Vertical distribution of meiofauna on reflective sandy beaches

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Financial Support: To UNIVALI-University of the Itajaí Valley, for providing sampling equipment and assistance. This study was financially and logistically supported by the Itajaí Harbour. This study was also supported by the Brazilian National Council for Technological and Scientific Development (CNPq - Process 158504/2014-3) wich provides PDS fellowships of TCMA and (CNPq - Process 140611/2008-8), which provided the PhD fellowship of MDD, and São Paulo Research Foundation (FAPESP - Process 2012/08581-0) which provide postdoctoral fellowships and grants for MDD.

Abstract

Extreme physical conditions usually limit the meiofauna occurrence and distribution in highly hydrodynamic environments such as reflective beaches. Despite sediment grains of the upper layers being constantly resuspended and deposited, the high energy of the swash zone besides depositing coarse sediments allows an ample vertical distribution of meiofaunal organisms. The effect of physical, chemical and sediment variables on the vertical distribution of meiofaunal organims and nematodes was analysed on two reflective exposed beaches. Sampling was conducted at three sampling points on each beach in the swash zone. The sediment collected was divided into four 10-cm strata (0-10 cm, 10-20 cm, 20-30 cm, 30-40 cm). The statistical differences between strata due to factors previously established (i.e. meiofaunal composition, density of most abundant taxa) were tested using a hierarchical PERMANOVA applied under similarity and euclidian distances. An inverse relation among average grain size, content of organic matter and sediment sorting was evident. Coarser sediment characterized the upper layers, while at deeper layers the sediment was very poorly sorted and presented a higher content of organic matter. A similar pattern in the vertical distribution of meiofaunal and nematofaunal composition and density was detected. The lowest densities were associated with the first stratum (0-10 cm), highly affected by hydrodynamics. The vertical distribution of organisms was statistically different only when the interaction among factors was considered. This result suggests that zonation and vertical distribution of meiofaunal organisms are determined by the within-beach variability.

Descriptors: Reflective beach, Vertical distribution, Spatial distribution, Meiofauna, Nematoda, Sediment.

Resumo

A ocorrência e distribuição da meiofauna em ambientes com alta energia hidrodinâmica, tais como praias refletivas, são normalmente limitadas por extremos físicos. Apesar de as camadas superficiais do sedimento serem afetadas, a alta energia na zona de espraiamento e a presença de areia grossa possibilitam que a meiofauna tenha ampla distribuição vertical. Para testar o padrão de distribuição vertical da meiofauna e de nemátodos em relação às variáveis físicas, químicas e sedimentológicas, duas praias refletivas expostas foram analisadas. As coletas ocorreram na zona de espraiamento em três pontos de cada uma dessas praias. O sedimento coletado foi dividido em quatro estratos de 10 cm (0-10, 10-20, 20-30 e 30-40 cm). A diferença entre os estratos foi analisada com o uso de PERMANOVA com modelo hierarquizado. A análise foi aplicada em matrizes de similaridade e de distância euclidiana, para estudo da composição da meiofauna e densidades específicas de táxons mais abundantes, respectivamente. O padrão granulométrico evidenciado caracterizou-se pela relação inversa entre o tamanho médio do grão e o teor de matéria orgânica aliado ao grau de selecionamento. Sedimentos mais grosseiros foram encontrados nos estratos superficiais e a maior concentração de matéria orgânica e sedimentos menos selecionados localizaram-se nos estratos inferiores. A composição e densidade da meiofauna e da nematofauna apresentaram padrão de distribuição vertical semelhantes, sendo que a camada superficial (0-10 cm), mais afetada pela energia hidrodinâmica, mostrou os mais baixos valores. Diferenças significativas na distribuição vertical dos organismos só foram detectadas quando considerada a menor interação entre os fatores, indicando que a variabilidade entre os pontos dentro de uma mesma praia são responsáveis pela estruturação espacial e vertical dos organismos meiofaunais.

Descritores: Praia reflectiva, Distribuição vertical, Distribuição espacial, Meiofauna, Nematoda, Sedimento.

http://dx.doi.org/10.1590/S1679-87592015095606304

INTRODUCTION

Variations in horizontal and vertical distributions are the major focus for understanding the causes of spatially structured ecological patterns of meiofauna (CHAPMAN et al., 2010; VIEIRA; FONSECA, 2013). On sandy beaches, the distribution is primarily controlled by the physical and chemical extremes of interstitial spaces (MCLACHLAN; BROWN, 2006; SCHLACHER et al., 2008). These extremes may be attributed to the degree of sorting, size and shape of the grains, primary production and local hydrodynamic energy (MCLACHLAN; BROWN, 2006; GRAY; ELLIOT, 2009).

Capillary forces, water retention, low infiltration and oxygenation, dominate the small interstitial spaces in fine and mud sediment habitats (FENCHEL; RIEDL, 1970; VIEIRA; FONSECA, 2013). In these interstitial habitats dominated by chemical extremes, the densities, number of species and species composition change immediately below the sediment surface (MCLACHLAN, 1989; STEYAERT et al., 2003; LEVIN, 2003). This is mainly to be explained in terms of food sources and redox potential (VIEIRA; FONSECA, 2013). Although the vertical distribution of mud and fine sediment is well understood (STEYAERT et al., 2003; JOINT et al., 1982; HEIP et al., 1985; PALMER, 1986), and the variability in the horizontal dimension is known to be as large on the centimeter scale as on that of meters and kilometers (GALLUCI et al., 2009; FONSECA et al., 2010), few tests have been carried out to correlate the vertical and horizontal dimensions (VIEIRA; FONSECA, 2013). This is specially true for exposed reflective beaches, which represent the opposite geomorphologic extreme controlled by physical limits (MCLACHLAN, 1989; DEFEO et al., 2001). The frequent incidence of large waves, with rising and falling tides in the intertidal zone, favors the deposition of coarse and asymmetrical grains (MASSELINK; RUSSEL, 2006; MASSELINK; PULEO, 2006), which creates a system with high sediment permeability and oxygenation. The grain size characteristics and the energy and hydrodynamic conditions result in the formation of a system with extensive interstitial spaces, which in some cases comprise as much as 40% of the total sediment volume (MCLACHLAN; BROWN, 2006). The three-dimensional spaces formed between the grains of sand create an extensive vertical layer that favors an extensive vertical distribution of meiofauna (MCLACHLAN; BROWN, 2006).

On exposed reflective beaches, meiofauna organisms such as Nematoda, Copepoda, Harpacticoida, Tardigrada, Gastrotricha, Annelida and Mystacocarida, exhibit high abundance (MCLACHLAN; BROWN, 2006; GIERE, 2009). These organisms inhabit different sediment layers; however, few studies have attempted to investigate their vertical distribution in reflective sandy beach sediments (PLATT, 1977; SHARMA; WEBSTER, 1983; NICHOLAS; HODDA, 1999; ALBUQUERQUE et al., 2007; MARIA et al., 2012; DI DOMENICO et al., 2014). The sediment oxygen concentration in reflective beaches is assumed to be the environmental variable that directly influences the vertical distribution of meiofauna communities (BRAECKMAN et al., 2011), as it is a non-limiting factor due to the great hydrodynamic force of the waves that break on the beach face (FENCHEL; RIEDL, 1970; RODRIGUEZ et al., 2001). The consequence of this assumption is the non-stratified distribution of meiofauna and Nematoda in reflective beach sediments. However, this assumption is frequently disregarded in studies on the distributions of sandy beach organisms (GHESKIERE et al., 2004; GHESKIERE et al., 2005; GHESKIERE et al., 2006; KOTWICKI et al., 2005). Other abiotic variables, such as grain size, salinity, redox potential, organic matter, temperature, water content, and depth of the water table (REISE; AX, 1979; STEYAERT et al., 1999), as well as biological interactions, may also determine the stratification patterns in reflective beaches.

The goal of this study was to test and correlate the vertical and horizontal distributions of meiofauna and Nematoda in response to the physical, chemical and grain size characteristics of two reflective beaches on the southeast/south Brazilian coast. Their overall geomorphological description was first made 15 years ago (KLEIN; MENEZES, 2001; PETTERMANN et al., 2006; DI DOMENICO et al., 2009) and they were then characterized by their large waves. The following hypotheses were tested: (H1) Nematoda and meiofauna are not stratified and (H2) are randomly distributed in the intertidal zone of reflective beaches.

MATERIAL AND METHODS

Study site

Two beaches - Estaleiro Beach and Estaleirinho Beach - previously characterized as exposed reflective beaches (KLEIN; MENEZES, 2001; PETTERMANN et al., 2006; DI DOMENICO et al., 2009), located on the centre-north coast of the state of Santa Catarina (Figure 1), were examined in June (i.e. late autumn) 2008. Both beaches exhibit a north-south orientation and are composed of sediments that are primarily characterized by coarse and medium sand, steep beach faces and the absence of a surf zone during the greater part of the year. When storm surges occur, these beaches exhibit narrow surf zones formed by sand banks and the beaches' morphodynamic profile becomes temporarily intermediate (KLEIN; MENEZES, 2001).

Sampling

Three points located more than 100 meters apart were sampled in the intertidal zone of each beach during low spring tide. Five replicates were collected at each sampling point for the meiofauna analysis and one replicate was collected for the grain size distribution analysis. The sampling was carried out on the same day.

Samples were collected using a PVC tube of 3.5 cm diameter and 1 m length, which was buried 40 cm into the sediment. The sediment collected was divided into four 10-cm strata, beginning with the most superficial layer (0-10 cm, 10-20 cm, 20-30 cm and 30-40 cm), and fixed in a 4% formaldehyde-saline solution.

Laboratory methods

The meiofauna was separated from the sediment through a floatation technique using colloidal silica LUDOX TM 50 (Sigma Aldrich, St. Louis, USA). The suspended material was separated using a 0.045 mm mesh sieve and stored in 4% formaldehyde. The collected organisms were quantified and identified by preparing permanent slides in accordance with SOMERFIELD and WARWICK (1996).

Samples for the grain size distribution analysis were processed according to SUGUIO (1973), and the grain size parameters were obtained using SIGA (*Sistema Gerenciador de Amostras Sedimentológicas* [Manager System of Sedimentologic Samples]) software. The organic matter concentration was determined using the weight difference after they had been burned in a muffle furnace at 800ºC for eight hours. The $CaCO_3$ concentration was determined by acid dissolution in 10% hydrochloric acid.

Chlorophyll a extraction from the sediment was performed by adding 90% acetone for 12 hours. Chlorophyll a concentrations were calculated according to the equation by LORENZEN (1967), using absorbances at 665 and 750 µm and measured in a spectrophotometer before and after acidification with 2 N HCl.

The sediment permeability was determined using a device developed by CAPUTO (1980). The salinity was measured using a HORIBATM analyzer and the temperature with a thermometer placed in contact with the sand in a hole dug with a shovel. The bathymetric profile was established using a tape measure and a transparent hose as a level. The measurements were performed crosswise to the beach line from the beginning of the sand bank to the intertidal zone.

Data analysis

The spatial variation of the environmental variables was analyzed using principal component analysis (PCA). The PCA was performed for the following variables: calcium carbonate (%), average grain diameter, sorting, skewness and organic matter and chlorophyll a concentrations. The selection of variables assumed non-collinearity and included the measurements of variables at all depths. The data matrix was standardized for the application of the PCA

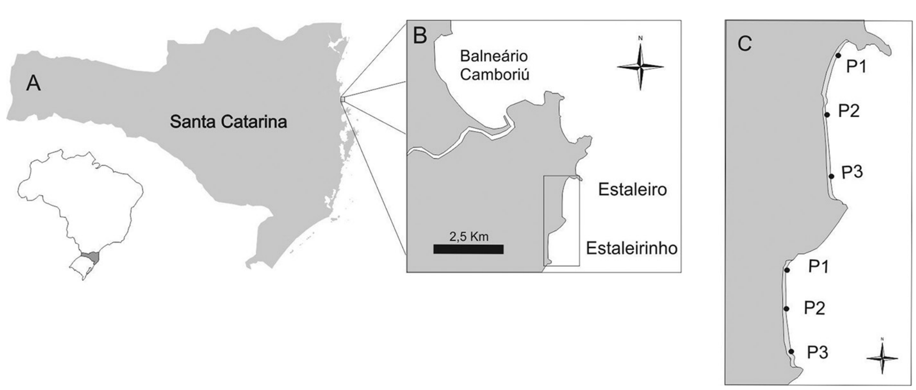

Figure 1. Location map of the studied sites and distribution of the sampling points at Estaleiro Beach and Estaleirinho Beach.

(LEGENDRE; LEGENDRE, 1998). The analysis of the abiotic factors to check for collinearity revealed a correlation between the sand and gravel proportions; therefore, these parameters were excluded from the analysis.

Hypotheses 1 and 2 (H1 and H2), which were tested on the specific abundances and total densities of organisms, were used to calculate the similarity and distance matrices, respectively. The similarities in the compositions of the meiofauna and Nematoda were measured by the Bray-Curtis coefficient and the Euclidean distance of total meiofauna density. A permutational multivariate analysis of variance (PERMANOVA) was performed using the resulting matrices by considering the following factors: strata (four fixed levels including 0-10, 10-20, 20-30, 30-40 cm), beaches (two random levels - Estaleiro Beach and Estaleirinho Beach - nested within the strata), and sampling points (three random levels - 1, 2 and 3 - nested within the beaches).

To identify the associations tested by the PERMANOVA, a proximity analysis (multidimensional scaling, MDS) was performed. The contributions of different taxa to the similarities amongst the strata were evaluated by the average similarity between the tested and significant factors, using a similarity percentage analysis (SIMPER). All statistical multivariate analyses were performed using the PRIMER 6.1.6. software (2008) (CLARKE; WARWICK, 2001).

RESULTS

Beach morphodynamics

Both beaches exhibited a large subaerial volume - 75-50 m wide at Estaleiro Beach and 40-50 m at Estaleirinho Beach - pronounced steepness and reflective beach characteristics. Estaleiro Beach exhibited a larger variation in the morphodynamic profile of the sampling points (Figure 2). The measured temperatures varied between 21 and 22ºC. Higher chlorophyll a concentrations were found in the more superficial strata; the highest concentration (215.29 µg/l) was observed in the 0-10 cm stratum of sampling point 3 on Estaleiro Beach and the lowest concentration (53.90 µg/l) was observed in the 30-40 cm stratum of sampling point 1 on Estaleirinho Beach (Table 1).

The beaches were characterized by a predominance of moderately sorted coarse sand, with modal peaks of grains between 1.0 and 2.0 phi. The grain-size distribution was similar amongst the strata, sampling points and beaches. Sampling point 3 on Estaleiro Beach exhibited higher heterogeneity amongst the strata, with the average grain size varying between 0.34 phi in the 20-30 cm stratum to 1.4 phi in the 0-10 cm stratum.

The principal component analysis (PCA) resulted in the extraction and interpretation of two factorial axes, which explained 61.63% of the total variation. Axis 1 separated Estaleiro Beach, which was positioned on the positive side of the axis, with a higher organic matter concentration and coarser sediments, from Estaleirinho Beach, which was positioned on the negative side of the axis and was characterized by smaller average grain sizes and a lower organic matter concentration. Axis 2 separated the sampling points of Estaleiro Beach from the 0-10 cm and 10-20 cm strata with higher chlorophyll a concentrations. The 20 to 40 cm strata were significant due to a greater quantity of sorted grains on Estaleiro Beach and a higher carbonate concentration on Estaleirinho Beach (Figure 3).

Meiofauna distribution

The meiofauna was composed of 15 taxonomic groups. Nauplius, which in this case belongs to the copepod, was the most abundant followed by adult Copepoda, Nematoda, Gastrotricha, Tardigrada, Platyhelminthes, Ostracoda and Polychaeta. The remaining taxa exhibited a total abundance lower than 5% (Table 2). The highest meiofauna densities were found in the intermediate strata (10-20 and 20-30 cm) and the lowest meiofauna densities were observed in the 0-10 cm stratum. The highest average meiofauna density (620.4 ind.10 cm^{-2}) was observed in the 20-30 cm stratum of sampling point 3 on Estaleirinho Beach. The lowest density (65.8 ind.10 cm^{-2}) was observed in the 0-10 cm stratum of sampling point 3 of Estaleiro Beach (Figure 4). Significant differences were observed at the lowest interaction point amongst the factors (beach (stratum)) (P-MC = 0.001) (Table 3), i.e., the vertical distribution patterns of the meiofauna depended on the sampling points and the beaches.

The multidimensional scaling (MDS) proximity analysis applied to the meiofauna groups showed the separation of the 0-10 cm stratum from the remaining strata (Figure 5). The analysis of the contributions of different species to the similarities amongst strata showed that the nematodes and turbellarians were the most representative in the 0-10 cm stratum by contributing more than 50% of the similarities amongst the samples. Below the 10-20 cm stratum, the copepods and Nauplius yielded the largest contributions to the similarities amongst the samples (Table 4).

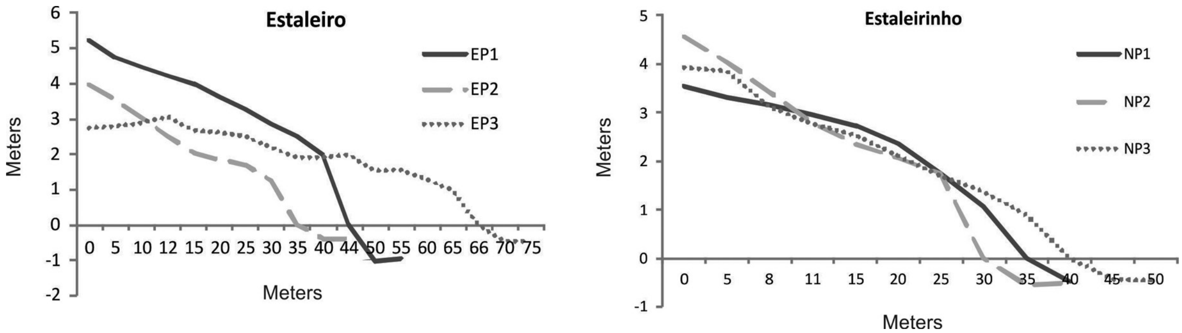

Figure 2. Topographic profiles of Estaleiro Beach and Estaleirinho Beach. The solid lines represent sampling point 1, the dashed lines represent sampling point 2 and the dotted lines represent sampling point 3.

Table 1. Sediment grain size and chlorophyll *a* concentration: (AGS) average grain size (phi), (Sort) sorting, (Skew) skewness (phi), (%$CaCO_3$) carbonate percentage, (%OrgMat) organic matter percentage and (Chl-*a*) chlorophyll *a* concentration.

Point	Depth	ºC	MGS	Sort	Skew	%$CaCO_3$	%OrgMat	Chl-a (µg/l)
Estaleiro - P1	10	20.8	0.8717	0.7107	-0.0560	3.03	0.15	132.336
	20		0.9891	0.6712	-0.0780	2.73	0.12	88.9239
	30		0.8845	0.7212	-0.0713	2.79	0.12	86.4936
	40		0.7651	0.7375	-0.0735	3.69	0.12	79.9762
Estaleiro - P2	10	22	1.1816	0.6414	-0.1871	2.73	0.14	101.296
	20		1.088	0.6593	-0.1015	2.93	0.09	149.237
	30		0.9498	0.7261	-0.0872	3.63	0.11	115.435
	40		0.8074	0.8027	-0.0729	3.42	0.14	84.7262
Estaleiro - P3	10	21.3	1.0208	0.6998	-0.0825	3.52	0.18	215.295
	20		1.4341	0.5808	-0.2718	2.95	0.12	125.046
	30		0.3476	0.9616	-0.0442	3.73	0.18	181.051
	40		1.1935	0.6374	-0.2331	3.36	0.09	111.569
Point	**Depth**	**ºC**	**MGS**	**Sort**	**Skew**	**%$CaCO_3$**	**%OrgMat**	**Chl-a (µg/l)**
Estaleirinho - P1	10	21.7	1.3041	0.6453	-0.1947	4.33	0.1	97.761
	20		1.3051	0.6656	-0.0823	4.43	0.1	85.7204
	30		1.1851	0.651	-0.0027	4.85	0.09	74.7844
	40		0.9623	0.684	0.0668	4.57	0.1	53.9066
Estaleirinho - P2	10	21.7	0.9105	0.8893	0.0201	4.58	0.11	92.6796
	20		1.2904	0.7141	-0.1382	4.72	0	128.47
	30		1.1866	0.7487	-0.0511	4.29	0.1	102.842
	40		1.2487	0.6784	-0.0385	4.97	0.11	76.9937
Estaleirinho - P3	10	21.3	1.2023	0.6846	0.0646	4.46	0.11	152.772
	20		1.2696	0.6484	-0.0049	4.61	0.1	132.668
	30		1.4509	0.6819	-0.1706	5.31	0.1	104.555
	40		1.3807	0.6006	-0.0990	5.03	0.09	128.139

Nematoda distribution

Nematoda belongs to 24 genera, the Epsilonema, Axonolaimus, Microlaimus, Theristus, Enoploides, Daptonema, Bathylaimus, Monoposthia and Sphaerolaimus being the most abundant, with 96% of the total number of organisms counted. The remaining genera exhibited a total abundance lower than 0.1% (Table 5).

The highest average nematode density (104.6 ind. cm^{-2}) was observed in the 20-30 cm stratum of sampling point 3 of Estaleirinho Beach, and the lowest (3.6 ind.cm^{-2}) was observed in the 20-30 cm stratum of sampling point

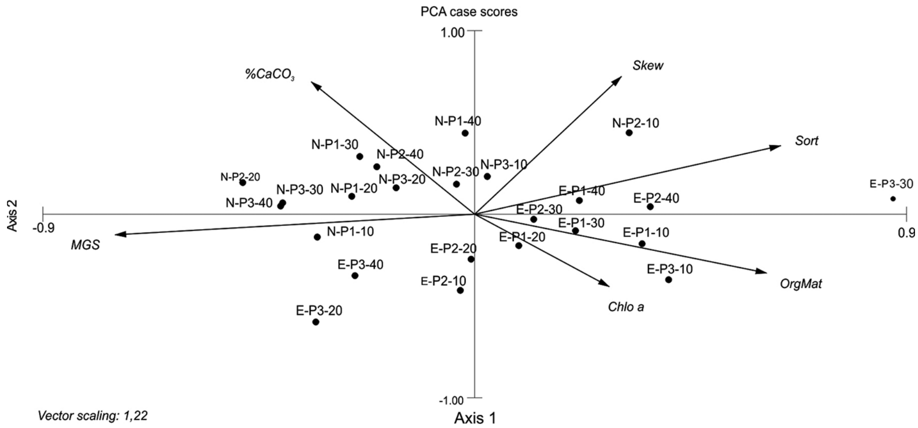

Figure 3. PCA for Estaleiro Beach and Estaleirinho Beach for different depths. The vectors represent skewness (Skew), sorting (Sort), organic matter (OrgMat), chlorophyll *a* (Chl-*a*), average grain size (AGS) and carbonate percentage (%$CaCO_3$). At the points, the first letter represents Estaleiro (E) Beach and Estaleirinho (N) beach, followed by the indication of the sampling points (P1, P2 and P3) and strata (0-10, 0-20, 0-30 and 0-40).

Table 2. Total abundance and frequency of meiofauna taxa.

Taxa	Abundance	(%)
Nauplius	8076	30.63
Copepoda	4443	16.85
Nematoda	3640	13.81
Gastrotricha	3151	11.95
Tardigrada	1642	6.23
Turbellaria	1604	6.08
Ostracoda	1440	5.46
Polychaeta	1129	4.28
Mystacocarida	776	2.94
Halacoroidea	235	0.89
Oligochaeta	163	0.62
Sarcomastigophora	48	0.18
Cnidaria	10	0.04
Bivalvia	9	0.04
Total	26366	100

1 of Estaleiro Beach (Figure 6). Significant differences were observed for the interaction point (beach (stratum)) (P-MC = 0.001) (Table 6), i.e., the vertical distribution patterns for the nematodes depended on the sampling points and beaches.

The proximity analysis (MDS) performed for the Nematoda genera matrix showed a trend towards a grouping of the 0-10 cm strata (Figure 7). The individual contributions of the different genera were similar for each stratum and beach. At Estaleiro Beach, the genus Daptonema contributed to the similarities in the most superficial layer (0-10 cm). The genus Theristus contributed to the similarities in the 30-40 cm stratum. On Estaleirinho Beach, Epsilonema and Microlaimus contributed to the similarities in the strata below 10 cm. The genus Axonolaimus contributed to the similarities in almost all strata of both beaches (Table 7).

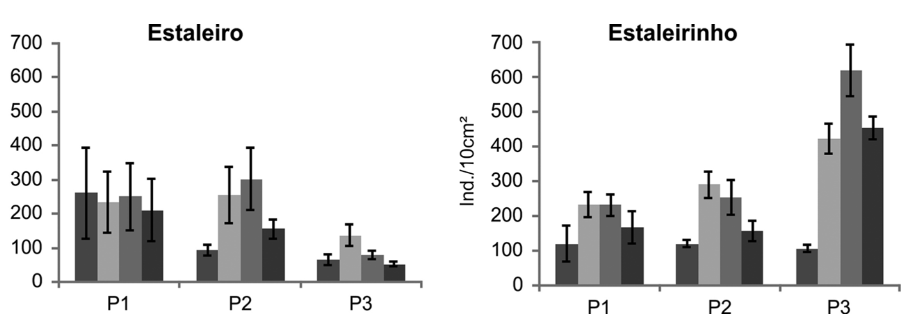

Figure 4. The density of meiofauna (ind./10 cm^2) at Estaleiro Beach and Estaleirinho Beach for different sampling points (P1, P2 and P3) and four sediment strata (0-10, 10-20, 20-30, 30-40 cm).

Table 3. Results of the PERMANOVA applied to the Euclidean distance matrix for the total density of meiofauna.

Source	df	SS	MS	Pseudo-F	P (perm)	perms	P (MC)
Stratum (St)	3	582.37	194.12	1.6875	0.319	105	0.319
Beach (St)	4	460.13	115.03	1.774	0.158	999	0.188
Point (Beach (St))	16	1037.5	64.842	3.8649	0.001	998	0.001
Res	96	1610.6	16.777				

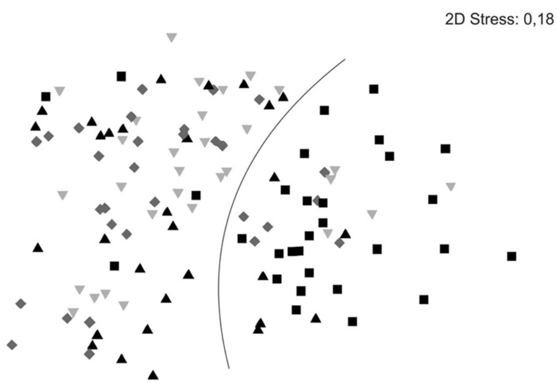

Figure 5. Representation of the similarities using a nonparametric MDS plot. Similarities calculated with the Bray-Curtis coefficient using the abundance values for the meiofauna groups observed at depths from 0 to 40 cm (stress = 0.18). 0-10 cm strata = black squares, 0-20 cm strata = black triangles, 0-30 cm stratum = dark grey diamonds and 0-40 cm stratum = grey triangles. Line separates superficial strata.

DISCUSSION

The spatial variability of the composition and densities of both meiofauna and Nematoda, were higher amongst the sampling points located on the same beach face, than amongst the different vertical strata. Different studies on meiofauna suggest that the meiofauna's variability on the horizontal dimension is large on the centimeter scale when compared to the meter and kilometer scales for mud and fine sediments (GALLUCI et al., 2009; FONSECA et al., 2010; VIEIRA; FONSECA, 2013). The horizontal and vertical distribution patterns were related to the beach profiles at each sampling point, which resulted from different areas of erosion and deposition. The large heterogeneity of the intertidal zones of reflective sandy beaches is primarily due to the formation of turbulent regions, which are caused by the direct impact of waves

Table 4. Contribution to the average similarity (SIMPER). Average density and contribution (%) to the taxa similarity for each depth strata of Estaleiro Beach and Estaleirinho Beach.

Estaleiro				Estaleirinho			
depth	Taxa	Average density	Cont. (%)	Depth	Taxa	Average density	Cont. (%)
	Nematoda	21.87	38.45		Nematoda	29	29.12
10	Turbellarians	17.47	32.42	10	Turbellarians	16.07	22.58
	Nauplius	61.67	8.16		Copepoda	29.4	22.55
	Copepoda	27.33	23.64		Nauplius	68.2	25.13
	Nauplius	78	23.05		Gastrotricha	54.6	19
20	Nematoda	16.13	14.31	20	Nematoda	49.67	17.73
	Ostracoda	25.4	13.6		Copepoda	40.27	15.08
	Nauplius	112.53	32.79		Nauplius	80.27	31.48
	Copepoda	30.13	26.13		Nematoda	63.33	18.54
30	Nematoda	9.6	10.41	30	Gastrotricha	56.13	16.74
	Nauplius	71.2	36.38		Nauplius	49.67	35.4
40	Copepoda	29.6	23.46	40	Nematoda	46.2	15.94
	Turbellarians	8.07	11.75		Gastrotricha	56.4	15.2

Table 5. Total abundance and frequency of nematode genera.

Taxa	Abundance	(%)
Epsilonema	1096	30.53
Axonolaimus	666	18.55
Microlaimus	461	12.84
Theristus	333	9.28
Enoploides	238	6.63
Bathylaimus	236	6.57
Daptonema	233	6.49
Monophostia	136	3.79
Sphaerolaimus	60	1.67
Oncholaimus	27	0.75
Camacolaimus	16	0.45
Viscosia	15	0.42
Eurystomina	14	0.39
Thichotheristus	12	0.33
Rhabdodemania	12	0.33
Terschellingia	11	0.31
Neotonchus	7	0.19
Chromaspirina	6	0.17
Enoplolaimus	5	0.14
Ascolaimus	2	0.06
Paracyatholaimus	1	0.03
Rhynchonema	1	0.03
Desmoscolex	1	0.03
Metachromadora	1	0.03
Total	3590	100

(MASSELINK; RUSSEL, 2006). A higher deposition of coarse grains was evident at the erosion points, and the accumulation of gravel composed primarily of shell fragments resulted in a lower stratification. These characteristics were more pronounced at sites where rip currents are formed, as the force of the water carries the finer sediment particles to those sites (SHORT, 1999; MASSELINK; RUSSEL, 2006). Associated with this physical factor, the patchy distribution characteristic of the meiofauna may be essential for the determination of vertical and horizontal distribution patterns (MCLACHLAN; BROWN, 2006). Similar results were found for the horizontal distribution of interstitial annelids on Estaleiro beach (DI DOMENICO et al., 2009), where differences among transects (i.e. points) on the same beaches are higher than on similar beaches.

In this study, the highest meiofauna densities were observed in the 10 to 30 cm strata. This contrasts with previous reports, according to which the highest meiofauna densities were generally observed in the top 10 cm of sediment (MCLACHLAN, 1978; OLAFSSON; ELMGREN, 1997; DE JESUS-NAVARRETE; HERRERA-GOMEZ, 2002; KAPUSTA et al., 2002; KOTWICKI et al., 2005). High densities at the sediment surface are generally related to the existence of an anoxic layer (chemical gradient) that forms immediately below the top centimeters of sediment in dissipative beaches (KOTWICKI et al., 2005), ultra-dissipative beaches (MARIA et al., 2012) and tidal flats

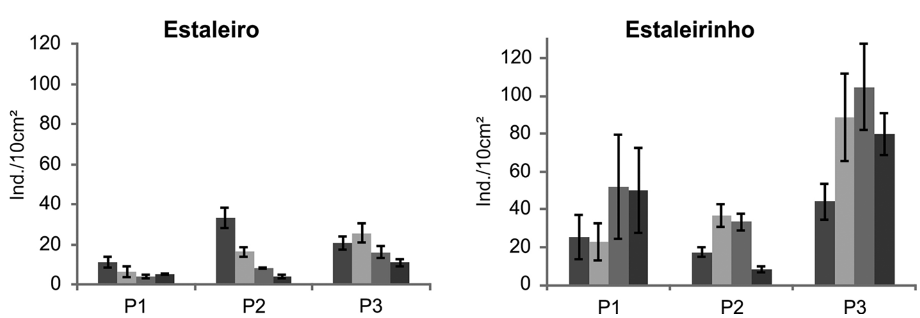

Figure 6. Nematode average density (nº ind./10 cm²) at Estaleiro Beach and Estaleirinho Beach for different sampling points (P1, P2 and P3), and depths from 10 cm to 40 cm.

Table 6. Results of PERMANOVA regarding the Nematoda taxonomic composition.

Source	df	SS	MS	Pseudo-F	P (perm)	perms	P (MC)
Stratum (St)	3	16300	5433.5	0.65686	0.684	105	0.802
Beach (St)	4	33088	8271.9	2.9776	0.003	999	0.002
Point (Beach (St))	16	44449	2778.1	3.5471	0.001	998	0.001
Res	96	75187	783.2				

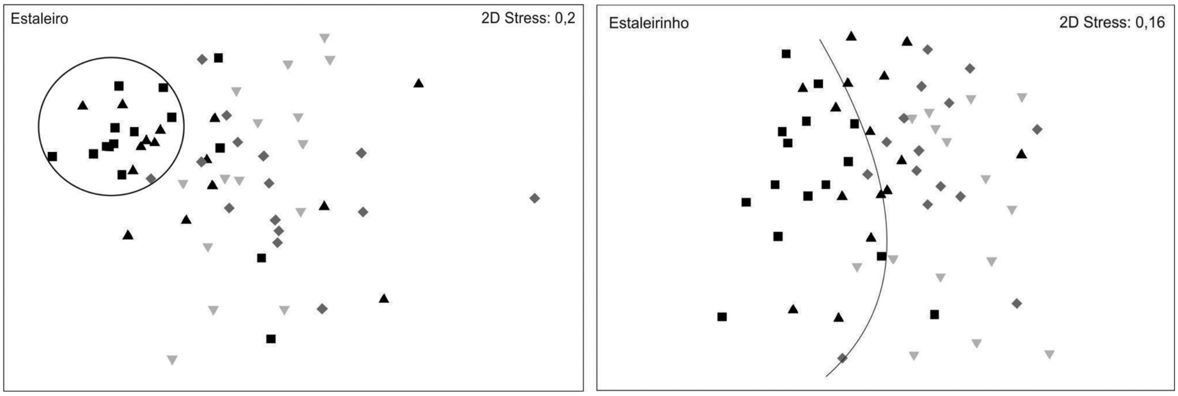

Figure 7. Nonparametric MDS plot. Similarities calculated with the Bray-Curtis coefficient using the nematode abundance values for Estaleiro Beach and Estaleirinho Beach. 0-10 cm strata = black squares, 0-20 cm strata = black triangles, 0-30 cm stratum = dark grey diamonds and 0-40 cm stratum = grey triangles. Circle and line separates superficial strata.

Table 7. Contribution to average similarity (SIMPER). Average abundance (ind./10 cm^2), average similarity, contribution (%) and cumulative contribution (%) of the Nematoda genera for each stratum of Estaleiro Beach and Estaleirinho Beach.

Estaleiro						Estaleirinho					
Depth	*Genus*	Average abundance	Similarity	Cont. (%)	Cum. (%)	Depth	Genus	Average abundance	Similarity	Cont. (%)	Cum. (%)
10	*Daptonema*	8.8	18.2	38.48	38.48	10	*Axonolaimus*	10	19.97	49.06	49.06
	Axonolaimus	5.33	11.88	25.11	63.59		*Theristus*	5.67	6.7	16.47	65.53
	Enoploides	2.47	5.96	12.59	76.19		*Enoploides*	3.2	5.64	13.86	79.39
20	*Axonolaimus*	4.33	10.88	28.24	28.24	20	*Axonolaimus*	10.73	14.03	37.14	37.14
	Enoploides	3.07	7.98	20.72	48.95		*Theristus*	4.33	4.27	11.32	48.46
	Theristus	2.4	7.38	19.14	68.09		*Microlaimus*	14.2	4.27	11.31	59.77
30	*Epsilonema*	2.13	14.87	38.9	38.9		*Monophostia*	3.07	4.25	11.26	71.03
	Theristus	2.27	9.97	26.08	64.99	30	*Epsilonema*	30.07	18.79	46.98	46.98
	Enoploides	1.93	5.92	15.49	80.48		*Axonolaimus*	6.8	8.32	20.81	67.79
40	*Enoploides*	1.53	9.84	24.46	24.46		*Microlaimus*	12.07	3.81	9.52	77.31
	Axonolaimus	1	9.32	23.19	47.65	40	*Epsilonema*	29.87	23.56	67.49	67.49
	Theristus	1.13	9.28	23.09	70.75		*Axonolaimus*	4.73	4.78	13.68	81.16

(VIEIRA; FONSECA, 2013). However, on reflective beaches, such as Estaleiro and Estaleirinho Beaches, the low densities in the 0-10 cm stratum resulted from the re-suspension of the top centimeters of sediment by the wave energy (MCLACHLAN, 1989; MCLACHLAN; BROWN, 2006), which conditioned the meiofauna to live in intermediate strata.

High chlorophyll a concentrations below the top layers of the sediment may somehow support microscopic chains and enable the proliferation of meiofauna and Nematoda in reflective beaches (JESUS et al., 2006). The combination of high values of skewness and average grain size produce larger interstitial spaces, greater water infiltration and penetration of sunlight below the top millimeters of sediment (JESUS et al., 2006).

Nauplius was the most abundant group. The high densities of these organisms are common in intertidal zones of coarse sand reflective beaches (RODRIGUEZ et al., 2001). The high oxygen concentration characteristic of these environments is optimal for these organisms as they are highly sensitive to reductions in interstitial oxygen (GHESKIERE et al., 2005; MCLACHLAN; BROWN, 2006).

Nematoda were responsible for the similarity patterns in the top 10 cm of sediment. Both beaches' concentrations of chlorophyll a and organic matter were slightly higher in the more superficial layers. Copepoda and Nauplius were the organisms most represented at the remaining depths.

Only tiny, well-adapted species such as Epsilonematid and Draconematid nematodes (GHESKIERE et al.,

2006) were expected to inhabit these highly dynamic zones (MCLACHLAN; BROWN, 2006). Amongst the nematodes, the genus Epsilonema was the most abundant as it existed at the deepest layers between 30 and 40 cm. The organisms belonging to this genus were small and can respond opportunistically given their high reproduction rates; thus they can attain high densities when food was available (VANAVERBEKE et al., 2004). The lower mobility of small organisms such as Epsilonema, hinder their efficient return to the surface after they have been washed away due to the high permeability in the zones of reflective beaches (GHESKIERE et al., 2005). Meanwhile, our horizontal distribution showed that the heterogeneity of the substrate of the same beach, as found at point 3 on Estaleiro, might show the ideal condition for Nematoda abundance.

The separate analysis of the vertical distribution of the different genera in the sediment column revealed that they are not homogeneously distributed. Each genus displays a preference for a given depth range. The preference of some species for given depths as suggested by the occurrence of exclusive genera in each stratum determines the vertical distribution patterns of Nematoda, which can occupy different ecological niches (WIESER 1952). In this study, different genera contributed differently to each stratum, which indicated a possible division of ecological niches.

Daptonema, Theristus and Axonolaimus, which are classified as non-selective deposit feeder nematodes, were responsible for the similarity between superficial strata, whereas the genus Enoploides (predators) made the largest contribution to the intermediate strata. The non-selective deposit feeder genera are confined to the superficial layers of the sediment due to the larger availability and variety of food at the surface and the presence of predators and copepod species (STEYAERT et al., 2003; MARIA et al., 2012).

The community distribution and species abundance in reflective sandy beaches is primarily determined by physical factors, such as sediment characteristics and hydrodynamic stress (MCLACHLAN et al., 1993). The low densities found in the superficial layer were a result of the direct impact of waves in the intertidal zone, which resulted in the vertical migration of organisms to escape the physical stress and the drying characteristics of these zones (URBAN-MALINGA et al., 2004). However, the existence of the Nematoda genera indicated a possible partitioning of the habitat, with preferential zones for non-selective deposit feeder species in superficial layers and predator species in deeper strata.

CONCLUSIONS

The meiofauna distribution in reflective beaches is primarily controlled by physical factors. In this scenario, our hypotheses regarding the absence of stratification, and its independence of the horizontal distribution patterns along the intertidal zone in the sediments of reflective beaches were partially rejected. We observed low densities in the top 10 cm of the sediment and that the higher concentration of organisms in intermediate strata (20 and 30 cm) were potentially caused by the migration of the organisms in an attempt to escape the physical stress caused by the wave impact and desiccation characteristic of the intertidal zone. Similarly, the lower density observed below a depth of 30 cm may be attributed to predators. Then the biological interactions assume a secondary role with predator species in deeper strata. However, significant differences in the vertical distribution of organisms were only detected when the lowest interaction between factors was considered, which indicates that the spatial variation on the beaches is a determinant of the vertical distribution of organisms.

ACKNOWLEDGMENTS

We wish to thank UNIVALI/University of the Itajaí Valley, for providing sampling equipment and assistance. This study was financially and logistically supported by the Itajaí Harbor authorities and also by the Brazilian National Council for Technological and Scientific Development (CNPq - Process 140611/2008-8), which provided MDD's PhD fellowship, and the São Paulo Research Foundation (FAPESP - Process 2012/08581-0) which provided MDD's postdoctoral fellowships and grants.

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