Estuarine, Coastal and Shelf Science 81 (2009) 555–568

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Sandy beach macrofaunal communities on the western coast of Portugal – Is there a steady structure under similar exposed conditions?

Sílvia C. Gonçalves[a,b,*], Pedro M. Anastácio[c], Miguel A. Pardal[b], Patrícia G. Cardoso[b], Susana M. Ferreira[a,b], João C. Marques[b]

[a] *GIRM – Grupo de Investigação em Recursos Marinhos, ESTM – Escola Superior de Tecnologia do Mar, Instituto Politécnico de Leiria, Campus 4, Santuário Na. Sra. dos Remédios, Apartado 126, 2524-909 Peniche, Portugal*
[b] *IMAR – Institute of Marine Research, Department of Zoology, Faculty of Sciences and Technology, University of Coimbra, 3004-517 Coimbra, Portugal*
[c] *IMAR – Institute of Marine Research, Department of Ecology, University of Évora, Rua Romão Ramalho 59, 7000-671 Évora, Portugal*

ARTICLE INFO

Article history:
Received 29 April 2008
Accepted 5 December 2008
Available online 14 December 2008

Keywords:
exposed sandy beaches
macrofaunal community structure
seasonality
key species
detritus subsidies

ABSTRACT

The structure of macrofaunal communities at two similar exposed sandy beaches on the western coast of Portugal was monitored for approximately 18 months by sampling all the beach area, from the shoreline to the base of the dunes. The beaches' physical environment, as well as community density and composition, seasonal variations and the potential relationships between biological data and environmental parameters were studied. The two beaches had similar exposure to wave action, but differed in terms of sediment grain size, extent of the intertidal area, sediment moisture content and, especially, in the potential food availability in the form of allochthonous debris. Differences were observed with regard to the communities' structure, namely regarding composition and relative contribution of the dominant species. Seasonality, especially temperature variations, and the interaction between seasons and the beach zones (supralittoral vs. intertidal) also had a strong influence on communities: controlling dominant species' density and the horizontal distribution of the dominant species, and promoting a differential utilization of the beach by several resident macrofaunal animals. The present study allows the identification of key species in exposed sandy beaches of western Portugal and demonstrates that a steady community structure does not persist in the similarly exposed conditions observed, which may be mainly a response to distinct detritus subsidies, combined with differences in sediment grain size, sediment moisture content and extent of the intertidal area.

1. Introduction

Sandy beaches are important dynamic coastal systems that border most of the shores worldwide. They are natural interfaces between sea and land, capable of absorbing large quantities of incoming wave and wind energy, despite of their relative fragility as ecosystems (Brown and McLachlan, 1990). Moreover, the human use of sandy shores is quickly increasing (e.g. construction of engineering structures and recreational facilities) at the expense of the ecological quality of the beach environment (e.g. Weslawski et al., 2000; Lercari and Defeo, 2003; Gheskiere et al., 2005).

Although apparently devoid of life, sandy beaches support several macrofaunal and meiofaunal populations, some of which are often very abundant. Macrofaunal communities of these systems are dominated by Crustaceans, Molluscs and Polychaetes, especially in the intertidal area, with different relative abundances according to the local exposure to wave action (Dexter, 1983, 1990). Insects are common inhabitants of the upper reaches of the shore and the dunes (Brown and McLachlan, 1990), associated with wrack and algal deposits stranded by tides and/or blown overland by the wind from a terrestrial origin.

Several recent studies have focused on macrofaunal communities of sandy beaches. Studies like those by Dexter (1983, 1990), McLachlan and Jaramillo (1995), Dugan et al. (2003) and Rodil et al. (2006) have analysed community structure, at distinct levels, and in terms of zonation patterns, while the impact of human activities on community composition and structure has been assessed for instance in Lercari and Defeo (2003), Junoy et al. (2005) and Veloso et al. (2006).

Dexter (1990) has pointed out that macrofaunal community structure is strongly influenced by exposure to wave action, and McLachlan and Jaramillo (1995) noted that general patterns found

---

[*] Corresponding author. GIRM – Grupo de Investigação em Recursos Marinhos, ESTM – Escola Superior de Tecnologia do Mar, Instituto Politécnico de Leiria, Campus 4, Santuário Na. Sra. dos Remédios, Apartado 126, 2524-909 Peniche, Portugal.

E-mail address: scgoncalves@estm.ipleiria.pt (S.C. Gonçalves).

0272-7714/$ – see front matter © 2008 Elsevier Ltd. All rights reserved.
doi:10.1016/j.ecss.2008.12.004

in sandy beach macrofauna exhibit a negative correlation between species richness, exposure rating and grain size, depending on beach type. Thus, a harsh and dynamic environment, mainly physically controlled, is expected in exposed sandy beaches. Exposed sandy beach communities will therefore have different compositions and distinct structures in comparison to more sheltered conditions, as demonstrated for instance by McLachlan et al. (1993) and Rodil and Lastra (2004).

In sandy beach ecology, studies on macrofaunal communities are frequently based on snapshot sampling events (e.g. McLachlan, 1990; Defeo et al., 1992; Rodil et al., 2006). Defeo and Rueda (2002) strongly criticised this approach because this could lead, for instance, to biases on the temporal and spatial abundance patterns observed for each species. Likewise, a fortnight sampling program, with a proper spatial replication across the beach area, appears to be extremely important if, for instance, the influence of seasons on community structure and function are to be assessed. However, this kind of sampling programs are very rare in sandy beach studies, and several parameters of the beach environment oscillate throughout the year (e.g. food supply, namely in the form of detritus subsidies; beach width; occurrence of storms). In exposed conditions, the oscillations on the beach environment may be even more pronounced. Thus, comprehensive and temporally replicated studies on sandy beach macrofaunal communities, covering all the beach area from the low tide watermark to the base of the dunes, are needed.

The objectives of the present study are to analyse the macrofaunal communities of two similarly exposed sandy beaches on the western coast of Portugal and to compare them from a structural point of view, focusing on density, composition, diversity and horizontal distribution between the supralittoral and intertidal areas. The structural analysis of these communities will also allow the identification of potential key species in these environments. Additionally, taking advantage of a fortnight sampling program, over 1.5 years of study, the role of seasonality and of several other environmental parameters, namely detritus subsidies, as community structuring mechanisms is also examined.

2. Materials and methods

2.1. Study sites

Two sandy beaches – Cabedelo and Quiaios – on the western coast of the Iberian Peninsula, located in the central region of Portugal (Fig. 1) were selected as study sites. The Cabedelo sandy beach (40°07’32″ N 8°51’49″ W) is 1 km south of the Mondego river mouth, in the vicinity of its estuarine environment, while Quiaios beach (40°12’21″ N 8°53’48″ W) is further north, approximately 8 km north from Cape Mondego. In general Quiaios and Cabedelo are relatively undisturbed beaches, receiving a moderate number of summer visitors. Cabedelo has probably been subjected to increasingly higher human pressure than Quiaios in the past few years, since it is closer to the town of Figueira da Foz, an important tourist centre where sandy beaches are the main attraction. These are exposed beaches, which present relatively similar conditions of exposure to wave action. Tides on the western Portuguese coast are semidiurnal and mesotidal, with a tidal range between 2 and 3.5 m.

During storms, Cabedelo may be almost completely submerged, causing depositions of large amounts of drift wrack, mainly composed of macroalgae from rocky shores located north of the beach and possibly also from the Mondego estuarine system. The input of drift wrack at Quiaios is clearly more limited, since there are no rocky shores or other potential sources of debris nearby. The exposed nature of both beaches meant that no vegetation was found on the supralittoral areas of these study sites. Supplementary characteristics of these two sandy beaches are provided in Table 1.

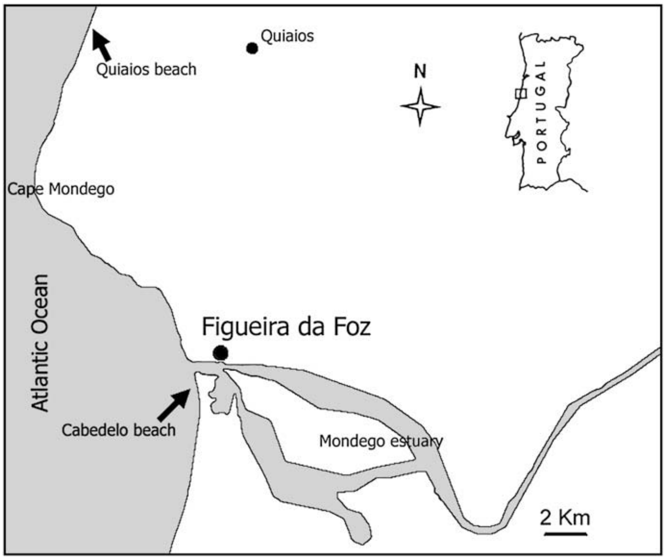

Fig. 1. Location of the sandy beaches used as study sites: Cabedelo and Quiaios (western coast of Portugal). Cabedelo: 40°07′32″N 8°51′49″W; Quiaios: 40°12′21″N 8°53′48″W.

2.2. Sampling procedures

The sandy beach macrofaunal communities were sampled fortnightly, during low neap tides, from January 1999 to June 2000 at Quiaios (18 months), and from March 1999 to June 2000 (16 months) at Cabedelo. Samples were taken on the supralittoral and intertidal zones. Sampling levels were defined at regular intervals along two transects arranged from the low tide watermark to the base of the dunes. For each transect, ten sampling levels were considered. The mean high water neap tide mark, left by the previous tide, was always used as a reference point to define, on each occasion, the supralittoral and the intertidal zones, preventing seasonal oscillations on the width of these areas throughout the year. For each transect, five sampling levels were sampled on each zone of the beach (supralittoral and intertidal), and the intervals between the levels necessarily adjusted through the year. This sampling procedure was able to account for differential horizontal distribution of the macrofauna during the year. Sampling was performed using a wooden square of 0.25 m^2 and removing the first

Table 1
Basic characteristics observed in the two sandy beaches used as study sites. For quantitative characteristics averages ± standard deviations for the period of study are given.

Characteristic	Cabedelo	Quiaios
Width of the beach (m)	60	100
Average slope (%)	2.0	1.8
Extension of the intertidal area (m)	Neap tides: 30 Spring tides: 45	Neap tides: 50 Spring tides: 75
Foredune height (m)	2.5–3	2.5–3
Sediment granulometry (mm)	Medium sand (0.250–0.500)	Coarse-sand (0.500–1.0)
Sediment moisture (%)	3.24 (±1.22)	2.64 (±0.95)
Supralittoral	2.53 (±1.44)	2.08 (±1.30)
Intertidal	4.11 (±1.88)	3.07 (±0.88)
Organic matter content (%)	0.15 (±0.05)	0.19 (±0.35)
Supralittoral	0.13 (±0.03)	0.19 (±0.35)
Intertidal	0.15 (±0.04)	0.21 (±0.38)

20 cm of the sand surface layer, with a small scoop. The sand was sieved through a 1 mm mesh and the animals collected were then separated in the laboratory and preserved in 70% alcohol, after fixation in 4% formalin. Sediment grain size composition was determined from seasonal samples to check for significant differences, and classified according to the Wentworth scale described in Brown and McLachlan (1990).

A set of physico-chemical parameters were measured over the study period to account for possible relationships between the macrofaunal communities and their environment. At the beaches debris quantity (potential food measured in g m^{-2}), organic matter in the sediment (AFDW), and sediment moisture content were determined according to the procedures described in Marques et al. (2003). The meteorological data were obtained from the nearest meteorological stations (Coimbra for temperature and precipitation and Figueira da Foz harbour for the other parameters): precipitation, temperatures, visibility, cloudiness, wave height, wave period, and wind velocity.

2.3. Data analysis

All the animals collected (marine, semi-terrestrial and terrestrial) were considered in the study. Density (individuals.m^{-2}) was calculated for each site using a proportionally weighted average approach regarding each level of the beach, and analysed through all sampling dates and for each season. Supralittoral and intertidal zones were compared with regard to density, horizontal distribution and species composition. Animals with a frequency of occurrence higher than 10% of the complete period of sampling were considered residents. Diversity trends were also analysed using the number of species as a measure of species richness and Shannon-Wiener's H' as a measure of heterogeneity.

Before developing any kind of statistical analyses, all the variables – faunal and environmental – were previously checked for normality, using the MINITAB 12.2 software package, and transformed whenever necessary. The physicochemical parameters measured at the beaches (debris quantity, organic matter in the sediment and sediment moisture content) and the faunal components were tested for differences using Two-Way ANOVA's with seasons and beaches as main factors. These variables were also tested with Two-Way Nested ANOVA's where, besides the factor seasons, beach zones (supralittoral and intertidal) nested on the beaches were also tested as a factor. In both cases, the significant effects detected were afterwards subjected to post-hoc tests: (1) the Tukey HSD and LSD tests to analyse the individual effects of the factors; (2) Bonferroni tests to analyse the significant interactions between the factors (pair wise comparisons). All these procedures were performed using the SPSS 16.0 software package.

Potential relationships between the density of resident species and environmental parameters were explored using multivariate techniques performed with the statistical software package CANOCO 4.0 for windows (ter Braak and Šmilauer, 1998). Multivariate methods, especially canonical analyses techniques (e.g. Redundancy Analysis and Canonical Correspondence Analysis), are important tools in community ecology because they can assess large-scale relationships between species data (response variables) and environmental factors (explanatory variables). For both data sets, all the biological data were square-root transformed in the analysis and there was no down-weighting of rare species. The environmental parameters tested as explanatory variables in the multivariate analyses were: debris quantity, organic matter of the sediment, sediment moisture content, precipitation, temperature, visibility, cloudiness, wind velocity, wave period and wave height. These variables were previously checked for multicolinearity, before performing the multivariable techniques.

The multivariate analysis technique used was selected following a sequence of procedures. Biological data matrixes were initially subjected to a Detrended Correspondence Analysis (DCA), with detrending by segments, to measure the gradient lengths. This procedure makes it possible to decide whether a linear species response-based or a unimodal species response-based ordination method should be used. In all cases, the gradient length of the first axis obtained was less than 3.0, suggesting that an analysis based on linear species response should be used. The constrained ordination method used, therefore, was Redundancy Analyses (RDA). The forward selection procedure was used with a Monte Carlo Permutation Test (999 permutations) to determine which environmental variables were significant ($p < 0.05$) and explain the largest amount of variation in each biological data set. The significance of the reduced RDA models finally obtained was also assessed using Monte Carlo Permutation Tests ($p < 0.05$ after 999 permutations).

3. Results

3.1. Beaches' physical environment

Quiaios beach is considerably wider than Cabedelo, and has a smaller average slope (Table 1). The seasonal variation of sediment grain size composition was not significant ($p < 0.05$). According to the Wentworth scale described in Brown and McLachlan (1990), Cabedelo had medium sand grains, while in Quiaios the sediment was coarse (Table 1). Considering the other parameters in McLachlan's (1980) rating scheme for assessing the degree of exposure in sandy beaches, Quiaios is classified as a very exposed beach (exposure rate: 16) and Cabedelo as exposed (exposure rate: 15). The two beaches can thus be considered relatively similar regarding exposure to wave action.

In autumn and summer, the moisture contents of the sand were significantly distinct and, regarding beach zones, 3 homogeneous subsets were identified (Table 2). Cabedelo beach had a much higher input of detritus subsidies, in average 4.5 times higher than Quiaios (Fig. 2c). This variable was significantly distinct between beach zones since, at the supralittoral of Cabedelo, the detritus quantity was higher (Table 2). The organic content of the sand did not reveal significant differences.

3.2. Communities structure

On both beaches, the communities' structure was dominated by arthropods. Crustaceans were the most abundant macrofaunal group, followed by insects (Table 3). Other groups of arthropods, along with molluscs, annelids and nemerteans, had only residual contributions (<1%), and most of them were quite rare. Amphipods and isopods were the most abundant crustaceans but were differently represented in the two beaches (Fig. 2a and b). Amphipod dominance at Cabedelo was very consistent (Fig. 2a). At Quiaios the community structure was far more changeable, although isopods were generally dominant (Fig. 2b). Amphipods became dominant in the winter of 1999 and in most autumn months, but in the spring of 2000 the two groups had similar proportions. ANOVA results showed that the beach had significant effects on the densities of amphipods and isopods (Table 2).

Although highly abundant, crustaceans were found in only 8 species at Cabedelo and 9 at Quiaios. Insects were the most diverse group but most of the species were very rare on samples. According to the ANOVA results, diversity indexes were similar between both beaches. Only a small number of the species were residents – 16 species at Cabedelo and 14 species at Quiaios (Table 4). This included crustaceans (mainly talitrid amphipods and isopods),

Table 2
ANOVA and post-hoc tests results for environmental and faunal responses considering the effects of beach (Cadedelo and Quiaios), seasons (Spring, Summer, Autumn and Winter), and beach zones (Supralittoral and Intertidal, nested on beaches) as factors. Only the variables that presented any kind of significant results are represented ($p < 0.05$). df – degrees of freedom; MS – Mean Square.

ANOVA				
Source of variation	df	MS	*F*-statistic	*p*-value
Environmental parameters				
Sediment moisture content (%)				
Seasons (A)	3	5.900	4.037	**0.013**
Beaches (B)	1	4.284	2.931	0.095
Zones nested in Beaches (C)	3	8.451	8.724	**0.000**
A × B	3	0.259	0.177	0.911
A × C	9	0.797	0.823	0.600
Detritus quantity (g m^{-2})				
Seasons (A)	3	11.521	0.302	0.823
Beaches (B)	1	118.818	3.119	0.085
Zones nested in Beaches (C)	3	215.546	7.386	**0.001**
A × B	3	9.907	0.260	0.854
A × C	9	10.193	0.349	0.950
Faunal components				
Anfipoda density (ind m^{-2})				
Seasons (A)	3	1792.857	0.803	0.496
Beaches (B)	1	40411.848	18.105	**0.000**
Zones nested in Beaches (C)	3	15893.302	10.878	**0.000**
A × B	3	2254.522	1.010	0.393
A × C	9	7411.327	5.073	**0.000**
Isopoda density (ind m^{-2})				
Seasons (A)	3	2868.977	0.843	0.475
Beaches (B)	1	23168.646	6.811	**0.011**
Zones nested in Beaches (C)	3	7819.636	2.801	**0.047**
A × B	3	1141.506	0.336	0.800
A × C	9	7706.712	2.760	**0.009**
Coleoptera density (ind m^{-2})				
Seasons (A)	3	4.696	1.817	0.152
Beaches (B)	1	2.938	1.137	0.290
Zones nested in Beaches (C)	3	22.225	13.957	**0.000**
A × B	3	3.221	1.246	0.299
A × C	9	3.346	2.101	**0.042**
Talitrus saltator density (ind m^{-2})				
Seasons (A)	3	3516.521	1.951	0.132
Beaches (B)	1	37935.353	21.052	**0.000**
Zones nested in Beaches (C)	3	12700.121	12.758	**0.000**
A × B	3	3481.211	1.932	0.135
A × C	9	7045.672	7.078	**0.000**
Talorchestia brito density (ind m^{-2})				
Seasons (A)	3	73.599	0.573	0.635
Beaches (B)	1	283.796	2.210	0.143
Zones nested in Beaches (C)	3	883.790	9.399	**0.000**
A × B	3	21.929	0.171	0.916
A × C	9	41.605	0.442	0.905
Tylos europaeus density (ind m^{-2})				
Seasons (A)	3	458.546	0.415	0.743
Beaches (B)	1	10058.335	9.094	**0.004**
Zones nested in Beaches (C)	3	5462.025	7.706	**0.000**
A × B	3	971.091	0.878	0.458
A × C	9	2722.404	3.841	**0.001**
Community density (ind m^{-2})				
Seasons (A)	3	4686.073	0.828	0.482
Beaches (B)	1	2486.363	0.439	0.509
Zones nested in Beaches (C)	3	4095.161	1.019	0.389
A × B	3	2016.931	0.356	0.785
A × C	9	19239.911	4.789	**0.000**
Number of species				
Seasons (A)	3	34.375	2.387	0.079
Beaches (B)	1	2.250	0.156	0.694
Zones nested in Beaches (C)	3	83.458	13.534	**0.000**
A × B	3	11.042	0.767	0.518
A × C	9	32.833	5.324	**0.000**

Table 2 (*continued*)

Post-hoc tests			
Dependent variable and factors tested	Test	Condition	*p*-value
Environmental parameters			
Sediment moisture content (%)			
Effect of seasons	Tukey HSD	comparison: autumn and summer	**0.032**
	LSD	comparison: autumn and summer	**0.006**
Effect of beach zones: Homogeneous subsets	Tukey HSD	subs. 1: Qsupra = Csupra	0.554
		subs. 2: Csupra = Qinter	0.400
		subs. 3: Qinter = Cinter	0.583
Detritus quantity (g m^{-2}): Effect of beach zones	Tukey HSD	comparison: Csupra and Cinter	**0.000**
		comparison: Csupra and Qinter	**0.000**
		comparison: Csupra and Qsupra	**0.013**
	LSD	comparison: Csupra and Cinter	**0.000**
		comparison: Csupra and Qinter	**0.000**
		comparison: Csupra and Qsupra	**0.003**
Faunal components			
Anfipoda density (ind m^{-2})			
Interaction: seasons × beach zones	Bonferroni	Spring	
		comparison: Cinter and Qinter	**0.019**
		comparison: Cinter and Qsupra	**0.002**
		Summer	
		comparison: Cinter and Qinter	**0.000**
		comparison: Cinter and Qsupra	**0.000**
		comparison: Cinter and Csupra	**0.000**
		Winter	
		comparison: Csupra and Cinter	**0.018**
		comparison: Csupra and Qsupra	**0.010**
Anfipoda density (ind.m^{-2})			
Interaction: seasons × beach zones	Bonferroni	Summer	
		comparison: Qinter and Cinter	**0.017**
		comparison: Qinter and Csupra	**0.008**
		comparison: Qinter and Qsupra	**0.003**
		Winter	
		comparison: Qsupra and Qinter	**0.035**
		comparison: Qsupra and Cinter	**0.024**
Coleoptera density (ind m^{-2})			
Interaction: seasons × beach zones	Bonferroni	Spring	
		comparison: Csupra and Qsupra	**0.023**
		comparison: Csupra and Qinter	**0.000**
		comparison: Csupra and Cinter	**0.000**
		Autumn	
		comparison: Csupra and Qinter	**0.001**
		comparison: Csupra and Cinter	**0.007**
Talorchestia brito density (ind m^{-2})			
Effect of beach zones: Homogeneous subsets	Tukey HSD	subs. 1: Qsupra = Csupra = Cinter	0.148
		subs. 2: Qinter	1.000
Talitrus saltator density (ind m^{-2})			
Interaction: seasons × beach zones	Bonferroni	Winter	
		comparison: Csupra and Qsupra	**0.013**
		comparison: Csupra and Qinter	**0.008**
		comparison: Csupra and Cinter	**0.010**
		Summer	
		comparison: Cinter and Qinter	**0.000**
		comparison: Cinter and Qsupra	**0.000**
		comparison: Cinter and Csupra	**0.000**
Tylos europaeus density (ind m^{-2})			
Interaction: seasons × beach zones	Bonferroni	Winter	
		comparison: Qsupra and Csupra	**0.000**
		comparison: Qsupra and Cinter	**0.000**
		comparison: Qsupra and Qinter	**0.000**
Community density (ind m^{-2})			
Interaction: seasons × beach zones	Bonferroni	Summer	
		comparison: Cinter and Qsupra	**0.001**
		comparison: Cinter and Csupra	**0.003**
		comparison: Qinter and Csupra	**0.001**
		comparison: Qinter and Qsupra	**0.000**
Number of species			
Interaction: seasons × beach zones	Bonferroni	Autumn	
		comparison: Qinter and Csupra	**0.003**
		comparison: Qinter and Qsupra	**0.012**
		Winter	
		comparison: Cinter and Qsupra	**0.000**
		comparison: Cinter and Csupra	**0.012**
		comparison: Qinter and Csupra	**0.018**
		comparison: Qinter and Qsupra	**0.000**
		Spring	
		comparison: Csupra and Qinter	**0.000**
		comparison: Csupra and Cinter	**0.000**

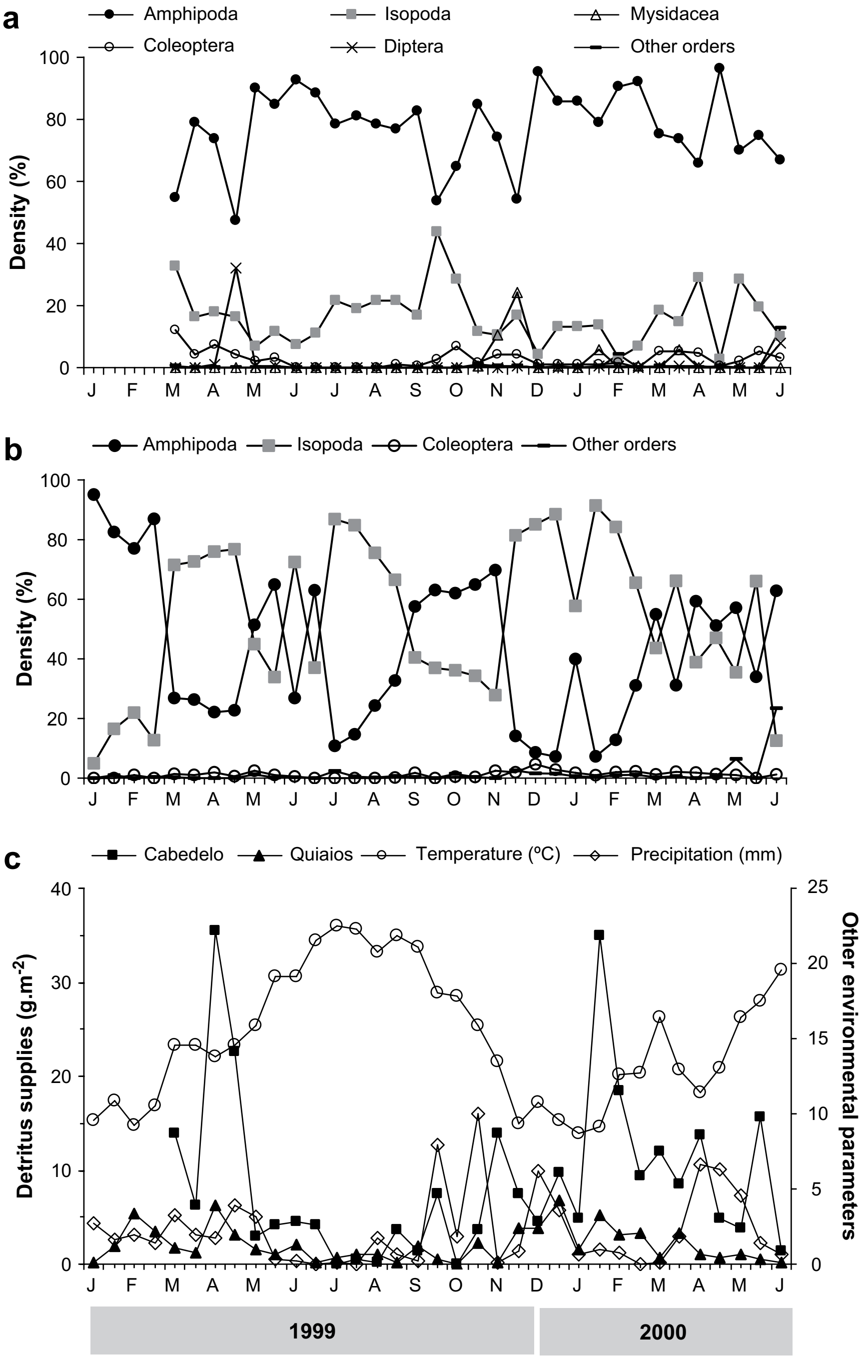

Fig. 2. Relative contribution of the different orders observed in the studied sandy beach communities at the western coast of Portugal and relevant environmental parameters during the study period. (a) – Cabedelo; (b) – Quiaios; (c) – Variation of the most relevant environmental parameters.

coleopterans (mainly tenebrionids and scarabids, besides different kinds of larvae) and dipterans larvae.

Some differences were observed between the communities regarding resident fauna composition. Species like the mysid *Gastrosaccus sanctus* and the coleopterans *Callicnemis latreillei*, *Aegiala arenaria* and *Saprinus* sp. occurred only at Cabedelo, whilst the coleopteran *Gonioctena olivacea*, and the mollusc *Cochlicella barbara*, residents in Quiaios, were never observed at Cabedelo.

The amphipods *Talitrus saltator* and *Talorchestia brito*, and the isopod *Tylos europaeus* were the most abundant animals found at both communities (Table 3; Fig. 3b and c). At Cabedelo, *T. saltator* was dominant, followed by *T. europaeus* and *T. brito*, while at Quiaios, *T. europaeus* was the most abundant species, followed by *T. brito* and, in much smaller numbers, *T. saltator*. Two-Way ANOVA revealed that *T. saltator* and *T. europaeus* presented significantly distinct means between both beaches (Table 2). Considering the whole communities, total densities were similar between both beaches – the ANOVA results obtained were not significant. Minimum and maximum density was always recorded, respectively, in January (winter) and July (summer) at both beaches (Fig. 3a). This clearly reflected the patterns of variation of the dominant species: *T. saltator* at Cabedelo and *T. europaeus* and *T. brito* at Quiaios (Fig. 3).

Table 3
Community structure in Cabedelo and Quiaios beaches based in selected species. Avg – average; SD – standard deviation; Occu. (%) – Percentage of occurrence; Avg % contrib. – Average percentual contribution; unidt. – unidentified; abs. – absent.

	Cabedelo				Quiaios			
	Density (ind m^{-2})		Occu. (%)	Avg % contrib.	Density (ind m^{-2})		Occu. (%)	Avg % contrib.
	Avg	SD			Avg	SD		
Crustacea								
Talitrus saltator	67.08	50.90	100	69.52	4.48	4.01	100	6.22
Tylos europaeus	14.66	11.07	100	15.19	47.50	77.07	100	65.95
Talorchestia brito	7.69	7.57	97	7.97	17.65	15.52	100	24.50
Gastrosaccus sanctus	1.13	4.26	23	1.17	abs.	–	0	–
Eurydice naylori	0.38	0.70	48	0.39	0.00	0.04	<10	0.01
Pontocrates arenarius	0.13	0.31	19	0.13	0.00	0.02	<10	0.00
Armadillidium album	0.07	0.13	26	0.07	0.22	0.49	29	0.31
Other Crustacea	0.01	0.06	10	0.01	0.01	–	<10	0.02
Total Crustacea				**94.45**				**97.01**
Insecta								
Coleoptera								
Scarabaeidae larvae	0.51	1.09	45	0.53	0.04	0.09	26	0.06
Elateridae larvae	0.41	0.54	58	0.43	0.16	0.28	43	0.22
Unidt. larvae *a*	abs.	–	0	–	0.06	0.18	17	0.08
Unidt. larvae *b*	abs.	–	0	–	0.02	0.06	14	0.03
Phaleria acuminata	0.49	0.67	61	0.50	0.18	0.36	46	0.25
Gonioctena olivacea	abs.	–	0	–	0.03	0.10	14	0.05
Callicnemis latreillei	0.13	0.28	26	0.13	abs.	–	0	–
Aegiala arenaria	0.12	0.23	32	0.13	abs.	–	0	–
Olisthopus rotundatus	0.04	0.13	13	0.04	0.01	0.04	6	0.01
Saprinus sp.	0.03	0.09	13	0.03	abs.	–	0	–
Tenebrionidae unidt. species 1	0.02	0.06	10	0.02	0.02	0.07	14	0.03
Psammodius porcicollis	0.01	0.04	7	0.01	0.02	0.06	14	0.03
Other Coleoptera	0.39	–	<10	0.41	0.16	–	<10	0.22
Sub-total				2.23				0.98
Díptera								
Cyclorrhapha larvae	1.29	1.33	16	1.33	0.01	0.04	9	0.02
Unidt. larvae	0.03	0.03	13	0.03	0.04	0.16	9	0.06
Other díptera	0.70	–	<10	0.73	0.71	–	<10	0.98
Sub-total				2.09				1.06
Hemiptera	0.63	–	<10	0.65	0.10	–	<10	0.14
Hymenoptera	0.27	–	<10	0.29	0.06	–	<10	0.09
Mecoptera	abs.	–	0	–	0.05	–	<10	0.08
Lepidoptera	abs.	–	0	–	0.01	–	<10	0.01
Total Insecta				**5.26**				**2.36**
Other Arthropoda	0.16	–	<10	0.17	0.04	–	<10	0.04
Mollusca								
Cochlicella barbara	abs.	–	0	–	0.03	0.07	14	0.04
Other Mollusca	0.10	–	<10	0.10	0.1	–	<10	0.14
Annelida								
Enchytraeidae unidt. species	0.02	0.08	<10	0.02	0.08	0.37	14	0.11
Other Annelida	0.00	–	<10	0.00	0.16	–	<10	0.21
Nemertea	abs.	–	0	–	0.06	–	<10	0.09
Total	**96.50**	**60.25**		**100**	**72.02**	**85.00**		**100**

3.3. Beach zones and seasons

The supralittoral and the intertidal zones of the beaches revealed differences in species composition, especially on the resident fauna (Table 4). For instance, the isopod *Armadillidium album*, the coleopterans *Callicnemis latreillei* and *Aegiala arenaria*, and the mollusc *Cochlicella barbara*, were only found in the supralittoral. Resident insect larvae (coleoptera and diptera), and the coleopterans *Phaleria acuminata* and *Psammodius porcicollis* exhibited a stronger supralittoral affinity, while the isopod *Eurydice naylori* was mainly found in the intertidal zone. The amphipod *Pontocrates arenarius* and the mysid *Gastrosaccus sanctus* were only observed in the lower intertidal zone. Regarding the three dominant species, *Talitrus saltator* was the most abundant organism in both the supralittoral and intertidal zones at Cabedelo, *Tylos europaeus* showed clear supralittoral affinity, and *Talorchestia brito* attained their highest density in the intertidal zone (Table 4).

The results from the Two-Way Nested ANOVA showed that the interaction between seasons and the beach zones had a significant effect on the density of amphipods, isopods and coleopterans (Table 2). In spring and summer, at the intertidal zone of Cabedelo, amphipods presented significantly higher density means, while in winter densities were significantly higher at the supralittoral zone of Cabedelo (Table 2). Regarding isopods, significantly higher densities were observed in winter at the supralittoral zone of Quiaios and during summer at the intertidal zone of this beach. Coleopterans presented significantly distinct density means at the supralittoral zone of Cabedelo in autumn and spring (Table 2).

Seasons and beach zones also presented a significant interaction on the densities of *Talitrus saltator* and *Tylos europaeus*, but for

Table 4

Comparative structure of supralittoral and intertidal communities at Cabedelo and Quiaios sandy beaches. Unidt. – unidentified; abs – absent; n.r. – not resident.

	Cabedelo				Quiaios			
	Average density (ind m^{-2})		Average contribution		Average density (ind m^{-2})		Average contribution	
Resident animals	Supral.	Inter.	Supral.	Inter.	Supral.	Inter.	Supral.	Inter.
Talitrus saltator	49.63	68.58	63.0%	73.6%	2.33	5.14	5.8%	7.7%
Talorchestia brito	2.33	11.62	3.0%	12.5%	2.22	25.63	5.5%	38.2%
Pontocrates arenarius	abs.	0.27	–	0.3%	abs.	n.r.	–	–
Tylos europaeus	20.90	9.60	26.6%	10.3%	34.43	36.25	85.0%	54.1%
Armadillidium album	0.13	abs.	0.2%	–	0.38	abs.	0.9%	–
Eurydice naylori	0.08	0.67	0.1%	0.7%	abs.	n.r.	–	–
Gastrosaccus sanctus	abs.	2.44	–	2.6%	abs.	abs.	–	–
Phaleria acuminata	1.05	n.r.	1.3%	–	0.43	n.r.	1.0%	–
Tenebrionidae unidt. spc.1	n.r.	n.r.	–	–	0.04	abs.	0.1%	–
Callicnemis latreillei	0.26	abs.	0.3%	–	abs.	abs.	–	–
Psammodius porcicollis	n.r.	abs.	–	–	0.03	n.r.	0.1%	–
Aegiala arenaria	0.27	abs.	0.3%	–	abs.	abs.	–	–
Saprinus sp.	0.09	abs.	0.1%	–	abs.	abs.	–	–
Elateridae larvae	0.85	n.r.	1.1%	–	0.29	n.r.	0.7%	–
Scarabaeidae larvae	0.92	n.r.	1.2%	–	0.21	abs.	0.5%	–
Coleoptera unidt. larvae a	abs.	abs.	–	–	0.09	abs.	0.2%	–
Coleoptera unidt. larvae b	abs.	abs.	–	–	0.05	abs.	0.1%	–
Diptera unidt. larvae spa	0.06	abs.	0.1%	–	n.r.	n.r.	–	–
Cyclorrhapha larvae	2.14	abs.	2.7%	–	n.r.	n.r.	–	–
Cochlicella barbara	abs.	abs.	–	–	0.04	abs.	0.1%	–
	Supralittoral		Intertidal		Supralittoral		Intertidal	
Total mean density (ind m^{-2})	79.5 (± 58.9)		96.2 (± 99.9)		41.1 (± 46.9)		68.8 (± 90.9)	
Total number of species	44		90		40		77	
Mean number of species	7.6 (± 4.2)		6.5 (± 12.7)		6.0 (± 4.4)		5.3 (± 7.9)	
Mean density of the resident community (ind m^{-2})	71.1 (± 60.4)		93.4 (± 93.7)		38.2 (± 46.1)		67.2 (± 88.9)	
Number of resident species	13		6		12		3	
Minimum density	Spring (May)		Winter (December)		Summer (July)		Winter (January)	
Maximum density	Summer (September)		Spring (May)		Winter (February)		Summer (July)	

Talorchestia brito only the beach zones had a significant effect since the intertidal zone of Quiaios was clearly distinct from the rest of the beach zones (average: 25.6 ind m^2 ± 21.6, highest average density recorded for this species) (Table 2). During winter, at Cabedelo, the densities of *T. saltator* at the supralittoral were significantly distinct and higher, while in summer this was observed at the intertidal zone. For *T. europaeus*, densities at the supralittoral zone of Quiaios were significantly distinct during winter from the remaining beach zones (Table 2).

Regarding communities' density at both zones, some interesting seasonal patterns of variation were observed at each study site (Fig. 4). Density was higher in the intertidal zone by the end of spring and during summer, becoming approximately similar at both zones in early autumn. From the end of this season and during winter, densities show an increase in the supralittoral and decrease in the intertidal zones. Two-Way Nested ANOVA results proved that there was a significant interaction between seasons and beach zones regarding community density, and that this component was significantly distinct between the intertidal and the supralittoral zones of both beaches during summer months (Table 2), attaining higher values in the intertidal. All these results reflect a variation in the horizontal distribution of abundant macrofaunal species over the year.

The total number of species observed in the intertidal zones was almost twice the number of species collected in the supralittoral (Table 4), but only a small proportion of these animals were residents. Actually, 86% of the species found in the intertidal at Cabedelo and 74% at Quiaios, mostly insects, were rare. Also, the supralittoral resident fauna was more diverse than the intertidal one in both beaches (Table 4). The interaction between seasons and beach zones had a significant effect on the number of species (Table 2). This faunal component presented distinct means in autumn at the intertidal zone of Quiaios (lowest values observed), and in spring at the supralittoral zone of Cabedelo (highest values observed). Also, in winter, the intertidal and supralittoral zones of the beaches were clearly different regarding the number of species, with higher values observed in the supralittoral.

Considering the beach as a whole, densities increase in spring and peak in summer, decrease by autumn, and attain the lowest values in winter (Fig. 3a), showing a similar pattern at both beaches. The density of *Talitrus saltator* and *Tylos europaeus* peaked in summer, but *Talorchestia brito* presented highest densities during summer and autumn months of 1999, and in spring 2000. The variation of the dominant species density in the supralittoral and intertidal zones of the beaches (not shown for simplification), as well as the periods of maximum and minimum density of the whole communities (Table 4), and the ANOVA results upon the effects of the interaction between seasons and beach zones on several faunal components, strongly suggest the occurrence of seasonal movements of abundant macrofaunal organisms in both beaches.

Crustaceans, like *Armadillidium album*, *Pontocrates arenarius* and *Gastrosaccus sanctus*, and insects, like *Callicnemis latreillei* and *Aegiala arenaria,* were only seasonally present in the beaches. The number of species was higher in spring and attained the lowest values during summer (Fig. 5b). Shannon-Wiener's H' also reached the lowest values in summer in both communities, but the highest values were attained in different seasons – autumn for Cabedelo and spring for Quiaios (Fig. 5a). However the analyses of variance revealed that diversity indexes were not significantly affected by the factor seasons individually.

3.4. Influence of the environmental variables on the communities' structure

Different environmental variables were considered significant regarding the Cabedelo and Quiaios resident communities after

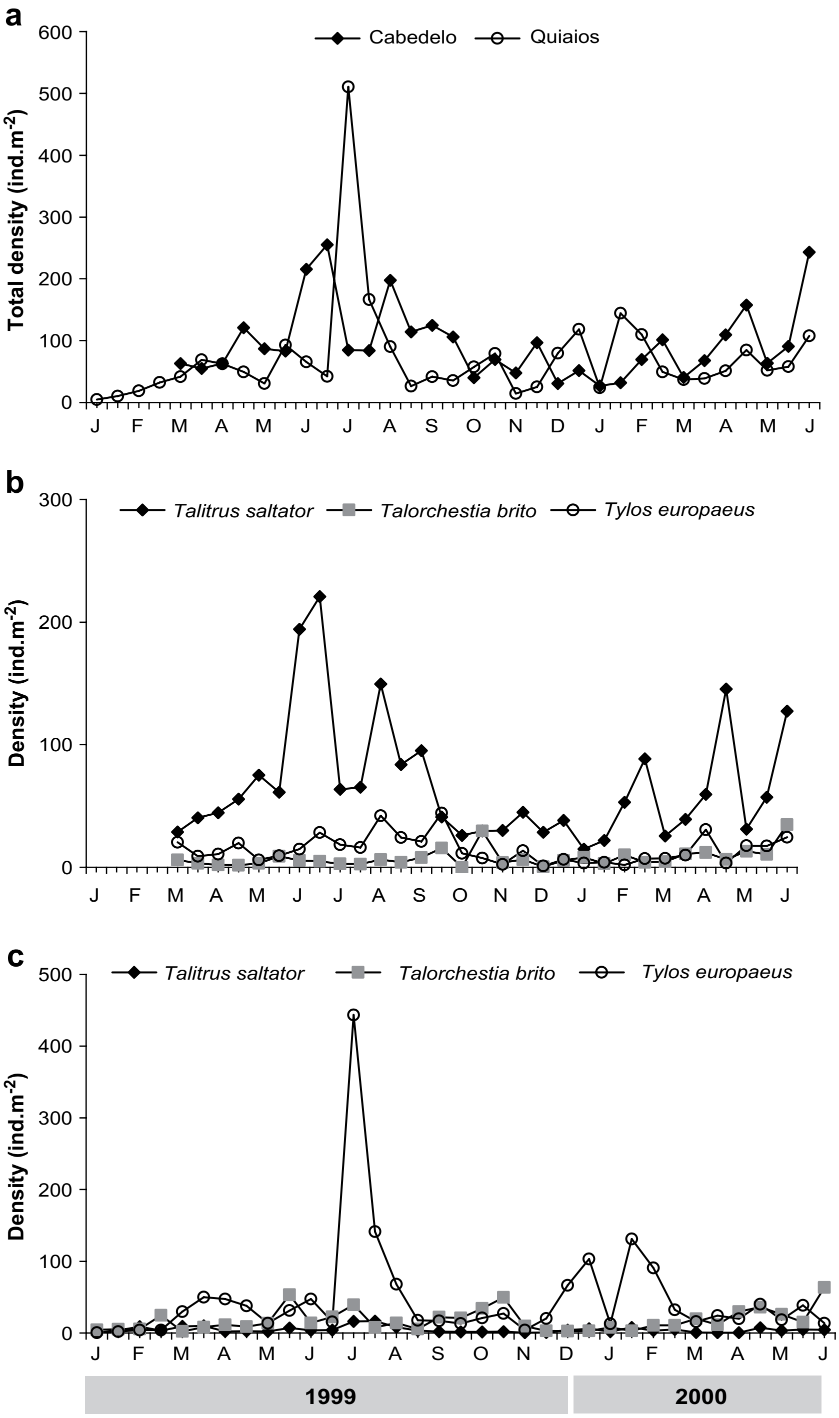

Fig. 3. Variation of community density in the western coast of Portugal. (a) Variation of total density in each community during the study period; (b) Variation of population density in the dominant species at Cabedelo during the study period; (c) Variation of population density in the dominant species at Quiaios during the study period.

forward selection procedures applied to Redundancy Analysis. Only temperature had a significant contribution ($p = 0.001$) in explaining the variance of the faunal data at Cabedelo. Therefore the first axis is constrained to this variable and the remaining axes unconstrained. The two first RDA axes accounted for 60% of the cumulative variance observed in faunal data. The second axis concerns the residual variance in the data, explained by a hypothetical environmental variable, which, according to the reduced RDA model obtained, has more influence than temperature. The significance of the final RDA, using temperature as the explanatory variable, was also significantly assessed using the Monte Carlo Permutation Test ($p = 0.002$, F-ratio: 8.80). The corresponding ordination diagram (Fig. 6a) showed that temperature had a strong and positive influence on *Tylos europaeus*. The crustaceans *Pontocrates arenarius*, *Gastrosaccus sanctus*, *Eurydice naylori* and *Armadillidium album*, as well as most of the insect larvae responded negatively to temperature, increasing their density from left to right along the first axis. *Talitrus saltator* and *Olisthopus rotundatus* were positively influenced by the second ordination axis. The talitrid presented the highest fit. The remaining coleopterans formed

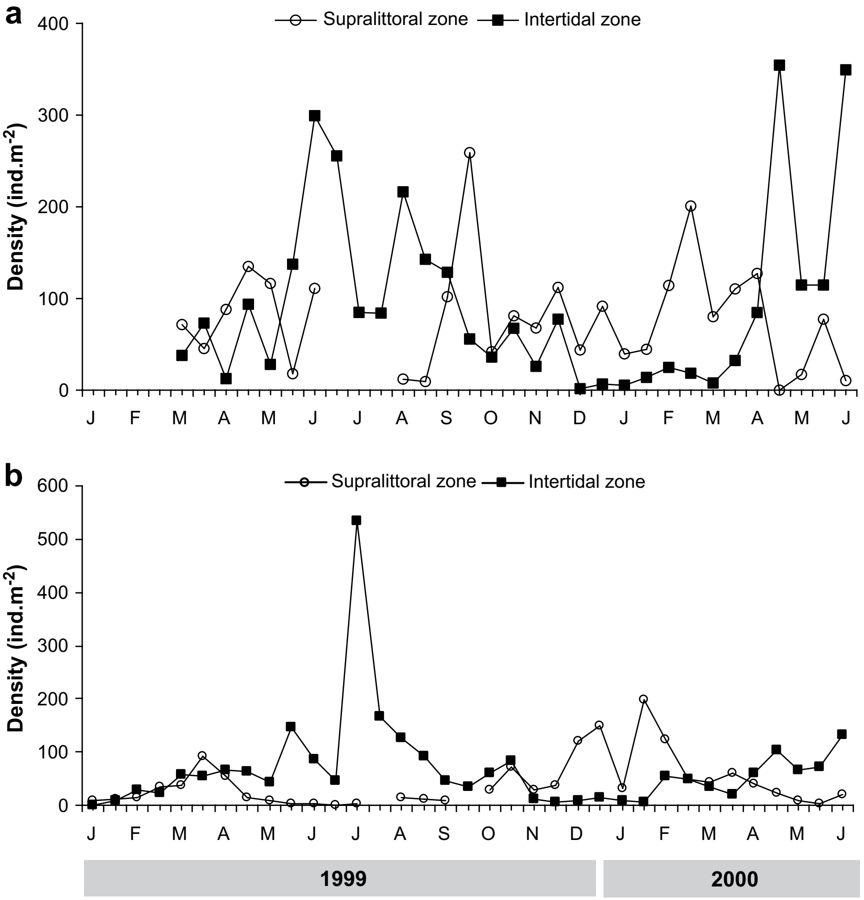

Fig. 4. Variation of total density in the supralittoral and intertidal zones of each study site between January 1999 and June 2000. (a) – Cabedelo; (b) – Quiaios.

an isolated group exhibiting a negative relationship with the second axis. Density variation of *Talorchestia brito* and Cyclorrhapha larvae was not explained by the ordination diagram.

Temperature ($p = 0.036$) and detritus ($p = 0.011$) were selected as explanatory variables regarding the Quiaios resident fauna. In this model, the first two axes of the RDA account for only 26% of the cumulative variance observed in the species data (Fig. 6b). The final RDA using these two explanatory variables was significant (Monte Carlo Permutation Test, $p = 0.004$, F-ratio: 5.48, for the test of significance of all canonical axes). Temperature had a strong, positive influence on the crustacean *Talorchestia brito* (Fig. 6b), and quantity of detritus a negative influence. The other two dominant crustaceans were negatively related to the first ordination axis. Several species were positively related to the quantity of detritus, but the coleopterans *Phaleria acuminata* and Elateridae larvae presented the strongest fit. The crustacean *Armadillidium album*, and the coleopterans *Psammodius porcicollis*, and the unidentified larvae *a*, formed a distinct group, positively related to the second axis and with quantity of detritus. Variations in density of *Gonioctena olivacea* and Scarabidae larvae were not explained by the ordination diagram.

4. Discussion

Regarding exposure to wave action, results demonstrated that both beaches can be considered relatively similar, since they present similar exposure rates. However relevant differences were observed between the sandy beaches in the extension of the intertidal area, sediment grain size, sediment moisture contents and detritus supplies. These characteristics may play important roles in community structuring mechanisms since several differences were observed with regard to community structure and composition between Cabedelo and Quiaios.

Although the communities studied were strongly dominated by crustaceans, insects (especially coleoptera and diptera) represented a much higher contribution than molluscs and polychaetes, and were also the most diverse group. Besides the studies on stranded wrack macrofaunal communities of sandy beaches (e.g. Inglis, 1989; Colombini et al., 2000; Jędrzejczak, 2002; Dugan et al., 2003; Jaramillo et al., 2006), little relevance is given to insects – the intertidal macrofauna is usually the focus of attention. Most of the allochthonous food resources stranded by tides are however consumed by scavengers (e.g. amphipods, isopods and insects) in the supralittoral. Sampling a transect across the entire beach back to the dunes, allowed a more accurate analysis of the macrofaunal communities and demonstrated that insects have an important place in their structure, especially in the supralittoral zone, where the relative importance of resident insects in the community's composition increases.

The number of resident macrofaunal species in the western coast of Portugal is equivalent to the observed by Rodil and Lastra (2004), in similar beaches of northern Spain, when only frequently found organisms were considered. Also, total mean densities recorded in the present study are equivalent to the observed values for other sandy beaches with similar conditions (e.g. Rodil and Lastra, 2004; Rodil et al., 2006). Regarding the abundant species – *Talitrus saltator*, *Tylos europaeus* and *Talorchestia brito* – the two communities studied did not present a steady structure and the

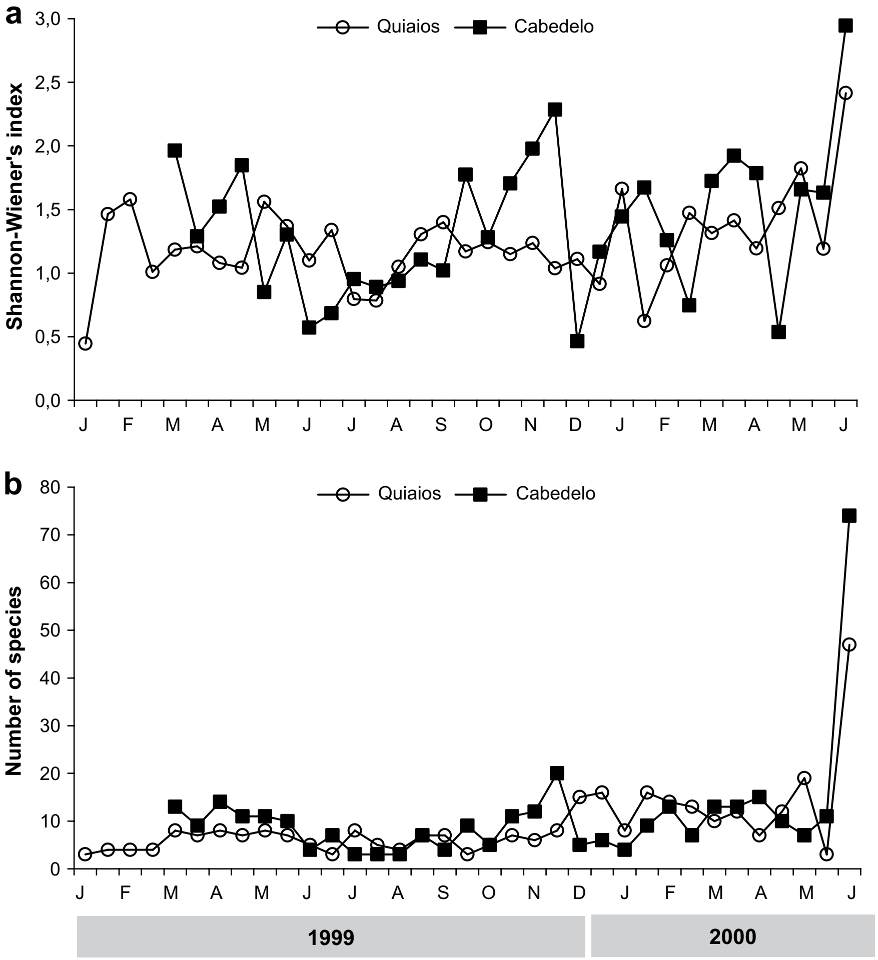

Fig. 5. Variation of diversity indexes in the studied sandy beach communities at the western coast of Portugal. (a) Variation of Shannon-Wiener's index in each community during the study period; (b) Variation of the number of species in each community during the study period.

factor beach had significant effects on the density of these species. These animals are the driving forces, at different levels, of the macrofaunal community structure of the sandy beaches on the western coast of Portugal. Talitrids and tylids may well have similar roles in other exposed sandy shores of Europe and even North Africa, where they are known to be frequently abundant. Furthermore, as dominant species that form abundant populations on exposed beaches, these animals constitute key species in these environments and may be used as indicators of environmental quality. However, to do so, their population dynamics, reproductive strategies and productivity must be studied as done by Marques et al. (2003), and Gonçalves et al. (2003, 2005).

Why is the relative dominance of the three key species so distinct in the Cabedelo and Quiaios communities? The differences observed must be mainly related to the different feeding habits and habitat preferences of the dominant species and the particular conditions observed in each sandy beach. The talitrids *Talitrus saltator* and *Talorchestia brito* are sympatric species but have distinct habitat preferences regarding their optimum zone on the beach: *T. brito* occupies the intertidal zone, taking advantage of the extended intertidal area of Quiaios, while *T. saltator* prefers the supralittoral area. Also, according to Lagardère (1966), *T. saltator* has a preference for finer sands, a condition observed at Cabedelo. The higher moisture content of the sand at Cabedelo beach may also be an advantage for *T. saltator* – it's easier to avoid desiccating conditions in sands with higher moisture contents. Moreover, although both can be considered scavengers *sensu lato*, *T. brito* is more of an herbivore which feeds on the interstitial flora of the sediment (Lagardère, 1966), and is therefore less dependent on detritus subsidies. The coarsest nature of Quiaios sands may even be an advantage, promoting the development of a richer and more abundant interstitial flora. Concerning the supralittoral isopod *Tylos europaeus*, a clear preference for coarse-sand beaches, avoiding fine sediments which hamper their locomotion (Kensley, 1974), explains the higher population densities recorded in Quiaios. This tylid is an important decomposer of stranded wrack (Kensley, 1974), but several animals were often observed associated with embryo dunes vegetation at Quiaios, namely *Otanthus maritimus* (personal observations). This suggests that *T. europaeus* possibly also feeds on living plants, as an alternative food resource when detritus are limited. However there is also possible competition with *T. saltator*, especially at Cabedelo, due to a considerable niche overlapping between both species.

Resident macrofaunal composition was similar to other Atlantic and Mediterranean sandy beaches of Europe, especially regarding semi-terrestrial and marine animals (e.g. Lagardère, 1966; Rodil et al., 2006). The talitrids and the tylid were abundant throughout the beach, although they are normally reported as abundant species only in the supralittoral (see for instance Lagardère, 1966; Rodil et al., 2006). Also, the important differences in resident scavenger insects composition observed (i.e. the coleopterans *Saprinus* sp., *Aegiala arenaria* and *Callicnemis latreillei*, exclusive to

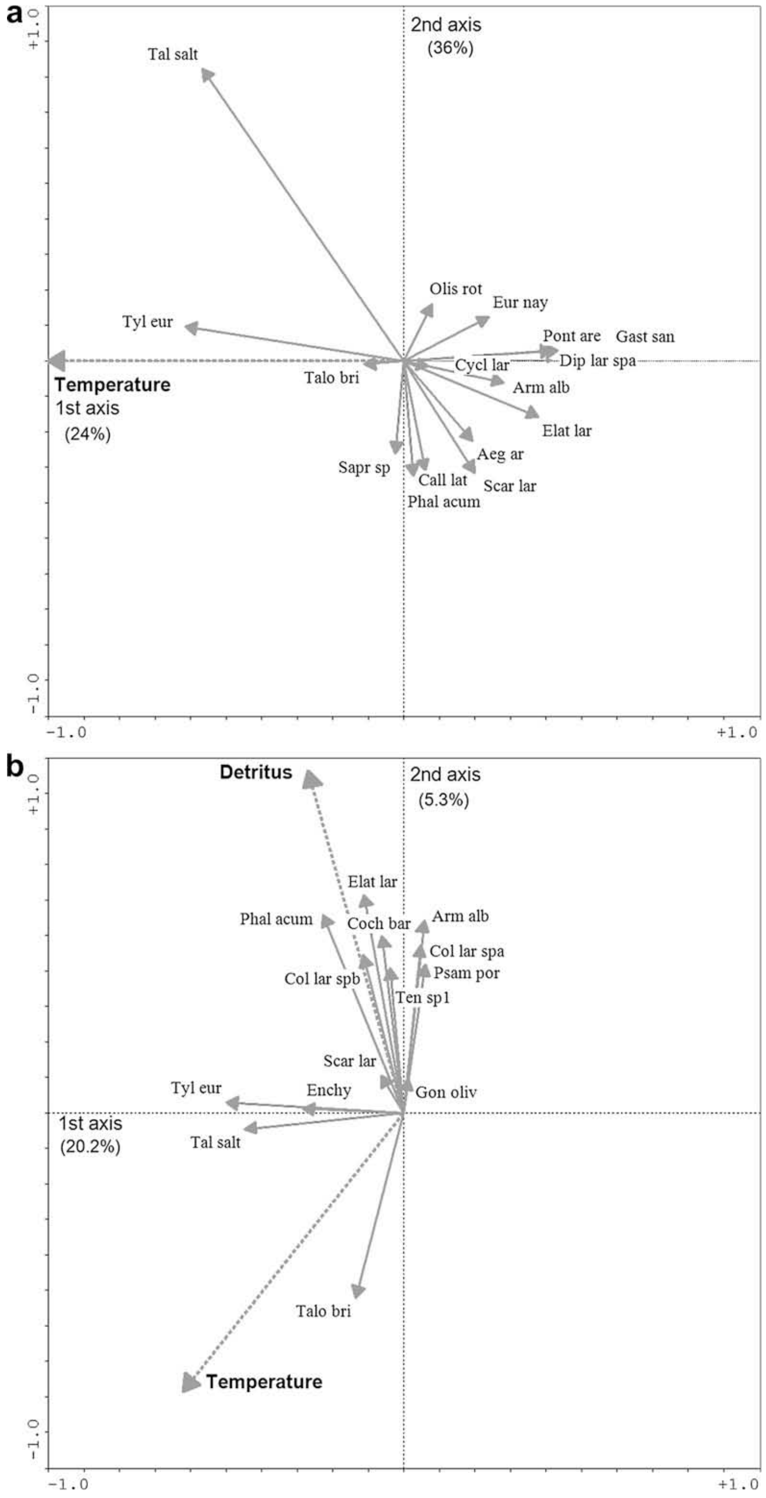

Fig. 6. RDA ordination diagrams of macrofaunal communities' data and environmental parameters at Cabedelo and Quiaios sandy beaches (western coast of Portugal). (a) – RDA ordination diagram of resident community data and environmental parameters at Cabedelo beach; (b) – RDA ordination diagram of resident community data and environmental parameters at Quiaios beach. Tyl eur – *Tylos europaeus*; Tal salt – *Talitrus saltator*; Talo bri – *Talorchestia brito*; Eur nay – *Eurydice naylori*; Pont are – *Pontocrates arenarius*; Gast san – *Gastrosaccus sanctus*; Arm alb – *Armadillidium album*; Dip lar – Diptera unidentified larvae; Cycl lar – Cyclorrhapha larvae; Olis rot – *Olisthopus rotundatus*; Aeg ar – *Aegiala arenaria*; Call lat – *Callicnemis latreillei*; Phal acum – *Phaleria acuminata*; Psam por – *Psammodius porcicollis*; Gon oliv – *Gonioctena olivacea*; Sapr sp – *Saprinus* sp.; Ten sp1 – Tenebrionidae unidentified species 1; Elat lar – Elateridae larvae; Scar lar – Scarabaeidae larvae; Col lar spa – Coleoptera unidentified larvae species a; Col lar spb – Coleoptera unidentified larvae especies b; Enchy – Enchytraeidae unidentified species; Coch bar – *Cochlicella barbara*.

Cabedelo), suggest that wrack subsidies can increase insect species richness on exposed beaches, as proposed by Dugan et al. (2003) for exposed beaches in California.

In western Portugal, the macrofaunal species composition in the beach zones reflected the typical patterns observed in sandy beaches worldwide. Nevertheless, the intertidal impoverishment recorded (only crustaceans were resident), although a common feature of exposed beaches (Brown and McLachlan, 1990), is not frequent in other studies on similar beaches (e.g. Bayed, 2003; Rodil et al., 2006). The present study revealed that the amphipod *Talitrus saltator* used both the supralittoral and the intertidal zones of the beach according to seasons. These results contrast with other studies where *T. saltator* is frequently reported as an exclusive species to the supralittoral (see for instance Rodil et al., 2006). However, contrarily to the present work, community studies are often based on snapshot sampling events, masking possible seasonal movements of the macrofauna on the beach. Regarding the other two abundant species, results were in accordance with the already mentioned supralittoral preference by *Tylos europaeus*, and the intertidal preference by *Talorchestia. brito*.

The interaction between seasons and beach zones presented significant effects on several faunal components, namely on the densities of amphipods, isopods, and the abundant species *Talitrus saltator* and *Tylos europaeus*. However, such a type of interaction was not detected for the talitrid *Talorchestia brito*, although beach zones influenced the density of this animal. These results confirm the occurrence of seasonal differences in the horizontal distribution of *T. saltator* and of *T. europaeus* on the beach, but regarding *T. brito* some doubts may remain. The populations' density increased in the intertidal zones in the warm seasons, while in the supralittoral increases were recorded in the coldest seasons. Previous studies (Gonçalves et al., 2003, 2005; Marques et al., 2003) suggested that the low winter densities observed in the populations of both talitrids and the tylid may be a consequence of a partial movement of these animals to the dunes, or even a displacement in their burrowing depth, as they burrow deeper into the sand. Similar seasonal fluctuations in horizontal distribution have been reported by Lagardère (1966) for *T. brito* and *T. europaeus* in France and by Williams (1995) for *T. saltator* in United Kingdom. Seasonal movements along the beach may avoid potential situations of desiccative stress and extreme temperatures, by burrowing in the beach zones where sand moisture content and sediment temperature create a more favourable microhabitat, thus enabling these animals to survive in such dynamic and severe environments (Williams, 1995; Tsubokura et al., 1997). This is also supported by the significant differences observed between seasons and between beach zones on sand moisture content in the present study.

The seasonal patterns of density variation observed in the abundant species are associated with their populations' dynamics (see Marques et al., 2003 for *Talitrus saltator*, Gonçalves et al., 2003 for *Talorchestia brito* and Gonçalves et al., 2005 for *Tylos europaeus*). The differences observed between the dynamics of *T. europaeus* and *T. brito*, especially the timing of recruitments and average population densities, were reflected in the seasonal variation in community structure dominance at Quiaios between isopods and amphipods. Seasons also have a clear influence on the bio-ecology of these abundant species demonstrated by: (1) the positive correlations between population density and temperature found in earlier studies on these populations (see Gonçalves et al., 2003, 2005; Marques et al., 2003); (2) the significant relationships observed with multivariate methods in the present study (namely *T. brito* and *T. europaeus*). However, several authors also indicate the photoperiod as an important reproduction regulating factor in talitrids (e.g. Williams, 1978) and oniscid isopods like *Tylos* (e.g. Souty-Grosset et al., 1991).

Several resident organisms were only seasonally observed on the beaches. The seasonal disappearance of terrestrial insects (e.g. *Callicnemis latreillei* and *Aegiala arenaria*) during the extreme seasons (summer and winter), reinforced by the significant ANOVA results observed for coleopterans on the interaction between seasons and beach zones, may be a way of avoiding extreme environmental conditions on the beach, viz. severe storms and extreme temperatures, while for marine crustaceans (e.g. *Gastrosaccus sanctus*) it may prevent dragging by winter storms. Temporal trends observed in the seasonal analysis of diversity indexes also support seasonal changes in the utilization of the beach by the macrofauna. Furthermore, the negative influence of temperature on the seasonally resident crustaceans *Pontocrates arenarius*, *G. sanctus*, *Armadillidium album* and *Eurydice naylori*, and on several insect larvae, showed by Redundancy Analysis techniques, also reinforce the relevance of seasons in controlling population densities and beach utilization by several organisms, including the abundant tylid and the talitrids – seasons shape the structure and composition of these communities.

In Cabedelo, many resident organisms were distinctly related to the second ordination axis, which had a higher influence than temperature on species data and produced two assemblages of species. *Talitrus saltator* and *Olisthopus rotundatus* were positively influenced by this hypothetical environmental variable, while all the resident scavenger coleopterans were negatively influenced. A combination of the variables detritus quantity and relative moisture content of detritus (fresh weight) appears to be a plausible explanation for these results. All these species are directly or indirectly (in the case of the predator *O. rotundatus*) associated with wrack deposits on sandy beaches. Several authors (e.g. Inglis, 1989; Colombini et al., 2000; Jędrzejczak, 2002) have demonstrated that wrack-associated macrofauna colonize the debris in a succession, invading it at different times according to their metabolic and trophic needs. Talitrid amphipods are primary colonizers of recently stranded fresh debris (e.g. Colombini et al., 2000; Jaramillo et al., 2006), and invasion by coleopteran predator species often coincides with amphipod and isopod colonization (e.g. Colombini et al., 2000; Jędrzejczak, 2002). Furthermore, Jaramillo et al. (2006) reported that the scavenger tenebrionid *Phalerisida maculata* on Chilean sand beaches was more abundant on old dry wrack deposits. Based on these evidences, the negative influence of the second ordination axis observed on the coleopteran scavengers' assemblage, including, for instance, one tenebrionid, might be related to a preference to consume older and drier debris. Therefore, although debris quantity was assessed (dry weight form), freshness and aging of the debris was not estimated in this study and it might be an important explanatory variable regarding wrack-associated macrofaunal abundances.

Besides temperature, the quantity of detritus was also selected as an explanatory variable at Quiaios, and several scavenger species were positively related to it. Since in this beach the input of debris is more irregular over time and more limited, these may lead to a more obvious and clear reflection in scavenger density and occurrence data at the community level, making the relationship clearer. The two distinct macrofaunal assemblages associated with the first and second ordination axes for this resident community are unclear and difficult to interpret, suggesting that other environmental variables should be tested in the future (e.g. sediment temperature).

5. Conclusions

On the whole, this study demonstrates that these similarly exposed sandy beaches on the western coast of Portugal present several differences regarding community structure, community composition and relative contribution of the abundant species. The absence of a steady structure is believed to be mainly associated with relevant differences in detritus subsidies and, to a lesser extent, with differences in sand grain size, sediment moisture content and extent of the intertidal area, which lead to distinct ecological responses of the abundant species. These findings agree with the Multicausal Environmental Severity hypothesis proposed by Brazeiro (2001), since the different species of the studied beaches appear to be controlled by the combined effects of the distinct environmental factors identified. Seasons, both as an isolated factor and when combined with the effects of beach zones, influence relevantly these communities by shaping some abiotic conditions of the sand (moisture content, temperature) and various community and population features differently throughout the year, as the significant relationships with seasons, seasons × beach zones and temperature demonstrated. Wrack deposits are believed to play an extremely important role in exposed sandy beaches where macrofaunal communities are dominated by supralittoral wrack-associated fauna and, they may overlap with the physical characteristics of the beach, as demonstrated by Dugan et al. (2003). This work further demonstrates that supralittoral macrofaunal organisms, especially talitrid and tylid crustaceans, play a relevant role in the structure of exposed sandy beach communities and should be considered key elements and potential indicators in future management options for these environments. However, the role of detritus subsidies, and especially the functioning of these macrofaunal communities, should be investigated more deeply in the future.

Acknowledgements

The present study was partially supported by the Projects WADI (INCO2003 – MPC2 – 015226) and EFICAS (POCI/MAR/61324/2004). The research complies with the current laws in the country where it was conducted. The authors are indebted with all the colleagues at IMAR-CIC who assisted in the field work, to Jean Burroughs for her valuable contribution on manuscript language revision, and with the two anonymous reviewers for their reviews and their helpful comments on the earlier versions of this manuscript.

References

Bayed, A., 2003. Influence of morphodynamic and hydroclimatic factors on the macrofauna of Moroccan sandy beaches. Estuarine, Coastal and Shelf Science 58S (Suppl. A), 71–82.

Brazeiro, A., 2001. Relationships between species richness and morphodynamics in sandy beaches: what are the underlying factors? Marine Ecology Progress Series 224, 35–44.

Brown, A.C., McLachlan, A., 1990. Ecology of Sandy Shores. Elsevier, Amsterdam, 328 pp.

Colombini, I., Aloia, A., Fallaci, M., Pezzoli, G., Chelazzi, L., 2000. Temporal and spatial use of stranded wrack by the macrofauna of a tropical sandy beach. Marine Biology 136, 531–541.

Defeo, O., Jaramillo, E., Lyonnet, A., 1992. Community structure and intertidal zonation of the macrofauna on the Atlantic coast of Uruguay. Journal of Coastal Research 8, 830–839.

Defeo, O., Rueda, M., 2002. Spatial structure, sampling design and abundance estimates in sandy beach macroinfauna: some warnings and new perspectives. Marine Biology 140, 1215–1225.

Dexter, D.M., 1983. Community structure of intertidal sandy beaches in New South Wales, Australia. In: McLachan, A., Erasmus, T. (Eds.), Sandy Beaches as Ecosystems. W Junk Publishers, The Hague, pp. 461–472.

Dexter, D.M., 1990. The effect of exposure and seasonality on sandy beach community structure in Portugal. Ciência Biológica, Ecológica e Systemática. Portugal 10, 31–50.

Dugan, J.E., Hubbard, D.M., McCrary, M.D., Pierson, M.O., 2003. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. Estuarine, Coastal and Shelf Science 58S (Suppl. A), 25–40.

Gheskiere, T., Vincx, M., Weslawski, J.M., Scapini, F., Degraer, S., 2005. Meiofauna as a descriptor of tourism-induced changes at sandy beaches. Marine Environmental Research 60, 245–265.

Gonçalves, S.C., Marques, J.C., Pardal, M.A., Bouslama, M.F., El Gtari, M., Charfi-Cheikhrouha, F., 2003. Comparison of *Talorchestia brito* (amphipoda, talitridae) biology, dynamics, and secondary production in Atlantic (Portugal) and Mediterranean (Tunisia) populations. Estuarine, Coastal and Shelf Science 58, 901–916.

Gonçalves, S.C., Pardal, M.A., Cardoso, P.G., Ferreira, S.M., Marques, J.C., 2005. Biology, population dynamics and secondary production of *Tylos europaeus* (Isopoda, Tylidae) on the western coast of Portugal. Marine Biology 147, 631–641.

Inglis, G., 1989. The colonisation and degradation of stranded *Macrocystis pyrifera* (L.) C. Ag. by the macrofauna of a New Zealand sandy beach. Journal of Experimental Marine Biology and Ecology 125, 203–217.

Jaramillo, E., de la Huz, R., Duarte, C., Contreras, H., 2006. Algal wrack deposits and macroinfaunal arthropods on sandy beaches of the Chilean coast. Revista Chilena de Historia Natural 79, 337–351.

Jędrzejczak, M.F., 2002. Stranded *Zostera marina* L. vs. wrack fauna interactions on a Baltic sandy beach (Hel, Poland): a short-term pilot study. Part II. Driftline effects of succession changes and colonisation of beach fauna. Oceanologia 44, 367–387.

Junoy, J., Castellanos, C., Viéitez, J.M., de la Huz, M.R., Lastra, M., 2005. The macroinfauna of the Galician sandy beaches (NW Spain) affected by the Prestige oil-spill. Marine Pollution Bulletin 50, 526–536.

Kensley, B., 1974. Aspects of the biology and ecology of the genus *Tylos* Latreille. Annals of the South African Museum 65, 401–471.

Lagardère, J.P., 1966. Recherches sur la biologie et l'écologie de la macrofaune des substrats meubles de la côte des Landes et de la côte Basque. Bulletin du Centre d'Etudes et de Recherches Scientifiques. Biarritz 6, 143–209.

Lercari, D., Defeo, O., 2003. Variation of a sandy beach macrobenthic community along a human-induced environmental gradient. Estuarine, Coastal and Shelf Science 58S (Suppl. A), 17–24.

Marques, J.C., Gonçalves, S.C., Pardal, M.A., Chelazzi, L., Colombini, I., Fallaci, M., Bouslama, M.F., El Gtari, M., Charfi-Cheikhrouha, F., Scapini, F., 2003. Comparison of *Talitrus saltator* (Amphipoda, Talitridae) biology, dynamics, and secondary production in Atlantic (Portugal) and Mediterranean (Italy and Tunisia) populations. Estuarine, Coastal and Shelf Science 58S (Suppl. A), 127–148.

McLachlan, A., 1980. The definition of sandy 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., Jaramillo, E., Donn, 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.

McLachlan, A., Jaramillo, E., 1995. Zonation on sandy beaches. An Annual Review. Oceanography and Marine Biology 33, 305–335.

Rodil, I.F., Lastra, M., 2004. Environmental factors affecting benthic macrofauna along a gradient of intermediate sandy beaches in northern Spain. Estuarine, Coastal and Shelf Science 61, 37–44.

Rodil, I.F., Lastra, M., Sánchez-Mata, A.G., 2006. Community structure and intertidal zonation of the macroinfauna in intermediate sandy beaches in temperate latitudes: North coast of Spain. Estuarine, Coastal and Shelf Science 67, 267–279.

Souty-Grosset, C., Chentoufi, A., Juchault, P., Mocquard, J.P., 1991. Combined effects of thermoperiod and photoperiod on the reproduction of the terrestrial isopod *Armadillidium vulgare* (Latreille): geographical variability. Journal of Thermal Biology 16, 233–240.

ter Braak, C.J.F., Šmilauer, P., 1998. CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (Version 4). Microcomputer Power, Ithaca, NY, USA, 351 pp.

Tsubokura, T., Goshima, S., Nakao, S., 1997. Seasonal horizontal and vertical distribution patterns of the supralittoral amphipod *Trinorchestia trinitatis* in relation to environmental variables. Journal of Crustacean Biology 17, 674–686.

Veloso, V.G., Silva, E.S., Caetano, C.H.S., Cardoso, R.S., 2006. Comparison between the macroinfauna of urbanized and protected beaches in Rio de Janeiro State, Brazil. Biological Conservation 127, 510–515.

Weslawski, J.M., Stanek, A., Siewert, A., Beer, N., 2000. The sandhopper (*Talitrus saltator*, Montagu 1808) on the Polish Baltic coast. Is it a victim of increased tourism? Oceanological Studies vol. 29, 77–87.

Williams, J.A., 1978. The annual pattern of reproduction of *Talitrus saltator* (Crustacea: Amphipoda: Talitridae). Journal of Zoology 184, 231–244.

Williams, J.A., 1995. Burrow-zone distribution of the supralittoral amphipod *Talitrus saltator* on Derbyhaven beach, Isle of Man – a possible mechanism for regulating desiccation stress? Journal of Crustacean Biology 15, 466–475.