and the major contributors to biomass were the amphipod *T. saltator* and the isopod *T. europaeus*. These were gradually replaced by polychaetes and bivalves, and the major contributors to biomass downshore were the bivalve *C. edule* and the polychaete *O. fusiformis*. The intraspecific zonation by size shown by *C. edule* is often recorded in molluscs, as well as in other species of sandy-beach macroinvertebrates (Ansell and Lagardère, 1980; McLachlan and Jaramillo, 1995). On the whole, the study site's macrofaunal assemblages were similar to other European beaches described by a number of authors (Withers, 1977; Dexter 1988, 1990; Junoy and Viéitez, 1992; Degraer *et al.*, 1999), with most differences at the species level.

The results of our multivariate analysis agree with a tripartite general zonation scheme for sandy beaches (see review by McLachlan and Jaramillo, 1995): 1) the supralittoral fringe, populated by air-breathing crustaceans; 2) the littoral or midshore region, characterised by the presence of truly intertidal species, especially cirolanid isopods and spionid polychaetes; 3) the sublittoral or lowshore region, typified by a diverse array of species (mostly polychaetes).

According to McLachlan and Jaramillo (1995), a valid zone should include the centre of gravity of at least one characteristic species, and should be clearly noticeable without recourse to sophisticated statistical techniques (e.g., it must be reasonably clear in kite diagrams). Using this principle, the UE and the ME in the midshore, and the LE and IF in the lowshore regions, may be considered as valid zones typified by *E. pulchra* (UE), *S. armiger* (ME), *P. elegans* (LE) and sublittoral polychaete species (IF). The five faunal zones match with the five sampling strata defined a priori, demonstrating that the macroscopic properties of the sediment on sandy beaches can be useful indicators of faunal zonation, despite their dynamic nature.

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REFERENCES

Ansell, A. D. and F. Lagardère. 1980. Observations on the biology of *Donax trunculus* and *D. vittatus* at Île d'Oleron (French Atlantic coast). *Marine Biology* 57: 287-300.

Buchanan, J. B. and J. M. Kain. 1971. Measurement of the physical and chemical environment. In: *Methods for the study of marine benthos.* N. A. Holme and A. D. McIntyre (eds.): 30-58. Blackwell Scientific Publications, Oxford.

Brown, A. C. and A. McLachlan. 1990. *Ecology of sandy shores.* Elsevier. Amsterdam: 328 pp.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18: 117-143.

Clarke, K. R. and R. M. Warwick. 2001. *Change in marine communities: an approach to statistical analysis and interpretation* (2nd edition). PRIMER-E, Plymouth.

Dahl, E. 1952. Some aspects of the ecology and zonation of the fauna on sandy beaches. *Oikos* 4: 1-27.

Degraer, S., I. Mouton, L. de Neve and M. Vincx. 1999. Community structure and intertidal zonation of the macrobenthos on a macrotidal, ultra-dissipative sandy beach: summer-winter comparison. *Estuaries* 22 (3B): 742-752.

Dexter, D. 1988. The sandy beach fauna of Portugal. *Arquivos do Museu Bocage. Nova Série* 1: 101-110.

Dexter, D. 1990. The effect of exposure and seasonality on sandy beach community structure in Portugal. *Ciência Biologica. Ecologia e Systematica* 10: 31-50.

Fenchel, T. M. and R. J. Riedl. 1970. The sulphide system: a new biotic community underneath the oxidised layer of marine sand bottoms. *Marine Biology* 7: 255-268.

Field, J. G., K. R. Clarke and R. M. Warwick. 1982. A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series* 8: 37-52.

John, D. M. and G. W. Lawson. 1991. Littoral ecosystems of tropical western Africa. In: *Intertidal and littoral ecosystems.* A. C. Mathieson and P. H. Nienhuis (eds.): 297-323. Elsevier. Amsterdam.

Junoy, J. and J. M. Viéitez. 1992. Macrofaunal abundance analyses in the Ria de Foz (Lugo, Northwest Spain). *Cahiers de Biologie Marine* 33: 331-345.

Lambshead, P. J. D., H. M. Platt and K. M. Shaw. 1983. The detection of differences among assemblages of marine benthic species based on an assessment of dominance and diversity. *Journal of Natural History* 17: 859-874.

McLachlan, A and E. Jaramillo. 1995. Zonation on sandy beaches. *Oceanography and Marine Biology: an Annual Review* 33: 305-335.

McLachlan, A and I. Turner. 1994. The interstitial environment of sandy beaches. *PSZNI. Marine Ecology* 15 (3/4): 177-211.

Meire, P. M. and J. Dereu. 1990. Use of the abundance/biomass comparison method for detecting environmental stress. Some considerations based on intertidal macrozoobenthos and bird communities. *Journal of Applied Ecology* 27: 210-223.

Orth, R. J. 1992. A perspective on plant-animal interactions in seagrasses: physical and biological determinants influencing plant and animal abundance. In: *Plant-animal interactions in the marine benthos.* D. H. John, S. J. Hawkins and J. H. Price (eds.): 147-165. Oxford University Press. Oxford.

Raffaelli, D. and S. Hawkins. 1996. *Intertidal ecology.* Chapman & Hall. London: 356 pp.

Reise, K. 1992. The Wadden Sea as a pristine nature reserve. In: *Present and future conservation of the Wadden Sea. Proceedings of the 7th International Wadden Sea Symposium* (1990. Ameland). N. Dankers, C. J. Smith and M. Scholl (eds.) 20: 49-53. Publication Series of the Netherlands Institute of Sea Research.

Santelices, B. 1991. Littoral and sublittoral communities of continental Chile. In: *Intertidal and littoral ecosystems.* A. C. Mathieson and P. H. Nienhuis (eds.): 347-370. Elsevier. Amsterdam.

Talling, J. F. 1974. Photosynthetic pigments. General outline of spectrophotometric methods. In: *A manual on methods for measuring primary production in aquatic environments.* R. A. Vollenweider (ed.): 22-26. Blackwell Scientific Publications. Oxford.

Vadas, R. L. and R. W. Elner. 1992. Plant-animal interactions in the north-west Atlantic. In: *Plant-animal interactions in the marine benthos.* D. M. John, S. J.Hawkins and J.H. Price (eds.): 33-60. Clarendon Press. Oxford.

Warwick, R. M. 1986. A new method for detecting pollution effects on marine macrobenthic communities. *Marine Biology* 92: 557-562.

Wetzel, R. G. and G. E. Likens. 1991. *Limnological analyses* (2nd edition). Springer Verlag. New York: 156-161.

Withers, R. G. 1977. Soft-shore macrobenthos along the southwest coast of Wales. *Estuarine and Coastal Marine Science* 5: 467-484.

Yentsch, C. S. and D. W. Menzel. 1963. A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. *Deep-Sea Researche* 10 (3): 221-231.

Zar, J. H. 1996. *Biostatistical analysis* (3rd edition). Prentice Hall, Simon and Schuster. Upper Saddle River. New Jersey.