



# Zonation of macrobenthos across a mesotidal sandy beach: Variability based on physical factors



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## ABSTRACT

The dynamic and unstable nature of sandy beaches results in a highly variable distribution of macroinfauna inhabiting the intertidal fringe. Storm-induced sediment movement on the beaches could alter the distribution of organisms, leading to an indistinct zonation scheme. In this context, the zonation pattern of macroinfauna was studied monthly during 2010 in an exposed mesotidal sandy beach on the SW Atlantic coast of Argentina (39°S). Faunal samples were collected with a plastic core (0.02 m<sup>2</sup>) at 10 to 12 levels along five replicated transects extending from above the drift line to the low tide swash zone. Sand samples were also taken at each level. Wave height and period were measured *in situ* and data of wind speed and direction were provided by the National Weather Service (SMN). The relationship between the formation of zonation schemes, meteorological data and the physical features of the beach were explored. The results show some significant trends: the supralittoral zone was characterized by the absence of organisms on all sampling occasions. During most of the year the zonation scheme comprised two zones, both within the littoral zone; during winter months, no zonation schemes were found. This contrasting pattern could have been determined by the harsh wind-driven waves, leading to sand movements and thus promoting variations in faunal distribution. Sedimentological changes driven by storms could therefore be the cause of a hidden zonation scheme occurring during winter months, highlighting the importance of a climatic variable in the detection of macrofaunal zonation patterns.

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## 1. Introduction

Sandy beaches are dynamic and unstable habitats and therefore the distribution of macrobenthic fauna across the intertidal zone has a highly variable spatial structure (McLachlan and Jaramillo, 1995; Brown, 1996; Schlacher et al., 2008; Schlacher and Thompson, 2013). Most of the studies evaluating zonation patterns on sandy beaches were conducted on microtidal beaches (tidal range < 2 m) (e.g. Defeo et al., 1992; Brazeiro and Defeo, 1996; Schlacher and Thompson, 2013; Santos et al., 2014) and report mostly the formation of zonation schemes in the intertidal zone. Dean's dimensionless parameter (Wright and Short, 1984) allow the classification of beaches into beach types, ranging from dissipative beaches, with wide surf zone, fine sand and flat beach profile, to reflective beaches, with short surf zone, coarse sand and steep slope. A series of intermediate states are recognized between the above extremes (Short, 1996). Dean's parameter is a good predictor of biological descriptors of benthic communities across different geographic regions and is also relevant in establishing the zonation patterns of macrofauna; the number of biological zones depends on the beach type and so, reflective beaches present fewer zones

than those dissipative (Defeo and McLachlan, 2005; Jaramillo et al., 1993) and on very harsh reflective beaches, only the supralittoral zone may be found. However, the model of Wright and Short (1984) was developed for microtidal environments (Masselink and Short, 1993). Tidal effects must be taken into account when the zonation patterns of a beach are studied, since elevated tidal energy (i.e. tidal range > 2–3 m) increase the degree of dissipativeness of a beach (McLachlan et al., 1996).

Tidal range also determines the vertical dimension of the intertidal habitat and therefore has an impact on the distribution of organisms. Far less is known about the zonation patterns on macro-to-mesotidal beaches than on microtidal beaches (Degraer et al., 2003; Veiga et al., 2014). Working on intermediate mesotidal exposed sandy beaches of Spain, Rodil et al. (2006) and De la Huz and Lastra (2008) found no distinct intertidal zonation for macrofauna. The same occurs on sandy beaches of the Gulf of Gabès (Pérez-Domingo et al., 2008) and along the coast of Scotland (Raffaelli et al., 1991). In a study comparing zonation patterns over a wide range of conditions including contrasting tidal ranges, McLachlan et al. (1996) found an indistinct zonation in most cases and no more than three zones on any of the beaches.

Sandy beaches with higher tidal ranges are usually more heterogeneous compared with microtidal beaches, displaying intertidal sandbars intercalated with runnels (Masselink and Short, 1993; Gingold et al.,

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2010). Wave action during storm events has different effects on beach profiles of different areas of a coastline (Lee et al., 1998). Several authors emphasize the damage caused on the Argentinian coast (39°S, Atlantic Ocean) by strong winds from the SE and SW quadrants (Marcomini and López, 1997; Caló et al., 2000; Fiore et al., 2009), which cause a significant rise in mean sea level (Marcomini and López, 1997), with the consequent change in sedimentary balance (loss-gain of sediments in the beach) (Bustos et al., 2011; Semeoshenkova et al., 2016). These events increase the erosive action of waves, changing the position of typical landforms, generating what is known as storm profiles or winter profiles, since these events occur mainly during winter. Beach profiles therefore show a significant seasonality: during summer they are characterized by a uniform profile of concave shape, almost no bars are distinguished and the prominent landform is the berm. During winter, the profiles are characterized by a convex shape associated with the accumulation of sediment in the area of the bar, a not very marked berm and in some cases the formation of bars and channels (Perillo, 2003). This natural variability can induce changes in the distribution of intertidal macroinvertebrates across the intertidal zone. Hence, temporal studies are needed for a full picture of zonation patterns, requiring intensive sampling to provide unbiased estimates (Defeo and McLachlan, 2005) and to accurately describe the spatial structure on many ocean-exposed sandy beaches (Schlacher and Thompson, 2013).

In this context, we hypothesize that storms-induced sediment movement could alter the distribution of the macrofauna. The biological zonation schemes along these intertidal coasts will therefore vary

strongly throughout the year, showing a subdivision in zones only during months not preceded by storms. To test this hypothesis, we examined the zonation structure of the intertidal macrobenthic community of an exposed mesotidal sandy beach during one year and explored the relationship between zonation schemes, meteorological data and the physical features of the beach.

## 2. Materials and methods

### 2.1. Study area

This study was conducted on an exposed dissipative sandy beach located along a continuous coastal fringe within the Provincial Nature Reserve Pehuen C6-Monte Hermoso (39°S; 61°W) (Fig. 1). The area has a mesotidal regime with semidiurnal tides, low slope, and is backed by extensive sand dunes. The intertidal zone spans a mean length of 120 to 170 m from the base of the dunes to the swash (Bustos, 2012; Huamantínco, 2012). The mean amplitude ranges between 2.32 and 3.35 m for neap and spring conditions respectively, with a mean value of 3.10 m (Servicio de Hidrografía Naval, 2009). A description of the physical features and the macrobenthic community of this area can be found in Carcedo (2014), Carcedo et al. (2015a) and Carcedo et al. (2015b). The area has a temperate climate; the average temperatures oscillate between 14 and 20 °C and the mean annual precipitation is 650 mm (Carbone, 2003; Campo de Ferreras et al., 2004). The storms characterized by winds from the sea (S, SW and SE quadrants) with

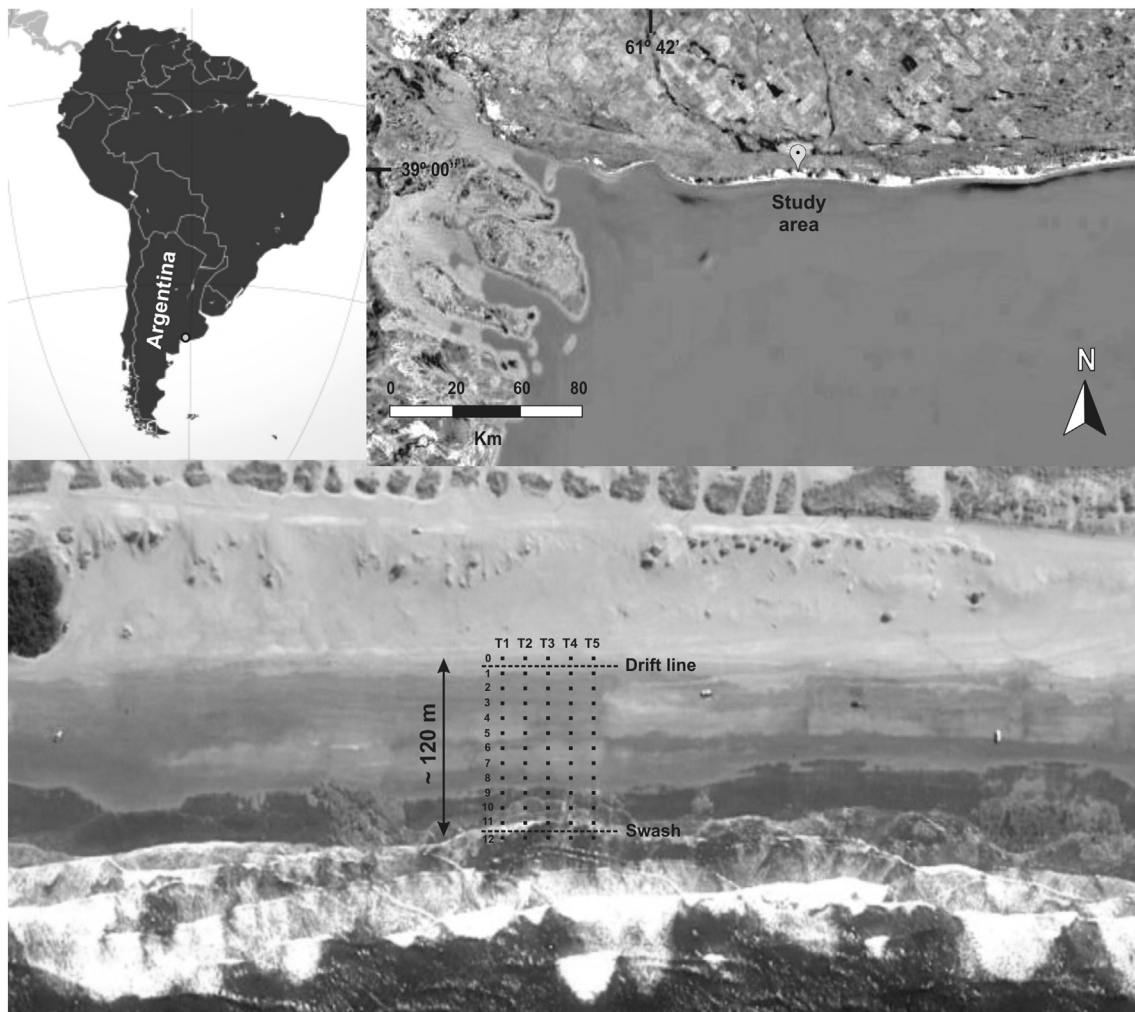


Fig. 1. Study area showing the location of the beach sampled and the spatial layout of the fauna collections.

speeds up to  $40 \text{ km} \cdot \text{h}^{-1}$ , generating wave trains above 2.5 m in height, cause considerable changes in sedimentary balance on this coast (Bustos, 2012; Huamantingo, 2012; Semeoshenkova et al., 2016).

## 2.2. Sampling design

Sampling was conducted during 12 months, from May 2010 to April 2011. On each sampling occasion, five equidistant (5 m) transects were performed perpendicular to the tide line, across the entire across-shore width, during daytime and low tide (Fig. 1). Each transect was divided into levels located every 10 m and depending on the low water level reached. At each level, one sample was taken per transect, the sampling unit (SU) consisted in a plastic core of 16 cm diameter and 40 cm depth (area =  $0.02 \text{ m}^2$ ). Core samples were softly sieved through mesh bags (1 mm aperture size) to separate the fauna from the sediment. Organisms retained were fixed in 10% formalin. Sand samples were collected at the same sites where biological samples were taken, using a plastic cylinder of 10 cm diameter and 10 cm depth (area =  $78.5 \text{ cm}^2$ ). Wave height (m) was determined by measuring breaking waves with graduated poles against the horizon (Emery, 1961). Wave period (s) was estimated as the time interval between consecutive breaking waves, measured with a stopwatch.

## 2.3. Laboratory procedure and data analysis

Non-metric multidimensional scaling analysis (nMDS) was used to represent the community under study. The technique was based on triangular matrix using the Bray Curtis similarity index on transformed data [ $\log_{10}(X + 1)$ ] to enhance the contribution of the less abundant taxa. To determine whether zonation can be objectively identified, raw species abundance data were subjected to cluster analysis using the group average clustering method (Clifford and Stephenson, 1975). Similarity profiles (SIMPROF) determine whether clusters represent patterns in community structure that are significantly ( $p < 0.05$ ) different from random spatial structure (Clarke et al., 2008). Similarity percentage analysis (SIMPER) was used to determine the organisms that contributed most to the zones differentiated in the cluster analysis. These analyses were performed with PRIMER-E® 6 (Clarke and Gorley, 2006). Levels without species were excluded from the analysis due to the subsequent incorrect interpretation of the graphical outputs. The species with the highest contributions in abundance (detected through SIMPER analysis) were selected to perform a graphical representation of the zonation patterns (contour plots). To map the distribution of species, the kriging interpolation technique was used (Rossi et al., 1992). Months where the species showed the highest abundances were selected to plot (one month per season). For each species, abundance per SU was used as data input. These analyses were performed with Surfer 8®.

Sand samples were washed, dried, homogenized and weighed before mechanically sieving through the traditional sieve column. Nine granulometric categories were used in relation to the phi scale or Udden-Wentworth scale (Wentworth, 1922). Mean sand size, sorting, skewness and kurtosis were computed according to Folk and Ward (1957) and results were expressed as phi ( $\varphi$ ) values ( $\varphi = -\log_2$  diameter in mm). The pelitic fraction (gr), defined as the silt-clay fraction ( $< 63 \mu\text{m}$ ) was also calculated for each sand sample. Canonical correspondence analyses (CCA) were carried out to establish the relationships between species, physical features of the sediment and levels within the beach width. Four CCA analyses were conducted (one analysis per season) based on all data from the three months of each season. In the graphic output of this analysis, arrows represent the environmental variables and their length indicates the importance of each variable; the projection of the species on the arrows shows the environmental preference of the species. The position of the species reflects their contribution to the variance explained by the first two axes (Ter Braak, 1986). To select the environmental variables which significantly explain

the variability in the abundance of macrofauna ( $p < 0.05$ ) a Monte Carlo permutation test was carried out. For this analysis only species with  $n > 5$  were included. These CCA's were performed using the statistical package XLStat Addinsoft® (Fahmy, 1999).

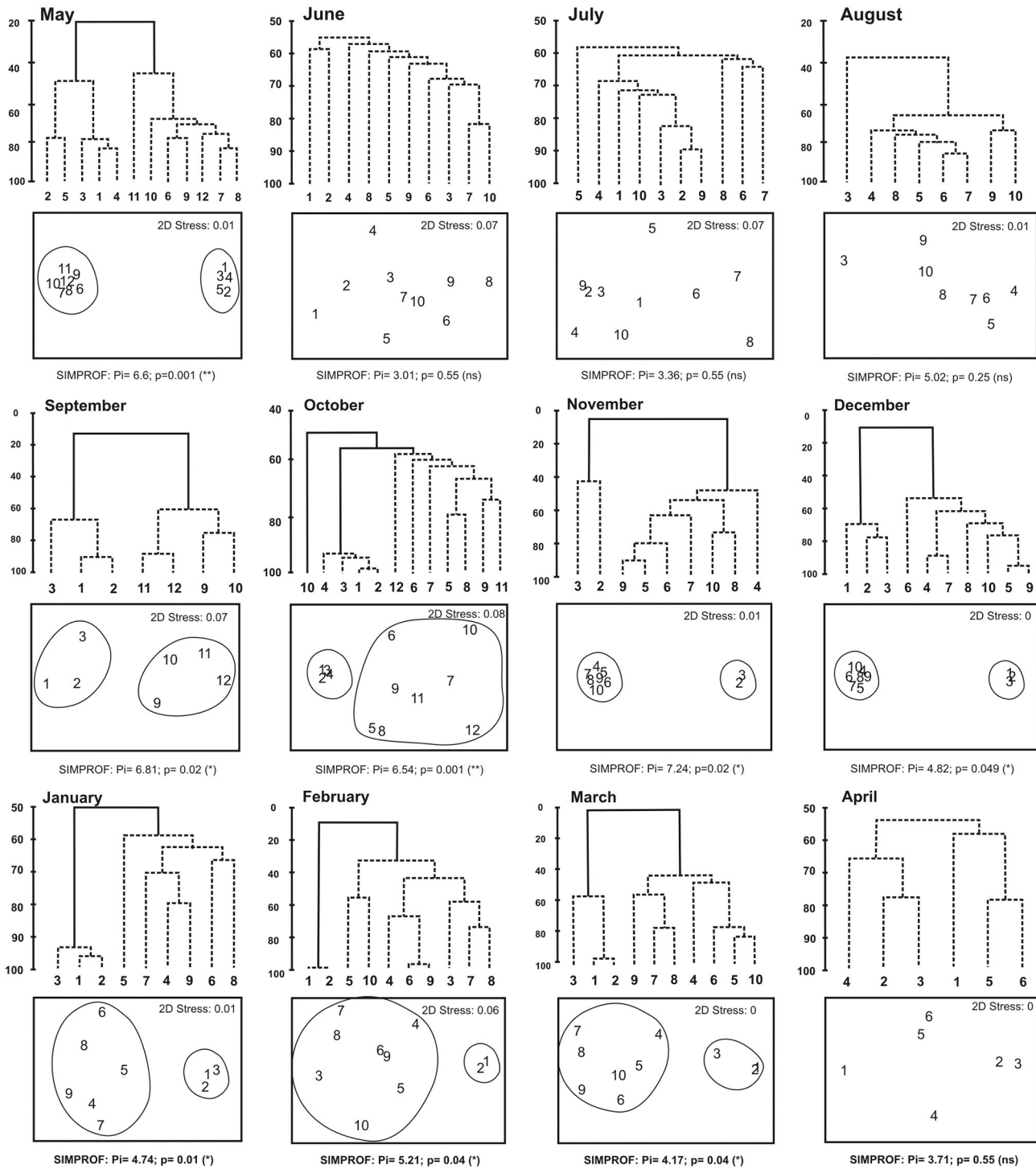
Data of wind speed and direction, recorded every 3 h during the study period, were provided by the National Weather Service (SMN). The occurrence of winds above  $40 \text{ km} \cdot \text{h}^{-1}$  was used to assess the impact of storms on the formation of zonation schemes. Wind speed ( $\text{km} \cdot \text{h}^{-1}$ ) occurred during fifteen days previous to each sampling occasion, and wave height and period measured *in situ* were compared between months when zonation scheme formation occurred (Z) and those in which there was no zonation scheme formation (nZ), applying Mann-Whitney tests given that normality was not assumed even after data transformation. Principal Component Analysis (PCA) using Spearman's rank correlation matrix was used to arrange and visualize the data, and to detect relationships among wind persistence and the formation of zonation schemes. The data used was the amount of hours with winds higher to  $40 \text{ km} \cdot \text{h}^{-1}$  occurred during fifteen days previous to each sampling occasion.

## 3. Results

### 3.1. Zonation patterns of macrobenthos

Cluster and MDS analyses were carried out for macrofaunal densities on each sampling occasions (Fig. 2). A measure of goodness-of-fit of the MDS ordination was given by the low stress value (2D stress  $< 0.1$ ). A zonation scheme was observed on eight of the twelve months sampled. The schemes found were characterized by the formation of two zones. The upper levels of the littoral zone (1 and 2, sometimes including level 3, 4 and 5) constitute one zone. The other zone comprises the rest of the sampled levels (5 to 10/12) (SIMPROF:  $p < 0.05$ ). On one occasion, the upper levels (1, 2 and 3) conformed one zone and the lower levels (9–10/12) another zone, with absence of organisms in the medium levels (4–8) (SIMPROF:  $p < 0.05$ ). This pattern revealed a significant difference in community composition between the upper and the medium and lower levels of the shoreline during most of the year. No ordination of organisms was observed during June, July, August and April months (SIMPROF:  $p > 0.05$ ).

The supralittoral zone (level 0) was characterized by the absence of organisms on all sampling occasions and was therefore not taken into account in the subsequent analysis. The SIMPER routine identified the species which contributed most to the differences observed between levels separated through multivariate analysis (Table 1). The isopod *Excirrolana armata* and a polychaete of the family Paraonidae characterize the upper levels of the littoral zone (~1–5), where the pea crab *Austinixa patagoniensis* was represented in higher densities only during October and January. The yellow clam *Amarilladesma mactroides* occurs at these levels mostly during December and February. The medium and lower levels of the littoral zone (~5–12) were characterized by higher densities of the pea crab. The yellow clam occurs at these levels mostly during May and September. These levels were also characterized by the presence of species that were not found in higher levels, as the case of the snails *Olivancillaria orbigny* and *Buccinanops duartei* during October, November and January. These same trends are evidenced from the results of the geostatistical analysis, which showed the graphical representation of the zonation patterns of the species with highest contributions percentages in the SIMPER analyses. Contour plots reveal that during July, the most abundant species, *A. patagoniensis* and *A. mactroides*, were more represented in higher levels of the intertidal area (Fig. 3). Contour plots also reveal that the areal distribution of the polychaete *Lepidasthenia* sp. and the ghost shrimp *Sergio mirim* does not changes between seasons, being distributed throughout the entire intertidal area. The distribution pattern of the isopod *E. armata* and the paraonid polychaete was restricted to the higher levels of the intertidal area (Fig. 3).



**Fig. 2.** n-MDS ordinations and clusters analysis of each month during one year. Numbers (1–12) are sampling stations. Dashed lines indicate groups of samples not separated ( $p < 0.05$ ) by SIMPROF analysis.

### 3.2. Habitat properties and species distributions

The CCA showed the relationship between the macrobenthic species and the physical features of the sediment (Fig. 4). The selected sedimentological variables were mean sand size, sorting, symmetry, kurtosis and pelitic fraction percentage. Results of permutation tests indicate that levels/species were linearly correlated with levels/variables during fall months (March, April and May,  $F = 1.52$ ;  $p = 0.04$ ), spring months (September, October and November,  $F = 1.64$ ;  $p = 0.02$ ) and summer

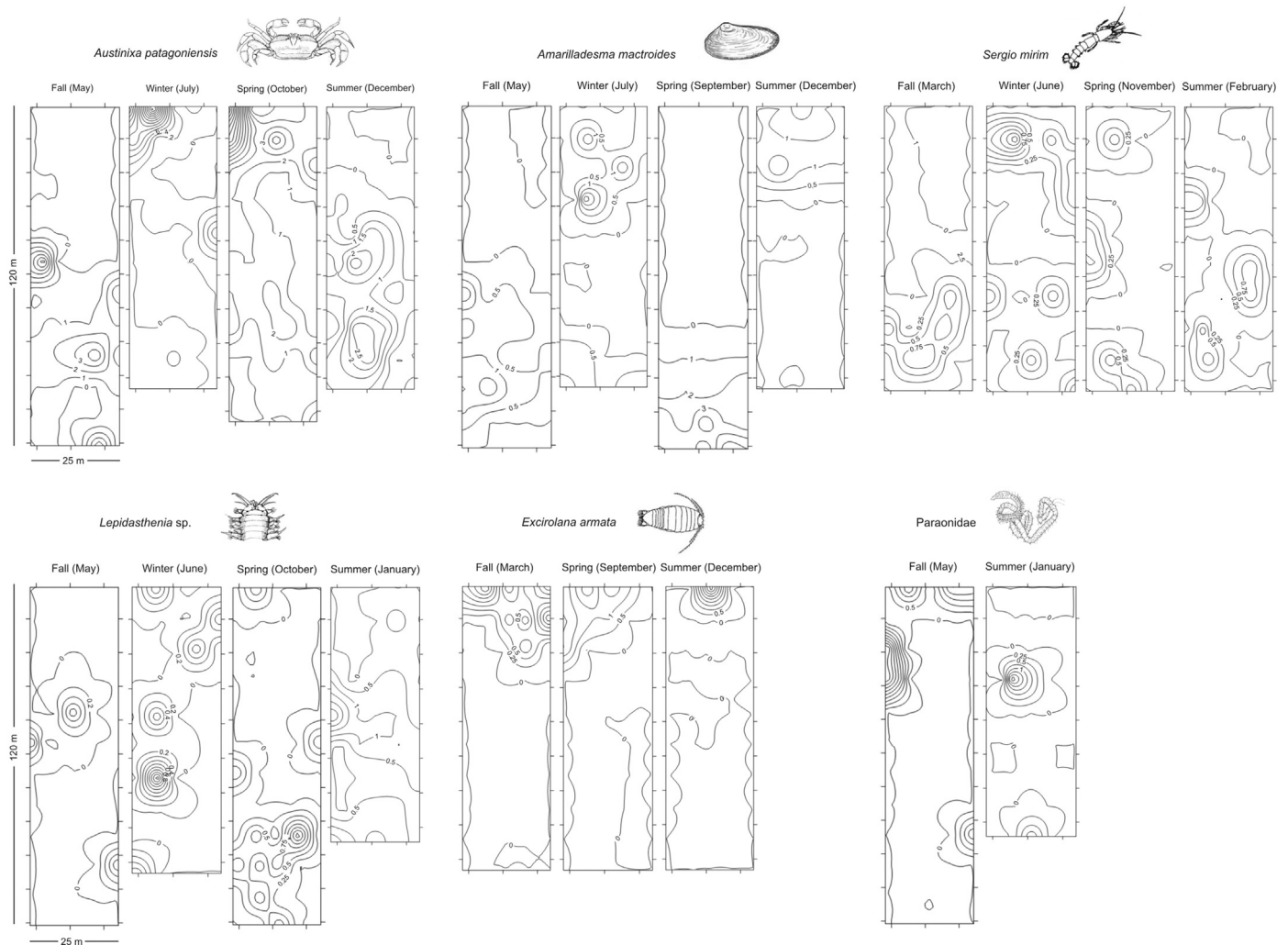
months (December, January and February,  $F = 1.24$ ;  $p = 0.01$ ). Only during winter (June, July and August), levels/species were not linearly correlated with levels/variables ( $F = 0.42$ ;  $p = 0.38$ ). During fall months, the isopod *Excirrolana armata* and the paraonid polychaete were associated with the levels 1–2 of the intertidal zone. *Amarilladesma mactroides* was associated with the levels 3–4 and with higher values of sorting. During spring months, *Olivancillaria orbigny*, *Diopatra viridis* and *Lepidasthenia* sp. were associated with fine sand present at the lower levels (9–10) of the intertidal zone. *A. mactroides*

**Table 1**  
Results of the SIMPER routine in average density (organisms · m<sup>-2</sup>). Av diss: average dissimilarity.

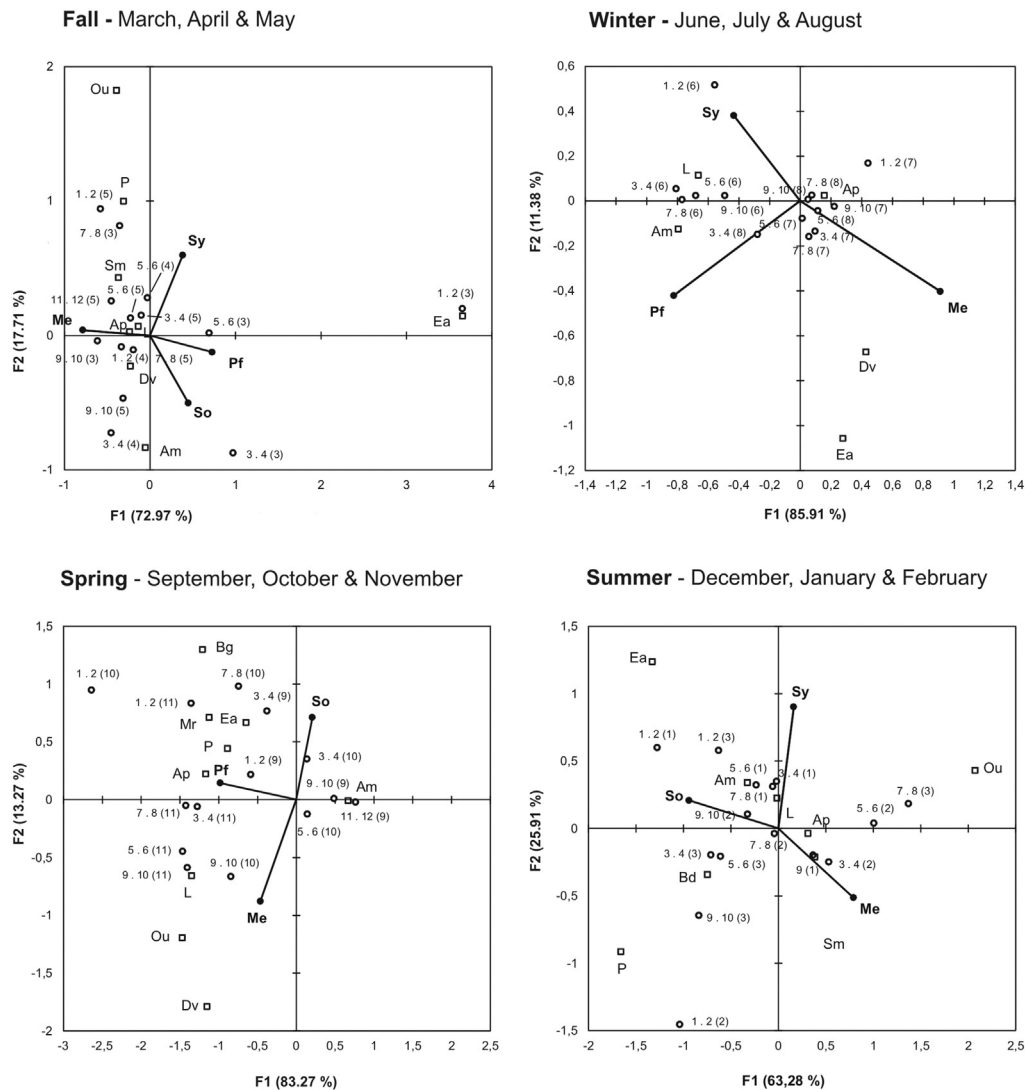
Levels/species	May		September		October		November		December		January		February		March	
	1–5	6–12	1–3	9–12	1–4	5–12	2–3	4–10	1–3	4–10	1–3	5–9	1–2	3–10	1–3	4–10
<i>Austinixa patagoniensis</i>	0	66.82	–	–	181.75	51.18	0	4.07	0	45.50	56.40	31.52	9.98	57.23	0	31.28
<i>Amarilladesma mactroides</i>	0	21.43	0	126.89	–	–	–	–	49.76	0	–	–	10.00	1.25	3.32	4.27
<i>Sergio mirim</i>	0	7.14	–	–	–	–	1.20	1.03	0	2.84	–	–	0	7.50	0	7.11
<i>Lepidasthenia</i> sp.	–	–	–	–	0	9.95	0	2.05	–	0	29.86	0	6.25	–	–	–
<i>Excirolana armata</i>	–	–	36.49	0	–	–	–	–	3.32	0	–	–	–	–	26.54	0
Paraonidae	22.00	1.43	–	–	–	–	–	–	–	0	4.98	–	–	–	–	–
<i>Buccinanops duartei</i>	–	–	–	–	0	11.37	–	–	–	0	3.32	–	–	–	–	–
<i>Corbula patagonica</i>	–	–	–	–	0	7.11	–	–	–	–	–	–	–	–	–	–
<i>Diopatra viridis</i>	–	–	–	–	–	–	3.04	0	–	–	–	–	–	–	–	–
<i>Olivancillaria orbignyi</i>	–	–	–	–	–	–	0	1.81	–	0	4.98	–	–	–	–	–
<i>Australonuphis casamiquelorum</i>	–	–	–	–	–	–	1.52	0	–	–	–	–	–	0	5.69	–
<i>Macrochiridothea robusta</i>	–	–	–	–	–	–	0	0.78	–	0	9.95	–	–	–	–	–

was also associated with lower levels, while *Austinixa patagoniensis* was associated with intermediate levels and with higher values of pelitic fraction. During summer *E. armata* and the paraonid polychaete were associated with the upper levels (1–2), whereas *A. patagoniensis* and *Sergio mirim* were associated with the fine sand present at lower levels (from 3 to 9) of the intertidal zone.

According to meteorological data, wind speed up to 40 km · h<sup>-1</sup> occur mostly during winter months, with 5 to 14 days between the event of strong winds and the non-formation of biological zonation schemes. The non-formation of a zonation scheme in April was more likely related to the tide level reached than to a strong wind event. Events of separate strong winds between 19 and 25 days from the



**Fig. 3.** Contour plot of the five more abundant macrobenthic species. Abundance per sampling unit (SU) was used as data input. Months were the species showed the highest abundances were selected to plot (one month per season). Seasons without representation for *Excirolana armata* and Paraonidae are due to the absence of the species.



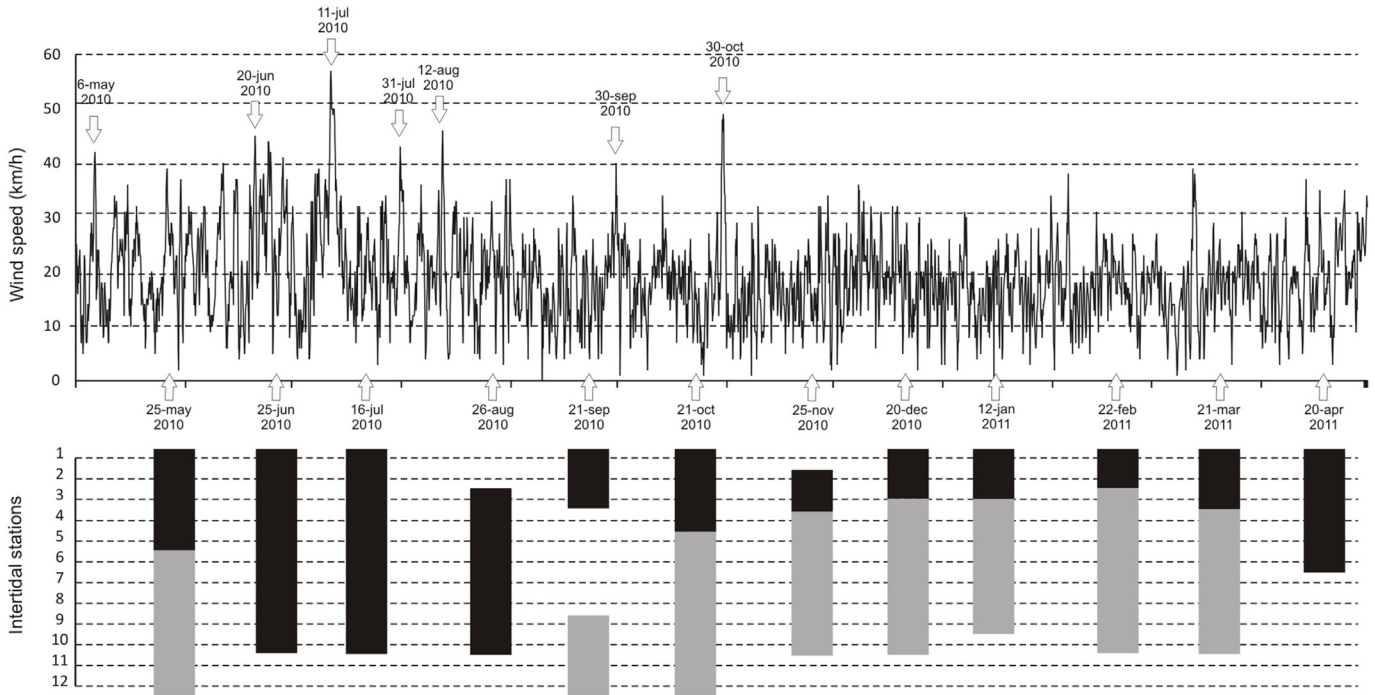
**Fig. 4.** Canonical correspondence analysis (CCA) during the four seasons, showing the position of species and sedimentological variables. Numbers (1–12) are sampling stations. Numbers in parentheses indicate the month. Ou: *Olivancillaria orbigny*, P: Paraonidae, Sm: *Sergio mirim*, Ap: *Austinixa patagoniensis*, Dv: *Diopatra viridis*, Am: *Amarilladesma macrooides*, Ea: *Excirrolana armata*, Bd: *Buccinanops duartei*, Bg: *Buccinanops deformis*, Mr: *Macrochiridothea robusta*. Sy: symmetry, Pf: pelitic fraction, Me: mean sand size, So: sorting.

biological samplings appear to have had no impact on the formation of zonation schemes (Fig. 5). Wind intensities were significantly higher in months with no zonation schemes formation - nZ ( $22.11 \pm 10.23 \text{ km} \cdot \text{h}^{-1}$ ) than in months with zonation schemes formation - Z ( $17.57 \pm 6.24 \text{ km} \cdot \text{h}^{-1}$ ) (Mann-Whitney *U* test,  $W = 459,473$ ;  $p < 0.0001$ ). Accordingly, wave height was significantly higher in months with nZ ( $1.19 \pm 0.42 \text{ m}$ ) than in months with Z ( $0.77 \pm 0.22 \text{ m}$ ) (Mann-Whitney *U* test,  $W = 2210$ ;  $p < 0.0001$ ), while wave period do not differ between month with nZ ( $6.34 \pm 2.78 \text{ s}$ ) and Z ( $6.52 \pm 2.96 \text{ s}$ ) (Mann-Whitney *U* test,  $W = 1575.5$ ;  $p = 0.75$ ). These results are in accordance with the Principal Component Analysis, where the first two components explained the 71.06% of total variance (Fig. 6). The first axis (PC1) was positively correlated to higher persistence of SW, SE, NW, NE and W winds, and with nZ. PC1 was negatively correlated with Z. The second axis (PC2) was positively correlated to higher persistence of S and N winds and negatively with higher persistence of SW, NE and W winds. Thus, the PC1 evidenced a zonation gradient, positioning the sampling dates with nZ on the right side (positive axis) of the plot associated to strong winds from SW, SE, NW, NE and W directions, whereas sampling dates with Z were located on the left side (negative axis) of the plot with no relation with any strong wind (Fig. 6).

#### 4. Discussion

The results of the present study indicate that there are two biological zones in the littoral area of this mesotidal sandy beach. The lack of zonation schemes, mainly during winter months, seems to be associated with the sand movements caused by harsh wind-driven waves, which in turn lead to changes in macrofaunal distributions. This study addresses the importance of the action of climatic factors such as strong winds in explaining biological variability in a sandy beach, particularly, in the detection of macrofaunal zonation patterns.

Several zonation schemes have been proposed for macrofauna of sandy beaches (McLachlan and Jaramillo, 1995): (a) no clear zonation; (b) 2 zones, air breathers above the drift line and water breathers below; (c) 3 zones based originally on Dahl's (1952), a supralittoral zone of air breathers, a littoral zone with intertidal species and a sublittoral zone a wide variety of species; (d) 4 physical zones based originally on Salvat's (1964) description of sediment moisture content, dry zone, retention zone, resurgence zone and saturation zone. In this study, the supralittoral zone or dry zone was characterized by the absence of organisms on all sampling occasions. This absence in the supralittoral zone had already been reported by Escofet et al. (1979) for the same section of the Argentinian coast, unlike the case of the

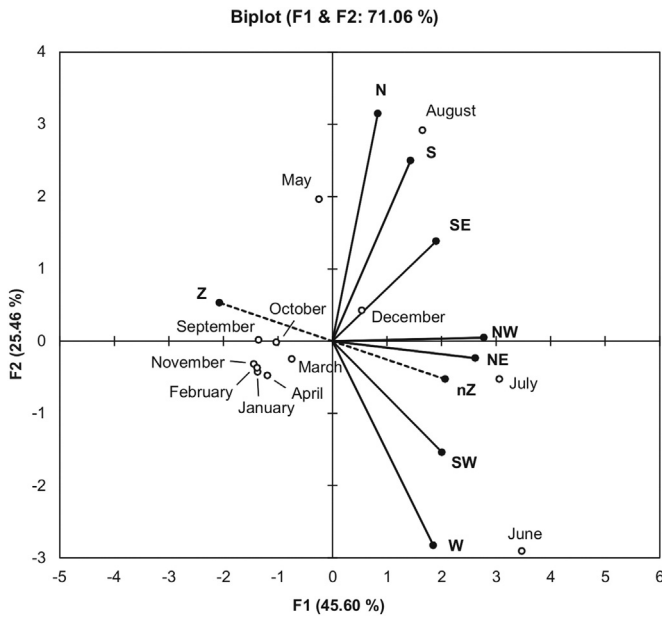


**Fig. 5.** Wind speed ( $\text{km} \cdot \text{h}^{-1}$ ) across the study period showing the relation between the occurrence of strong winds and the non-formation of biological zonation schemes. Dates when occur wind speeds up to  $40 \text{ km} \cdot \text{h}^{-1}$  are indicated in the figure. Dates when biological samplings were conducted are indicated in the figure: two-color bars (black and grey) indicate the formation of two zones within the intertidal area. The black bar indicates the no formation of zonation scheme.

closest Uruguayan beaches, where this zone is characterized by the presence of air-breathing crustaceans like talitrid amphipods (e.g. species of the genera *Talorchestia*, *Orchestia* and *Talitrus*) and ocypodid crabs (e.g. species of the genera *Ocyopode*) (Escofet et al., 1979). Talitrid amphipods live in the supralittoral zone, where the drifting macrophytes (wrack) are deposited through interactions between wave exposure, coastal topography and seasonality (Barreiro et al., 2011). It is known that species richness increases from beaches with low to those with very high wrack subsidies, since wrack represents a habitat which can be colonized by more species than the bare sediment

(Barreiro, 2013). In these areas, wrack reduces the physical stress in the sediment, rendering the environment suitable for less tolerant taxa. Wrack also signifies greater availability of food and provides shelter from predation (Dugan et al., 2003; Lewis et al., 2007; Barreiro, 2013). Particularly, it has been studied that a wrack removal diminished the density of the sandhopper *Talitrus saltator*, a dominant species in the supralittoral zone of sandy beaches, showing the important role of wrack as food or refuge for talitrid amphipods (Ruiz-Delgado et al., 2015). It is likely that the low and inconstant supply of wrack in the coastal area of these beaches could be the reason for the absence of talitrid amphipods or other species on the supralittoral zone of the beach. The other air-breathing crustaceans inhabiting the supralittoral zone are the ocypodid crabs, which are common around the drift line and therefore considered a typical species of the supralittoral zone (Koepcke and Koepcke, 1952, 1953; Barros, 2001; Quijón et al., 2001; Lucrezi et al., 2009). However, the genus *Ocyopode* is restricted to warm temperate and tropical waters (Dahl, 1952), so the absence of this genus from the studied coastal fringe could be due to low ambient temperatures (see Bally, 1983 for South African coasts).

The littoral zone is characterized by cirrolanid isopods (Brazeiro and Defeo, 1996); in the present study, the isopod *Excirrolana armata*, together with a polychaete of the family Paraonidae, characterize the upper levels (retention zone, sensu Salvat, 1964). The medium and lower levels of the littoral zone could be compared to the resurgence and saturation zones defined by Salvat (1964) and in this study were characterized by the polychaete *Lepidasthenia* sp., the callianasid crab *Sergio mirim* and its commensal, the pea crab *Austinixa patagoniensis*. This level was also characterized by subtidal species at the upper limits of their distribution, such as *Olivancillaria orbigny* and *Buccinanops duartei*. These carnivorous snails make incursions into the swash zone and lower intertidal to prey upon suspension-feeders (Gianuca, 1983; McLachlan and Brown, 2006). Another species found in the littoral is the yellow clam *Amarilladesma mactroides*; during winter, the clams can be found near the low tide level (saturation zone), whereas in spring they start migrating to the high tide level (retention zone) where they will remain during the summer; during fall they begin migrating to their overwintering position (Coscarón, 1959; Fiori et al.,



**Fig. 6.** Principal Component Analysis (PCA) considering hours of winds above  $40 \text{ km} \cdot \text{h}^{-1}$ . N: northern wind, S: southern wind, W: western wind, SE: southeastern wind, SW: southwestern wind, NE: northeastern wind, NW: northwestern wind. Z: zonation, nZ: no zonation.

2004). The seasonal migration of species to their lower levels of distribution is due to the lower temperatures during the fall and winter (Defeo et al., 1986; De Alava and Defeo, 1991; Gimenez and Yannicelli, 1997; Jaramillo et al., 2000): as temperature fluctuations are smaller in water than in the sand, species move to lower levels, where they stay covered by water longer, thus avoiding extreme variations and attaining an optimal temperature (thermoregulation) (Brazeiro and Defeo, 1996).

The distribution of macrobenthic invertebrates across the intertidal zone of the studied coastal fringe showed in general two types of schemes. During most of the year, two faunal zones were distinguished: the upper zone of the intertidal area and the median and lower zones together. The statistical analyses detected no clear intertidal zonation schemes during winter samplings, the lack of zonation schemes appearing to be associated with the storm pattern on these shores. These events generate trains of waves higher than 2.5 m, causing significant changes in sedimentary balance (Masselink et al., 2006; Bustos, 2012; Huamantínco, 2012) and thus leading to variations in faunal distribution. Meteorological data indicate that winds were more intense and persistent during months with no formation of zonation schemes. *In situ* measurements of wave height were consistent with these results, showing higher wave heights during the same months. More than 30 days after a storm, the beach recovered sand and a biological zonation scheme was consequently formed. It is known that for the study area, beach profile recovery starts 7 or 8 days after the storm event (Bustos, 2012). This same pattern was registered on beaches at Cádiz (Spain), where Anfuso and Del Río (2003) observed a uniform recovery rate of one to three months after an erosional event, despite the different morphological characteristics. Storms are powerful modifiers of coastal areas and their dynamic naturally alters the distribution of organisms. This is evident in the distribution of the yellow clam *Amarilladesma mactroides* (Fig. 3). Contrary to expectations, the clams were registered in the upper part of the intertidal zone (high tide level) in the winter month of July, when the strongest and most persistent storms were recorded; normally in this month they would be found near the low tide level to avoid the lower temperatures (Defeo et al., 1986). This change in the distribution pattern could be due to the unintentional displacement of the fauna caused by the large-scale movement of sand during a storm event. These results therefore support the working hypothesis that macrofaunal zonation along this coastal fringe varies widely throughout the year in response to storm-induced sediment movement taking place through the intertidal zone.

These findings are also consistent with those reported by the CCA, which indicate that during most of the year, the distribution of some species correlates with sediment characteristics whereas during winter no correlation between species and physical properties was observed. It is known that sediment particle size plays an important role in determining interstitial environmental conditions, and therefore, in structuring the benthic community (Fenchel and Riedl, 1970; Cunha and Ravara, 2003; McLachlan and Brown, 2006). In the present study, the sand grain sizes showed differences along the beach profile, characterized by higher representation of coarse sands in the upper intertidal zone, while the lower intertidal zone was characterized by the presence of fine sand. This environmental gradient leads to the typical pattern of more variable and extreme conditions in the upper part of the intertidal zone (Raffaelli and Hawkins, 1996) and reveals different levels of species tolerance to this gradient across the intertidal zone (Griffith and Telford, 1985; Alexander et al., 1993; Dugan et al., 2000; McLachlan and Brown, 2006). Species inhabiting the upper intertidal levels must not only adapt to a larger sand grain size, but must also be able to spend long periods of time not covered by water; this situation becomes more extreme in meso to macrotidal beaches. In this study, the upper zone was most clearly defined on almost all sampling occasions when a zonation scheme was evident (Fig. 2). In this sense, data are consistent with McLachlan and Jaramillo (1995), who report that zones at the top

of the shore are the most distinct, with the distinctions becoming less clear down shore.

Defeo and McLachlan (2005) underline the importance of macrofaunal zonation in relation to beach type, the number of biological zones increase from reflective to dissipative beaches (Jaramillo et al., 1993; McLachlan and Jaramillo, 1995), with up to four zones recognized on wide dissipative beaches. It would therefore expect to find up to four zones on dissipative sandy beaches with higher tide ranges (meso to macrotidal beaches). However, McLachlan et al. (1996) tested the hypothesis that more than three faunal zones can be distinguished on beaches across the continuum from microtidal to macrotidal sandy beaches, and concluded that zonation was indistinct in most cases and no more than three zones could be distinguished on any of the beaches. Some authors, working on macro-to-mesotidal beaches, found no clear intertidal zonation of the macrofauna, even though the beaches had two zones in common: a supralittoral zone (dry zone) and a littoral zone. Subdivision of the lower part including retention, resurgence and saturation zones (Salvat, 1964) could not be clearly established (Raffaelli et al., 1991; Rodil et al., 2006; De la Huz and Lastra, 2008; Pérez-Domingo et al., 2008). In this study, the dry zone could not be established as a faunal zone due to the absence of organisms and the littoral zone could be divided in two zones, matching retention zone and resurgence-saturation zones together. Therefore, no more than two zones were detected in this study, unlike the scheme of three zones valid for microtidal beaches (McLachlan and Jaramillo, 1995; Schlacher and Thompson, 2013).

It is crucial to take into account the particular characteristics of a beach when carrying out comparisons. For example, the use of the BSI (which considers tidal range) instead of  $\Omega$  shows an improved fit of the data on the regression line for species abundance over a range of beaches and locations (McLachlan et al., 1993); this indicates that tidal effects have an impact on animal abundance and should therefore be included when investigating beach morphodynamics and macrofaunal abundance (Hacking, 1998). Likewise, it is important to take into account the tidal range when making assumptions in relation to the number of zones and beach type. Variables such as latitude, degree of exposure and tidal range represent important sources of variability, in both the identity of their species and how they are distributed. The seasonal variability is also important in the detection of zonation patterns, being able to be detected in studies longer than one year. Finally, the strict use of statistical analysis (i.e. randomized cluster and SIMPROF) is necessary to explore zonation patterns of macrofauna (Veiga et al., 2014) in order to be able to prove the existence of defined biological zones and to perform adequate comparisons between intertidal environments.

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