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Two year study of swash zone suprabenthos of two Galician beaches (NW Spain)

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ABSTRACT

The suprabenthos is considered a major food resource for some fish and birds. Moreover, it plays a key role in the food chain and in nutrient regeneration in the surf zone. The aim of this study was to determine the factors that regulate this fauna and the differences between the suprabenthic groups, to study the possibility of seasonal variations and to compare these results with those of other studies conducted in Europe. A study and geographical comparison was conducted of the temporal patterns of the suprabenthos in the swash zone at two sandy beaches on the NE Atlantic coast (Altar and Ladeira beaches) in the NW of Spain. The study was carried out from September 2005 to August 2007 (24 months). To study the fauna, 60 m^2 was sampled monthly with a suprabenthic sledge, and a total of 101 species belonging to Peracarida and Decapoda were recorded. Total densities ranged from 0.42 $ind \cdot m^{-2}$ to 178.75 $ind \cdot m^{-2}$. Ladeira beach showed higher densities and species richness than Altar beach, and the biocoenosis showed a different dynamic over the 24 months and between years and locations. These results indicate that there is no clear seasonality in the dynamic of suprabenthic species, although the variance of Peracarida orders was explained in diverse degree by environmental variables. The environmental models implemented explained between 27.7% and 93.8% of the faunal data, and hydrodynamic factors and daily global irradiance were selected as the best factors to explain the temporal variations.

1. Introduction

The intertidal zone on sandy beaches is one of the most inhospitable natural environments for life due to constant sudden changes in environmental conditions, and the fauna which inhabits this zone must be adapted to marine and semi-terrestrial conditions, a circumstance which excludes sensitive species. Variability in the fauna found on sandy beaches in temperate latitudes is linked to species life cycle, physical and chemical characteristics, climatic events and accretion–erosion dynamics (Lastra et al., 2006). The water layer just above the seabed is inhabited by small fauna collectively known as the suprabenthos (Mees and Jones, 1997), which is considered a major food resource for some fish, birds and marine mammals (e.g. McLachlan, 1983; Murison et al., 1984) since it forms a very important link in the marine food chain and in nutrient regeneration in the surf zone (Cockcroft et al., 1988). Furthermore, this fauna has the capacity to structure the zooplankton biocoenosis (Fulton, 1982), and it has even been suggested that such predation may play an important role in regulating meiofaunal densities (Johnston and Lasenby, 1982).

The suprabenthos biocoenosis is fundamentally formed by peracarids (mysids, cumaceans, amphipods and isopods) and decapods (Heyns and Froneman, 2010; San Vicente et al., 2009). A limited number of studies have been conducted of the suprabenthos inhabiting sandy European beaches on the coasts of the North Sea and Baltic Sea (Beyst et al., 2001; Lock et al., 1999), the United Kingdom (Colman and Segrove, 1955), the Bay of Biscay (San Vicente and Sorbe, 2001) and the Mediterranean Sea (Munilla and San Vicente, 2005). To date, the only study of the suprabenthic community in Galicia (NW Spain) was conducted on the ría de A Coruña and continental platform (Frutos, 2006), and thus, there is no prior data for the sandy beaches. Previous studies do not show a clear pattern for the dynamics of peracarid fauna, although it has been suggested that the differences between fauna groups are determined by diverse environmental factors. To elucidate these questions, two sandy beaches were sampled over 24 consecutive months. The beaches sampled were Altar beach (Cantabrian Sea) and Ladeira beach (Atlantic Ocean), both of which were affected in 2002–2003 by the Prestige oil spill, to a greater (Ladeira) or lesser (Altar) extent (Junoy et al., 2005). The present research was carried out almost 3 years after the oil spill, in September 2005.

2. Materials and methods

2.1. Study area and sampling

The swash zones of two sandy beaches in Galicia (NW Spain) were selected as study sites. Altar beach (43°34′N 7°14′W) is located at the mouth of the ría de Foz, forming a 1 km long sandbar with a N–NE orientation. Ladeira beach (42°34′N 9°03′W) is 1.2 km long, with a SW orientation, and is a protected area forming part of the Corrubedo Natural Park (Parque Natural del Complexo dunar de Corrubedo e lagoas de Carregal e

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Vixán) (Fig. 1). Tides are semidiurnal and mesotidal, with maximum ranges of between 1.35 and 4.1 m (Vilas et al., 1986). Monthly monitoring was carried out from September 2005 to August 2007 (24 months).

All samples were taken from the swash zone (<1 m depth) 1 h before and after low tide, using a suprabenthic sledge. Measuring 50 cm wide and 20 cm high and equipped with a 0.5 mm mesh, the sledge was designed to skim over the surface of the sediment in order to collect the fauna swimming within the 0–20 cm near-bottom water layer. The beaches were divided into three zones; four tows were taken in each zone, and a total of 60 m^2 (12 tows) was sampled monthly on each beach. All samples were taken by the same operator to avoid operator bias. Samples were fixed in 7% formalin and Rose Bengal was added to facilitate animal sorting. Then, in the laboratory, all animals were sorted, identified to species level, counted and preserved in 70% alcohol. Peracarids and decapods represented more than 97% of the total fauna and only these taxa were employed in the analyses in order to reduce the potential bias caused by using taxa with scant occurrence and abundance.

2.2. Environmental variables

A monthly sediment sample was collected from the swash zone in each of the three beach zones for grain size analysis and organic matter content. Particle size analysis was performed by dry sieving (Buchanan, 1984). Wave height (m), water temperature (°C) and salinity (ups) were recorded hourly from the oceanographic buoys WANA1052075 (43.75°N 7.00°W) and Cabo Peñas (43.74°N 6.17°W) for Altar beach and from WANA1044070 (42.50°N 9.00°W) and Cabo Silleiro (42.12°N 9.43°W) for Ladeira beach (National Ports Authority, Spanish Ministry of Development). The data are expressed as the monthly average value

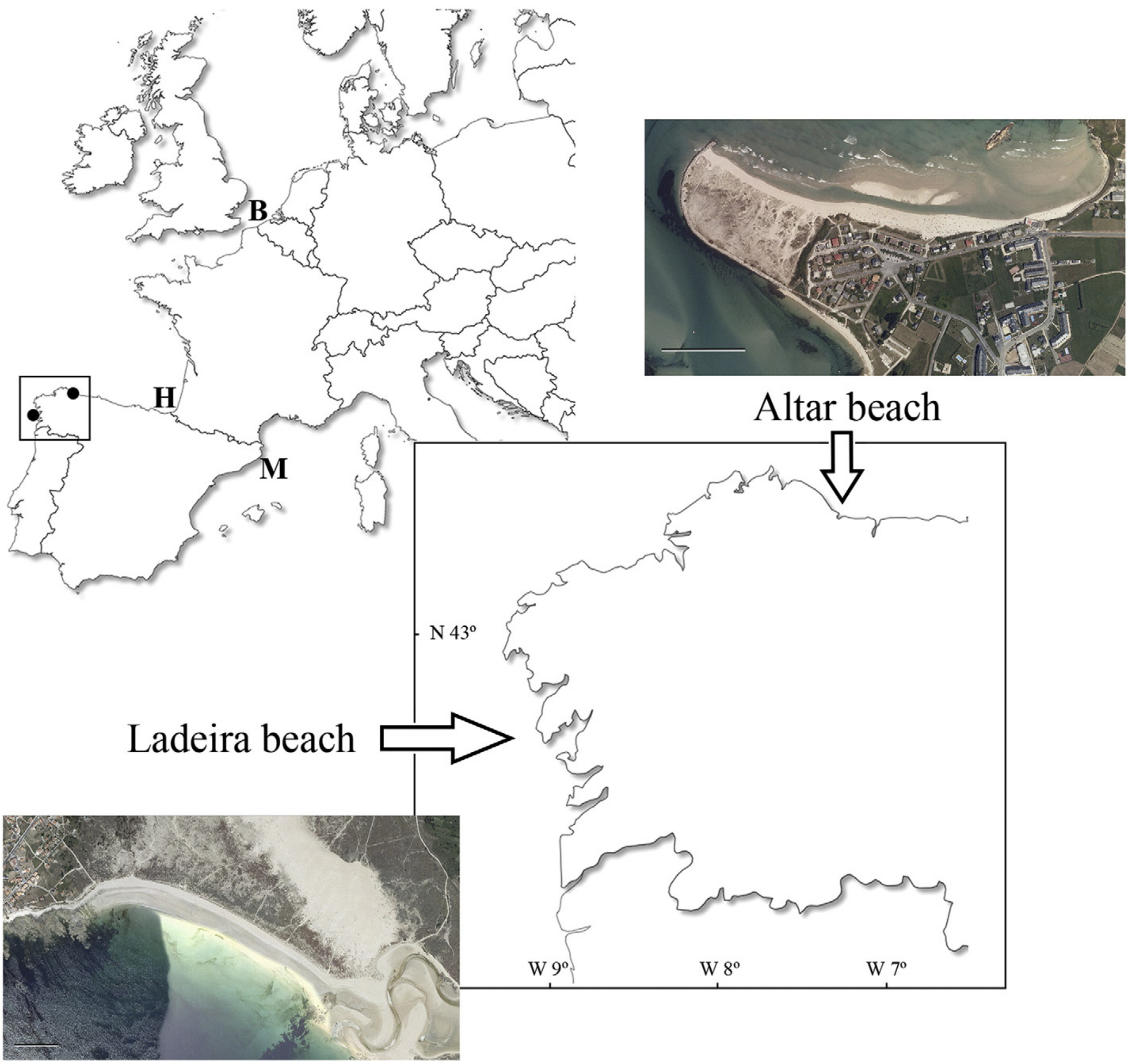

Fig. 1. Location of the suprabenthic studies on European sandy beaches: B = Belgian coast, M = Catalan coast, H = Biscay bay, Circles = Altar and Ladeira beaches; Localization of studied beaches: Ladeira (42°34′N 9°03W) and Altar (43°34′N 7°14′W) (Orthoimage from Instituto Geográfico Nacional, Spain; scale bar: 200 m).

Table 1
List of taxa collected in Altar and Ladeira, and their presence (+) in other European sandy beaches: Belgian coast (B), Bay of Biscay (H), and Mediterranean Catalan beaches (M).

Species	Beaches		
	Altar	Ladeira	Others
Amphiphoda			
Amphipoda indet.	+	+	
Ampithoe gannaroides		+	
Ampithoe ramondi		+	M
Ampithoe sp.		+	
Aoridae sp.		+	
Apherusa bispinosa		+	H
Apherusa jurinei		+	H
Apherusa sp.	+	+	
Apohyale prevosti		+	B
Atylus swammerdami	+	+	B, H, M
Bathyporeia elegans		+	
Bathyporeia pelagica	+	+	
Bathyporeia pilosa		+	B, H
Bathyporeia sarsi	+	+	B
Bathyporeia sp.	+	+	
Caprella acanthifera		+	M
Caprella linearis		+	B
Caprellidae indet.		+	
Dexamine spinosa		+	H, M
Dexamine thea		+	H
Ericthonius punctatus		+	M
Gammarellus angulosus		+	
Gammaropsis sp.		+	
Gammarus finmarchicus	+		
Gammarus locusta	+	+	B
Gammarus oceanicus	+		
Gammarus sp.	+	+	
Haustorius arenarius		+	B, M
Hyale sp.		+	
Ischyriceridae indet.	+	+	
Jassa falcata		+	B, M
Jassa marmorata		+	B, H, M
Jassa ocia		+	M
Jassa pussila	+		
Jassa sp.		+	
Leucothoe procera		+	
Lysianassa ceratina		+	
Lysianassidae indet.		+	
Mellita palmata	+		B
Microdeutopus sp.		+	
Monocorophium acherusicum		+	B, M
Monocorophium insidiosus		+	B
Monocorophium sp.		+	
Nannonyx sp.		+	
Parajassa sp.		+	
Peltocoxa dammoniensis		+	
Perrierella audouiniana		+	
Phtisica marina		+	B, M
Pontocrates altamarinus	+	+	B, H, M
Pontocrates arenarius	+	+	B, H, M
Pseudoprotella phasma		+	
Siphonoecetes kroyeranus		+	H, M
Stenothoe sp.		+	
Synchelidium maculatum		+	
Urothoe atlanticus	+		
Urothoe brevicornis	+		
Isopoda			
Eurydice affinis	+	+	B, M
Eurydice naylori	+	+	
Eurydice pulchra	+	+	B, H
Gnathia sp.	+	+	M
Idotea balthica	+	+	B, M
Idotea chelipes	+	+	
Idotea emarginata	+	+	B, M
Idotea linearis		+	B, M
Idotea metallica	+		B
Idotea neglecta	+		M
Idotea pelagica	+	+	B, M
Idotea sp.		+	
Isopoda indet		+	
Lekanesphaera rugicauda		+	

Table 1 (*continued*)

Species	Beaches		
	Altar	Ladeira	Others
Lekanesphaera teissieri	+	+	
Lekanesphaera weilli	+	+	M
Cumacea			
Bodotria arenosa		+	
Cumella sp.		+	
Cumopsis fagei	+	+	H
Cumopsis goodsir	+	+	B, M
Cumopsis longipes	+	+	
Eocuma dollfusi		+	H
Vaunthompsonia sp.		+	
Mysida			
Gastrosaccus roscoffensis	+	+	H, M
Gastrosaccus spìnifer	+		B, H, M
Hemimysis sp.	+	+	
Heteromysis armoricana		+	
Heteromysis lamornae	+		
Heteromysis sp.		+	
Leptomysis lingvura		+	M
Leptomysis mediterranea		+	M
Mysidella typica		+	
Neomysis integer	+		B, M
Paramysis arenosa		+	H, M
Praunus flexuosus	+		B
Praunus neglectus	+		
Schystomysis ornata	+		
Schystomysis parkeri	+	+	H
Schystomysis spiritus	+	+	B, H
Siriella armata	+	+	B, H, M
Siriella clausi	+	+	B, M
Caridea			
Crangon crangon		+	H, M
Crangonidae indet	+	+	
Philocheras trispinosus	+	+	H, M

of the hourly data; monthly data are more adequate than instant data collected at sampling occasion. In order to correctly characterise the wave dynamic, it was necessary to propagate the waves in deep waters near the area of study (CEPRECO, 2006). Wave height at surf zone for Deans's parameter was calculated according to the expression given by Rattanapitikon and Shibayama (2000).

The atmospheric variables, air temperature (°C), wind speed (km/h), sun hours (h), Daily Global Irradiance (10 kJ/(m^2·day)) (DGI hereafter), precipitation (dm^3/m^2/month), and insolation (%), were taken from the weather stations at Corrubedo (42.56°N 9.03°W) and Ribadeo (43.54°N 7.08°W), and are expressed as the monthly average value, except for hours of sun (absolute monthly values).

2.3. Statistical analysis

Temporal patterns of the multivariate suprabenthic fauna assemblages (SFA) were examined by performing Permutational Multivariate Anova (PERMANOVA) (Anderson, 2001) and canonical analysis of principal coordinates (CAP) (Anderson and Robinson, 2003; Anderson and Willis, 2003) analyses using PERMANOVA v.6 software. Prior to analysis, a square root transformation was performed on the abundance data in order to retain information regarding relative abundances and to reduce differences in scale among the variables (e.g. Clarke and Green, 1988). The Bray–Curtis similarity index was calculated between all pairs of samples for subsequent analyses (Bray and Curtis, 1957) and the zero-adjusted Bray–Curtis similarity was performed to avoid possible fluctuations due to near-blank samples (Clarke et al., 2006); similarity tests, based on the multivariate extension of Levene's (1960) test for differences in multivariate dispersion of beach and season, were performed using the PERMDISP tool (Anderson, 2006) from PERMANOVA v.6 software, using distances from centroid and p-values for 9999 permutations (e.g. Anderson, 2001; Manly, 1997). The assumption of normality was avoided due to the use of PERMANOVA (e.g. Johnsons and Field, 1993; Mardia, 1971; Olson, 1974), which was employed to check the existence of significant differences between the beaches and the seasons using a reduced model of the permutation method (Freedman and Lane, 1983) and applying 9999 permutations.

Constrained ordination (CAP) was used to study multivariate patterns among plots on the basis of the Bray–Curtis dissimilarities, having previously conducted a study to determine correlations between the environmental variables in order to avoid redundant information. Environmental variables with negative estimates for the variance components (Fletcher and Underwood, 2002) or with p-value > 0.25, "rule-of-thumb" (Underwood, 1997; Winer et al., 1991) were removed one by one (Fletcher and Underwood, 2002; Thompson and Moore, 1963). These screens were performed by means of the Draftsman plot and DISTLM tool from PERMANOVA v.6 software (Legendre and Anderson, 1999; McArdle and Anderson, 2001).

The environmental variable selection process was based on the capacity to explain the greatest amount of variance for the suprabenthic data using the DISTLM tool. The "BEST" selection procedure from the DISTLM tool was used to choose the predictors and the "Akaike Information Criterion" AIC (Akaike, 1973) and "Bayesian Information Criterion" BIC (Schwarz, 1978) were the selection criteria chosen to decide the best model. Models explaining the greatest amount of variance and selected according to the above criteria (AIC, BIC) were considered the best models for each dependent variable (Anderson et al., 2008). The dependent variables for the models were as follows: i) individual orders as taxonomic rank (Amphipoda, Isopoda, Mysida and Cumacea), ii) monthly abundance on each beach and iii) monthly richness on each beach. Subsequent canonical correlation analyses were performed to study the percentage of variation explained by the predictors selected in DISTLM for the taxonomic ranks and monthly abundance and richness on both beaches. Canonical correlation analyses were tested using 9999 unrestricted random permutations of the raw data (Manly, 1997). In addition, canonical discriminant analyses were performed to classify the SFA according to the factor beach-season.

Furthermore, individual multivariate analyses were performed of the species which accounted for a minimum of 10% in one month, in order to examine the seasonal parameters by contrast analyses using PERMANOVA; these analyses were conducted to compare one season with the other three in order to study species variance as regards density.

3. Results

3.1. Beaches physical environment

Altar beach had medium sand sediment (median particle diameter ranged from 0.21 to 0.48 mm,) and Ladeira had fine to medium sands (median particle diameter ranged from 0.13 to 0.38 mm), according to the Wentworth scale (Buchanan and Kain, 1971). Degree of exposure, according to McLachlan's (1980) rating scheme, was 15 for Altar beach and 14 for Ladeira beach, hence both beaches were classified as exposed. The mean value of Dean's dimensionless parameter (Ω) throughout the entire study was 3 ± 1.67 for Altar beach and 4 ± 1.46 for Ladeira beach. However, monthly values of Ω ranged from 1.16 to 8.17 for Altar beach and 1.85 to 8.06 for Ladeira beach. Both beaches were categorised as intermediate beaches (values ranged from 1 to 5) in morphodynamic state for all months except March 2006 and January 2007 (Altar beach) and April and October 2006 (Ladeira beach), when they presented a dissipative state (values > 5.5) (Wright and Short, 1984).

The total mean wave height at breaking zone was 1.5 ± 1.21 m for Altar beach, and 1.4 ± 0.8 m for Ladeira beach. Both showed the maximum value for this parameter in March 2006 (4.14 m and 3.37 m for Altar and Ladeira surf zone, respectively) and the minimum in September 2005 (0.22 m on Altar and 0.52 m on Ladeira). Average water temperature was 16.1 ± 2.83 °C on Altar, and 15.6 ± 1.56 °C on Ladeira. Maximum temperatures on Altar beach were attained in August 2006 (20.8 °C), and on Ladeira beach in July 2007 (18.4 °C). Both beaches reached lowest values in March 2006 (12.1 °C and 13 °C on Altar and Ladeira beaches, respectively). Water salinity showed a mean value of 35.6 ± 0.14 on Altar beach and 35.8 ± 0.13 on Ladeira beach.

3.2. SFA composition

A total of 101 species were identified; 47 taxa on Altar beach and 86 taxa on Ladeira beach, with 32 species being common to both beaches. Amphipods were the most diverse group, with 63 species (Table 1). A total of 5228 individuals were collected on Altar beach, where amphipods (46% of the specimens) were the most abundant group (mainly *Pontocrates arenarius*). In contrast, 36,050 individuals were collected on Ladeira beach, where isopods (38% of the specimens) were the most abundant group (mainly *Eurydice affinis*) (Table 2).

The monthly number of species (5–19 on Altar beach, 9–32 on Ladeira beach) was higher in summer (15.8 ± 3.4 on Altar beach, 21.7 ± 7.7 on Ladeira beach) and autumn (12.3 ± 4.3 on Altar beach, 20.2 ± 6.5 on Ladeira beach), whilst lowest values were mainly obtained during winter (10.2 ± 4.4 on Altar beach, 14.2 ± 2.9 on Ladeira beach) (Fig. 2A). Shannon-Wiener's index for Altar beach ranged from 0.86 to 3.4 decits/ind, while the index for Ladeira beach was from 1.10 to 3.19 decits/ind (Fig. 2B).

Amphipods and mysids were the predominant groups on Altar beach. Amphipods dominated during the winter and early spring of 2006 and 2007whereas mysids were more frequent in the spring and summer (Fig. 3A). The main groups on Ladeira beach consisted of isopods, cumaceans and mysids.

The biennial mean density was noticeably higher on Ladeira beach (26.95 ± 40.99 $indv \cdot m^{-2}$) than on Altar beach (4.33 ± 3.80 $indv \cdot m^{-2}$). The highest monthly densities for Altar beach were observed in August 2007 (14.02 $ind \cdot m^{-2}$) and for Ladeira beach in November 2005 (178.75 $ind \cdot m^{-2}$). The high density value in the latter case was due to a large concentration of the isopod *Idotea pelagica* (72.95 $ind \cdot m^{-2}$) and the cumaceans *Cumopsis longipes* (40.21 $ind \cdot m^{-2}$) and *Cumopsis fagei* (35.36 $ind \cdot m^{-2}$) (Fig. 4A, B). The lowest densities were recorded in the winter months, and the minimum was in January 2007 (Altar beach: 0.42 $ind \cdot m^2$, Ladeira beach: 1.50 $ind \cdot m^2$). Many of the most common species showed one or more density peaks, but the majority of these were not repeated in the same period in both years (*Idotea balthica*, August 2007 Fig. 4G). Nevertheless, some species presented repeated high densities in specific seasons but with substantial differences in their intensity over the 24 month study period (*Atylus swammerdami*, and *Eurydice pulchra* in summer. Fig. 4E, H). In other cases, these density peaks were extended over more than one month (*Gastrosaccus roscoffensis*, *Schistomysis parkeri* and *P. arenarius* Fig. 4C, D and F, respectively). *P. arenarius* was the most frequent species identified in the study. It was present over the entire 24 months on both beaches, but its abundance varied widely between the first and second year. During the first 12 months, it showed two abundance peaks; the first in October (2005) and the second in the spring. In contrast, abundance remained at very low levels throughout most of the second year, showing a single growth peak in spring on Ladeira beach, and there was no peak on Altar beach.

Amphipod and mysid species highlighted the dissimilarity in fauna between the two beaches. Decapod crustaceans, making a scant contribution to total density, consisted of two common species, *Philocheras trispinosus* and *Crangon crangon*.

3.3. SFA analysis

The PERMANOVA analyses revealed statistically significant differences between the two beaches as regards densities, diversity and seasonality. Beach analysis was significant with a p (perm) value of 0.001 and a Pseudo-F value of 13.03. Season analysis was significant

Table 2
Main species and taxa from Altar and Ladeira beaches. $\bar{x}$ = abundance mean of the 24 months; SD = standard deviation; Occu. (%) = Occurrence in the 24 months of sampling; Abund. (%) = relative abundance.

	Altar				Ladeira			
	Density (ind·m^{-2})		Occu. (%)	Abund. (%)	Density (ind·m^{-2})		Occu. (%)	Abund. (%)
	$\bar{x}$	SD			$\bar{x}$	SD		
Amphipoda								
Atylus swammerdami	0.48	1.45	63	12.16	0.32	0.59	63	1.19
Bathyporeia sarsi	0.02	0.03	46	0.58	0	0.02	8	0.02
Gammarus sp.	0.13	0.34	58	3.17	0.01	0.05	13	0.04
Pontocrates arenarius	1.1	1.85	100	28.02	1.14	1.38	100	4.22
Other Amphipoda	0.07	0.12	83	1.85	0.36	0.48	96	1.35
Total Amphipoda				45.79				6.82
Isopoda								
Eurydice affinis	0	0.01	8	0.07	5.92	16.4	100	21.44
Eurydice naylori	0.01	0.02	25	0.19	0.35	1.1	58	1.31
Eurydice pulchra	0.03	0.05	50	0.79	0.36	0.63	75	1.35
Gnathia sp.	0.03	0.05	33	0.65	0.03	0.05	50	0.11
Idotea balthica	0.2	0.63	63	4.97	0.01	0.03	21	0.03
Idotea pelagica	0.15	0.52	24	3.75	3.09	14.88	54	11.38
Lekanesphaera weilli	0.03	0.06	42	0.88	0.39	1.1	71	1.45
Other Isopoda	0.03	0.1	33	0.83	0.3	1.12	67	1.15
Total Isopoda				12.14				38.22
Cumacea								
Cumopsis fagei	0.12	0.27	63	2.98	4.39	7.71	96	16.29
Cumopsis goodsir	0.12	0.17	75	3.08	0.04	0.2	13	0.16
Cumopsis longipes	0.08	0.12	58	2.12	3.57	8.26	92	13.15
Other Cumacea	–	–	–	–	0.03	0.09	33	0.12
Total Cumacea				8.17				29.72
Mysida								
G. roscoffensis	0.67	1.96	75	16.96	5	8.09	96	18.49
Paramysis arenosa	–	–	–	–	0.2	0.85	13	0.76
Schistomysis parkeri	0.53	0.61	96	13.37	1.38	2.66	88	5.12
Schistomysis spiritus	0	0.01	4	0.04	0.11	0.48	17	0.39
Other Mysida	0.03	0.04	50	0.69	0.11	0.17	63	0.4
Total Mysida				31.05				25.16
Caridea								
P. trispinosus	0.06	0.1	42	1.43	0.01	0.04	29	0.05
Other Caridea	0.06	0.14	29	1.41	0.01	0.03	21	0.04
Total Caridea				2.85				0.09

with a p (perm) value of 0.003 and a Pseudo-F value of 2.14. Nevertheless, the interaction between beach and season did not give a significant result. CAP analysis showed a significant effect for the Beach factor with a squared canonical correlation of $\delta^2 = 0.8516$ ($p = 0.0001$). There was also a significant effect for Season of $\delta^2 = 0.6805$ ($p = 0.0011$) (Fig. 5). The canonical axes separated the 2 main factors, SFA and season, between Ladeira beach (open figures) and Altar beach (black figures).

The relative distinctiveness of the assemblages was also clearly demonstrated by differences in the leave-one-out allocation success from the CAP analysis, but seasonality for individual beaches was not so clear (Table 3).

3.4. Species correlated

Species which represented a minimum of at least 10% of the abundance in one month were analysed by contrast analyses using PERMANOVA to identify significant differences between the seasons. The results indicate that *A. swammerdami*, *Gammarus* sp. *E. pulchra*, *I. balthica*, *C. fagei*, *Cumopsis goodsir* and *Philocheras trispinosum* showed

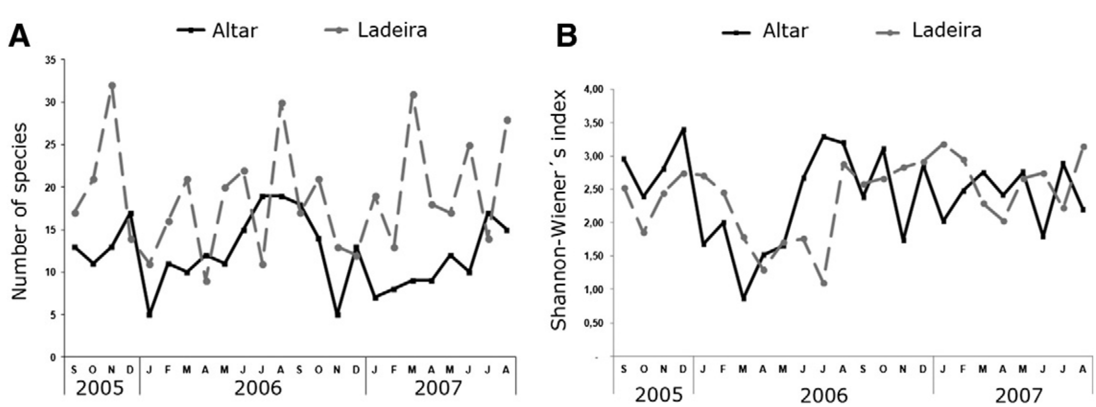

Fig. 2. (A) Number of species and (B) Shannon-Wiener's index (ind/decit) for Altar and Ladeira beaches during the study period.

significant differences in occurrence and abundance in summer compared to the other seasons, as did *Lekanesphaera weilli* and *C. goodsir* in autumn and *E. pulchra Gammarus* sp. and *P. trispinosum* in winter. No species showed significant differences in spring and some of the most abundant species (*P. arenarius*, *Gastrosaccus roscofensis* and *S. parkeri*) did not show significant differences for any season throughout the two years of study. All contrast analyses obtained a p-value of less than 0.05.

3.5. Environmental analysis

The environmental factors selected for the DISTLM analyses were wind speed, air temperature, Daily Global Irradiance (DGI), wave height, water temperature, salinity and Dean's parameter. The precipitation factor was removed since it obtained negative estimates for variance components and had a p-value > 0.25. DGI was the most frequently selected factor for the environmental analyses, whilst wave height and Dean's parameter were exclusively selected for abundance and richness analyses. The sun hour factor was the only one that was not selected by any model. Water and air temperature were selected as the best explanatory variables for variance in mysid abundance. Variance in the abundance of the remaining Peracarida orders (amphipods, cumaceans and isopods) was explained by DGI. Cumacean and amphipod variance was also explained by salinity, whilst isopod variance was explained by wind speed. Variance in Altar abundance and Ladeira richness was explained by wave height and DGI (for Altar abundance) and salinity (for Ladeira richness) (Table 4). Total abundance was positively related with DGI, salinity and air and water temperature and it was negatively related with Dean's parameter and wave height (Fig. 6). DGI and salinity factors were employed in the model for total SFA (24 months and the 2 beaches together). These two factors explained 25.28% of the total sample variation. The percentage of variation explained for each group ranged from 27.77% to 93.8% (Table 4). All models obtained a p-value of less than 0.004 except for Ladeira richness, which obtained a p-value of 0.03.

4. Discussion

4.1. SFA structure

In agreement with other studies of macrofauna assemblages on sandy Atlantic coast beaches (e.g. Gonçalves et al., 2009; Lastra et al., 2006), there was considerable variation between the beaches as regards the number, diversity and temporal distribution of the suprabenthic biocoenosis. The suprabenthos structure consisted mainly of peracarids and decapods, similar to that recorded on other beaches (Heyns and Froneman, 2010; San Vicente et al., 2009). However, the dominant suprabenthic groups on the beaches studied for this research differed from the dominant group reported in previous studies, the mysids (Beyst et al., 2001; Mees and Hamerlynck, 1992; Mees et al., 1993, 1995; San Vicente and Sorbe, 1999). As regards total abundance, amphipods were the dominant group on Altar beach; however, monthly dominance alternated between amphipods and mysids.

Monthly dominance on Ladeira beach alternated between mysids, isopods and cumaceans. Dominance and abundance varied according to season and between the two years of the study, a finding which has been reported for other medium term studies of surf zone ichthyofauna (Lasiak, 1984; Modde and Ross, 1981). The total number of species recorded on Altar beach was 47, a figure similar to other temporal studies of sandy beaches. In contrast, the number of species on Ladeira beach was 86, which is high for a single beach (Table 5). The average number of species collected per month in this study (12 ± 4 Altar beach, 19 ± 7 Ladeira beach) was lower than in other studies (22–31 species) (Beyst et al., 2001; Munilla and San Vicente, 2005; San Vicente and Sorbe, 2001). However, sampling effort (number of months), number of sites studied and depth have all previously been recognised as confounding factors in the number of species compared (Allen, 1985; Gibson, 1973; Riley et al., 1981; Ross, 1983; Ross et al., 1987).

The higher species richness of Ladeira beach may be explained by beach configuration and recent history. Ladeira beach forms part of Corrubedo Bay, a 5 km long sandy shore only interrupted by a lagoon discharge channel situated south of Ladeira beach (see Fig. 1), and rocks, and could thus be considered a single long beach; the positive relationship between beach length and number of species has been observed by many authors (Lastra et al., 2006; McLachlan et al., 1993). Ladeira beach was more affected than Altar beach by the Prestige oil spill in autumn 2002–winter 2003, whereas Altar beach was affected by the construction of a jetty in 1986–88 and beach replenishment (Castellanos et al., 2003). Although the two beaches have some similar environmental characteristics (e.g. grain size), they differ on the coast and recent history that might explain some differences. Both beaches are used for recreational purposes in the summer (mainly July and August), and Ladeira beach forms part of an environmentally protected area. The human impact on intertidal macrofauna due to recreational use is not significant (Jaramillo et al., 1996), but there is no data on this factor as regards the suprabenthos. The potential impact of these disturbances on the fauna is unclear, but it cannot be ignored.

A small number of species dominated throughout the two years of study, with only five species accounting for more than 75% of the specimens collected (*P. arenarius*, *G. roscoffensis*, *S. parkeri*, *A. swadermmani* and *I. balthica* on Altar beach and *E. affinis*, *G. roscoffensis*, *C. fagei*, *C. longipes* and *I. pelagica* on Ladeira beach). This dominant condition has been reported in other temporal studies of the suprabenthos (e.g. San Vicente and Sorbe, 2001), and the dominance of a few species on beaches is a well-known circumstance among the macrofauna and ichthyofauna (Allen, 1985; Gonçalves et al., 2009; Lasiak, 1984; Lastra et al., 2006; Rodil et al., 2006; Ross, 1983; Ross et al., 1987). The mean density values were similar to those reported in other studies of the suprabenthos (Beyst et al., 2001; Heyns and Froneman, 2010; San

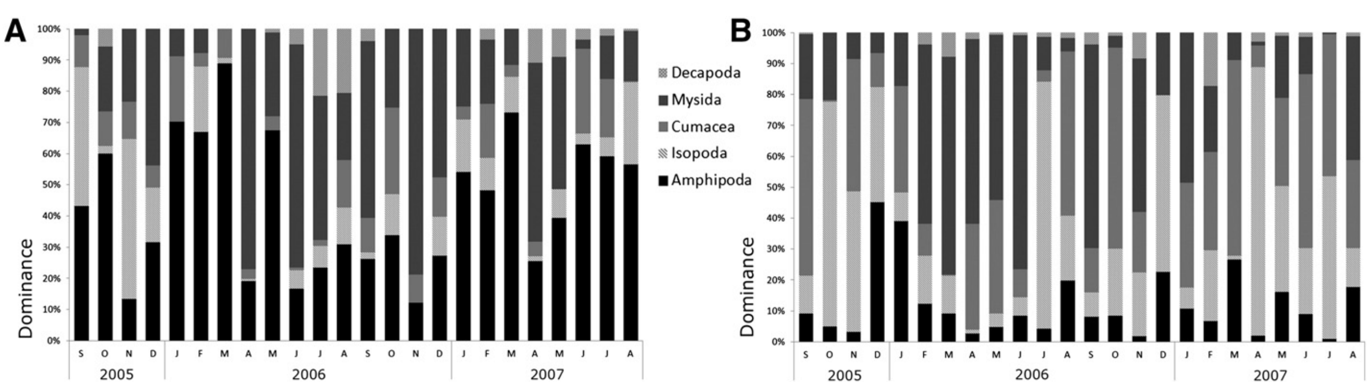

Fig. 3. Dominance of different taxonomic groups along the two years of study on Altar beach (A) and Ladeira beach (B).

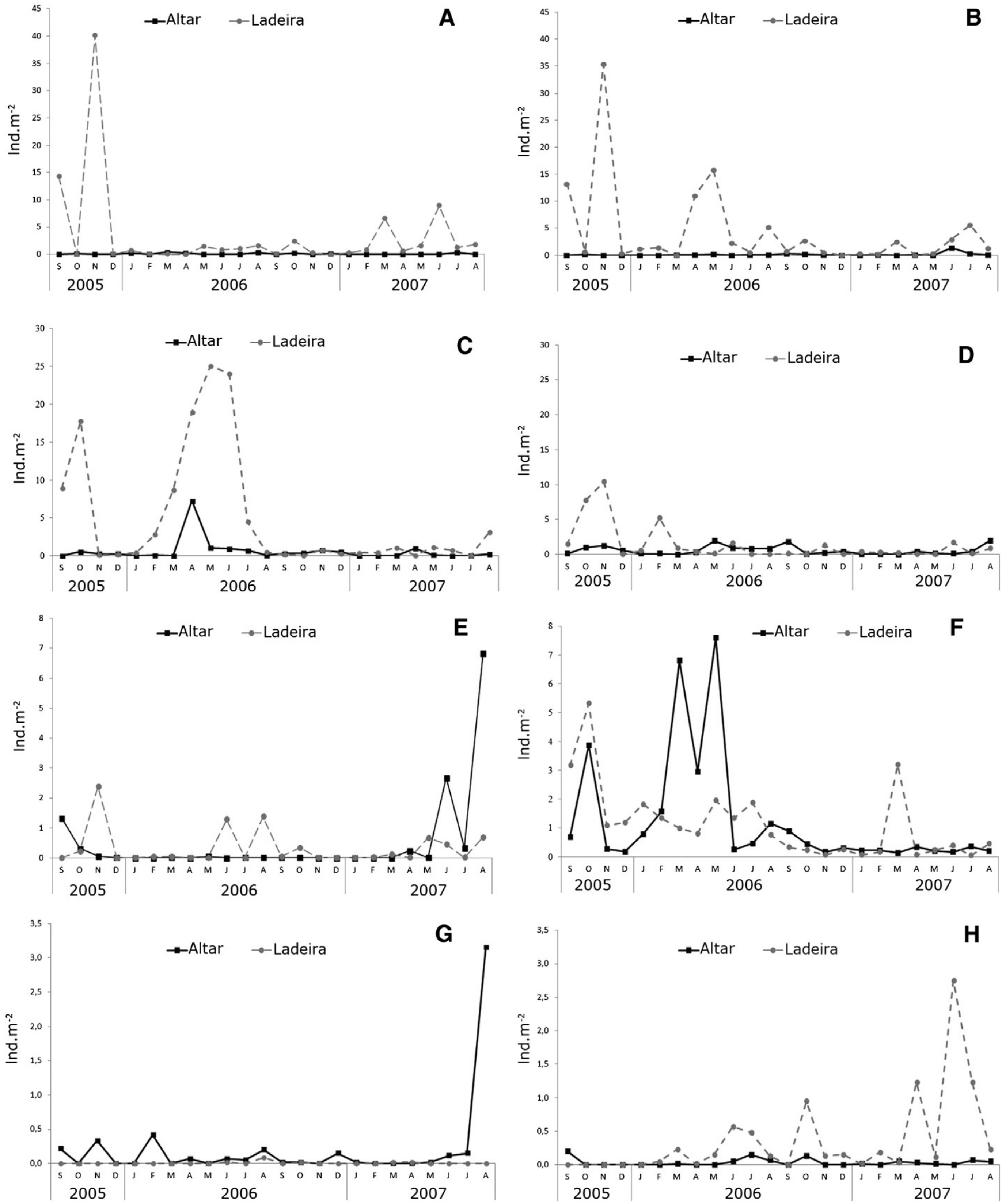

Fig. 4. Abundance of selected suprabenthic species on Altar and Ladeira beaches: (A) *Cumopsis longipes*, (B) *Cumopsis fagei*, (C) *Gastrosaccus roscoffensis*, (D) *Schistomysis parkeri*, (E) *Atylus swammerdami*, (F) *Pontocrates arenarius*, (G) *Idotea balthica*, and (H) *Eurydice pulchra*.

Vicente and Sorbe, 2001). Occurrence and abundance of the different species did not show any regular pattern in the two years analysed, hindering the identification of species seasonality. All species presented very marked peaks in abundance for a short period over the entire study. One noticeable peak was due to *I. pelagica*, an isopod typical of rocky shores; the presence of a species from this genus on Ladeira and

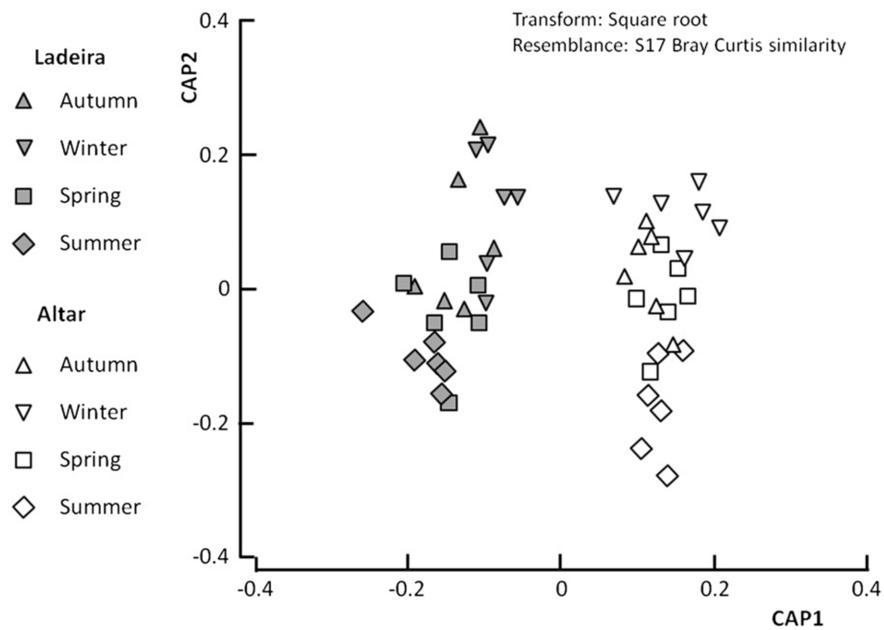

Fig. 5. Two-dimensional scatter plot of the canonical axes, for beach–season factor.

Altar beaches was related to drift algae, a frequent occurrence from September onwards, and especially in October and November, due to the waves.

4.2. Seasonal pattern

Seasonal distribution has been discussed in previous studies of the suprabenthos inhabiting diverse areas and depths (Beyst et al., 2001; Colman and Segrove, 1955; Dauvin et al., 2000; Heyns and Froneman, 2010; Mees et al., 1993; San Vicente and Sorbe, 2001). However, none of these previous studies lasted more than 18 months, curtailing the possibility of conducting a temporal analysis of the normal variations in the entire SFA for a specific area. Our results suggest that seasonal intra-beach variation is too complex to be analysed in one year alone, and peaks in abundance observed over the course of one year might produce inaccurate seasonality. Thus, the marked differences observed between the present and previous studies may be explained by the temporal limitations of the latter. Although the duration of this study (24 months) permitted the observation of significant differences in the occurrence, dominance and abundance of the species between seasons and years, it was nonetheless limited as regards elucidating the natural cycles of the suprabenthic community. Although the two beaches were sampled at the same time, the present study did not reveal any synchrony in the suprabenthic fauna.

The factors affecting the occurrence and abundance of the surf zone fauna can be ranked hierarchically (Ross et al., 1987). In the present study, only the first and third ranks, local climatic events and physical and chemical factors, respectively, were analysed, whilst the second rank factors of timing of reproduction and feeding movements were not taken into account. Thus, much of the variance remained unexplained following the analyses. Table 1 shows the geographical distribution of suprabenthic species inhabiting sandy European beaches (Belgian coast (Beyst et al., 2001), Hendaye beach on the Bay of Biscay (San Vicente and Sorbe, 2001) and Catalonian beaches in the NW Mediterranean (Munilla and Corrales, 1995; Munilla and San Vicente, 2005; San Vicente and Sorbe, 2001)). Several of the most frequent species on the Altar and Ladeira beaches were also the most common species on Hendaye beach (San Vicente and Sorbe, 2001), and whilst *Siriella armata* and *A. swammerdami* were reported in all the studies, *Bathyporeia pilosa*, and *E. pulchra* were only collected on Atlantic coast beaches.

4.3. Faunistic group and environmental factor

The environmental factor which best explained variance in mysid abundance was water temperature; previous surveys have shown a correlation between low water temperatures and decreased mysid density (Beyst et al., 2001; Van der Baan and Holthuis, 1971; Zatkutskiy, 1970). Specifically, *G. roscoffensis* and *S. parkeri* presented population peaks in spring, summer and autumn, coinciding with those recorded by San Vicente and Sorbe (2001). Moreover, the reduced abundance observed in winter supported the reports of several authors (Colman

Table 3
Results of canonical analysis of principal coordinate (CAP) analysis examining the effects of beach, season and their interaction with the suprabenthic fauna assemblages. Var (%) = percentage of the total variation explained by the first *m* principal coordinate axes; Allocation success = percentage of points correctly allocated into each group; δ^2 = squared canonical correlation; Aut (Autumn), Win (Winter), Spr (Spring), Sum (Summer).

Factor	m	Var (%)		Allocation success (%)					δ^2	P
				Group 1	Group 2	Group 3	Group 4	Total		
Beach	5	95.83		100 Ladeira	100 Altar			100	0.885	0.0001
Season	7	27.08		50 Aut	75 Win	50 Spr	66.67 Sum	60.42	0.654	0.0011
Beach–Season	7	41.67	Ladeira	0 Aut	83.33 Win	50 Spr	66.67 Sum	52.08	0.954	0.0001
			Altar	50 Aut	66.67 Win	33.33 Spr	66.67 Sum			

Table 4
Environmental variables selected by the criteria AIC and BIC. D.G.I = Daily Global Irradiance.

	Wind speed	Air T^a	Sun hours	D.G.I	Wave height	Water T^a	Salinity	Dean	R^2
Total fauna				X			X		25.28
Amphipoda	X			X					27.77
Isopoda				X			X		33.57
Mysida		X				X			40.55
Cumacea				X			X		45.56
Ladeira abundance				X				X	82.04
Altar abundance		X		X	X				87.10
Altar richness	X			X			X	X	92.76
Ladeira richness					X		X	X	93.80

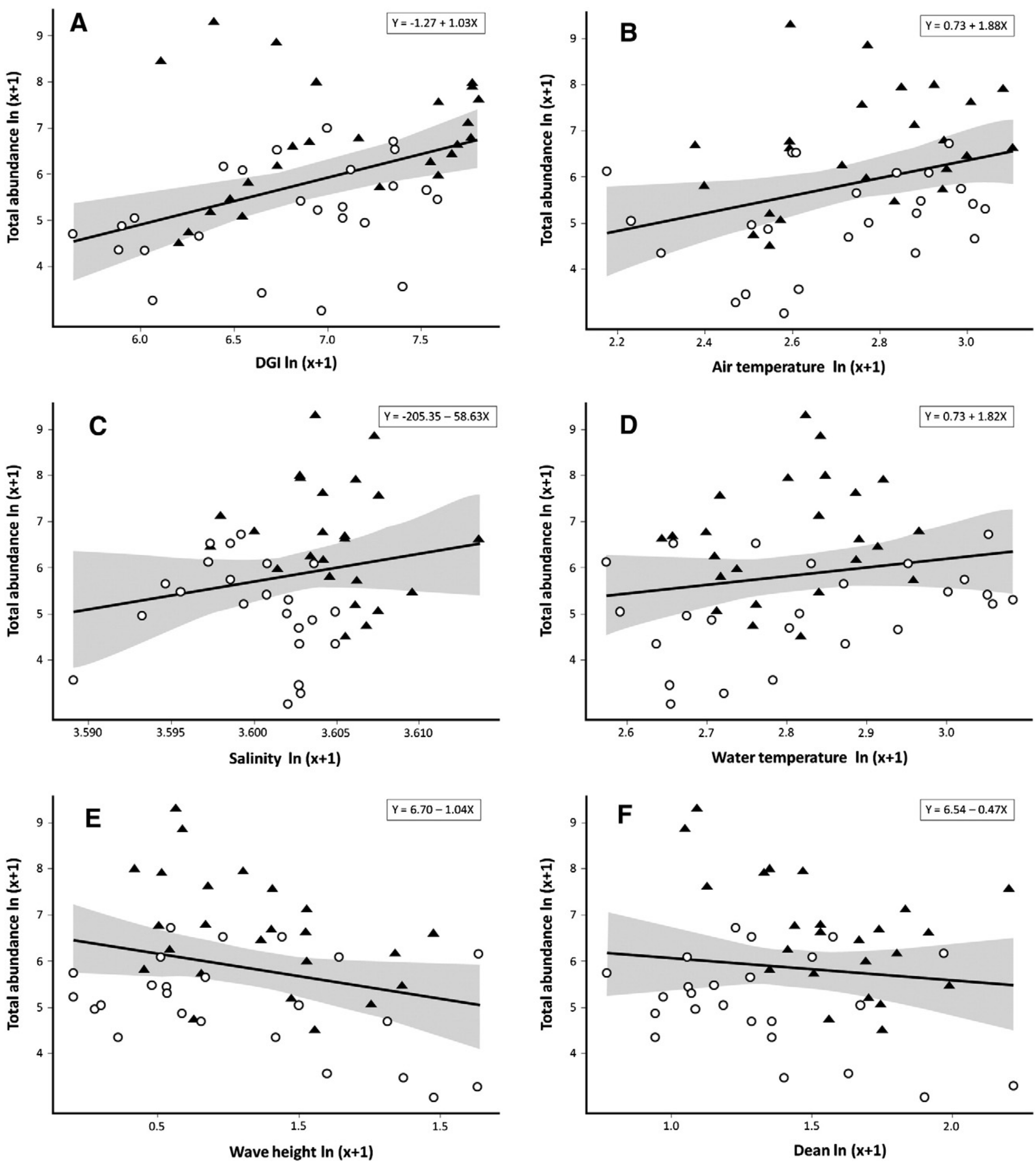

Fig. 6. Linear-regression analyses of total fauna vs. (A) Daily Global Irradiance (DGI), (B) air temperature, (C) salinity, (D) water temperature, (E) wave height and (F) Dean's parameter in the swash zone.

Table 5
Comparative of different suprabenthos studies on European sandy beaches. S = number of species (only crustaceans). G = Galician coast; C = Catalan coast; B = Belgian coast; H = Bay of Biscay.

Beach	S	Sampling effort			Location	Reference
		Area sampling (m^2)	Months	Total area (m^2)		
Altar	47	60	24	1440	G	Present study
Ladeira	86	60	24	1440	G	id.
Aluet	23	50	1	50	M	Munilla and San Vicente (2005)
Cambrils	27	50	1	50	M	id.
Castelldefels	11	50	1	50	M	id.
Creixell	72	50	1	50	M	id.
Estartit	12	50	1	50	M	id.
La Fosca	8	50	1	50	M	id.
Masnou	7	50	1	50	M	id.
Pals	8	50	1	50	M	id.
Platja d'Aro	3	50	1	50	M	id.
Roses	18	50	1	50	M	id.
S'Agaró	20	50	1	50	M	id.
Sta. Cristina	9	50	1	50	M	id.
Trabucador	15	50	1	50	M	id.
Belgium*	80	475	14	6650	B	Beyst et al. (2001)
Hendaye	44	50	12	600	H	San Vicente and Sorbe (2001)

* Total data from Oostduinkerke, Lombardsijde, Wenduine and Knokke beaches in Belgium.

and Segrove, 1955; Mauchline, 1980) concerning the ability of mysids to migrate to deeper areas when weather conditions are severe, this species being an active swimmer which migrates to deeper waters in the winter. As regards the amphipods, peaks in *A. swammerdami* abundance coincided with those described for the Voordelta coastal area in the Netherlands (Cattrijsse et al., 1993) and the A Coruña Bay (Frutos, 2006). Our results showed that the most frequently selected factors in the temporal variation models were DGI and salinity. This is the first time that DGI has been considered in this kind of research, and the preferential selection of DGI in the models suggests that this factor might, directly or indirectly, be a very important regulator of the dynamic of the swash zone suprabenthos. To a greater or lesser extent, shifts in the SFA were explained by physical, chemical and hydrodynamic parameters, although earlier suprabenthic studies have related them to parameters such as salinity gradients, Secchi disc depth, temperature, precipitation, oxygen concentration and sediment characteristics (Beyst et al., 1999; Drake et al., 2002; Mees and Hamerlynck, 1992; Mees et al., 1993, 1995; Morgado et al., 2003). In addition, ichthyofauna density was related to wind speed and direction, wave height, tidal movements, water temperature and light (Ross et al., 1987). These latter relationships may be an indirect response, because this group feeds on the suprabenthos. Hydrodynamic factors may affect the SFA through modifying the environmental conditions, promoting the circulation of food and affecting spawning and larval survival (Beyst et al., 2001). There is a complex relationship between the SFA and environmental variables; our results show that the variables for explaining total fauna variance are different to those explaining specific taxa variance.

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