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The forgotten dimension in sandy beach ecology: Vertical distribution of the macrofauna and its environment

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ABSTRACT

Spatial and temporal environmental heterogeneity influences biodiversity distribution patterns and dynamics on sandy beaches. In these ecosystems, the microscale vertical distribution adds a dimension to the analysis of biological and physical processes, whose ecological patterns have been rarely described. An intensive across-shore sampling in a dissipative beach was conducted, using a stratified corer to analyze small-scale vertical variations in macrofaunal and physical variables. Sediment temperature decreased towards the swash zone and at deeper sediments. Conversely, moisture, grain size and organic content increased seaward, concurrently with the highest vertical variability. Species richness and density increased from the dunes to the swash zone, being highest at the surface, whereas biomass was higher in sediments deeper than 15 cm as a consequence of larger individual sizes. Sediment moisture and temperature showed a consistent correlation with biological descriptors. Deconstructed by taxonomic group, a significant vertical segregation of body size was observed, suggesting different microhabitat preferences and burrowing abilities. Species spatial patterns varied according to life history traits and differential susceptibility to variations in environmental conditions. This study provides novel insights on vertical environmental and biological variations across the dune-shore axis in a dissipative beach. Expanding the findings of this research to larger spatio-temporal scales is a short-term need to decipher the processes underlying the community and population patterns outlined here.

1. Introduction

Ecology is scale-dependent (Levin, 1992; Gotelli et al., 2009; McGill, 2010a). Individual and population processes operating at the microscale (e.g., competition) potentially impact the distribution and abundance of organisms at large spatial scales (e.g., species' ranges). Therefore, they can also be influential in predicting macroscale patterns of diversity, community abundance and structure (McGill, 2010a, b). In addition, spatial and temporal environmental heterogeneity influences biodiversity distribution patterns and dynamics at different scales (Sutherland et al., 2013; Cabral et al., 2017; Dietze, 2017). Thus, the explicit consideration of scale provides additional insights about the factors controlling the distribution and abundance of organisms and therefore the structure of faunal communities and the potential underlying processes.

Sandy beaches are dynamic environments placed on the land-sea interface, where physical and biological factors operating over three main spatial scales govern macrofaunal patterns and processes (Defeo and McLachlan, 2005): 1) the macroscale, which concerns biogeographic patterns in community and population features, including also variations over beaches with different morphodynamics; 2) the mesoscale, which concerns variations within a single beach, both in the alongshore and across-shore directions; and 3) the microscale, which encompasses the area of influence of an individual and thus refers to biological and physical processes occurring at distances from millimetres to meters within a beach. Filling existing gaps between small and large scales will help elucidating how local dynamics operating at the organismal level of ecological organization link to macroecological patterns and dynamics at the community level in sandy beach ecosystems (Defeo et al., 2017; McLachlan and Defeo, 2018).

The microscale is of utmost importance in soft bottom ecosystems, including sandy shores. This scale includes a third dimension, given by the vertical distribution of organisms in the sand, and mainly concerns fine-scale environmental gradients, interactions between individuals (Defeo and McLachlan, 2005) and the density experienced by an individual at a certain neighborhood (i.e., concentration and crowding:

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Orensanz et al., 1998). At this scale, sandy beach meio and macrofauna may be strongly affected by environmental gradients and by intra- and interspecific interactions (Croker and Hatfield, 1980; Defeo, 1996a, b, 1998; Dugan et al., 2004; Maria et al., 2012; Fanini et al., 2017). This third dimension is thus critical for horizontal and vertical partitioning in the sand. Burrowing capability has been identified as a mechanism of space partitioning at this scale (McLachlan, 1998; Nel, 2001; Dugan et al., 2004). As burrowing rates are closely and directly related to individual size, smaller individuals burrowing faster than larger ones, body size is also a critical indicator of the capacity of the macrofauna to occupy different depths in the sediment, as shown for mole crabs (Dugan et al., 2000; Defeo et al., 2001), amphipods (Poulin and Latham, 2002), ghost crabs (Watson et al., 2018), and bivalves (McLachlan et al., 1995; Fiori and Carcedo, 2015).

Strong environmental gradients are particularly influential at the small scale. Waves, tides and sediment type interact in sandy beaches to determine the texture and movement of sediments, moisture gradients and the swash climate. These variables define the immediate environment experienced by macrobenthic species, including (McLachlan and Defeo, 2018): 1) the sand in which they burrow (grain size and compaction); 2) the swash water movement over the sand, i.e., the swash climate, which could affect burrowing and feeding times; and 3) the gradient of exposure to air, which generates strong fine-scale variability in temperature and moisture, causing desiccation stress and altering the ability to burrow into the sand (Nel et al., 1999, 2001; de la Huz et al., 2002; Sassa et al., 2014). Extreme temperatures and dry sediments are generally encountered in the upper few centimeters at upper beach levels above the drift line, becoming more stable towards the sea and down into the sediment. Thus, the extent of these fine-scale environmental gradients also varies markedly across the dune-sea axis, affecting in a dissimilar way the across-shore distribution, abundance and burrowing abilities of faunal components according to specific environmental preferences (McLachlan et al., 1995; Nel et al., 1999; Dugan et al., 2000; Defeo et al., 2001).

Surprisingly, microscale studies have been rarely conducted in exposed sandy beaches at different levels of ecological organization. Most efforts in this direction were made for meiofauna (McLachlan, 1978; Maria et al., 2012) and macrofauna in sheltered beaches (e.g. Croker, 1967; Croker and Hatfield, 1980; Rodil et al., 2008). In this paper, small-scale vertical variations in species richness, density, biomass and body size of sandy beach macrofauna across the dune-shore axis were investigated, together with the potential effects of variations in physical factors on biological descriptors. To this end, a very intensive sampling design was conducted in a high-energy dissipative beach on the Uruguayan Atlantic coast with a four-layer stratified corer, from the base of the dunes to the lower level of the swash zone. The macrofaunal community was also deconstructed in main taxonomic groups, in order to better understand biological patterns in relation to vertical and across-shore variations in the beach environment. Patterns at the species level were also compared, considering supralittoral and intertidal forms, different development modes and feeding habits (Defeo and McLachlan, 2011). It is hypothesized that the third dimension of the sandy beach habitat influences species richness, abundance, biomass and body size, but the relative importance of different environmental predictors will vary across shore and among macrofaunal components. Considering the existing knowledge about intertidal abiotic heterogeneity and specific susceptibilities of macrofaunal members to physical conditions, differences in the structure and composition of the community are predicted: a) among depths and b) in the across-shore dimension of the beach. It is also expected that organisms with different body size show a differential vertical distribution (habitat partitioning) according to their burrowing capacity.

2. Material and methods

2.1. Study area, sampling design and laboratory analyses

The study was conducted at Barra del Chuy, a wave-dominated dissipative beach (sensu McLachlan et al., 2018) of Uruguay (33°49′S, 53°27′W) with a wide surf zone, a gentle slope and fine to very fine well-sorted sands (Fig. S1a). The sampling was carried out in late spring. Sampling levels (SL) were placed at 4 m intervals following a linear transect (perpendicular to the shoreline) from the base of the dunes to the lower limit of the swash zone. Environmental information at each SL was obtained in four depth strata (S5: 0–5 cm, S10: 5–10 cm, S15: 10–15 cm and S > 15: > 15 cm). At each SL, sediment temperature was registered in all the four strata (± 0.1 °C) and sediment samples were collected using a stratified plastic corer for laboratory determination of mean grain size, moisture and organic matter content. Mean grain size was assessed by sieving the sediment through a 9- sieve column ranging from 2.0 to 0.006 mm mesh. The sediment retained on each sieve was weighed to estimate mean grain size (Folk's method) using the GRADISTAT software (Blott and Pye, 2001). Moisture was determined by the difference in weight between wet and dried sediment (at 80 °C for 24 h), while the organic matter content was determined by the difference between dry and incinerated sediment sample weights at 500 °C for 5 h.

Biological samples were taken at each SL by triplicate, along transects spaced 8 m apart, from the base of the dunes to the lower limit of swash zone. Samples were extracted with a PVC cylinder (15 cm diameter) subdivided into four 5 cm strata mentioned above (Fig. S1b). Samples were field-sieved through a 0.5 mm mesh and the organisms retained were fixed (5% buffered formalin) and, in the laboratory, identified to the species level, counted and weighed (wet weight ± 0.001 g). Macrobenthic community was described in both dimensions (i.e., across shore and vertical) in terms of species richness (registered species number considering all transects), density (ind·m^{-3}), biomass (g·m^{-3}) and body size (g·ind^{-1}). A specific length-based analysis was performed for the yellow clam *Mesodesma mactroides*, where organisms were also measured (maximum valve length ± 0.1 mm) and three population components were determined (Defeo, 1998): recruits (< 10 mm), juveniles (10–43 mm) and adults (> 43 mm).

2.2. Statistical analyses

In order to explore the spatial variations of environmental and biological variables, the Natural Neighbor interpolation method (Sibson, 1981) was used to create contours maps considering the coordinate scheme as: X: distance from dunes, Y: depth, and Z: analyzed variable. This method does not extrapolate beyond the limits of the data locations and it is based on the Delaunay triangulation of a set of observation points, creating a new set of gridded observations including the gridded points and the observation points (Sibson, 1981). Biological and environmental data from the observation points were weighted by the area of overlap between a new cell corresponding to the grid point and the original cell corresponding to the observation point. The weighted values were summed and divided by the sum of the weights to determine the value at the grid point (Watson, 1994; Beletsky et al., 2003). Linear and non-linear models were also used to assess across-shore trends, selecting in all cases the model that maximized the goodness of fit (R^2).

A two-dimensional (2D) ordination of environmental and biological information was performed using non-metric multidimensional scaling (nMDS). Environmental variables were log-transformed and the nMDS was based on Euclidean distance matrix. The same approach was employed to assess between-strata similarity in density (root-root transformed data) and biomass (range transformation) using the Bray-Curtis similarity index. Similarity percentages (SIMPER: Clarke, 1993) were calculated to identify typifying species (contribution > 10% of similarity intra-groups) and discriminating species (contribution to dissimilarity between groups > 5%) between depth strata. To assess which combination of environmental variables best explained vertical variations in density and biomass, the BIOENV approach was followed (Clarke and Ainsworth, 1993). All multivariate analyses were carried out using the PRIMER 6.1.4 software package (Clarke and Gorley, 2006).

An Analysis of Covariance (ANCOVA) was initially considered to assess vertical differences in environmental and biological variables, using depth stratum as a main factor and the distance from dunes as a covariate. However, the homogeneity of slopes (parallelism assumption) was not fulfilled, suggesting contrasting patterns in vertical variations of response variables according to the distance from dunes. This fact precluded the application of ANCOVA. Therefore, the covariate (distance from dunes in this case) was partitioned and considered as a second fixed factor in order to perform two-way ANOVAs following Underwood (1997). Across-shore beach zones were then defined using the results previously obtained by nMDS (see above) and two-way ANOVAs were performed, using beach zone and depth stratum as main fixed factors. Data were transformed to meet the normal distribution and homoscedasticity assumptions when required. When significant differences were found, multiple comparisons were assessed by a Tukey HSD test for multiple comparisons ($p < 0.05$).

3. Results

3.1. The environment

Environmental variables showed clear across-shore and vertical patterns at Barra del Chuy beach (Fig. 1). Sand temperature decreased linearly from dunes to the sea and significantly differed between depth strata, with the highest values always occurring in S5 (Fig. 1a and S2, Table 1 and S1). Sand moisture significantly increased asymptotically from the dunes to the swash zone, and the highest values tended to be

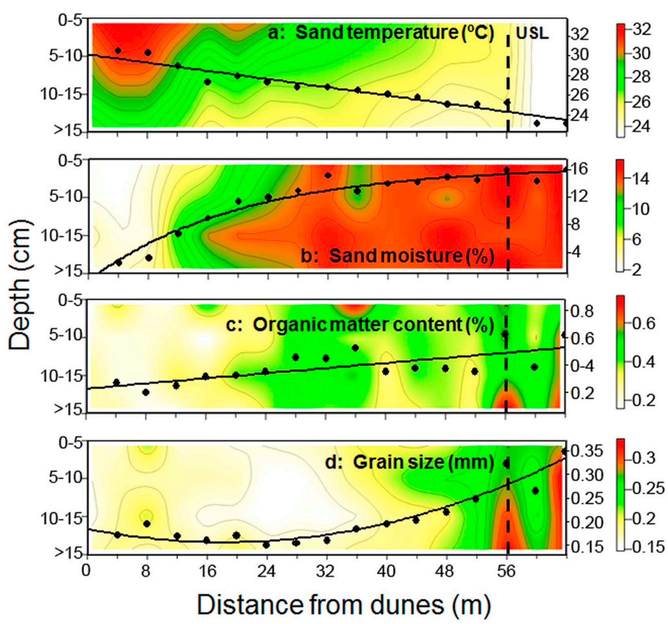

Fig. 1. Contours of physical parameters of sediment variables at Barra del Chuy beach. Best models ($p < 0.001$) fitted between mean values of sediment variables per sampling level and the distance from dunes are shown (details in Table S1). USL: upper swash limit at sampling time.

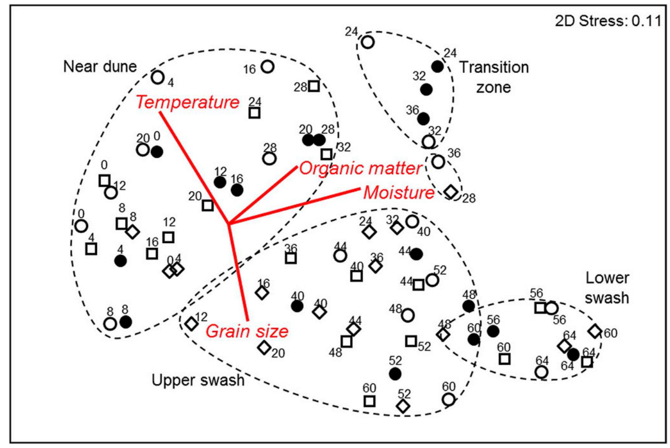

Fig. 2. Non-metric multidimensional scaling (nMDS) of sediment variables at Barra del Chuy beach. Numbers next to markers indicate the distance from dunes (m). Depth strata (cm) defined as follows:○: S5; □: S10; ●: S15 and ◇: S > 15. Dashed lines enclose groups formed at 45% resemblance level. Vectors of multiple correlations with environmental variables are shown in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

found in the deepest sediment layers throughout the across-shore axis (Fig. 1b). Sediment organic matter increased linearly towards the sea, presenting high variability between depth strata (Fig. 1c). Grain size significantly increased towards the two extremes of the dune-sea axis, particularly towards the swash zone, which showed the coarsest sediment with the highest variation among depth strata (Fig. 1d).

Environmental nMDS grouped samples that roughly revealed four beach zones (Fig. 2): 1) near dunes (ND), clustering samples up to 20 m from dunes; 2) transition zone (TZ), extended between 20 and 32 m from dunes; 3) upper swash (US) and 4) lower swash (LS), defined from 32 to 52 m from dunes, respectively.

Two-way ANOVA revealed differences between strata and beach zones (i.e., the four beach zones defined by nMDS in Fig. 2) in sand temperature (Table 1), decreasing across the shore until reaching water temperature values. Variability among strata also decreased towards the lower swash zone (Fig. S2, Table S2). Moisture, organic matter and

Table 1
Summary of ANOVA results performed on environmental and biotic data recorded at Barra del Chuy beach. Temperature, abundance and biomass were log-transformed. Significant results are highlighted (*$p < 0.05$; ***$p < 0.001$). SS: sum of squares.

		Beach zone	Depth stratum	Beach zone · Depth stratum
Temperature (°C)	SS	0.36	0.1	0.03
	$F_{3,3,9}$	**83.90*** **	**23.93*** **	**2.23***
Moisture (%)	SS	1104	23	26
	$F_{3,3,9}$	**55.57*** **	1.15	0.43
Organic matter (%)	SS	0.69	0.02	0.13
	$F_{3,3,9}$	**19.16*** **	0.61	0.34
Grain size (mm)	SS	0.13	0.002	0.004
	$F_{3,3,9}$	**71.99*** **	1.13	0.77
Species richness	SS	35.3	50.6	42.9
	$F_{3,3,9}$	**16.13*** **	**23.14*** **	**6.53*** **
Density (ind·m^{-3})	SS	182.27	208.03	169.69
	$F_{3,3,9}$	**9.75*** **	**11.12*** **	**3.02*** **
Biomass (g·m^{-3})	SS	122.1	34.41	61.65
	$F_{3,3,9}$	**10.84*** **	**3.06***	1.82

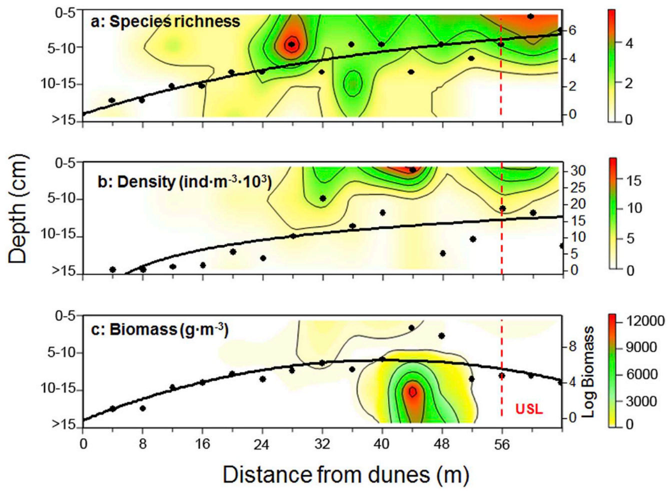

Fig. 3. Contours of community metrics at Barra del Chuy beach. Best models ($p < 0.001$) fitted between mean values of biotic variables for each beach level and the distance from dunes are shown (details in Table S1). USL: upper swash limit at sampling time.

grain size of the sediment significantly differed only between beach zones (Table 1), with ND showing lower values than the other three zones (Table S2).

3.2. Macrofauna community

The macrofauna community was represented by mollusks, polychaetes and crustaceans (Table S3). Crustaceans were most represented (5 species) and had the greatest density, being the isopod *Excirolana armata* and the amphipod *Phoxocephalopsis* spp. the most abundant species. The highest biomass corresponded to mollusks, mainly represented by the bivalve *Mesodesma mactroides*. The polychaete *Euzonus furcifera* had the highest density and biomass among polychaetes (Table S3).

Species richness increased asymptotically from the dunes to the swash zone, where the highest number of species was recorded (Fig. 3a, Table S1). Density also significantly increased in the seaward direction according to a logarithmic model (Table S1), being highest at the US zone (Fig. 3b, Table 1). Significant differences between strata and beach zones in species richness and density were found (Table 1). Moreover, the stratum x beach zone interaction was significant (Table 1), meaning that the effect of one factor is not independent of the presence of a particular level of the other factor. Cautious interpretation of post-hoc analysis (Table S2) showed that the ND zone had significant lower richness and density than the other three beach zones. Regarding depth, the two superficial strata (S5 and S10) had significantly higher richness and density than S15 and $S > 15$ (Table S2).

Biomass was highest at 44 m from the dunes (US zone) and decreased towards both ends of the across-shore axis (Fig. 3c), following a quadratic model (Table S1). The two-way ANOVA showed significant differences between zones and depth strata (Table 1). The US had significantly higher biomass than the other three beach zones, where biomass was significantly higher in the deepest stratum (> 15 cm) (Table S2).

Ordination (nMDS) based on density (Fig. 4a) and biomass (Fig. 4b) revealed a well-defined grouping of samples, reflected in very low stress values that indicate a robust 2D representation of the groups within the 45% similarity boundary. Superficial strata (S5 and S10) were clearly separated from deeper sediment layers, and this segregation tended to be consistent in the across-shore axis. Density-based nMDS showed that superficial strata (S5, S10) provided three clearly distinguishable groups according to the across-shore position on the beach (Fig. 4a).

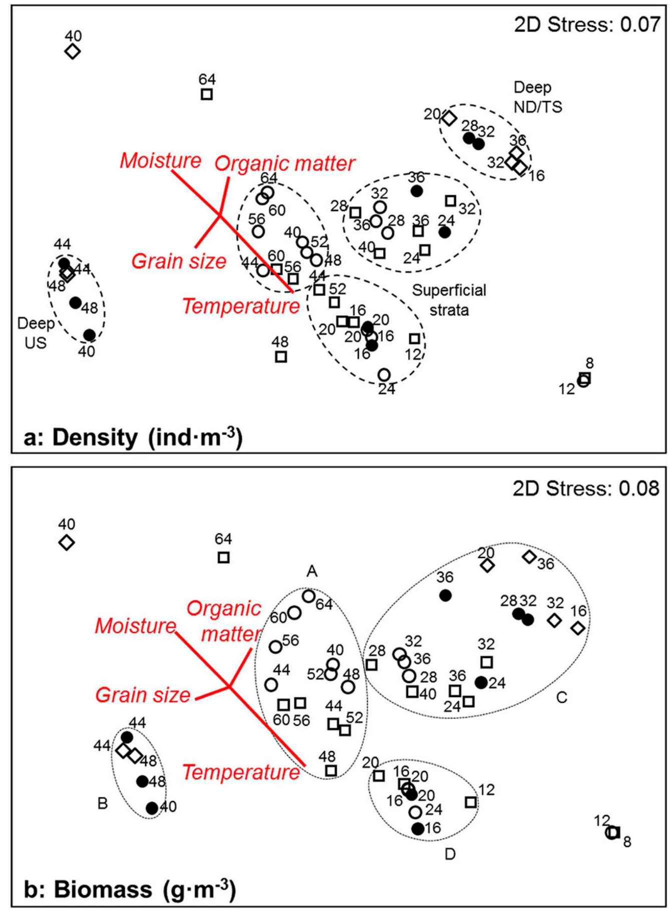

Fig. 4. Non-metric multidimensional scaling of macrofaunal a) density ($ind{\cdot}m^{-3}$) and b) biomass ($g{\cdot}m^{-3}$) at Barra del Chuy beach. Numbers next to markers indicate the distance from dunes (m). Dashed lines enclose groups formed at 45% resemblance level. Vectors of multiple correlations with environmental variables are shown in red. Depth strata (cm) defined as follows:○: S5; □: S10; ●: S15 and ◇: $S > 15$. ND: Near dunes; TZ: Transition zone; US: Upper swash; LS: Lower swash. Groups are: A: swash superficial strata (US, LS); B: deeper US; C: all strata mainly from TZ and US; D: mid-superficial strata of upper beach levels (ND and TZ). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Samples from the deeper strata formed two groups, one clustering samples of ND and TZ (right) and another encircling samples from the US zone (left). Biomass-based ordination showed four main groups: A) superficial strata of the swash zone (US, LS); B) deeper strata from the US; C) all depth strata mainly from TZ and US zones; and D) S5, S10 and S15 strata clustering samples from upper beach levels (ND and TZ). Vectors of multiple correlation superimposed on nMDS plots showed two abiotic axes grouping biological samples (Fig. 4): 1) sand temperature and moisture; and 2) grain size and organic matter content.

Sediment moisture and temperature showed, either isolated or combined, the most consistent correlations with density and biomass (Table 2). The degree of correlation between biotic and environmental variables tended to decrease with depth. Density and biomass were strongly correlated with: 1) sediment moisture in S5; 2) sediment moisture and temperature in S10; 3) temperature and grain size in S15; and 4) temperature in $S > 15$ (Table 2).

Individual body size showed significant vertical trends ($p < 0.001$), both for the whole macrofauna and deconstructed by taxonomic group. Body size for all taxa pooled, Crustacea and Mollusca increased exponentially with depth (Fig. 5a, b and d respectively), whereas Polychaeta decreased with depth and reached the highest body size at S5 (Fig. 5c).

Table 2
Rank correlation coefficients (Rho) as a measure of agreement between environmental and biological matrices for depth strata, based on BIOENV results. $p < 0.01$ in all cases. S5: 0–5 cm, S10: 5–10 cm, S15: 10–15 cm and S > 15: > 15 cm.

	Biological Variables	Environmental variables	Rho
S5	Density	Moisture	0.715
	Biomass	Moisture	0.703
S10	Density	Temperature-Moisture	0.722
	Biomass	Temperature-Moisture	0.674
S15	Density	Temperature-Grain size	0.548
	Biomass	Temperature-Grain Size	0.489
S > 15	Density	Temperature	0.385
	Biomass	Temperature	0.394

3.3. Species-level analyses

All depth strata presented low mean similarity and high mean dissimilarity values both for density (Table 3a) and biomass (Table 3b). In terms of biomass (4.1%) and density (5.8%), S > 15 presented the lowest values of mean similarity, while always exhibiting dissimilarity values > 90% with the remaining strata. By contrast, S10 presented the highest similarity in biomass (36.5%) and density (34.0%), and the lowest mean dissimilarity with S5.

Excirolana armata typified the two superficial strata in density and biomass and also best discriminated between strata, except for S > 15 vs. S15, where the yellow clam *Mesodesma mactroides* best discriminated in biomass and the polychaete *Euzonus furcifera* in density (Table 3). *E. furcifera* also typified the two deepest strata in density (S15 = 44.3%, S > 15 = 83.5%) and biomass (S15 = 52.8%, S > 15 = 69.5%). The contribution of *E. armata* to the similarity and dissimilarity within and between strata was consistent across the entire dune-sea axis, due to its wide across-shore distribution. By contrast, the contributions of *E. furcifera* and *M. mactroides* were restricted to the intertidal zone.

The foregoing results suggest contrasting responses of sandy beach species to environmental factors according to their across-shore and/or vertical location in the sediment. These responses were confirmed by spatial density patterns of selected typifying or discriminating species (Fig. 6). The ovoviviparous sandhopper *Atlantorchestoidea brasiliensis* was mostly concentrated in the supralittoral (ND, TZ), with the highest density located in S10 (Fig. 6a). The deposit-feeder *E. furcifera* restricted its distribution to intermediate beach zones (TZ, US) and mostly occurred in S5 and S10 (Fig. 6b). The ovoviviparous isopod *E. armata* was distributed across the entire dune-sea axis and was particularly concentrated close to the sediment surface (Fig. 6c). The broadcast spawner *M. mactroides* showed a bimodal distribution, with small organisms occurring close to the surface (S5) and large organisms distributed in the deeper strata S15 and S > 15 of upper and lower swash zones (US, LS; Figs. 6d and 7). This segregation by size was statistically confirmed by an ANCOVA using "distance from dunes" as a covariate and "depth strata" as fixed factor ($F_{3,89} = 1053.4$, $p \ll 0.001$), with clams in strata S5 and S10 being significantly smaller than those found in S15 and S > 15 (Tukey HSD test: $p < 0.001$).

4. Discussion

This paper shows novel spatial structuring findings in the environment and the biota on a sandy beach, notably in a vertical dimension that was seldom considered in ecological studies in these ecosystems. Community descriptors showed strong mesoscale (across the beach) and microscale (vertical) distribution patterns in response to an environment that is spatially structured by sharp, small-scale gradients. Species richness and density were highest at the surface layers, whereas biomass was higher in sediments deeper than 15 cm as a consequence of larger individual sizes of bivalves and crustaceans. These vertical patterns were accompanied by a clear increase in species richness, abundance and biomass from the dunes to the swash zone. Main environmental descriptors of biological patterns were sediment moisture and temperature. Spatial patterns varied according to differences in life histories and differential susceptibility of each species to variations in environmental conditions.

Sediment temperature clearly decreased towards the swash zone and at deeper sediments, being highly variable on the surface at near dune levels, and becoming more stable towards the sea and deep into the sediment (Fig. S2). Extreme temperatures higher than 30 °C were only found in the upper stratum (0–5 cm) at mid-to-high beach levels with intense solar radiation, concurrently with low sediment moisture. Otherwise, most of the beach face had temperatures similar to those of

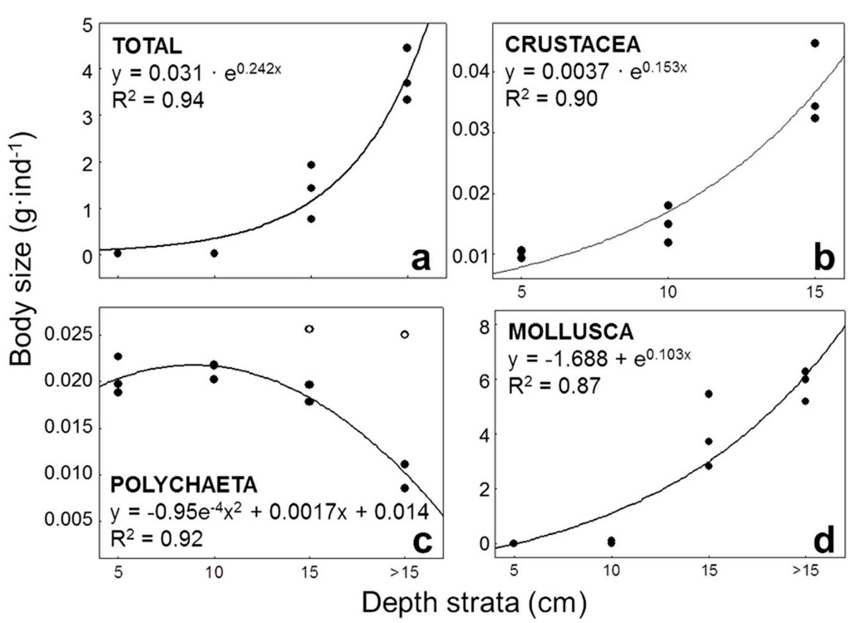

Fig. 5. Vertical variations in body size of total (a) and selected (b–d) macrofaunal taxa at Barra del Chuy beach. Statistical models ($p < 0.001$) relating body size to sediment depth are shown. Open circles indicate outliers that were not considered in the model.

Table 3
Similarity percentages of typifying (> 10%) and discriminating (> 5%) species in the average similarity (within-group) and dissimilarity (between-groups) identified by SIMPER procedure (Bray Curtis Similarity matrices) for vertical macrofauna variations in a) density and b) biomass at Barra del Chuy beach.

a) DENSITY (ind·m^{-3}) **Typifying species**			S5	S10	S15	S > 15
Excirolana armata			63.6	69.6	33.3	
Phoxocephalopsis spp			24.2	18.1		
Euzonus furcifera					44.3	83.5
Mesodesma mactroides					22.4	16.5
Mean similarity			**32.0**	**34.0**	**9.0**	**5.8**
Discriminating species	**S5 vs. S10**	**S5 vs. S15**	**S5 vs. S > 15**	**S10 vs. S15**	**S10 vs. S > 15**	**S15 vs. S > 15**
Excirolana armata	30.9	38.4	38.4	36.4	37.2	19.4
Phoxocephalopsis spp	24.2	19.3	18.9	17.7	17.3	
Euzonus furcifera	18.7	18.3	17.5	21.2	20.0	41.
Mesodesma mactroides		13.3	11.0	11.1	8.9	19.1
Atlantorchestoidea brasiliensis		6.0	6.3	9.1	9.3	
Mean dissimilarity	**65.7**	**88.3**	**95.9**	**87.4**	**95.7**	**92.6**
b) BIOMASS (g·m^{-3})						
Typifying species			**S5**	**S10**	**S15**	**S > 15**
Excirolana armata			72.5	75.6	16.8	
Phoxocephalopsis spp			15.9	13.5		
Euzonus furcifera					52.8	69.5
Mesodesma mactroides					30.4	30.5
Mean similarity			**31.6**	**36.5**	**7.1**	**4.1**
Discriminating species	**S5 vs. S10**	**S5 vs. S15**	**S5 vs. S > 15**	**S10 vs. S15**	**S10 vs. S > 15**	**S15 vs. S > 15**
Excirolana armata	35.8	38.5	41.9	38.2	41.7	14
Phoxocephalopsis spp	17.1	11.8	12.2	12.6	13.5	
Euzonus furcifera	20.7	17.9	16	21.1	19.3	38.2
Mesodesma mactroides	6.6	17.8	14.3	17.0	12.9	41.5
Atlantorchestoidea brasiliensis	10.0	5.4	6.2	8.0	8.8	
Mean dissimilarity	**65.1**	**90.4**	**97.2**	**89.5**	**97.1**	**93.1**

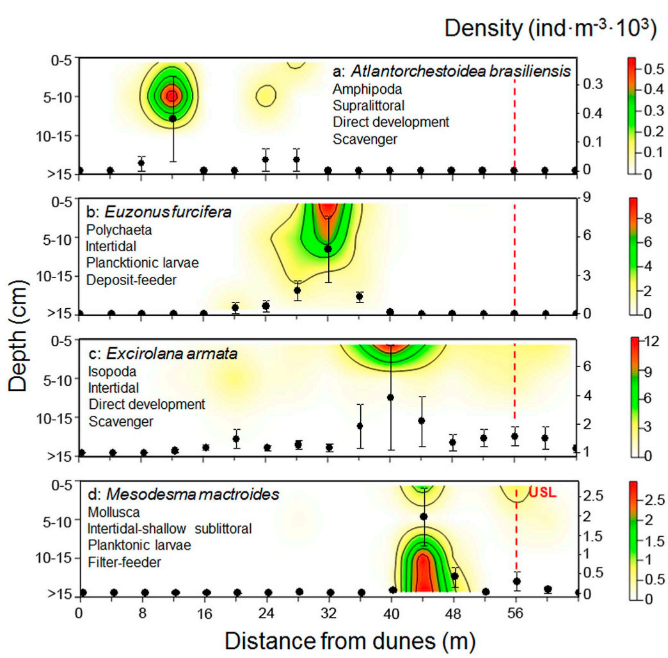

Fig. 6. Density contour maps (mean ± SE) of selected macrofaunal species at Barra del Chuy beach. Information about taxonomy, across-shore position, feeding and development mode, is also provided. USL: upper swash limit at sampling time.

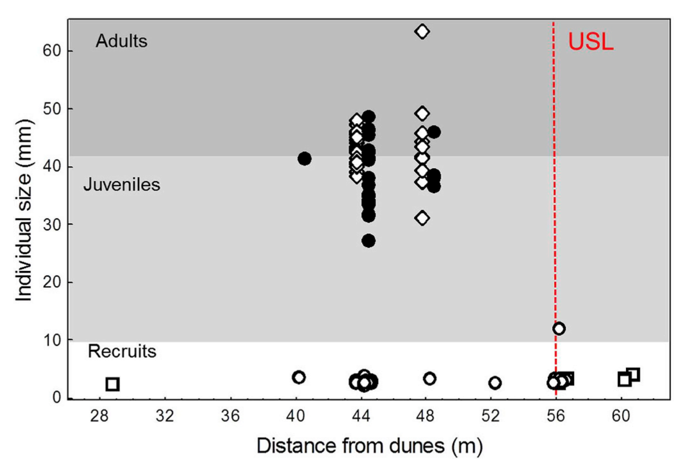

Fig. 7. Spatial variations in individual size of the yellow clam *Mesodesma mactroides* at Barra del Chuy beach. Shadows define population components. Depth strata (cm) as follows: ○: S5; □: S10; ●: S15 and ◇: S > 15. USL: upper swash limit at sampling time. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

the adjacent sea, where sediment moisture also showed the lowest variability, reaching saturation at swash levels. Grain size and organic matter content increased towards the swash zone, concurrently with the highest vertical variability. The linear increase in sediment organic matter content towards the sea reflects a major influence of waves and tides in the resuspension of organic matter (McLachlan and Defeo, 2018), which also coincided with coarser sediments.

Aggregated community descriptors showed strong mesoscale (across the beach) and microscale (vertical) distribution patterns, being highest towards the swash zone and at the upper 10 cm of sediment (with the exception of biomass). A previous work conducted in an estuarine sheltered beach also found that species richness and abundance were highest in the top 5 cm, concurrently with high values of organic matter and a well-developed reduced layer (Rodil et al., 2008). This layer strongly influenced the vertical distribution of the macrofauna on sheltered beaches, an effect that was absent in ocean oxygenated dissipative beaches as Barra del Chuy (Charbonnier et al., 2016; McLachlan and Defeo, 2018). The distinctive spatial structure across the intertidal identified here was related to environmental gradients, and the marked between-species differences in across-shore patterns reveal different physiological tolerances to environmental variability (Brazeiro and Defeo, 1996; Schlacher and Thompson, 2013; Scapini, 2014). This was reflected in clear zonation patterns identified by multivariate analysis, although these arrangements are dynamic because of short-term reactions to environmental conditions, passive transport by the swash and active microhabitat selection (de Alava and Defeo, 1991; McLachlan and Jaramillo, 1995; Brazeiro and Defeo, 1996; Giménez and Yannicelli, 1997; Defeo and Rueda, 2002).

Sediment moisture and temperature showed, isolated or combined, a consistent correlation with biological descriptors. Extreme (or suboptimal) conditions for macrofauna at higher beach levels, including high temperature and low moisture, increase the risk of desiccation (Fanini et al., 2009; Scapini, 2014). These characteristics, together with the limited availability of resources (organic matter), could explain the low values of richness, abundance and biomass near the sand dunes. Towards the swash zone, the environmental stress is gradually attenuated as sand moisture increases and temperature decreases. Escape from desiccation by burial and tidal migrations enable the more mobile macrofauna to move back and forth across the shore to select an optimal microhabitat (McLachlan and Defeo, 2018).

The community was mainly concentrated towards superficial strata and community metrics were correlated with lower temperature, higher moisture and smaller grain size, especially with less variability in moisture and temperature at lower beach levels (i.e., swash zone). The positive relationship between vertical variations in biological descriptors (species richness, density and biomass) and sediment water content reflects the critical importance of the swash in reducing the variability in environmental conditions. Thus, variations in the swash water movement over the sand could be considered as a crucial descriptor that modulates the across-shore (Giménez and Yannicelli, 1997) and vertical macrofaunal distribution. The swash level could then be considered as an “aggregate variable” (sensu Hall, 1983) which carries itself different effects produced by the strong environmental gradients observed across the shore and in the vertical axis. Consequently, the spatially-continuous gradients in the physical environment, co-occurring at different spatial scales on two orthogonal axes (vertical and across-shore), interacted to develop the aggregated macrofaunal distribution patterns observed in the field.

The significant vertical space partitioning found in this work strongly suggests a non-random vertical distribution of the macrofauna. Different species occupied characteristic microhabitats along the gradient of sediment moisture and temperature, together with an increase in body size towards the swash zone and in the deepest strata (see Figs. 5–7). Uruguayan shores are almost devoid of wrack drifted in the supralittoral zone where the talitrid *A. brasiliensis* occupied subsurface strata, and therefore morphological adaptations for active motion independent of swash movements (Giménez and Yannicelli, 1997), burrowing and orientation become critical for survival in this zone with low moisture and higher temperatures (Fanini et al., 2017). Thus, species with different body size typified or discriminated different vertical levels of the sediment. *E. armata* typified in terms of biomass and abundance the upper strata S5 and S10, and was also the species that best discriminated the vertical structure of the sandy beach community. This species has been reported as a high substrate-specific to fine and wet sands, which characterize TZ and US zones where it the species performs intense across-shore migrations that might explain its wide distribution pattern across the beach (de Alava and Defeo, 1991). The yellow clam *M. mactroides* had the largest body size and, together with the polychaete *E. furcifera*, typified the deepest strata in terms of biomass. This species performs intense chemical and physical sediment remobilization and has been recognized as important nutrient recycler on sandy shores (Otegui et al., 2012). The increasing total biomass towards the swash was also mainly driven by *M. mactroides*, whose smaller individuals were found in the upper strata and the larger ones deeper into the sediment. The dissimilar 3-dimensional distribution arrangement of the species may reflect a differential burrowing ability according to individual size (Fiori and Carcedo, 2015), thus facilitating space and resource partitioning at the microscale and reducing the potential extent of biological interactions (Maria et al., 2012). As burrowing depth is positively related with individual size (McLachlan et al., 1995; Dugan et al., 2000; Defeo et al., 2001), the significant vertical segregation by size observed for all taxa combined and by taxonomic group could indicate different microhabitat preferences and burrowing abilities (McLachlan and Jaramillo, 1995; Cardoso and Veloso, 2003; Dugan et al., 2004). A spatial segregation by population component can occur, with small individuals (recruits) displaced by dominant competitors (adults) towards suboptimal microhabitats (from de Alava and Defeo, 1991). It is also essential that the fauna display a high degree of mobility and ability to deal with the swash climate. Indeed, burrowing behavior must be both rapid and powerful on high-energy sandy beaches (such as Barra del Chuy) to avoid organisms being swept away by the swash (McLachlan and Defeo, 2018). Thus, burrowing is a key adaptation to avoid the risk of desiccation (McLachlan et al., 1995; Scapini, 2014; Fiori and Carcedo, 2015) and the extent of inter- and intraspecific interactions (Croker and Hatfield, 1980; Haddon et al., 1987; Maria et al., 2012).

Other variables (e.g., sand salinity, nutritional value of sand organic matter content, redox potential, suction) could provide additional insights on microscale faunal patterns (Rodil et al., 2008; Sassa et al., 2014). For example, recent studies showed the important role of suction (a process caused by differences between porewater and atmospheric pressures in association with groundwater level), in determining the across-shore distribution of amphipods, isopods and bivalves in sandy beaches (Sassa et al., 2011, 2014). This variable is also directly related to moisture and governs sand hardness and compaction (Sassa et al., 2014), and its contribution as an explanatory variable of microscale patterns in macrofaunal communities needs to be assessed.

In summary, this study provides novel insights on vertical variations in the environment and in community and population metrics across the dune-shore axis in a dissipative beach. This spatial dimension of population and community processes and patterns has received little attention in sandy beach ecology, thus overlooking the paradigm of spatial structuring, a critical determinant of how ecosystems function. Scaling up the findings of this research to larger (e.g., along the shore, beaches with contrasting morphodynamics) and longer (e.g., seasonal, annual) scales is a short-term need. Such analysis could provide further insights on disentangling cause-and-effect relationships to better understand processes that underlie the microscale patterns in sandy beaches.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2018.11.008.

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