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Littoral meiofauna community structure in San Julián bay, Santa Cruz province, Argentina

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Abstract. For the first time, standing stocks and community structure have been reported in San Julián Bay, located in the Santa Cruz province, toward the southern tip of South America, within the sub-Antarctic region. The mean density of the meiofauna found was 6724 individuals/10 cm^2, with a high dominance of nematodes (97.69%). Multivariate studies (PERMANOVA) revealed two distinct meiofauna assemblages: one, in an upper littoral salt marsh habitat and other, in a medium to low soft bare sediment. In the middle of the bay —in front of San Julián city— salt marsh habitats had the highest meiofaunal density, while bare sediments (medium-low levels) were the lowest. The mean average in the salt marsh area was 12246 individuals/10 cm^2, with nematodes being dominant followed by oligochaetes as the subdominant taxa. The mean average in bare sediments (medium to low levels) was 3962 individuals/10 cm^2, with nematodes as dominant and turbellarians, mastigophorans and maxillopodos (harpacticoid copepods) as subdominant taxa. Bare sediments related to Patagonian mussel's populations presented the lowest meiofauna densities. Diversity showed an opposite trend, with a maximum in medium-low levels and a minimum in salt-marshes habitat. Richness in number of taxa ranged from 8 to 12, with a total number of 18 taxa. Despite dominance of nematodes in meiofauna assemblages is known, maximum density found in San Julián bay is much higher than previously found for estuaries from north and mid-latitudes littoral sandy beaches and in the nearby region of the Straits of Magellan and Beagle Channel and other sub-Antarctic and Antarctic sites. On the other hand, the number of meiofauna taxa (no nematodes) is low, and its community structure differs from what has been reported in previous studies. The meiofauna taxa assemblages provide evidence that, in salt-marsh habitats, they have the highest densities, but the lowest diversity when compared with lower levels. This is likely due to adaptation problems of meiofauna communities to a semi-terrestrial habitat.

[Keywords: salt marshes, bare-sediments, nematodes, sub-Antarctic, coastal area]

Resumen. Comunidad de meiofauna litoral de la bahía San Julián, provincia de Santa Cruz, Argentina. Este trabajo reporta por primera vez la densidad y la estructura comunitaria de la meiofauna para la Bahía San Julián, Santa Cruz, Argentina. La densidad media fue 6724 individuos/10 cm^2, con dominancia de nematodos (97.69%). Estudios multivariados (PERMANOVA) revelan la existencia de dos asociaciones: una, en el litoral alto (ambiente de marisma) y otra, en los niveles medios y bajos (sedimentos desnudos). Los valores de densidades más altos y más bajos fueron hallados en la zona media de la bahía, frente a la ciudad de San Julián; los mayores, en el litoral superior, y los menores, en el inferior. La densidad media en el área de marismas fue 12246 individuos/10 cm^2, siendo los nematodos dominantes, seguidos por oligoquetos como taxón subdominante. La media de densidad en sedimentos desnudos fue 3962 individuos/10 cm^2, con una dominancia de nematodos, y turbellarios, mastigóforos y maxillópodos (copépodos harpacticoideos) como subdominantes. Los sedimentos desnudos relacionados con poblaciones de moluscos presentaron densidades de meiofauna más bajas. La diversidad presentó un máximo en sedimentos desnudos y un mínimo en marismas. La riqueza de taxones varió entre 8 y 12, con un total de 18 taxones. Aunque la dominancia de nematodos en las asociaciones de meiofauna es conocida, las densidades halladas para San Julián son mayores a las reportadas, tanto para estuarios, para latitudes intermedias o para zonas cercanas como el estrecho de Magallanes, el canal de Beagle y otras zonas sub-antárticas o antárticas. Por otro lado, el número de taxones (no nematodos) es bajo y su estructura comunitaria es diferente a la reportada en trabajos previos. Las asociaciones de meiofauna proporcionan evidencia de que en las marismas tiene lugar la mayor densidad, aunque la más baja diversidad, en comparación con los niveles del litoral medio e inferior. Esto podría deberse a problemas de adaptación de la comunidad de meiofauna al hábitat semiterrestre.

[Palabras clave: marisma, sedimentos desnudos, meiofauna, nematodos, zona sub-antártica]

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Introduction

Tidal flats are on the border between marine and terrestrial biosphere, exposed during the tidal cycle to the atmosphere or the overlaying water, with a resident biota that must be able to cope with both aquatic and semiterrestrial environments twice a day (Heip et al. 2005). These environments can be found in estuaries, bays or on open coasts all over the world. Tidal flats areas have high commercial value for shellfish exploitation, fish and birds nursery or feeding, and for humans as eco-tourism (Heip et al. 2005). The importance of tidal flats increases when they appear related to macrotidal areas. Due to the intertidal extension, a high number of different habitats and microhabitats are created, increasing biodiversity (e.g. Maria et al. 2013). Santa Cruz province presents this kind of tidal flats, they constitute a great extension of bare sediment, with their upper-littoral borderline carpeted with halophytes.

Several authors characterized the Patagonian tidal flats in Santa Cruz province. The first studies in the Ría Deseado locality (47°45′ S - 65°55′ W), from the early sixties to the late seventies, were descriptive of different taxa and/or assemblages: 1) macrofauna (Ringuelet et al. 1962; Ringuelet 1963a; Ringuelet 1963b; Zaixso 1975; Zaixso and Pastor 1977); 2) meiofauna: Mastigophora (Foraminifera) taxonomy and ecology (Boltovskoy 1963, 1970), Maxillopoda (Harpacticoidea) and Kinorhyncha taxonomy (Pallares 1966, 1970) and Nematode taxonomy and ecology (Pastor 1987, 1998), and 3) Cyanobacteria taxonomy and ecology (Halperín 1963, 1967, 1969, 1974).

Salt marshes from Santa Cruz province were less studied than their tidal flats. Halperín (1963), as a pioneer, reported that a typical Cyanobacteria assemblage was hosted by *Sarcocornia perennis* inside the estuary of the Puerto Deseado river. Meanwhile, Kühnemann (1969) described an upper littoral association of halophytes of the genus *Sarcocornia* and *Spartina*. Salt marshes from southern cold areas (from Coyle River to San Sebastián bay, Tierra del Fuego, 53°04′ S - 68°20′ W) were first mentioned as important wetlands by Collantes and Faggi (1999). These salt marshes were described as parallel fringes to the coast, in bays, estuaries and along the main-south Patagonian river openings (i.e. Coyle, Chico, Gallegos), covering most of the upper-littoral level in the form of a carpet and dominated by the halophyte *Sarcocornia perennis* ('jume', as native name) and a grass, *Puccinellia biflora*. *S. perennis*, from these salt marshes, covers 100% of sediment, and *P. biflora* grows between the first one standing out in a laminar plane, covering only 1% (Collantes and Faggi 1999) (Figure 1e). They are completely submersed in water only during spring tides; other tides cover only muddy tidal flats. The main characteristics of these salt marshes (with their vegetation working as an ecosystem engineer) and their medium-low levels seem to be their capacity to stabilize the sediment, providing areas of fish nursery and birds foraging, and playing an essential role in coastal nutrient filtration with a particular channel circulation (Perillo et al. 1996; Bianciotto et al. 2003). The San Julián bay salt marshes fit perfectly with the previous description, differing from Buenos Aires province and north Patagonia salt marshes (Isacch et al. 2006) in two main aspects: littoral extension and the dominance of *S. perennis* and the absence of plants of the genus *Spartina*.

Until the late 2010s, San Julián bay was only studied as part of extensive research all along Patagonia on various unrelated topics: heavy metals and hydrocarbons concentrations in mussels and sediments (Gil et al. 1996), bird colonies (Yorio and Quintana 1996, 1997), and macrofaunal distribution at salt marshes (Bortolus et al. 2009). The following decade was more prolific, with a variety of topics studied in the area: diatoms (Espinosa et al. 2015), nematodes (Pastor et al. 2015), macrobenthic fauna (Zaixso et al. 2017; Martin et al. 2019b), mussels (Sar et al. 2018), salt marshes (Martin et al. 2019a) and different environmental parameters in sediment (heavy metals) and water (hidrocarbons and coliform bacteria) (Pereyra et al. 2020).

The meiofauna is formed by small metazoans, which in the biomass/size benthos spectra are in between macrofauna and microfauna (Schwinghamer 1981). Technically defined, meiofaunal organisms are those that pass through a 0.5 mm mesh, but are retained by a 63 μm mesh (Higgins and Thiel 1988). Several taxa are responsible for the meiofauna community structure: Nematoda, Copepoda, Gastrotricha, Kinorhyncha, Polychaeta, larvae and eggs. In the southwest Atlantic coasts, only three studies have been carried out on the structure, diversity and density of meiofaunal communities in salt marshes and muddy/sandy littoral zones: two in the south (Rosa and Bemvenuti 2005a; Tarragô et al.

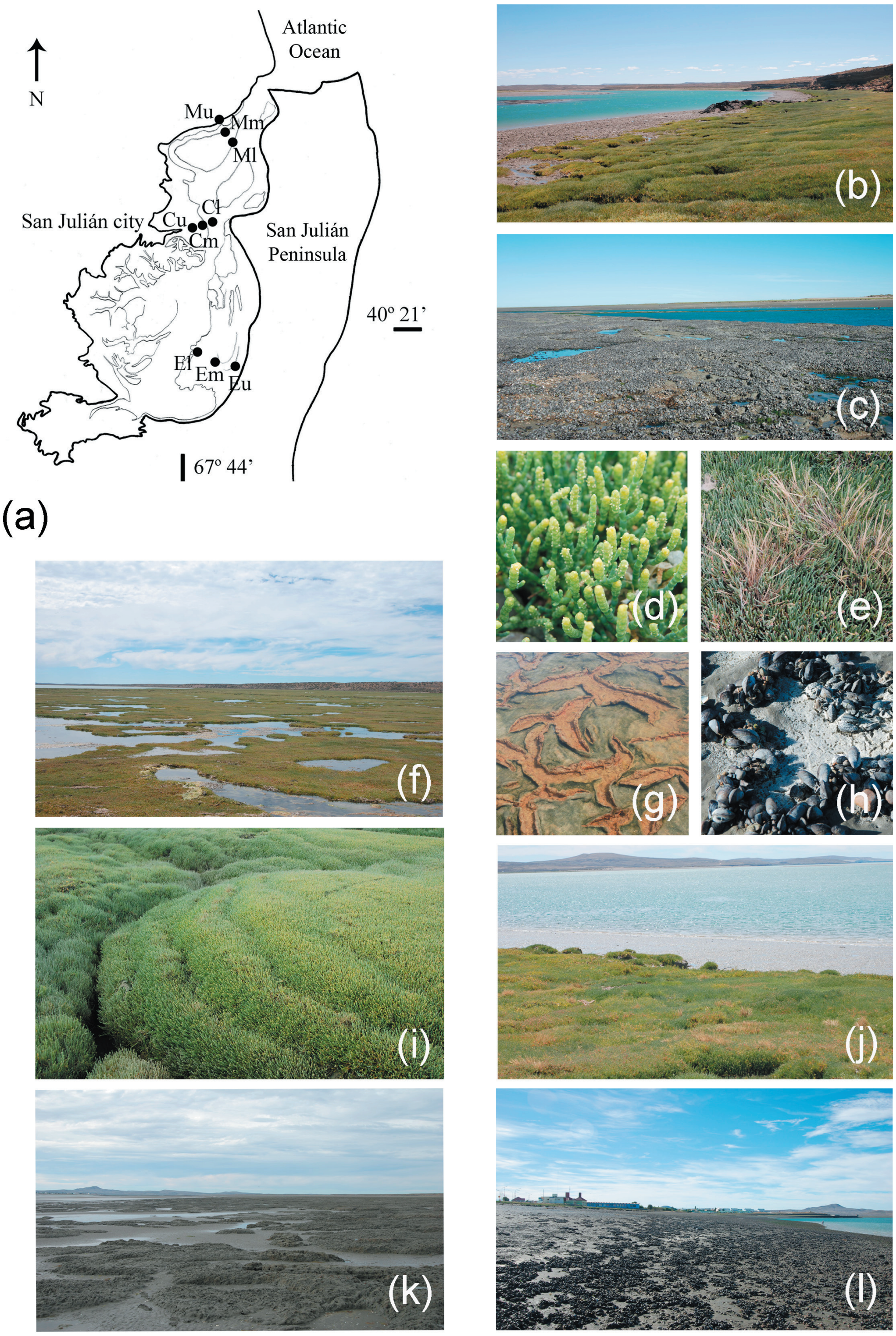

Figure 1. a) San Julián bay, Argentine; b) Upper and middle littoral at La Pingüinera site (Mu, Mm); c) Low littoral at La Pingüinera site (Ml); d) Stems detail of *Sarcocornia perennis*; e) *Puccinellia biflora* plant; f) Upper littoral at El Rincón site (Eu); g) Detail of cyanophytes inside lagoons at El Rincón site (Eu); h) Detail of mussels in sediment at La Rural site (Cl); i) Middle littoral at El Rincón site (Em); j) Upper and middle littoral at La Rural site (Cu, Cm); k) Low littoral at El Rincón site (El); l) La Rural site low littoral (Cl).

Figura 1. a) Bahía de San Julián, Argentina; b) Litoral superior y medio en el sitio La Pingüinera (Mu, Mm); c) Litoral inferior en el sitio La Pingüinera (Ml); d) Detalle de los tallos de *Sarcocornia perennis*; e) Planta de *Puccinellia biflora* ; f) Litoral superior en el sitio El Rincón (Eu); g) Detalle de cianofíceas en las lagunas internas en El Rincón (Eu); h) Detalle de mejillones en el sedimento en el sitio La Rural (Cl); i) Litoral medio en el sitio El Rincón (Em); j) Litoral superior y medio en el sitio La Rural (Cu, Cm); k) Litoral inferior en el sitio El Rincón site (El); l) Litoral inferior en La Rural (Cl).

2017) and north (Netto et al. 1999) of Brazil, and one in Puerto Madryn, Chubut, Argentina (Harguinteguy et al. 2012). There are several studies not focused on the local meiofauna, but on some ecological process that may affect it, and hence provide an accessory description of it. In salt marshes, such studies have been carried out in southern Brazil (32°02′ S - 52°05′ W) (Rosa and Bemvenuti 2005b), in Mar Chiquita (37°44′ S - 57°25′ W), Argentina (Botto and Iribarne 1999; Alvarez et al. 2013; Alvarez et al. 2015), and in Bahía Blanca (38°47′ S - 62°17′ W), Argentina (Escapa et al. 2008).

The meiofauna has been better studied in sublittoral than in littoral communities in subarctic and Antarctic districts. Chen et al. (1999) described meiofauna from muddy bottoms between 8 and 550 m depth around the Strait of Magellan and Chilean fjords; Vanhove et al. (1998), in sediments collected 10 m depth in the South Orkney Islands. de Skowronski and Corbisier (2002) reported meiofauna distribution as a function of food availability at 15 m depth in Martel Inlet, King George Island (Antarctica). Kotwicki et al. (2005) were the first to sample meiofauna from Arctic to Antarctic sandy littoral beaches trying to follow latitudinal patterns, but no data for sub-Antarctic districts were included.

This is the first study focused on total meiofauna taxa performed on the sub-Antarctic littoral of the Santa Cruz coast. The objective of this study is to describe the meiofauna community structure and diversity in relation to tidal levels, from the mouth to the end of San Julián bay. In addition, this study aims to explore the relationships between community structure and diversity with environmental parameters, identify different engineering processes involving the meiofauna community, and compare results with previous studies in sub-Antarctic and Antarctic areas.

Materials and Methods

Study area

San Julián bay is in Santa Cruz province (49°13′ to 49°24′ S - 67°40′ to 67°49′ W) on the Atlantic coast of South America (Figure 1a). It is situated in the high latitude Patagonian desert, characterized by constant winds (>9 m/s), with an annual mean of 25 km/h (Gassó and Stein 2007), dust storms, low irregular rain regimes (<200 mm/year), air temperatures between 2.5 and 15 °C and seawater temperatures between 1.8 and 14.5 °C. The bay is an inlet that runs parallel to the coast and is separated from the sea by a long and narrow peninsula. The bay is 19.9 km long and has two distinct areas within: one, near the entrance to the bay (length/width 6.8/5.3 km); the other, towards the very end (length/width 11.8/8.2 km). They are separated by a narrow passage where the city of Puerto San Julián is located. The peninsula has two very different coasts: the one facing the Atlantic Sea presents extended beaches of pebbles and erosion platforms. The other, facing the bay, has extensive salt marshes followed by muddy tidal flats, mostly occupied by mussel beds (*Mytilus edulis platensis*). The peninsula (with the internal islands) was declared a provincial reserve in 1986 due to its importance as a breeding ground for several marine bird species.

Tidal currents are the most important water movements affecting the area. The tidal regime is semidiurnal, with a maximum amplitude of 9 m. During low spring tides, a large part of the bay is exposed as the water recedes.

For this study, three sites were chosen (Figure 1a). The first site, called La Pingüinera (M), was near the opening of the bay to the sea (Figure 1b,c), with an upper salt marsh and middle-lower levels with high-density mussel bed (*Mytilus edulis platensis*) assemblages. The second site, named La Rural (C), is located in front of the city of San Julián (Figure 1j,l), with upper salt marsh and middle-lower levels with medium-density mussel beds. And the third one is at the end of the bay El Rincón (E) (Figure 1f,i,k), with an upper salt marsh and middle-lower levels with infaunal *Darina solenoides* assemblages.

Sampling techniques and treatment

At each sampling site, three levels of tidal were chosen, upper-littoral (high tide, salt marsh habitat), middle-littoral (mean tide, bare sediment habitat with mussel or *Darina* beds), and low-littoral (low tide, bare sediment habitat, also with mussel or *Darina* beds). At each site and level location, eight replicates were sampled with a PVC syringe (internal diameter 29 mm), separated 5-10 m each: four for meiofauna counts, two for organic matter and two for granulometry analyses. In total, 36 samples for meiofauna, 18 for granulometric analyses and 18 for organic matter were collected. The granulometric analyses samples were oven dried at 85 °C for 24 h and subsequently sieved through a series of sieves (2, 1, 0.5, 0.125, 0.063 mm mesh) and the grain size was determined based on the weight of each size fraction (Giere et al. 1988). They included the mean grain size (MGS) in micrometers and the percentage of silt-clay fraction (%FF). Organic matter (OM) content was determined by oven drying samples at 85 °C for 48 h and then combusting them at 550 °C for 12 h (Giere 1993) and was expressed as g ash dry sediment/100 g sediment. For each sampling site, the following data were gathered: date, geographical position (GPS), depth redox layer (DRL), penetrability (PEN) in centimeters, following Jaramillo and McLachlan (1993), temperature (TEMP) in Celsius degrees, salinity (SAL) in UPS and interstitial concentration of oxygen (O) in mg/L.

The meiofauna was extracted from the samples using the LUDOX TM (colloidal silica polymer) elutriation/decantation method at a specific gravity of 1.15, quantifying only organisms that pass through a 500 μm and are then retained by a 63 μm mesh. The samples were evaporated to anhydrous glycerol and permanent slides were made (Somerfield and Warwick 2013). All organisms were counted, and the value obtained was extrapolated from the syringe area to 10 cm^2. The classification for the systematic position of the meiofauna taxa was by Higgins and Thiel (1988).

Data analysis

As the first step, a PERMDISP test with Monte Carlo permutation was performed. This is an analysis to test the null hypothesis of no differences in the within-group multivariate dispersion among groups (analogous to a univariate test for homogeneity of variances prior to ANOVA). Permutational multivariate analysis of variance (PERMANOVA) (Anderson et al. 2008) with Bray-Curtis similarity was employed to test the significance of the experimental factors (site and levels, as fixed factors) for meiofauna community datasets and to assess the relative proportion of variation that each factor contributed. Hellinger standardization and fourth root transformation were used; the distances were replaced by ranks and Monte Carlo probability values were calculated using 9999 permutations. Finally, the SIMPER routine was applied to determine the contributions of different taxa to treatment differences (Clarke et al. 2014). This routine decomposes the average dissimilarities between all pairs of samples into percentage contributions from each species.

The relationships between the meiofauna assemblage's structure and environmental variables were assessed using the BEST routine in BIO-ENV mode. The routine aims to find the 'best' match between the multivariate among-sample patterns among samples of an assemblage and those of the abiotic data associated with those samples to explain them (Clarke and Gorley 2015). To do this, the test combines k environmental variables at a time to find which variable or combination of variables has the highest correlation possible. Before running the BIO-ENV, a draftsman plot was performed to evaluate the correlations between variables. As MGS has a strong correlation with %FF, it was not included in the BEST routine. Then, only seven environmental variables were included (%FF, PEN, DRL, OM, TEMP, SAL, %O).

The meiofauna abundance data was presented as k-dominance plots, in which taxa were ranked in decreasing order of dominance and percentage cumulative abundance was then plotted against the species rank. The diversity of meiofauna was studied through five indices: species richness (S), Margalef's index (d), Pielou's evenness index (J'), Shannon diversity index (H') and Simpson index (1-Lambda). Analysis of variance (ANOVA) was used to investigate the environmental parameters and the diversity indexes. Four replicates were used for each variable. The Meiofauna diversity index was not transformed. The homogeneity of the variance was assessed by the Cochran test prior to analysis. All multivariate analyses were performed using PRIMER version 6.0 and PERMANOVA+ f/Windows software (Anderson et al. 2008; Clarke et al. 2014).

Results

Multivariate analysis of the meiofauna community

The PERMDISP test showed that the groups have a homogeneous dispersion (nonsignificant differences); thus, the PERMANOVA test could be performed. The main PERMANOVA test with Hellinger distances found significant differences for the meiofauna community at locations (pseudo-F_2=8.16; P=0.0001) and tidal levels (pseudo-F_2=13.09; P=0.0001) and significant interaction (pseudo-F_4=3.87; P=0.0001) (Table 5). Pairwise comparisons (P=0.01) with Bonferroni correction revealed that all sites were significantly different from each other in the assemblages of the meiofauna community, and salt marshes were different from the lower levels (m and l), which did not differ from each other (Table 5).

The taxa primarily responsible for the differences in community structure between salt marsh and bare sediment are shown in Table 1. The averaged percentage contributions for all samples from both habitats are shown there, together with their contributions to the overall differences between habitats. Taxa are listed in descending order of importance, and numbers are bolded to show which habitat supported the higher dominance. Up to 64% of the cumulative contribution is made up of Nematoda (Adenophorea), Platyhelminthes, Oligochaeta, Maxillopoda (Copepoda, Harpacticoidea), Mastigophora and Polychaeta, which are hence responsible for the differences between salt-mashes and bare-sediments.

Environmental variables

The sediments at the three sites (M, C, E) in San Julián bay were heterogeneous and characterized by low median grain size, varying between coarse silt (58 μm) and fine sand (180 μm) with a variable clay-silt content (6.72-63.78%), see Table 2. The lowest median grain size and the highest percentage of silt-clay fraction were found at the upper littoral level of site E. By comparison, the highest median grain size, the lowest percentage of silt-clay fraction and the minimum organic matter were found around the mid to low littoral level from E site; more specifically, the site sampled at the far inner end of the bay.

Relation between the structure of the meiofauna community and environmental parameters

Results of BEST in BIO-ENV mode analysis found that the main variables that explained the differences were the percentage of silt-clay fraction and temperature (r=0.490). They were followed by the percentage of silt-clay fraction, temperature and percentage of oxygen (r=0.474), and the percentage of silt-clay fraction, penetrability, temperature and percentage of oxygen (r=0.436).

Density composition of the meiofauna

A total of 22 higher groups (ranging from seven at stations Mu and Em to 12 at stations Mm and Ml) of meiofauna were found in San Julián bay (Table 3). The Classes/Phyla Nematoda, Oligochaeta, Maxillopoda (Copepoda, Harpacticoidea), Euglenozoa, Platyhelminthes, Polychaeta, Gnathostomulida, Ostracoda and Arachnida (Halacaroidea) were found at the three sites. The overall average density of the meiofauna at all stations was 6724±5153 individuals/10 cm^2 (n=36) and ranged from 1576 individuals/10 cm^2 (site C-low) to 19726 individuals/10 cm^2 (site C-up). Nematoda was the most abundant taxon, and the average density was 6568±5156 individuals/10 cm^2 (n=36) which contributed 97.69% to the total meiofauna. The lowest

Table 1. SIMPER results show taxa which were primarily responsible for the differences between locations in the meiofauna community structure (Av. Abund.=average abundance; Av. Diss.=average dissimilarity; Diss./SD=dissimilarity and standard deviation ratio; Contrib.%=individual contribution of taxa; Cum.%=cumulative contribution of dominant and subdominant meiofauna).

Tabla 1. Resultados del SIMPER que muestran los principales taxones responsables de las diferencias encontradas entre localidades en la estructura comunitaria de la meiofauna (Av. Abund.=abundancia promedio; Av. Diss.=promedio de no similitud; Diss./SD=relación entre la no similitud y la desviación estándar; Contrib.%=contribución de cada taxón; Cum.%=contribución acumulativa de meiofauna dominante y subdominante).

Taxa	Salt marsh Av. Abund.	Sediment Av. Abund.	Av. Diss.	Diss./SD	Contrib.%	Cum.%
Nematoda	**8.93**	6.64	7.56	1.36	**17.39**	**17.39**
Platyhelminthes	0.08	**1.85**	5.64	2.3	**12.99**	**30.38**
Oligochaeta	**2.02**	0.75	5.37	1.41	**12.35**	**42.73**
Maxillopoda	1.28	**1.59**	3.66	1.31	**8.42**	**51.15**
Euglenozoa	**1.13**	0.98	3.28	1.16	**7.54**	**58.7**
Polychaeta	0.1	**0.88**	2.66	1.11	**6.13**	**64.83**
Arachnida	0.91	0.27	2.6	1.21	5.98	70.81
Ostracoda	0.36	0.63	2.45	1.02	5.63	76.45
Ciliophora	0	0.76	2.37	0.71	5.46	81.9
Insecta	0.76	0	2.3	0.95	5.3	87.2
Gnathostomulida	0	0.69	1.97	0.85	4.54	91.74

Table 2. Location of sampling stations and their mean environmental variables. (M=La Pingüinera; C=La Rural; E=El Rincón; u=upper littoral; m=middle littoral; l=low littoral; MGS=medium grain size; %FF=percent silt-clay fraction; PEN=penetrability; DRL=depth redox layer; TEMP=temperature; SAL=salinity; O=oxygen; OM=organic matter).

Tabla 2. Ubicación de las estaciones de muestreo y las medias de las variables ambientales. (M=La Pingüinera; C=La Rural; E=El Rincón; u=litoral superior; m=litoral medio; l=litoral inferior; MGS=tamaño medio de partícula; %FF=porcentaje de fracción fina; PEN=penetrabilidad; DRL=profundidad de la capa redox; TEMP=temperatura; SAL=salinidad; O=oxígeno; OM=materia orgánica).

Site	Lat. S	Long. W	MGS (µm)	%FF	PEN (cm)	DRL (cm)	TEMP (°C)	SAL PPM	O (mg/L)	OM (g)
Mu	49°16.187	67°42.681	70.00	55.56	2.00	0.52	21.00	34.40	7.74	4.02
Mm	49°16.211	67°42.694	80.00	37.39	6.00	0.24	17.30	32.90	4.84	4.60
Ml	49°16.237	67°42.724	120.00	37.08	6.16	0.08	16.60	32.10	4.11	7.65
Cu	49°18.604	67°42.960	60.00	51.98	2.36	0.18	24.30	33.20	6.70	5.95
Cm	49°18.575	67°42.947	90.00	43.38	3.30	0.84	16.90	28.80	8.40	2.48
Cl	49°18.558	67°42.919	140.00	26.55	3.40	0.20	15.50	33.00	8.00	5.00
Eu	49 21.352	67 41.480	60.00	63.78	1.80	21.00	22.90	46.30	2.83	15.95
Em	49°21.276	67°41.704	60.00	13.48	2.30	1.72	20.70	34.90	2.73	1.19
El	49°20.990	67°42.091	180.00	6.72	2.40	3.00	18.10	35.20	3.80	0.70

densities of nematodes occurred at site C-low (1520 individuals/10 cm^2, n=4) and the highest at site C-up (19597 individuals/10 cm^2, n=4). Oligochaeta, Maxillopoda (Copepoda, Harpacticoidea), Mastigophora and Platyhelminthes were subdominant taxa (34; 31; 29 and 25 individuals/10 cm^2 mean densities, respectively, n= 36) and the four taxa together represented only 1.8% of the available meiofauna. The meiofauna taxa between sites and levels were not similar. The highest density of Oligochaeta was at sites M-upper and C-upper (112 and 105.52 individuals/10 cm^2, respectively) and the lowest at levels C-low and E-low, where no individuals were found. The highest density of Maxillopoda (Copepoda, Harpacticoidea) copepods occurred at site M-middle (81 individuals/10 cm^2) and the lowest at site E-middle, where no individuals were found. Mastigophora specimens were more abundant in site E-low (215 individuals/10 cm^2) than in the rest of sites/levels. Platyhelminthes specimens were more abundant at E-low, E-middle and M-middle (73.86, 60.06 and 58 individuals/10 cm^2, respectively). The average density for each level was 12247 individuals/ 10 cm^2 for the upper level (salt marsh), 5198 individuals/10 cm^2 at the middle level and 2728 individuals/10 cm^2 in the low-level bare-sediments (Figure 2).

Diversity of the meiofuna community

ANOVA analysis showed a significantly different taxa diversity (S, d, H', J' and 1-Lambda) between salt-marshes levels and medium-low levels, some of them with interaction (ANOVA, SNK, $p<0.05$) (see Table 4, Figure 3). The diversity increased from the upper to the lower level, with salt marshes exhibiting lower diversity compared to the medium and low levels. The K-dominance curve shows higher biodiversity in bare sediments than in salt marsh (Figure 4). The sediments at site E show higher dominance

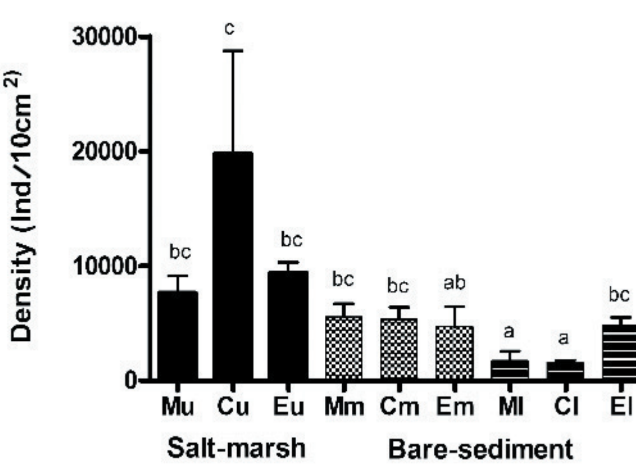

Figure 2. Mean abundance (individuals/ 10 cm^2, averaged across four replicates per site and level) of total meiofauna taxa; M=La Pingüinera; C=La Rural; E=El Rincón;u=Upper littoral; m=Middle littoral; l=Low littoral; black bars=Upper littoral; dotted bars=Middle littoral; striped bars=Low littoral. ANOVA, SNK, $p<0.05$; a,b,c: similar letters mean no differences.

Figura 2. Abundancias medias del total de los taxones de meiofauna (individuos/10 cm^2, promediados entre las cuatro réplicas por sitio y nivel). M=La Pingüinera; C=La Rural; E=El Rincón; u=Litoral superior; m=Litoral medio; l=Litoral inferior; barras negras=Litoral superior; barras punteadas=Litoral medio; barras rayadas=Litoral inferior. ANOVA, SNK, $p<0.05$; a,b,c: letras iguales implican diferencias no significativas.

Table 3. Mean values (individuals/10 cm^2) in three locations (M, C, E) and three levels (u, m, l).
Tabla 3. Valores medios (individuos/10 cm^2) en los tres sitios (M, C, E) y tres niveles (u, m, l).

Site/ Littoral Level (n=4)	Mu	Mm	Ml	Cu	Cm	Cl	Eu	Em	El	Total	%	Mean	SD
Nematoda	7466.48	5307.13	1629.20	19597.27	5184.58	1520.79	9281.81	4618.69	4512.99	59118.95	97.69	6568.77	5156.73
Oligochaeta	112.01	10.15	49.51	105.52	6.90	0.00	19.07	0.41	0.00	303.57	0.50	33.73	42.70
Harpacticoidea	61.28	80.88	43.43	6.09	42.61	24.35	4.46	0.00	19.07	282.18	0.47	31.35	26.17
Sarcomastigophora	0.41	2.03	4.06	4.06	0.00	3.25	25.57	4.46	214.69	258.52	0.43	28.72	66.15
Platyhelminthes	0.00	57.96	14.20	0.41	12.18	8.93	0.00	60.06	73.86	227.60	0.38	25.29	28.08
Ciliophora	0.00	12.78	0.00	0.00	92.13	9.33	0.00	0.00	0.00	114.24	0.19	12.69	28.46
Polychaeta	0.81	45.45	1.62	0.00	0.00	2.03	0.00	5.68	0.00	55.60	0.09	6.18	13.99
Gnathostomulida	0.00	36.36	0.41	0.00	3.65	0.00	0.00	0.00	10.55	50.97	0.08	5.66	11.34
Ostracoda	0.00	1.06	2.03	0.00	1.62	3.65	20.29	2.03	3.65	34.34	0.06	3.82	5.96
Halacaroida	6.90	0.81	0.00	7.71	0.41	2.44	1.22	0.00	0.00	19.48	0.03	2.16	2.85
Insecta	0.00	0.00	0.00	4.87	0.00	0.00	10.55	0.00	0.00	15.42	0.03	1.71	3.47
Gastrotricha	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.96	10.96	0.02	1.22	3.44
Nemertea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.93	8.93	0.01	0.99	2.81
Polychaeta larvae	0.00	0.00	1.62	0.00	0.00	0.00	0.00	0.81	2.03	4.46	0.01	0.50	0.76
Bivalvia larvae	0.41	0.41	1.62	0.00	0.00	1.62	0.00	0.00	0.00	4.06	0.01	0.45	0.65
Kinorhyncha	0.00	2.03	0.00	0.41	0.00	0.00	0.00	0.00	0.00	2.44	0.00	0.27	0.63
Aranae	0.00	0.00	0.00	0.00	0.00	0.00	1.22	0.00	0.00	1.22	0.00	0.14	0.38
Isopoda	0.00	0.00	0.00	0.00	0.00	0.00	1.22	0.00	0.00	1.22	0.00	0.14	0.38
Amphipoda	0.00	0.00	0.81	0.00	0.00	0.00	0.00	0.00	0.00	0.81	0.00	0.09	0.26
Loricifera	0.00	0.00	0.00	0.41	0.00	0.00	0.00	0.00	0.00	0.41	0.00	0.05	0.13
Crab larvae	0.00	0.00	0.41	0.00	0.00	0.00	0.00	0.00	0.00	0.41	0.00	0.05	0.13
Tardigrada	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.41	0.41	0.00	0.05	0.13
Total	7648.30	5557.05	1748.93	19726.74	5344.08	1576.39	9365.41	4692.15	4857.14	60516.19	100.00	6724.02	5153.55

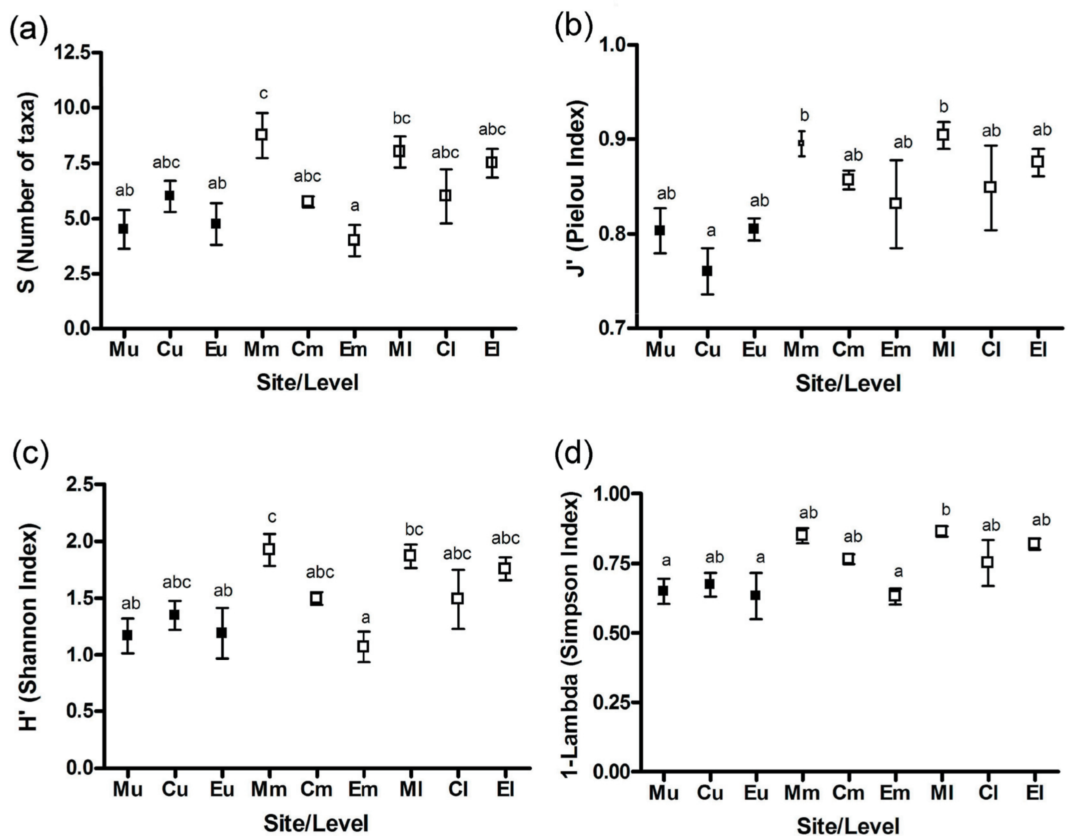

Figure 3. Diversity index from San Julián bay; a) Richness; b) Pielou index; c) Shannon index; d) Simpson index; M=La Pingüinera; C=La Rural; E=El Rincón; u=Upper littoral; m=Middle littoral; l=Low littoral. ANOVA, SNK, p<0.05; a,b,c: similar letters mean no differences.

Figura 3. Índices de diversidad para la bahía de San Julián; a) Riqueza; b) Índice de Pielou; c) Índice de Shannon; d) Índice de Simpson; M=La Pingüinera; C=La Rural; E=El Rincón; u=Litoral superior; m=Litoral medio; l=Litoral inferior. ANOVA, SNK, p<0.05; a,b,c: letras iguales implican diferencias no significativas.

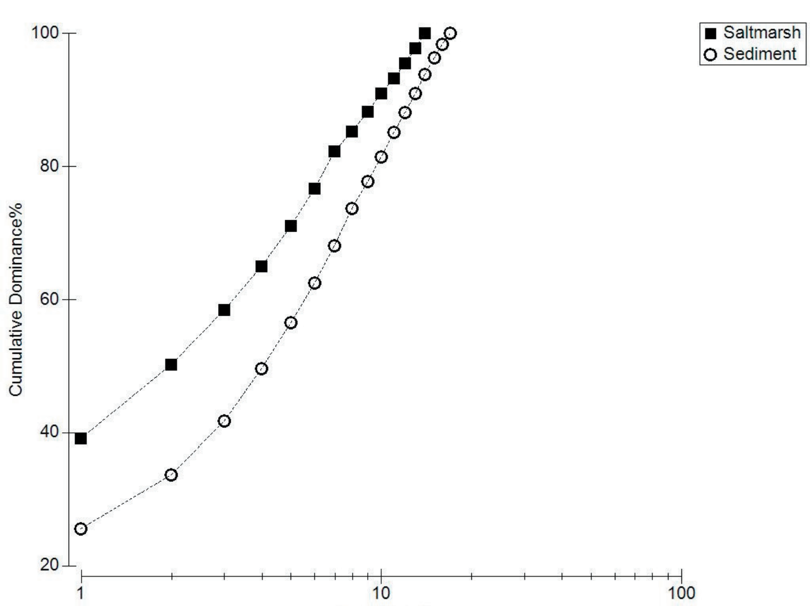

Figure 4. K-dominance curve from San Julián bay.

Figura 4. Curva de K-dominancia para la bahía de San Julián.

Table 4. ANOVA results for meiofauna diversity Index in the San Julián bay, Argentina.

Tabla 4. Resultados del ANOVA para los índices de diversidad de meiofauna en la bahía de San Julián, Argentina.

	Source		
Diversity index	MS	F	P
S-Sites	8.78	3.19	0.06
S-Levels	13.03	4.74	0.02*
S-Sites x Levels	10.61	3.86	0.01*
d-Sites	0.88	3.42	0.05
d-Levels	1.82	7.09	<0.01*
d-Sites x Levels	0.78	3.05	0.03*
j'-Sites	0.01	2.36	0.11
j'-Levels	0.03	9.41	<0.01*
j'-Sites x Levels	1.60E-03	0.60	0.66
H'-Sites	0.31	3.19	0.06
H'-Levels	0.66	6.82	<0.01*
H'-Sites x Levels	0.31	3.16	0.03*
1-Lambda-Sites	0.03	2.97	0.07
1-Lambda-Levels	0.08	8.65	<0.01*
1-Lambda-Sites x Levels	0.02	2.03	0.12

and the lowest was in the upper salt marsh of the C site. The richness in the number of groups ranged from eight to 12, with a total number of 18 taxa. In salt marsh, the average was eight and in bare sediment, 10 taxa.

Discussion

The maximum meiofaunal density (19726 individuals/10 cm^2) in San Julián bay is much higher than previously recorded in the nearby region of the Straits of Magellan and Beagle Channel (Chen et al. 1999), and was later found to be higher than that in other coastal sediments sampled in sub-Antarctic and Antarctic sites following de Skowronski and Corbisier (2002) revision (Supplementary Material-Table S1). Vanhove et al. (2000), on coastal Signy Island (Antarctica), found 0.7-18.8x10^6 individuals/m^2, but using a wider range of meshes (1000-38 μm). The number of meiofauna taxa in this study also greatly differs from those previous papers, presenting a low number of taxa. In similar studies in

Table 5. Results of PERMANOVA analysis test on meiofauna for the effects of levels between locations. df=degrees of freedom; SS=sum of squares; MS=mean square; Pseudo-F=pseudo-F statistic; P (perm)=permutation P-value; Unique perms=number of unique permutations; P(MC)=Monte Carlo P-values.

Tabla 5. Resultados del análisis de PERMANOVA sobre meiofauna para el efecto de los niveles entre localidades. df=grados de libertad; SS=suma de cuadrados; MS=cuadrados medios; Pseudo-F=estadístico pseudo-F; P(perm)=valores de P en base a permutaciones; Unique perms=número de permutaciones únicas; P(MC)=valores de P basados en Monte Carlo.

Main Test	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)	
Source								
Level (Le)	2	8780.1	4390	13.094	0.0001	9943	0.0001	*
Location (Si)	2	5475.2	2737.6	8.1655	0.0001	9933	0.0001	*
Level x Location (Le x Si)	4	5192	1298	3.8715	0.0001	9931	0.0001	*
Residual	27	9052.2	335.27					
Total	35	28499						

Pairwise test	t	P(perm)	Unique perms	P(MC)	
Location					
C, M	2.0379	0.0036	9946	0.0087	*
C, E	2.9462	0.0001	9962	0.0001	*
M, E	3.3224	0.0001	9962	0.0001	*
Level					
u, m	4.2294	0.0001	9946	0.0001	*
u, i	4.691	0.0001	9963	0.0001	*
m, i	1.7793	0.0065	9956	0.0197	
Interaction					
Within level, 'C' of factor 'Si'					
u, m	3.9478	0.0271	35	0.0016	*
u, i	3.645	0.0279	35	0.0013	*
m, i	1.9885	0.0299	35	0.0251	
Within level, 'M' of factor 'Si'					
u, m	2.5384	0.0285	35	0.0061	*
u, i	2.6457	0.029	35	0.0063	*
m, i	2.0949	0.026	35	0.0182	
Within level , E' of factor 'Si'					
u, m	2.3558	0.0273	35	0.0181	
u, i	2.6293	0.0291	35	0.0032	*
m, i	2.06	0.0277	35	0.0257	

estuaries from north latitudes (Bolam et al. 2006; Pascal et al. 2013; Semprucci et al. 2016; Soetaert et al. 1995) and from mid-littoral sandy beaches along a latitude gradient (Kotwicki et al. 2005), the density found was lower than in San Julián bay. The density found in the Lynher estuary (Warwick and Price 1979) was the only comparable with the present study and is even a little higher. Still, we cannot compare the number of taxa because the studies are not entirely equivalent. They count only nematodes, not the whole meiofaunal community.

In our study, nematodes accounted for 97% of the total meiofauna, with its most significant number in salt marshes. This was probably due to *S. perennis* acting as an autogenic ecosystem engineer. This plant, with its root system and woody subsediment stems, adds structure to the sediment (Zaixso 1975; Zaixso and Pastor 1977) (Figure 1 d,e), creating a variety of microenvironments protected from sediment erosion, transport and deposition (Escapa et al. 2008). In the inner part of the bay, such as the location E or El Rincón (Figure 1 f,i,k), as well as in other salt marshes along the coasts of the south Santa Cruz province (Perillo et al. 1996), the strong accretion of sediment around plants is so great that salt marsh areas grow into the sea, modifying the slope of the beach (Figure 1i). This sediment deposition probably also modifies the depth of the water table (Li et al. 2006), increasing temperatures in the surface sediment of the salt marsh as found in San Julián bay. This feature seems to be characteristic of the Santa Cruz province area (Perillo et al. 1996; Adam 1997).

In the long term, the presence of vegetation cover leads to the development of tidal channels, levees, and basins (Temmerman et al. 2005). In the short term, during single inundation events, vegetation has the strongest control on flow routing and the spatial sedimentation pattern (Temmerman et al. 2005). This flow, in turn, brings a profuse arrival of microphytobenthos as cyanobacterial biofilms (Halperín 1963) (Figure 1h) that probably suffers variations in their species diversity with spring and neap tides (Da Rodda and Parodi 2005). This group, along with bacteria and algae, act as an autogenic ecosystem engineer (sensu Jones et al. 1994), offering structure, shelter against flow erosion, desiccation, temperature fluctuation, UV-radiation and predation (Majdi et al. 2023), attractive odours compounds (Höckelmann et al. 2004) and food for meiofauna. At the same time, the meiofauna plays a role as an allogenic engineer indirectly by poking holes in the cohesive matrix and through their excretion and secretions (Majdi et al. 2023). Furthermore, variations in the sequential suspension of Protists (Shimeta and Sisson 1999) and Cyanobacteria biofilms could enhance microbial food-web dynamics on the benthic boundary layer and sediment, with the direct effect of increasing meiofaunal density. For example, in the sub-Antarctic Kerguelen islands, the presence of a dense microphytobenthos as primary production has been stated as the best reason to support a high meiofauna density in intertidal muds (Bouvy 1988). A future study on the microphytobenthos of San Julián bay would be needed to confirm this hypothesis.

The abundances of meiofauna were higher at the salt marshes, descending toward the low littoral level. An important feature to highlight is that the structure of the meiofauna community at taxa level stays nearly constant in the three salt marshes, even with the great physical differences shown between them. This suggests that the presence of *S. perennis* is a very important structure factor of meiofauna. Another feature found in the bay is the low densities of meiofauna community (especially Nematodes) in the lower levels of sites M and C. These areas have, as a distinguishing feature, high densities of mussels (*Mytilus edulis platensis),* which can live directly on sediment attached to pebbles or aggregate to each other (Figure 1c,h,l) in protected bays like San Julián. Considering the suspension of micro- and meiofauna from tidal forces because of mussel disturbance (Garstecki et al. 2002), the decrease in nematode abundance could be produced by at least two different ways: a high level of predation from *Mytilus edulis platensis* filtration (Dittmann 1990) or patchiness because of heterogeneity of habitat (Gingold et al. 2010; Hasemann and Soltwedel 2011). In contrast, the site El Rincón (Figure 1k), with a similar tidal position and without mussels, where only small suspension feeders bivalves (such as *Darina solenoides*) were found, a much higher meiofauna community density was observed.

The importance of crabs as a modulating factor of sediments and meiofauna in salt marsh habitats (Botto and Iribarne 1999) was found to be positive in the inter-tidal areas of Mar Chiquita, but negative in Lagoa Dos Patos, Brazil (Rosa and Bemvenuti 2005a). Even though some small crab species, such as *Halicarcinus planatus*, have been reported for the study area (Huespe, personal communication), no crabs were observed in the study sites. Thus, the high meiofauna densities observed in this study may not be related to the engineering activity of crabs.

The BEST routine selected as main variables the percentage of fine fraction (%FF), temperature (TEMP) and percentage of oxygen (O%). No wonder, the percentage of the fine fraction was one of the main variables structuring the community since the finer sediments are preferred by nematodes (Coull 1985), the observed dominant taxa. The percentage of oxygen can be interpreted as resulting from nematode bioturbation. Nematodes are here acting as ecosystem engineers producing because of their burrowing and feeding activities, physical disturbances to the mineral and organic particles comprising the substrate. As a result, they provide a direct physical enhancement to the oxygen flux and an indirect stimulatory effect on microbial activity (Alkemade et al. 1992; Aller and Aller 1992). As a self-reinforcing process, this increase in aerobic organic matter decomposition first increases bacterial densities and, as a result, increases meiofauna density (positive feedback). This process was recently studied through a laboratory experiment (Bonaglia et al. 2020). The authors demonstrated that increasing meiofauna bioturbation plays an important role in deepening oxygen penetration, counteracting euxinia and structuring microbial diversity. Thus, we prove the neutral interaction between ecosystem engineers (bacteria and meiofauna). This interpretation agrees with the findings of higher meiofauna densities in salt marshes sites M, C and E.

Conclusions

It is known that salt marshes act as ecotone areas or, in other words, as narrow and well-defined transition zones between terrestrial and marine ecosystems. They may intensify or concentrate the flow and processing of materials and organisms between systems and may affect the exchange rates of materials and organisms across community boundaries, thereby concentrating nutrients and increasing organism diversity (Traut 2005). In the assemblages of present study, the meiofauna taxa provide evidence that, in salt marsh habitats, they have the highest densities. However, contrary to Traut's work with spider assemblages (2005), the meiofauna shows the lowest taxa diversity compared with medium-low levels. This shows a decrease in the structural complexity of meiobenthos with the progression from a minimum salinity condition (low-level tide) towards maximum salinity as found in salt marshes (upper-level tide), like that found in European estuarine tidal flats (Heip et al. 2005). These findings agree with previous studies on macrofauna from Santa Cruz province's salt marshes (Bortolus et al. 2009). This is probably also due to adaptation problems of the meiofauna communities to a semi terrestrial habitat and to the distinct characteristics of Santa Cruz province's salt marshes in having only a dominant halophyte plant (*S. perennis*) as a structuring factor and to increasing environmental fluctuations given the land-sea border (Ott and Machan 1971).

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