



Variations in macrobenthic community structure in relation to changing environmental conditions in sandy beaches of Argentina



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ABSTRACT

This study describes for the first time the intertidal macrobenthic community of exposed sandy beaches located near the Bahía Blanca Estuary (38°S) and reports the physical characterization of this coastal fringe. The main objective of the study was to link environmental variables to biotic information, analyzing the results in the context of the *Swash Exclusion Hypothesis (SEH)* and possible estuarine influence. Four beaches were sampled seasonally at different distances from the mouth of the Bahía Blanca Estuary. To characterize the morphodynamic state of the beaches, the Dean parameter (Ω) was calculated. Multivariate analyses were used to assess benthic community structures and their relationships with physical variables. The two beaches located closest to the Bahía Blanca Estuary were classified as intermediate and those located further from the estuary as dissipative. Richness, diversity and biomass of intertidal macrobenthic communities varied with the *SEH*, increasing towards the dissipative beaches. However, total density was higher on intermediate beaches, possibly because of nutrient-rich silt-clay sediment input from the estuary, enabling them to maintain a higher density of organisms than dissipative beaches. The estuary acts as a moderator of habitat hardness, which together with the morphodynamic state of the beaches is an important factor in the structuring of the macrobenthic community along this coastal fringe.

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1. Introduction

Sandy beaches are the most common environments on coastal zones and these dynamic ecosystems are defined by three factors: tidal regime, wave climate and sediment type. The interactions between these factors determine the morphodynamic state of beaches, which span a continuum from harsh reflective beaches (narrow and steep, under conditions of small tides, low energy waves and coarse sand) to benign dissipative systems (wide and flat, under conditions of large tides, high wave energy and fine sand) with intermediate states between the above extremes (see Short, 1996).

The benthic fauna of sandy beaches includes representatives of most invertebrate groups and is generally dominated by mollusks, crustaceans and polychaetes (Bertness, 1999). The relationships between the intertidal benthic macrofauna and beach morphodynamics have been critical in beach ecology studies and focused on elucidating spatial and temporal patterns along a gradient of contrasting morphodynamic types (McLachlan et al., 1981; McLachlan, 1990; Defeo et al., 1992; Jaramillo et al., 1995; Rodil and Lastra, 2004). These studies showed that the richness, diversity, density and biomass of the macroinvertebrate community generally increase towards the more dissipative morphodynamic beach type. This is called *Swash Exclusion Hypothesis (SEH)*: (McLachlan et al., 1993) and constitutes the fundamental principles of beach ecology, which are integrated into a coherent framework (Defeo and McLachlan, 2005; McLachlan and Dorvlo, 2005).

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Furthermore, sandy beaches are closely linked to their adjacent ecosystems such as estuaries, rivers, streams and coastal lagoons in terms of sediment, freshwater, exchange of organic matter and nutrients (Lercari and Defeo, 1999, 2003, 2006; Lercari et al., 2002). These environments are generally responsible for changes in salinity, temperature, grain size and nutrient load and can also affect the biological organization of the macroinfauna on sandy beaches. In this context, the concurrent effects of beach morphodynamics and the influence of adjacent environments should be considered when modeling large-scale variations in macrofaunal biological descriptors of benthic communities (Lercari and Defeo, 2006). Despite the ecological importance of these interactions, considerable gaps exist in our understanding of the processes involved in the ecological coupling between exposed sandy shores and adjacent ecosystems.

The coastline closest to the Bahía Blanca Estuary in Argentina is characterized by extensive exposed sandy beaches that vary slightly in their morphodynamic state. In contrast to other estuarine areas, the salinity in the external zone of the Bahía Blanca estuary is similar to that of the adjacent continental shelf (Martos and Piccolo, 1988; Piccolo and Perillo, 1990) and the estuary therefore does not generate a strong salinity gradient along the coast. However, it does contribute with high loads of suspended sediment to the adjacent coast (Perillo et al., 2000) and consequently, it appears to be a significant source of nutrients and organic matter. This work describes the intertidal macrobenthic community and the physical features of sandy beaches adjacent to the Bahía Blanca Estuary, to interrogate the relationships between environmental variables and changes in community structure.

2. Materials and methods

2.1. Study area

This study was conducted into a continuous coastal fringe of exposed sandy beaches within the Provincial Nature Reserve Pehuen-Có – Monte Hermoso (39°S; 61°W). The area has a mesotidal regime with semidiurnal tides, low slope and is backed by extensive sand dunes. 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). 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 prevailing wind directions are from N, NW and NE, whereas the strongest winds come from the S, SE and SW, especially in spring and summer (Servicio Meteorológico Nacional, 1992).

The Bahía Blanca Estuary (38°S; 62°W) has an elongated shape, the inner reach of the estuary is narrow and the mouth is wide and opens to the southwestern Atlantic Ocean. It is a mesotidal estuary, formed by a system of interconnected channels separated by islands and wide tidal flats. The Sauce Chico River and the Naposta Grande creek provide most of the freshwater inflow. However, based on the salinity distribution, only the inner reach behaves as a partially mixed estuary, while the outer one is homogeneous with mean salinities similar to those of the adjacent continental shelf (Martos and Piccolo, 1988; Piccolo and Perillo, 1990).

2.2. Sampling design

Sampling was conducted seasonally during 2010 at four beaches along this continuous coastal fringe, at 25, 27, 50 and 54 km from the external zone of the Bahía Blanca Estuary (Base Baterías), designated as beach 1, 2, 3 and 4 respectively (Fig. 1). At each sampling site, five transects were established equidistant from each

other (5 m) and perpendicular to the tide line, from the upper to the lower intertidal zone (swash zone), during daytime and low tide. Each transect was divided into levels, located every 10 m in the middle and upper intertidal, and every 5 m in the lower intertidal. At each level, one sample was taken per transect, with a plastic core of 16 cm diameter and 40 cm depth (area = 201 cm²) and sieved through a 1 mm mesh. Organisms retained were fixed in 10% formalin and identified to the highest taxonomic separation possible. The wet weight was determined for each species at all sites.

2.3. Environmental characterization

In order to detect environmental variation along the coast studied; the physical variables were measured at the same coastal sites as the biology. Sand samples (six) were taken along a transect perpendicular to the tide line, from the upper to the lower intertidal zone (swash zone), with a plastic cylinder of 10 cm diameter and 10 cm depth (area = 78.5 cm²). Sand samples were washed, dried, homogenized and weighted before mechanically sieving through the traditional sieves column. Mean grain size, sorting, skewness and kurtosis were computed according to Folk and Ward (1957) and results were expressed as ϕ values ($\phi = -\log_2$ diameter in mm). The pelitic fraction (gr), defined as the silt-clay fraction (<63 μm) was also calculated for each sand sample. 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 stop-watch. Temperature (°C), turbidity (UNT) and salinity were obtained with a digital multisensor Horiba U-10. Salinity was measured using the Practical Salinity Scale. To characterize the seasonal morphodynamic state of the beaches, the Dean parameter (Ω) was employed. This index allows to define how reflective or dissipative a beach is, and is defined as:

$$\Omega = \text{Hb}/\text{Ws} \cdot \text{T},$$

where Hb is the wave height of the surf (m), Ws is sand fall velocity (m s^{-1}) and T is the wave period (s). The values of $\Omega < 2$ represent reflective beaches, whereas $\Omega > 6$ defines dissipative ones and $2 < \Omega < 6$ characterizes intermediate beach states (Short, 1996).

The physical variables measured (temperature, salinity, wave height, wave period, turbidity) and the variables calculated (mean grain size and pelitic fraction of the sediments) were compared between beaches by one-way ANOVA. Environmental variables were also analyzed by non-metric multidimensional scaling analysis (nMDS), from a similarity matrix calculated by the Euclidean distance index (with normalized data). The differences between groups was evaluated by one-way analysis of similarities (ANOSIM method, global test and pairwise tests), at a significance level of $p < 0.05$ and R statistic > 0.5 .

2.4. Biological characterization

Species abundance (IST, individuals m^{-1}) and biomass (BST, g m^{-1}) per strip are given by averaging the density or biomass q (individuals m^{-2} or g m^{-2}) in each sampling station i of all m samples pertaining to transect r (q_m) and multiplying by the corresponding width of the surveyed area (w) (Defeo, 1996):

$$\text{IST}, \text{BST} = \left[\sum_{i=1}^m (qi)/n \right] w$$

Both measures were employed in order to avoid biased results as a consequence of changing beach profile during rough and calm

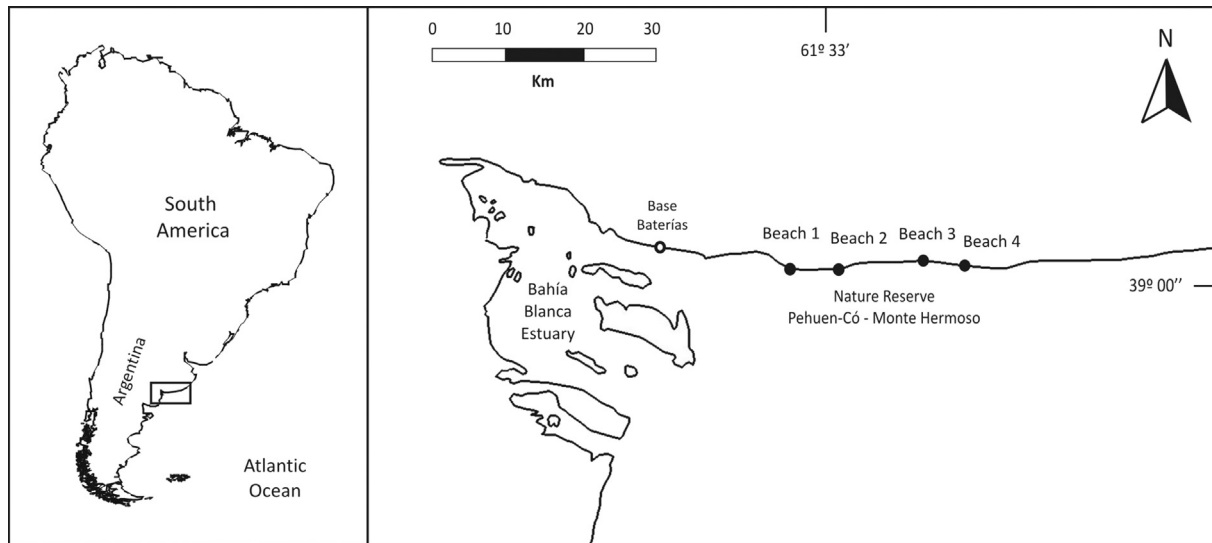


Fig. 1. Study area showing the location of sandy beaches along the Argentinian coast.

conditions, which may lead to changes in the distribution and density of organisms within the beach (McLachlan, 1983; Defeo, 1993).

Dominance (D%) and presence (P%) were calculated for each species. Species richness (S), density (individuals m^{-1}), biomass ($g m^{-1}$), the Shannon diversity index (H') and the Pielou diversity index (J') were calculated for each sampling occasion. Two-way ANOVA (beaches and seasons as factors) was used to compare the biological parameters calculated and the total density, total biomass and the densities of the dominant species. Normality and homoscedasticity were tested with the Kolmogorov–Smirnov and Bartlett tests, respectively (Sokal and Rohlf, 1995).

Non-metric multidimensional scaling analysis (nMDS) was used to represent the community under study (one nMDS per season). 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 (Clarke and Warwick, 1994). Species abundances were compared between beaches. The differences between groups due to the presence of benthic organisms was evaluated by one-way analysis of similarities (ANOSIM method, global test and pairwise tests), at a significance level of $p < 0.05$ and R statistic > 0.5 . Similarity percentage analysis (SIMPER) was used to determine the organisms that contributed most to the differences observed. These analyses were performed with PRIMER 6 (Clarke and Gorley, 2006).

2.5. Relationship between physical features and macrobenthic community

A principal component analysis (PCA) by Spearman rank correlation matrix was applied to detect relationships among environmental and biological variables and their association with the study sites. Beaches were included as a supplementary variable to determine their spatial arrangement according to data input. We used the following data as inputs: temperature ($^{\circ}C$), salinity, turbidity (UNT), wave height (m), wave period (s), mean sand size (ϕ), pelitic fraction (g), richness, diversity indices (H' and J'), biomass ($g m^{-1}$), density (individuals m^{-1}) and the densities of the dominant species.

3. Results

3.1. Environmental characterization

The environmental variables (mean and SD) of the four beaches are given in Table 1. All beaches demonstrated little variation for temperature ($F_{(3,12)} = 0.02$; $p = 0.99$) and salinity ($F_{(3,12)} = 0.20$; $p = 0.89$). There were no significant differences in mean sand size between beaches ($F_{(3,12)} = 2.74$; 0.08). However, at beach 1, 83% of samples were classified as fine sands, and 16% as medium sands and 1% as coarse sands; at beach 2, 75% of the samples were classified as fine sands, 20% as medium sand and 5% as coarse sands; at beach 3, 100% of the samples were classified as fine sands and at beach 4, 50% of the samples were classified as fine sands and 50% as medium sands. At beach 1, 2 and 3 all samples were moderately sorted, while at beach 4, 80% of the samples were moderately sorted and 20% were poorly sorted. Curves of cumulative frequency were negative asymmetric and from leptokurtic to platikurtic. Turbidity was significantly higher at beaches 1 and 2 ($F_{(3,12)} = 3.53$; $p = 0.048$) and also the pelitic fraction of the sediments was significantly higher at beaches 1 and 2 ($F_{(3,92)} = 2.78$; $p = 0.045$). Wave height was significantly higher at beaches 3 and 4 ($F_{(3,12)} = 8.89$; $p = 0.002$) while wave period showed no significant differences between beaches ($F_{(3,12)} = 1.41$; $p = 0.28$).

Table 1
Physical parameters of the beaches during the study period.

Sites/Physical variables	Beach 1	Beach 2	Beach 3	Beach 4
	Mean \pm SD	Mean \pm SD	Mean \pm SD	Mean \pm SD
Temperature ($^{\circ}C$)	16.82 \pm 5.51	17.5 \pm 5.59	17.46 \pm 5.25	17.7 \pm 5.73
Salinity	31.2 \pm 3.59	32.5 \pm 5.07	32.5 \pm 4.04	30.75 \pm 2.99
Turbidity (UNT)	49.25 \pm 3.77	51.70 \pm 6.03	46.75 \pm 7.52	45.75 \pm 2.98
Wave height (m)	0.85 \pm 0.39	0.75 \pm 0.10	1.32 \pm 0.25	0.95 \pm 0.37
Wave period (s)	7.58 \pm 1.41	5.93 \pm 0.68	4.95 \pm 0.42	4.65 \pm 0.82
Grain size (ϕ)	2.43 \pm 0.23	2.28 \pm 0.21	2.43 \pm 0.13	1.85 \pm 0.30
Selection (ϕ)	0.69 \pm 0.12	0.75 \pm 0.08	0.69 \pm 0.05	0.87 \pm 0.09
Symmetry (ϕ)	-1.05 \pm 0.35	-1.32 \pm 0.52	-1.17 \pm 0.08	-0.71 \pm 0.49
Kurtosis (ϕ)	0.88 \pm 0.41	1.03 \pm 0.34	0.83 \pm 0.19	1.46 \pm 0.29
Fine fraction (g)	0.55 \pm 0.27	0.71 \pm 0.58	0.46 \pm 0.36	0.40 \pm 0.29
Dean parameter (Ω)	4.74 \pm 0.51	3.79 \pm 1.03	8.52 \pm 1.16	7.27 \pm 1.89

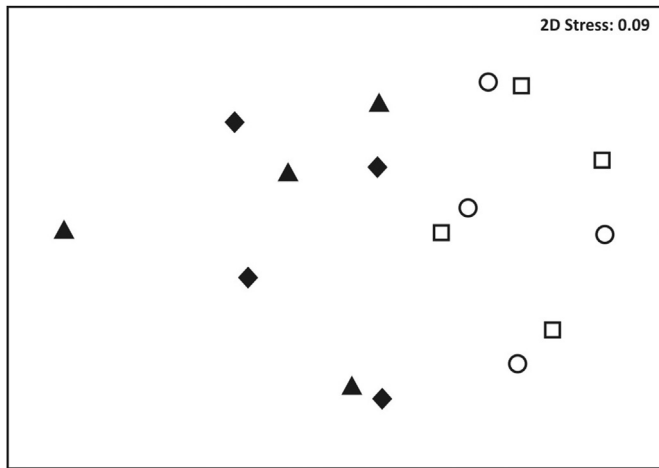


Fig. 2. Multidimensional Scaling (nMDS) plots of environmental data (Bray–Curtis similarity) between beaches. Beach 1: ◆; Beach 2: ▲; Beach 3: □; Beach 4: ○.

The non-metric multidimensional scaling (nMDS) showed the ordination of beaches (Fig. 2). One-way ANOSIM showed significant differences in physical variables among sites ($R = 0.25$, $p = 0.018$). Pairwise test showed significant differences in 4 of the 6 pairs of comparisons ($R > 0.4$; $p < 0.05$), no significant differences were

found between beaches 1 and 2 ($R = -0.21$; $p > 0.05$) and between beaches 3 and 4 ($R = -0.28$; $p > 0.05$). Morphodynamic states indicated that beaches 1 and 2 represent intermediate beaches ($\Omega = 4.74 \pm 0.51$ and $\Omega = 3.79 \pm 1.03$ respectively) while beaches 3 and 4 were characterized as dissipative beaches ($\Omega = 8.52 \pm 1.16$ and 7.27 ± 1.89 respectively). This trend did not change during the four seasons (Table 1)

3.2. Biological characterization

We found a total of 1281 organisms belonging to 26 morpho-species: 9 Crustaceans represented by Decapoda (4 species), Isopoda (3 species) and Amphipoda (2 species); Mollusca included 7 species, mostly Gastropoda (4 species) and Bivalvia (3 species); Polychaeta included 7 species belonging to five different families. Other less represented groups as Nematoda, Nemertea and Ophiuroidea were represented by a single morphospecies (Table 2). Crustaceans were the dominant group (70.43%), followed by Polychaeta (14.16%) and Mollusca (12.25%). The dominant species was the pea crab *Austinixa patagoniensis* (357.9 individuals m^{-2}), which was found as a commensal in the underground galleries of the callianasid crab *Sergio mirim*. However, the density of *S. mirim* was probably underestimated (20.21 individuals m^{-2}) given the fast burrowing activity of individuals, which led to avoidance of the sampling device. The other dominant species was the yellow clam *Amarilladesma mactroides* (52.35 individuals m^{-2}). Some other

Table 2

Community structure of the coastal fringe of sandy beaches studied. Average (av) and standard deviation (SD) of species abundance (IST), biomass (BST) and percentage of dominance (%D) and presence (%P) are presented.

	IST (individuals m^{-2})		BST (individuals m^{-2})		%D	%P
	Av	SD	Av	SD		
Phylum Arthropoda						
Class Malacostraca						
Order Decapoda						
<i>Austinixa patagoniensis</i>	357.90	332.75	40.84	36.02	64.09	93.75
<i>Sergio mirim</i>	20.21	32.80	33.07	69.00	3.62	33.75
<i>Blepharipoda doelloi</i>	2.15	6.99	6.31	24.19	0.38	8.75
<i>Cyrtograpsus angulatus</i>	0.28	2.53	0.00	0.04	0.05	1.25
Order Isopoda						
<i>Excirrolana armata</i>	13.06	42.45	0.64	2.55	2.34	13.75
<i>Macrochiridothea robusta</i>	4.64	15.34	0.23	0.79	0.83	11.25
<i>Sphaeroma serratum</i>	1.24	7.82	0.09	0.82	0.22	2.50
Order Amphipoda						
Phoxocephalidae	8.71	48.18	0.27	1.41	1.56	6.25
<i>Monocorophium insidiosum</i>	0.62	5.56	0.01	0.08	0.11	1.25
Phylum Annelida						
Class Polychaeta						
<i>Lepidasthenia</i> sp.	32.48	46.10	10.75	17.68	5.82	48.75
Paraonidae	19.54	45.62	0.52	1.82	3.50	25.00
<i>Diopatra viridis</i>	12.61	26.64	35.40	99.29	2.26	27.50
<i>Glycera americana</i>	2.49	10.91	1.25	7.84	0.45	5.00
Polynoidae	6.63	17.12	1.70	6.06	0.19	15.00
<i>Australonuphis casamiquelorum</i>	4.64	13.73	6.32	22.40	0.83	11.25
Syllidae	0.83	5.38	0.03	0.21	0.15	2.50
Phylum Mollusca						
Class Gastropoda						
<i>Olivancillaria orbigny</i>	3.11	13.35	7.50	30.56	0.56	7.50
<i>Buccinanops globosulus</i>	1.24	6.74	1.57	10.41	0.22	3.75
<i>Buccinanops duartei</i>	0.62	3.91	1.32	9.11	0.11	2.50
<i>Notochlis isabelleana</i>	0.62	5.56	0.88	7.86	0.11	1.25
Class Bivalvia						
<i>Amarilladesma mactroides</i>	52.35	67.19	334.76	487.62	9.37	51.25
<i>Corbula patagonica</i>	4.90	15.94	1.94	7.23	0.88	11.25
<i>Amiantis purpurata</i>	3.11	13.93	27.74	138.74	0.56	5.00
Other						
Nematode	1.24	11.13	0.005	0.04	0.35	5.00
Nemertino	1.97	8.88	0.15	1.02	0.22	1.25
Ophiura	0.93	4.76	0.75	6.25	0.22	3.75

invertebrates were present in more than 25% of the samples, the polychaetes *Lepidasthenia* sp. and *Diopatra viridis*.

The biological variables showed significant interactions between beaches and seasons: Margalef index (d) ($F_{(9,64)} = 4.60$; $p = 0.0001$), Pielou index (J') ($F_{(9,62)} = 5.37$; $p < 0.0001$), Shannon index (H') ($F_{(9,64)} = 7.23$; $p < 0.0001$), density ($F_{(9,64)} = 4.13$; $p = 0.0003$), biomass ($F_{(3,64)} = 9.81$; $p < 0.0001$) and the densities of the dominant species: *Austinixa patagoniensis* ($F_{(3,64)} = 30.84$; $p < 0.0001$) and *Amarilladesma mactroides* ($F_{(3,64)} = 9.53$; $p < 0.0001$).

Due to the presence of significant interactions for all variables, these were analyzed separately for each season. Richness (d) showed significant differences between beaches, being greater at beach 4 in the fall ($F_{(3,16)} = 6.21$; $p = 0.005$) and at beach 3 in winter ($F_{(3,16)} = 9.00$; $p = 0.001$). Diversity (H' y J') also showed significant differences between beaches: higher values of Shannon index (H') were registered at beach 3 (winter: $F_{(3,16)} = 10.73$; 0.0004), beach 4 (fall: $F_{(3,16)} = 11.85$; $p = 0.0002$) and at beaches 3 and 4 (spring: $F_{(3,16)} = 3.80$; $p = 0.03$ and summer: $F_{(3,16)} = 6.66$; $p = 0.004$), while higher values of Pielou index (J') were registered at beaches 3 and 4 (summer: $F_{(3,16)} = 11.02$; $p = 0.0004$ and fall: $F_{(3,16)} = 10.82$; $p = 0.0004$) and in site 2, 3 and 4 (winter: $F_{(3,15)} = 13.47$; $p = 0.0002$) (Fig. 3).

Higher values of total biomass were registered at beach 3 during winter ($F_{(3,16)} = 8.09$; $p = 0.001$) and spring ($F_{(3,16)} = 58.10$;

$p < 0.0001$), at beach 3 and 4 in fall ($F_{(3,16)} = 15.44$; $p = 0.0001$) and at beach 1 during summer ($F_{(3,16)} = 3.36$; $p = 0.04$). The general trend of total biomass varied according to the density pattern of the dominant species in biomass: the yellow clam *Amarilladesma mactroides*. The highest densities of the yellow clam were registered at beaches 3 and 4 (fall: $F_{(3,16)} = 153.5$; $p < 0.0001$, winter: $F_{(3,16)} = 9.46$; $p = 0.0008$ and spring: $F_{(3,16)} = 42.02$; $p < 0.0001$) (Fig. 3).

Total density was significantly higher at beach 1 during winter ($F_{(3,16)} = 10.02$; $p = 0.0006$) and summer ($F_{(3,16)} = 7.43$; $p = 0.002$); total density varied according to the density of the crab *Austinixa patagoniensis*. The highest densities of this pinnotherid crab were found at beach 1 during winter ($F_{(3,16)} = 313$; $p < 0.0001$) and summer ($F_{(3,16)} = 14.01$; $p = 0.0001$) and at beaches 1 and 2 during fall ($F_{(3,16)} = 7.13$; $p = 0.002$) (Fig. 3).

The non-metric multidimensional scaling (nMDS) showed the ordination of beaches in each season: during fall, (Fig. 4A) one-way ANOSIM showed significant differences in community structure among beaches ($R = 0.7$, $p = 0.001$). A pairwise test showed significant differences in all pairs of comparisons ($R > 0.6$, $p < 0.05$), with the exception of the comparison between beaches 1 and 2 ($R = 0.15$; $p > 0.05$). During winter, (Fig. 4B) one-way ANOSIM showed significant differences in community structure among beaches ($R = 0.8$, $p = 0.001$). Pairwise test showed significant differences in all pairs of comparisons ($R > 0.3$, $p < 0.05$). During

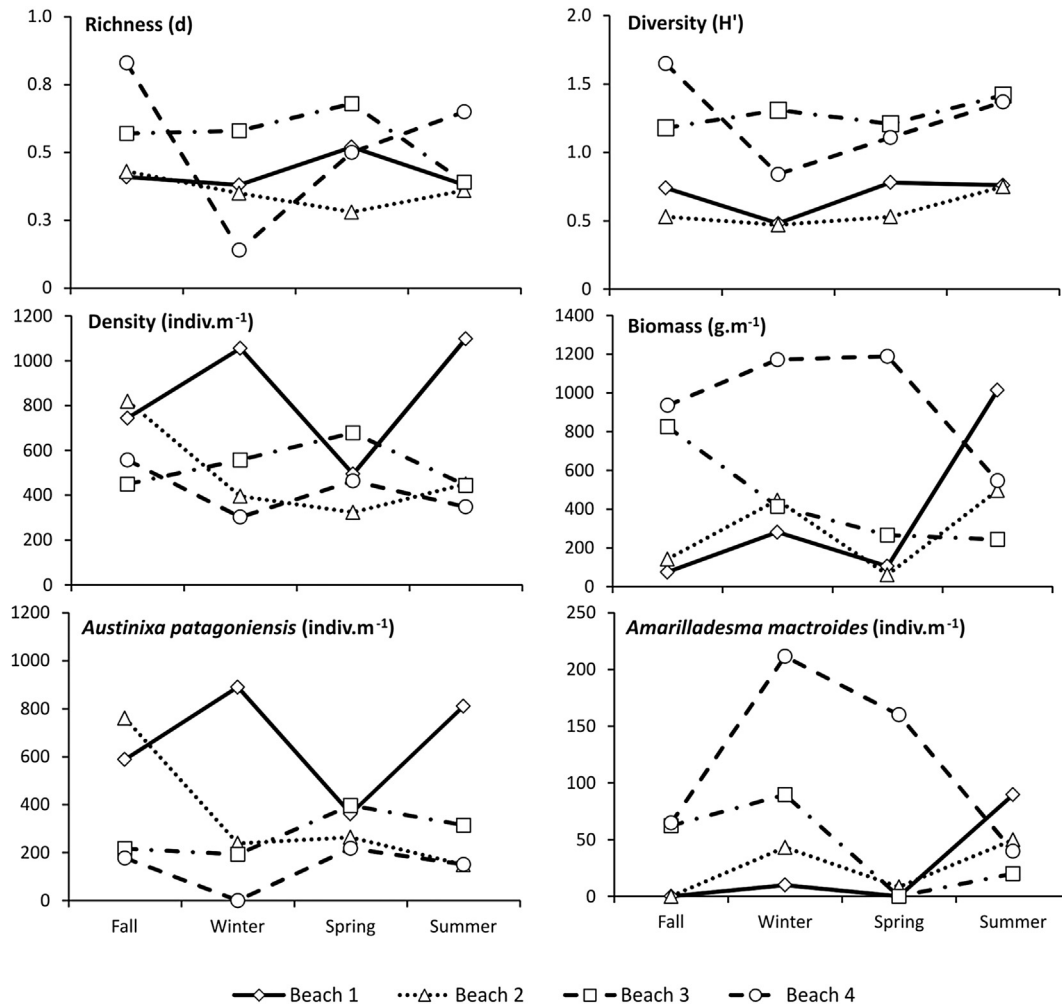


Fig. 3. Mean value and standard deviation (SD) of Margalef index (d), Shannon index (H'), total biomass (BST), total density (IST) and the densities of the dominant species, for each beach and season.

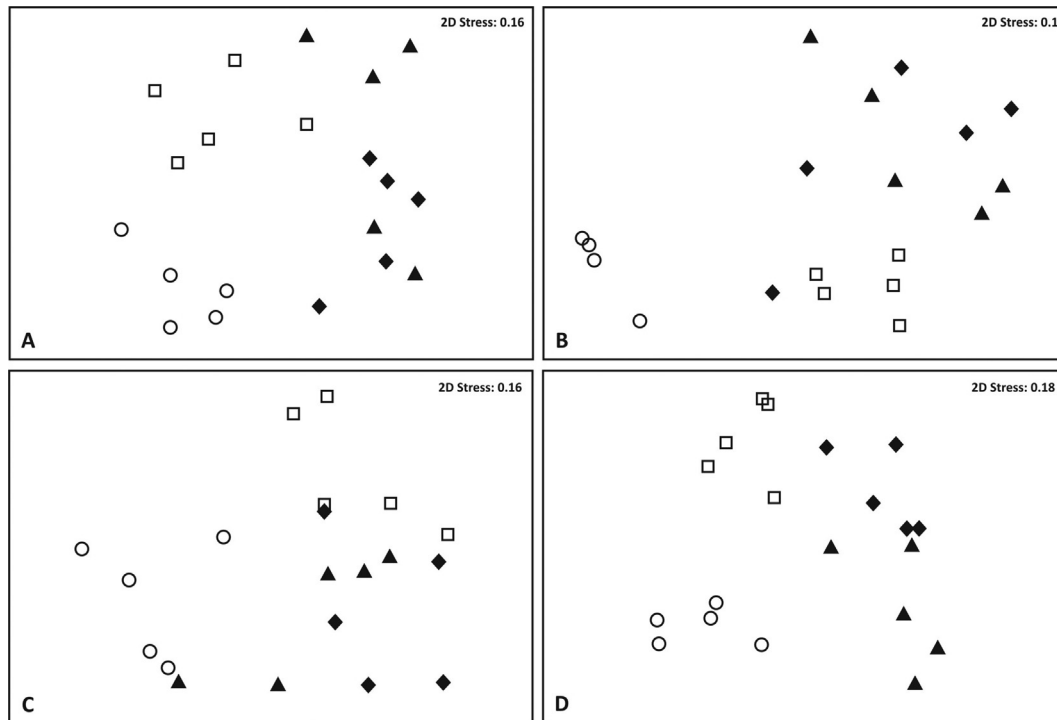


Fig. 4. Multidimensional Scaling (nMDS) plots of macrobenthic community data (Bray–Curtis similarity) between beaches. A. fall; B. winter; C. spring; D. summer. Beach 1: ◆; Beach 2: ▲; Beach 3: □; Beach 4: ○.

spring, (Fig. 4C) one-way ANOSIM showed significant differences in community structure among sites ($R = 0.46$, $p = 0.002$). Pairwise test showed significant differences in all pairs of comparisons ($R > 0.3$, $p < 0.05$), with the exception of the comparison between beaches 1 and 2 ($R = -0.03$; $p > 0.05$). During summer, (Fig. 4D) one-way ANOSIM showed significant differences in community structure among beaches ($R = 0.8$, $p = 0.001$). Pairwise test showed significant differences in all pairs of comparisons ($R > 0.5$, $p < 0.05$). The SIMPER routine identified 13 species which contributed most to the differences observed (Table 3). The crab *Austinixa patagoniensis* showed an increment in density from the beach 1 to the beach 4, where the species showed the greatest density. The yellow clam *Amarilladesma mactroides* showed the opposite trend, with increasing density from the beach 4 to the beach 1, where the species showed the greatest density. The seaworms *Diopatra viridis* and *Paraonidae* and the isopod *Macrochiridothea robusta*

characterized the beaches 1 and 2, being absent at beach 4, which was mainly inhabited by the isopod *Excirrolana armata*. Some species were present only in spring as the case of the snails *Buccinopsis globulosus* and *Olivancillaria orbigny*, while the seaworm *Australonuphis casamiquelorum* was present only during summer.

3.3. Relationship between physical features and macrobenthic community

The principal component analysis (PCA) exposed relationships among the analyzed variables (Fig. 5). The first two principal components (PC1 and PC2) explained 45.46% and 15.83% of the total variance, respectively and revealed significant correlations among the analyzed variables. The first axis (PC1) of the PCA was positively correlated to wave height, mean sand size, total biomass, diversity (H' and J') and the density of *Amarilladesma mactroides*

Table 3

SIMPER analysis (analysis of similarities), showing the organisms which most contributed to the observed differences between beaches. Av ab: Average abundance.

Beaches/Species	Fall				Winter				Spring				Summer			
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
	Av ab	Av ab	Av ab	Av ab	Av ab	Av ab	Av ab	Av ab	Av ab	Av ab	Av ab	Av ab	Av ab	Av ab	Av ab	Av ab
<i>A. patagoniensis</i>	587.9	760.1	216.7	177.1	889.7	238.2	192.8	0	361.6	264	396.4	217.6	810.3	149.3	314	150.8
<i>S. mirim</i>	9.9	9.1	20.7	79.6	9.9	29.8	34.8	0	0	0	34.8	14.9	0	9.95	44.8	24.8
<i>A. mactroides</i>	0	0	62.2	64.7	9.9	43.1	89.6	211.5	0	8.3	0	149.2	89.6	49.8	19.9	39.8
<i>Lepidasthenia</i> sp.	74.6	36.2	4.1	58.1	59.7	0	29.8	0	24.8	33.2	99.5	19.9	29.8	44.79	44.8	0
<i>D. viridis</i>	9.9	22.6	16.6	0	14.9	29.8	0	0	19.9	8.3	19.9	0	0	59.7	0	0
<i>Paraonidae</i>	29.8	9.1	70.5	0	0	0	0	0	9.9	4.1	0	0	99.5	89.6	0	0
<i>M. robusta</i>	19.9	4.5	0	0	0	0	0	0	24.8	0	14.9	0	0	0	0	0
<i>C. patagonica</i>	4.9	4.5	0	39.8	0	4.9	19.9	0	0	0	0	0	0	0	0	0
<i>G. americana</i>	0	0	0	19.9	0	0	0	0	0	0	0	0	0	0	0	0
<i>A. casamiquelorum</i>	0	0	0	0	0	0	0	0	0	0	0	0	4.9	0	0	39.8
<i>E. armata</i>	0	0	0	0	9.9	0	0	109.5	0	0	0	0	0	0	0	79.6
<i>O. orbigny</i>	0	0	0	0	0	0	0	0	4.9	0	39.8	0	0	0	0	0
<i>B. globulosus</i>	0	0	0	0	0	0	0	0	4.9	0	4.9	9.9	0	0	0	0

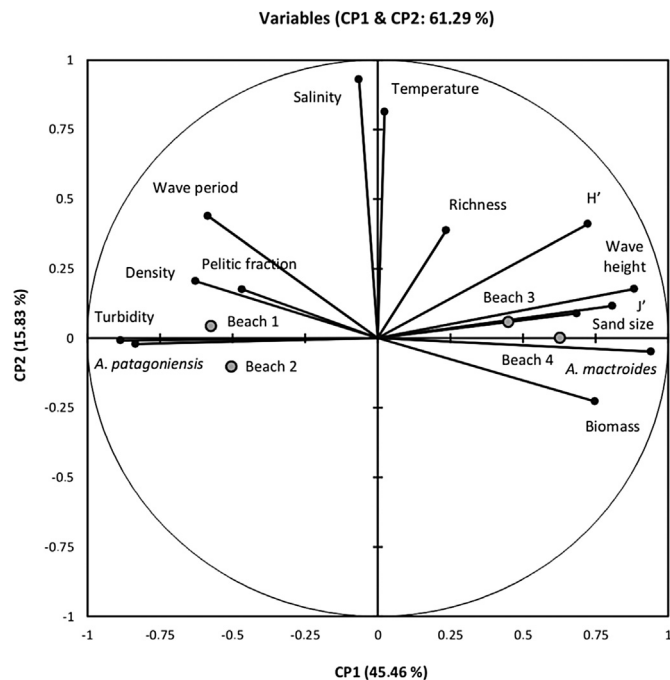


Fig. 5. Principal component analysis (PCA) plot of environmental and biological variables. Beaches are represented as supplementary variables.

and negatively with the density of *Austinixa patagoniensis* and the total density. The second axis (PC2) was positively correlated to salinity, temperature and wave period. Significant positive correlations were found between *A. mactroides* and wave height, mean sand size, total biomass and the diversity indices (H' and J') ($p < 0.05$). *A. patagoniensis* showed the opposite trend, with significantly negative correlations with wave height, mean sand size and the diversity index (J') ($p < 0.05$) and showed significant positive correlations with turbidity ($p < 0.05$). Wave height showed significantly positive correlations with mean sand size, biomass and diversity indices ($p < 0.05$), while wave period showed significant positive correlations with pelitic fraction ($p < 0.05$). The pelitic fraction showed significant negative correlations with diversity and total biomass ($p < 0.05$).

Variables were spatially linked with the sampling sites and arranged in opposite quadrants, showing spatial ordination on PC1. Beach 2 was positively correlated with turbidity and with *Austinixa patagoniensis* density ($p < 0.05$); while beaches 3 and 4 were associated with mean sand size, the diversity index (J'), total biomass and *Amarilladesma mactroides* density ($p < 0.05$).

4. Discussion

The studied beaches varied in their morphodynamic state, i.e. in terms of the interactions between wave climate and sediment type; the two beaches located closest to the mouth of the Bahía Blanca Estuary were classified as intermediate and the two located furthest from the mouth of the estuary as dissipative. The beaches also varied in terms of the turbidity and pelitic fraction of the sediments, those closest to the estuary having the highest values. This variation in turbidity and in the amount of fine sediments can be explained by the export of high loads of suspended sediment from the Bahía Blanca Estuary to the inner shelf where these sandy beaches are located (Perillo and Sequeira, 1989; Perillo and Cuadrado, 1990; Perillo et al., 2000), the effect being more significant on beaches located closer to the mouth of the estuary.

Consistent with the pattern of salinity in this estuary, which does not receive significant amounts of freshwater and therefore does not generate a strong salinity gradient along the coast, salinity did not differ among beaches (Martos and Piccolo, 1988; Piccolo and Perillo, 1990).

The intertidal macrobenthic community inhabiting the described coastal fringe is similar to that on other temperate and subtropical open sandy beaches in terms of species richness and the dominance of filter feeders, mainly crustaceans and bivalves (Brazeiro and Defeo, 1996; Brazeiro et al., 1998; Barros et al., 2001; Jaramillo et al., 2001; Monteiro Neves and Bemvenuti, 2006; Ramalho Fernandes and Soares-Gomes, 2006; Das Neves et al., 2008; Pérez-Domingo et al., 2008). However, the study area shows faunal impoverishment in relation to the Uruguayan and Brazilian coasts, probably due to the fact that the La Plata River constitutes an ecological barrier to the southern dispersal of species (Escofet et al., 1979).

The numerically dominant species along this coastal fringe was the pea crab *Austinixa patagoniensis*, this species; a commensal of a wide variety of benthic invertebrate hosts (Schmitt et al., 1973; Williams, 1984; Manning and Felder, 1989; Harrison and Hanley, 2005), has not been previously described for the study area. The other dominant species was the yellow clam *Amarilladesma mactroides* which historically was the most abundant species along this coast but which, since the mid-1990s, has undergone recurrent mass mortality causing strong fluctuations in population density (Fiori and Cazzaniga, 1999; Fiori et al., 2004). The present study was conducted during a post-mortality period, so the recorded densities are lower than historical data (544 indiv m^{-2} in 1989; Bastida et al., 1991). Our study is also the first to report high densities of *A. patagoniensis* living in the burrows of the callianasid crab *Sergio mirim* along the Argentinian coastline; previous research provided only isolated records of the two species (Boschi, 1964, 1979; Ferrari, 1981; Elías et al., 2007).

The macrobenthic community structure shows little seasonal variation in community descriptors or in dominant species. The most significant seasonal change observed in the community was the appearance of species such as the snails *Buccinanops globulosus* and *Olivancillaria orbigny* during the warm season in the intertidal zone. These carnivorous snails represent subtidal species found at the limits of their distribution and which migrate to the intertidal zone from deeper waters for feeding (McLachlan and Brown, 2006).

Most biological descriptors of the macrobenthic community varied between beaches in accordance with the Swash Exclusion Hypothesis (SEH: McLachlan et al., 1993), which predicts an increase in community descriptors from harsh reflective beaches to benign dissipative beaches, may be due to the harsh swash climate and coarse sands, as reflected by the strong relationship between community attributes and compound indices of beach state (such as the Dean parameter) or individual physical factors (McLachlan, 1990; Defeo et al., 1992; Borzone et al., 1996; Ricciardi and Bourget, 1999; Jaramillo et al., 2000; Rodil and Lastra, 2004; McLachlan and Dorvlo, 2005). As predicted, the dissipative beaches along this coastal fringe show higher values of richness, diversity and biomass.

The species that contributes most to the observed biomass distribution pattern was the yellow clam *Amarilladesma mactroides*, whose density increases towards the dissipative beaches. The yellow clam is mainly restricted to dissipative beaches (McLachlan et al., 1995; Fiori and Defeo, 2006) and its abundance pattern is better predicted by single physical variables such as grain size, rather than composite indices such as the Dean Index (Thompson and Sánchez De Bock, 2009). Recent studies show that the burial ability of *A. mactroides* is clearly affected by sand particle size and is higher in medium-to-fine sands and lower or more difficult in

extreme grain sizes (coarse or very fine), where the clam ability to bury rapidly is reduced, thus increasing their exposure time to predators (Fiori and Carcedo, unpublished).

The *SEH* prediction for density does not hold along these coasts. Total density was higher in sites corresponding to intermediate beaches and this parameter varied in accordance with the density of the pea crab *Austinixa patagoniensis*. The distribution of *Sergio mirim* on sandy beaches is restricted to semi-protected beaches (Alves dos Santos et al., 2005; Peiro et al., 2011) or exposed beaches, but influenced by nutrient-rich systems such as coastal lagoons (Manning and Felder, 1989; dos Santos Alves and Pezzutto, 1998). In addition, Vega et al. (1989) indicated that *S. mirim* galleries have a high percentage of pelitic fraction (silt-clay) in their composition. Accordingly, the export of large quantities of nutrient-rich silt-clay from the Bahía Blanca Estuary (Perillo and Sequeira, 1989; Perillo and Cuadrado, 1990; Perillo et al., 2000) favors an increase in density of species dependent on this sediment fraction, in the present case the callianasid crab *S. mirim*, and indirectly in the density of its commensal, *A. patagoniensis*. The influence of the Bahía Blanca Estuary through the input of fine sediment to the adjacent coastal fringe of exposed sandy beaches could therefore explain the distribution pattern of total density along these coasts, in contrast with the predictions of the *Swash Exclusion Hypothesis*. Therefore, the proximity of the studied beaches to the estuary could moderate habitat hardness, allowing intermediate beaches to maintain a higher density of organisms than dissipative ones. The influence of this adjacent environment and the morphodynamic state of beaches themselves are both important factors in structuring the intertidal macrobenthic community of this coastal fringe.

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References

- Barros, F., Borzone, C.A., Rosso, S., 2001. Macrofauna of six beaches near Guaratuba Bay, southern Brazil. *Braz. Arch. Biol. Technol.* 4, 351–364.
- Bastida, R., Roux, A., Bremec, C., Gerpe, M., Sorensen, M., 1991. Estructura poblacional de la almeja amarilla (*Mesodesma mactroides*) durante el verano de 1989 en la provincia de Buenos Aires, Argentina. *Frente Marítimo* 9, 83–92.
- Bertness, M.D., 1999. The Ecology of Atlantic Shorelines. Sinauer Associates, Massachusetts, p. 417.
- Borzone, C.A., Souza, J.R.B., Soares, A.G., 1996. Morphodynamic influence on the structure of inter and subtidal macrofaunal communities of subtropical sandy beaches. *Rev. Chil. Hist. Nat.* 69, 565–577.
- Boschi, E.E., 1964. Los crustáceos decápodos Brachyura del litoral bonaerense. *Boletín del Inst. Biol. Mar.* 6, 1–76.
- Boschi, E.E., 1979. Geographic distribution of Argentinian marine decapod crustaceans. *Bull. Biol. Soc. Wash.* 3, 134–143.
- Brazeiro, A., Defeo, O., 1996. Macrofauna zonation in microtidal sandy beaches: is it possible to identify patterns in such variable environments? *Estuarine. Coast. Shelf Sci.* 42, 523–536.
- Brazeiro, A., Rozbaczylo, N., Fariña, J.M., 1998. Distribución espacial de la macrofauna en una playa expuesta de Chile central: efectos de la morfodinámica intermareal. *Investig. Mar.* 26, 119–126.
- Campo de Ferreras, A., Capelli de Steffens, A., Diez, P., 2004. El clima del suroeste bonaerense. *EdiUNS, Bahía Blanca*, p. 105.
- Carbone, E., 2003. Hidrografía del arroyo Claromecú. Tesis Doctoral. Universidad Nacional del Sur, Bahía Blanca, Argentina, p. 198.
- Clarke, K.R., Gorley, R.N., 2006. *PRIMER Version 6: User Manual/Tutorial*. PRIMER-E Ltd, Plymouth, p. 190.
- Clarke, K.R., Warwick, R.M., 1994. *Change in Marine Communities: an Approach to Statistical Analysis and Interpretation*, first ed. Plymouth Marine Laboratory, Plymouth, UK.
- Das Neves, L.P., Rodrigues da Silva, P., Bemvenuti, C.E., 2008. Temporal variability of benthic macrofauna on Cassino beach, southernmost Brazil. *Iheringia Ser. Zool.* 98, 36–44.
- Defeo, O., 1993. The Effect of Spatial Scales in Population Dynamics and Modelling of Sedentary Fisheries: the Yellow Clam *Mesodesma mactroides* of a Uruguayan Exposed Sandy Beach. Doctoral Thesis. Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional, Mérida, Mexico, p. 308.
- Defeo, O., 1996. Experimental management of an exploited sandy beach bivalve population. *Rev. Chil. Hist. Nat.* 69, 605–614.
- Defeo, O., McLachlan, A., 2005. Patterns, processes and regulatory mechanisms in sandy beach macrofauna: a multi-scale analysis. *Mar. Ecol. Prog. Ser.* 295, 1–20.
- Defeo, O., Jaramillo, E., Lyonnet, A., 1992. Community structure and intertidal zonation of the macrofauna in the Atlantic coast of Uruguay. *J. Coast. Res.* 8, 830–839.
- Dos Santos Alves, E., Pezzutto, P.R., 1998. Population dynamics of *Pinnixa patagoniensis* Rathbun, 1918 Brachyura: Pinnotheridae a Symbiotic crab of *Sergio mirim* Thalassinidea: Callianassidae in Cassino Beach, Southern Brazil. *Mar. Ecol.* 19, 37–51.
- Dos Santos Alves, E., Rodrigues, S.A., Pezzutto, P.R., 2005. Estudo do crescimento relativo de *Austinixa patagoniensis* (Rathbun) (Decapoda, Pinnotheridae) simbiote de *Callichirus major* (Say) (Decapoda, Callianassidae) no mesolitoral da praia de Balneário Camboriú, Santa Catarina, Brasil. *Rev. Bras. Zool.* 22, 784–792.
- Elías, R., Iribarne, O., Bremec, C., Martínez, D., 2007. Comunidades bentónicas de fondos blandos. In: Piccolo, M.C., Hoffmeyer, M.S. (Eds.), *El ecosistema del estuario de Bahía Blanca*. Instituto Argentino de Oceanografía, Bahía Blanca, pp. 179–190.
- Emery, K.O., 1961. A simple method of measuring beach profiles. *Limnol. Oceanogr.* 6, 90–93.
- Escofet, A., Gianuca, N.M., Maitia, S., Scarabino, V., 1979. Playas arenosas del Atlántico Sudoccidental entre los 29° y 43° LS: consideraciones generales y esquema biocenológico. In: *Seminario sobre Ecología Bentónica y Sedimentación de la Plataforma continental del Atlántico Sur*, Montevideo, pp. 254–258.
- Ferrari, L., 1981. Aportes para el conocimiento de la familia Callianassidae (Decapoda, Macrura) en el Océano Atlántico sudoccidental. *Physis* 39, 11–21.
- Fiori, S.M., Cazzaniga, N.J., 1999. Mass mortality of yellow clam *Mesodesma mactroides* (Bivalvia: Macrura) in Monte Hermoso beach Argentina. *Biol. Conserv.* 89, 305–309.
- Fiori, S.M., Defeo, O., 2006. Large-scale and long-term patterns in life history traits of an endangered species: the yellow clam (*Mesodesma mactroides*) of Atlantic sandy beaches of South America. *J. Coast. Res.* 22, 872–880.
- Fiori, S.M., Vidal-Martínez, V., Simá-Álvarez, R., Rodríguez-Canul, R., Aguirre-Macedo, M., Defeo, O., 2004. Field and laboratory observations of the mass mortality of the yellow clam *Mesodesma mactroides* in South America: the case of Isla del Jabalí, Argentina. *J. Shellfish Res.* 23, 451–455.
- Folk, R.L., Ward, W.C., 1957. Brazos River Bar: a study in the significance of grain size parameters. *J. Sedimentol. Petrol.* 27, 3–27.
- Harrison, J.S., Hanley, P.W., 2005. *Austinixa aidae* Righi, 1967 and *A. hardyi* Heard and Manning, 1997 (Decapoda: Brachyura: Pinnotheridae) synonymized, with comments on molecular and morphometric methods in crustacean taxonomy. *J. Nat. Hist.* 39, 3649–3662.
- Jaramillo, E., McLachlan, A., Dugan, J., 1995. Total sample area and estimates of species richness in exposed sandy beaches. *Mar. Ecol. Prog. Ser.* 119, 311–314.
- Jaramillo, E., Duarte, C., Contreras, H., 2000. Sandy beach macrofauna from the coast of Ancud, Isla de Chiloe, Southern Chile. *Rev. Chil. Hist. Nat.* 73, 771–786.
- Jaramillo, E., Contreras, H., Duarte, C., Quijón, P., 2001. Relationships between community structure of the intertidal macrofauna and sandy beach characteristics along the Chilean coast. *Mar. Ecol.* 22, 323–342.
- Lercari, D., Defeo, O., 1999. Effects of freshwater discharge in sandy beach populations: the mole crab *Emerita brasiliensis* in Uruguay. *Estuar. Coast. Shelf Sci.* 49, 457–468.
- Lercari, D., Defeo, O., 2003. Variation of a sandy beach macrobenthic community along a human-induced environmental gradient. *Estuar. Coast. Shelf Sci.* 58, 17–24.
- Lercari, D., Defeo, O., 2006. Large-scale diversity and abundance trends in sandy beach macrofauna along full gradients of salinity and morphodynamics. *Estuar. Coast. Shelf Sci.* 68, 27–35.
- Lercari, D., Defeo, O., Celentano, E., 2002. Consequences of a freshwater canal discharge on the benthic community and its habitat on an exposed sandy beach. *Mar. Pollut. Bull.* 44, 1392–1399.
- Manning, R.B., Felder, D.L., 1989. The *Pinnixa Cristata* Complex in the Western Atlantic, with a Description of Two New Species (Crustacea: Decapoda: Pinnotheridae). Smithsonian Institution Press, Washington, p. 36.
- Martos, P., Piccolo, M.C., 1988. Hydrography of the Argentine continental shelf between 38° and 42° S. *Cont. Shelf Res.* 8, 1043–1056.
- McLachlan, A., 1983. Sandy beach ecology - a review. In: McLachlan, A., Erasmus, T. (Eds.), *Sandy Beaches as Ecosystems*. Junk, The Netherlands, pp. 321–380.
- McLachlan, A., 1990. Dissipative beaches and macrofauna communities on exposed intertidal sands. *J. Coast. Res.* 6, 57–71.
- McLachlan, A., Brown, A., 2006. *The Ecology of Sandy Shores*, second ed. Elsevier Academic Press, Burlington, MA.
- McLachlan, A., Dorvlo, A., 2005. Global patterns in sandy beach macrobenthic communities. *J. Coast. Res.* 21, 674–687.
- McLachlan, A., Erasmus, T., Dye, A.H., Woolridge, T., Van der Horst, G., Rossouw, G., Lasiak, T.A., McGwynne, L., 1981. Sandy beach energetics: an ecosystems approach towards a high energy interface. *Estuar. Coast. Shelf Sci.* 13, 11–25.
- McLachlan, A., Jaramillo, E., Donn Jr., T.E., Wessels, F., 1993. Sandy beach macrofauna communities and their control by the physical environment: a geographical comparison. *J. Coast. Res.* 15, 27–38.

- McLachlan, A., Jaramillo, E., Defeo, O., Dugan, J., de Ruyck, A., Coetzee, P., 1995. Adaptations of bivalves to different beach types. *J. Exp. Mar. Biol. Ecol.* 187, 147–160.
- Monteiro Neves, F., Bemvenuti, C.E., 2006. Spatial distribution of macrobenthic fauna on three sandy beaches from northern Rio Grande do Sul, Southern Brazil. *Braz. J. Oceanogr.* 54, 135–145.
- Peiró, D.F., Pezzuto, P.R., Mantelatto, F.L., 2011. Relative growth and sexual dimorphism of *Austinia aida* (Brachyura: Pinnotheridae): a symbiont of the ghost shrimp *Callinectes major* from the southwestern Atlantic. *Lat. Am. J. Aquat. Res.* 39, 261–270.
- Pérez-Domingo, S., Castellanos, C., Junoy, J., 2008. The sandy beach macrofauna of Gulf of Gabes (Tunisia). *Mar. Ecol.* 29, 51–59.
- Perillo, G.M.E., Cuadrado, D.G., 1990. Nearsurface suspended sediments at Monte Hermoso Beach, Argentina: I. Descriptive characteristics. *J. Coast. Res.* 6, 981–990.
- Perillo, G.M., Sequeira, M.E., 1989. Geomorphologic and sediment transport characteristics of the middle reach of the Bahía Blanca Estuary (Argentina). *J. Geophys. Res. Oceans* (1978–2012) 94, 14351–14362.
- Perillo, G.M.E., Piccolo, M.C., Parodi, E., Freije, R.H., 2000. The bahía blanca estuary, Argentina. In: Seeliger, U., Kjerfve, B. (Eds.), *Coastal Marine Ecosystems of Latin America*, Environmental Science Series. Springer Verlag, Berlín, pp. 205–217.
- Piccolo, M.C., Perillo, G.M.E., 1990. Physical characteristics of the bahía blanca estuary (Argentina). *Estuar. Coast. Shelf Sci.* 31, 303–317.
- Ramalho Fernandes, R.S., Soares-Gomes, A., 2006. Community structure of macrobenthos in two tropical sandy beaches with different morphodynamic features, Rio de Janeiro, Brazil. *Mar. Ecol.* 27, 160–169.
- Riccardi, A., Bourget, E., 1999. Global patterns of macroinvertebrate biomass in marine intertidal communities. *Mar. Ecol. Prog. Ser.* 185, 21–35.
- Rodil, I.F., Lastra, M., 2004. Environmental factors affecting benthic macrofauna along a gradient of intermediate sandy beaches in northern Spain. *Estuar. Coast. Shelf Sci.* 61, 37–44.
- Schmitt, W.L., McCain, J.C., Davidson, E.S., 1973. Decapoda I: Brachyura I: Fam. Pinnotheridae. *Crustac. Cat.* 3, 1–160.
- Servicio de Hidrografía Naval, 2009. Tablas de Marea. Buenos Aires. Departamento de Artes Gráficas del Servicio de Hidrografía Naval, pp. 140–144. Publicación H-610.
- Servicio Meteorológico Nacional, 1992. Estadísticas Climatológicas 1981–1990. Serie B, 37. Secretaría de Aeronáutica, Buenos Aires, p. 709.
- Short, A.D., 1996. The role of wave height, period, slope, tide range and embaymentisation in beach classifications: a review. *Rev. Chil. Hist. Nat.* 69, 589–604.
- Sokal, R., Rohlf, F., 1995. In: Freeman, W.H. (Ed.), *Biometry the principles and practice of statistics in biological research*, p. 877. New York: New York.
- Thompson, G.A., Sánchez De Bock, M.F., 2009. Influence of beach morphodynamics on the bivalve *Donax hanleyanus* and *Mesodesma mactroides* populations in Argentina. *Mar. Ecol.* 30, 198–211.
- Vega, V., Rodríguez, S., Valente, M., 1989. Shallow marine and fluvial environments of Quaternary deposits in Pehuen-Có beach, Buenos Aires, Argentina. *Quat. S. Am. Antarct. Peninsula* 7, 51–80.
- Williams, A.B., 1984. *Shrimps, Lobsters and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida*. Smithsonian Institution, Washington, p. 550.