

Patterns of Spatial Variation of Meiofauna in Sandy Beaches of Northwestern Mexico with Contrasting Levels of Disturbance

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Received: 15 February 2017 / Published online: 7 August 2017
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Abstract Despite the high abundance and diversity of meiofauna in sandy beach habitats, their patterns of spatial distribution have not been well characterized. This study analyzed the horizontal distribution of the intertidal meiofaunal community in sandy beaches of Todos Santos Bay (TSB), northwestern Mexico, and related it with levels of disturbance. Ten sandy beaches were sampled for meiofauna and sediment along the western coast of TSB at lower, mid, and upper levels of the intertidal. The meiofaunal community included five major groups viz. Amphipoda, Copepoda, Nematoda, Oligochaeta, and Polychaeta, and was mostly dominated by nematodes, regardless of the intertidal level. Meiofauna and nematode abundances differed significantly across the beach slope, increasing towards the upper level; this pattern varied along the shoreline, changing particularly where the beach was heavily modified due to costal development. Multivariate analyses significantly differentiated lower, mid, and upper levels of the intertidal, mostly due to differences in copepod abundance. Sediment grain size significantly differed among intertidal levels (i.e., smaller in the upper intertidal)

and was negatively correlated with meiofaunal abundance. Moreover, meiofaunal abundance was negatively impacted by the degree of disturbance as highly urbanized/disturbed beaches of TSB showed lower meiofaunal abundance. As costal development continues to increase, findings from ecological surveys should play a pivotal role in characterizing and monitoring the health status of sandy beaches to aid in their management and conservation.

Keywords Intertidal meiofauna · Mexico · Sandy beach · Todos Santos Bay · Zonation

Introduction

Sandy beaches are dynamic environments governed by waves, currents, tides, and winds, which in turn contribute to sediment accretion/erosion affecting the distribution of benthic organisms (Brown and McLachlan 2002). Tidal regimes produce cyclical exposures to air, direct sunlight, and temperature, changing sediment moisture and the horizontal/vertical distribution of benthic meio- and macrofauna (Gheskiere et al. 2005a; McLachlan and Brown 2006; Defeo and McLachlan 2013). Within the sediment, oxygen levels (i.e., anoxic conditions) limit vertical migration of meiofaunal organisms during tide fluctuations (Walters 1988; Coull 1999; Steyaert et al. 2001). Moreover, sediment grain size and organic matter are known to be key factors determining the distribution of benthic communities in soft sediments (Rodríguez et al. 2001; Rodríguez 2004; Defeo and McLachlan 2005).

Sandy beaches are amongst the most widely distributed ecosystems in the planet (Dexter 1992; Schlacher et al. 2015). In addition to their ecological roles [e.g., nutrient remineralization, habitat to innumerable invertebrate species, and nesting sites for endangered vertebrates, Schlacher et al.

Electronic supplementary material The online version of this article (doi:10.1007/s41208-017-0038-x) contains supplementary material, which is available to authorized users.

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(2008)], these environments offer important services to society including recreational areas for tourism (Houston 2008), buffer zones for coastal development (Defeo et al. 2009), and a variety of food sources to organisms (McLachlan and Brown 2006). Sandy beach meiofauna is often dominated by nematodes, copepods, polychaetes, and oligochaetes; these organisms play key ecological roles including nutrient recycling and transferring energy and matter into benthic and pelagic food webs (Alkemade et al. 1992; Coull 1999; Schlacher et al. 2008). Owing to their high abundance, diversity, and quick response to anthropogenic disturbance, marine nematodes are often used as bioindicators (Schratzberger et al. 2000; Warwick and Robinson 2000; Austen 2004; Alves et al. 2013; Zeppilli et al. 2015).

In Mexico, the coastal area is comprised of about 11,122 km and sandy beach ecosystems are extremely important to the economy due to their high demand for tourism, leading the Mexican authorities to apply different strategies and actions to promote sustainable touristic activities along the coast (Sectur 2002). Understanding the biological structure and functioning of sandy beaches is therefore fundamental to maintaining their quality and sustainability. Sandy beaches are under many threats (e.g., erosion, coastal occupation, pollution, and heavy/unsustainable tourism) due to human pressures, a scenario likely to worsen with global change (e.g., sea level rise, ocean acidification). As a result, sandy beach communities might be negatively impacted [e.g., reduction of diversity, Brown and McLachlan (2002)]. Owing to their high ecological and socio-economic value and high vulnerability to anthropogenic impacts, the study of sandy beaches including the spatial and temporal variation of living organisms is key to their preservation (Brown and McLachlan 2002; Schlacher et al. 2015; Félix et al. 2016).

This study characterizes the structure of meiofaunal communities in sandy beaches of Todos Santos Bay (TSB), Baja California, Mexico. Specifically, meiofaunal abundance and diversity is evaluated across lower, mid, and upper intertidal of sandy beaches differing in levels of anthropogenic activity. We hypothesize that meiofaunal communities will vary according to the intertidal level and degree of disturbance. Particularly, we expect to find lower meiofaunal diversity and abundance in sandy beaches under high levels of disturbance.

Material and Methods

Study Area

The TSB is located in Ensenada, Baja California, northwestern Mexico (31° 40' – 56' N and 116° 36' – 50' W), around 100 km south of the Mexico-USA border (Fig. 1). Considered a semi-protected bay, TSB has 116 km² of water surface with

50 km of coastline; the northern portion (delimited by Punta San Miguel) is mostly bordered by rocky beaches, whereas the southern coast of the Ensenada harbor (about 40% of TSB) has exclusively sandy beaches (Jiménez-Pérez et al. 1992; Peña-Manjarrez et al. 2005). The city of Ensenada, with about 519,813 habitants, (INEGI 2015) is located northeast of TSB and the Ensenada harbor near site 1 (Fig. 1).

Environmental conditions of TSB are strongly related to the California Current; Peña-Manjarrez et al. (2005) registered the lowest surface temperature in March (14 °C) and the highest in June (21 °C), with a mean temperature of 17.2 °C. Upwelling events are mostly common through spring and summer, bringing cold water into TSB during warmer months (Espinosa-Carreón et al. 2001). Winds predominantly from the northwest quadrant are the main factor controlling surface currents in TSB; wave activity is more frequent during fall and winter seasons (Ladah et al. 2005; Peña-Manjarrez et al. 2005). Salinity at 25 m depth ranged from 33.42 in January to 33.65 in September (Espinosa-Carreón et al. 2001).

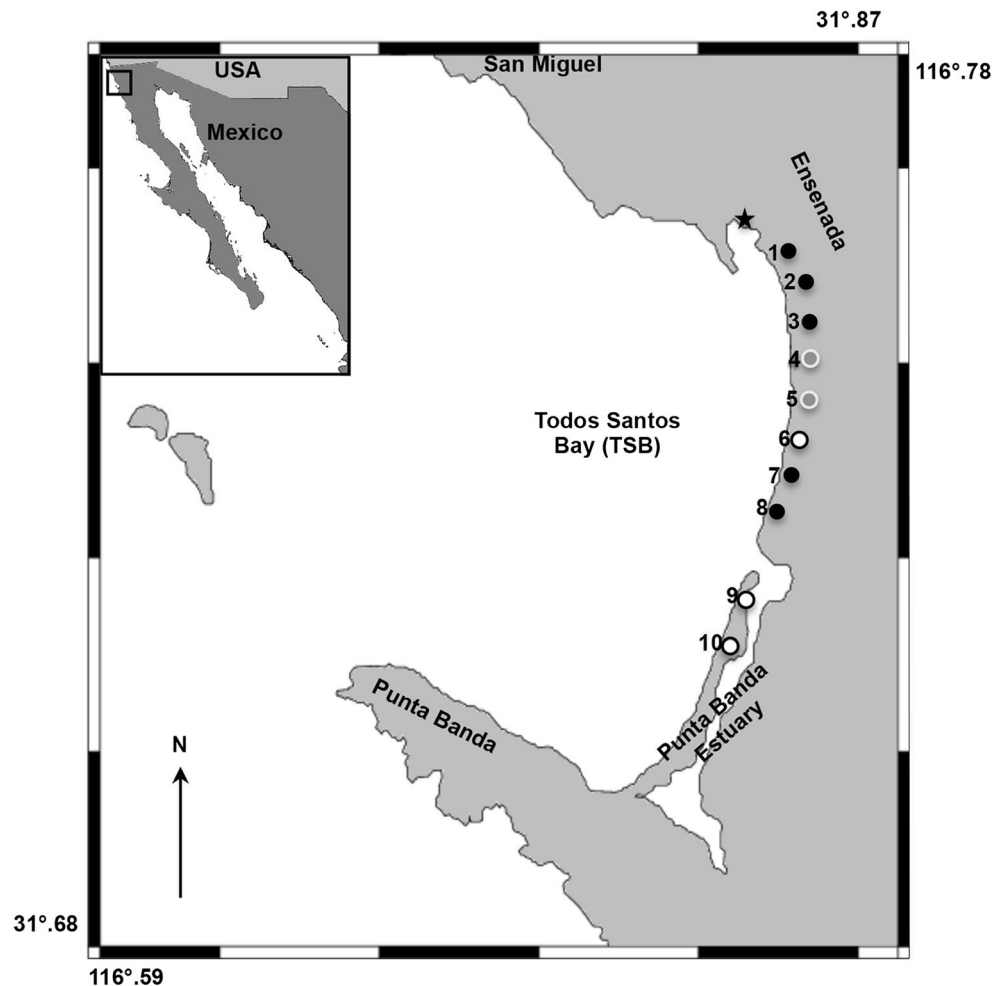
Sampling

Sampling was performed in July 13 and 14 of 2006 during the lowest spring tide. Perpendicular transects to the shoreline were distributed in 10 different sandy beaches of TSB, including disturbed (northern, near to Ensenada city/harbor) and undisturbed (southern region) sites (Fig. 1; Table 1). Parameters including intensity of urbanization/coastal development, sewage discharge, presence of domestic animals and vehicles, and intensity of tourism were considered to group the sandy beaches into three levels of disturbance: none to low, low to medium, and medium to high (Table 1). Sampling across the beach slope included the three intertidal zones of Dahl (1952): lower, near the water line during low tide; mid, about the mid-tide level; upper, the highest level of the tide during high tide; meiofaunal samples (two replicates per zone, 60 in total) were collected using a transparent corer (2.7 cm of diameter and 9.8 cm of long). Additional sediment samples, covering the three intertidal levels, were collected for sediment analyses. In the laboratory, meiofaunal samples were immediately fixed with a heated (70 °C) 4% buffered formaldehyde water solution (Heip et al. 1985).

Meiofauna Extraction and Identification

Meiofaunal samples were washed with filtered (2 µm) tap water over a 1 mm sieve to exclude macrofauna and large debris and then decanted over a 63 µm sieve. Organisms were extracted from the sediment according to Somerfield and Warwick (1996). Briefly, samples were transferred to a 250 ml beaker, saturated with Ludox™ 50 [specific density 1.15, Jonge and Bouwman (1977)] carefully stirred, left undisturbed for 50 min, after which the floating meiofauna was

Fig. 1 Distribution of sampling sites (10 transects/beaches) along the sandy coastline of TSB. Next to numbers are circles to represent sandy beaches under none to low (*white*), low to medium (*gray*), and medium to high (*black*) levels of disturbance, respectively. *Star* indicates the location of Ensenada harbor (for details, see Table 1)



collected on a 63 μm sieve. This process was repeated three times for each sample to maximize the extraction of organisms. Samples were stored in formalin 4% for posterior quantification and identification.

For each meiofaunal sample, the extract was placed into a beaker, made up to a standard volume (47 ml) with filtered (2 μm) tap water and homogenized into suspension before an aliquot (43%) was taken with a semi-automatic pipette for permanent mounts. Organisms were transferred from formalin to glycerol, mounted in glycerin slides (Seinhorst 1959), and identified to major meiofaunal groups under a light microscope (ZEISS Axiostar plus).

Sediment Analyses

Samples were initially dried out at 40 $^{\circ}\text{C}$ for 24 h to reach constant weight. As the sediment was mostly composed by fine sand, approximately 50 g of each sample were used for sieving (Carver 1971) following the classic methods described by Suguio (1973). Finally, sediment characteristics

(i.e., classification, sediment grain size, sorting and sandy percentages) were determined.

Statistical Analyses

Faunistic data were analyzed using univariate and non-parametric multivariate techniques (Clarke and Warwick 1994) to explore patterns of distribution of meiofauna in the sandy beaches of TSB. Meiofaunal structure was analyzed by non-metric multi-dimensional scaling (nMDS) based on a similarity distance matrix using Bray-Curtis index. Analysis of similarity (ANOSIM) was used to test for significant differences among intertidal levels (lower, mid, and upper) and beaches (none to low, low to medium, and medium to high disturbance). The similarity percentages analysis (SIMPER) was applied to determine the contribution of higher meiofaunal taxa towards the discrimination of groups (Clarke 1993). All multivariate analyses were performed using $\log(x + 1)$ transformed data to adjust the contribution of dominant and rare species (Clarke 1993). Univariate descriptors included the number of meiofaunal

Table 1 Sandy beaches sampled along the TSB shoreline. Environmental conditions were established based on the history of each site and observations during sampling

Transect/Beach	Latitude (31°N)	Longitude (116°W)	Levels of disturbance	Distance from harbor (m)	Environmental conditions
1- Arroyo El Gallo	50' 28.1"	36' 45.7"	medium to high	253	Heavy coastal development (housing), sewage, near to the Ensenada harbor.
2- Cueva de los Tigres	49' 58.4"	36' 38.4"	medium to high	1191	Moderate sewage and coastal development (housing).
3- Conalep	49' 36.6"	36' 34.4"	medium to high	1876	Sewage, highly visited for recreational purposes, heavy coastal development, impacted by vehicles.
4- El Naranjo	48' 49.9"	36' 35.2"	low to medium	3314	Low coastal development.
5- El Ciprés Norte	48' 23.1"	36' 43.0"	low to medium	4156	Moderately visited for recreational purposes, low coastal development.
6- El Ciprés Sur	47' 46.8"	36' 48.5"	none to low	5298	Rarely visited for recreational purposes, no coastal development
7- Playa Corona	47' 20.0"	37' 00.6"	medium to high	6182	Recreational zone, upper level of intertidal highly modified for housing purposes (trailer park).
8- Playa El Faro	46' 48.3"	37' 11.2"	medium to high	7201	Highly visited for recreational purposes, impacted by vehicles and animals.
9- Barra Arenosa Norte	45' 51.0"	37' 43.1"	none to low	9168	No human occupation, ecological reserve (close to the mouth of Punta Banda estuary).
10- Barra Arenosa Sur	44' 55.0"	38' 09.0"	none to low	11,023	Low human occupation, exclusive recreational (housing) area

major taxa (richness; S), density (inds. 10 cm^{-2} ; N), Shannon-Wiener diversity index (\log_2 ; H'), and Pielou's evenness index (J'). Multivariate community analyses (ANOSIM and SIMPER) as well as calculations of univariate descriptors were performed using the PRIMER v6 software package (Clarke and Gorley 2006).

Differences in univariate community descriptors among intertidal levels (lower, mid, and upper) and sandy beaches (transects 1 – 10) were tested with a two-way ANOVA in STATISTICA v7.1 (StatSoft 2005). Cochran's C tests were applied to test for homogeneity of variances, and data were $\log(x + 1)$ transformed when needed. Tukey's multiple comparison tests were used when significant differences between factors were detected [$P < 0.05$, Sokal and Rohlf (1995)]. For sediment (i.e., mean grain size), one-way ANOVA was used to test for differences among intertidal levels. A nested ANOVA (i.e., intertidal level nested under beach) was performed to test for significant differences among beaches under different levels of disturbance. A linear regression was also applied plotting meiofaunal and nematode abundances against beach distance from the Ensenada harbor (highly disturbed) to explore for a possible north-south disturbance gradient.

Results

Sediment Characterization

Overall, sediment in TSB was characterized as fine sand, either well sorted or very well sorted along the different levels

of the intertidal level (i.e., lower, mid, and upper) and beaches (i.e., transects 1 – 10). Medium sand, moderately sorted was only found at the lower level of transect 8 (El Faro beach). Sediment grain size ranged from 184.80 μm to 326.92 μm with an average of 227.77 μm . Although, sediment composition along TSB seems to be relatively homogenous (i.e., lacking silt, clay and coarse sand), mean grain size showed a clear gradient with respect to the different intertidal levels, with lower grain size in the upper level increasing towards the lower level (Fig. 2). According to one-way ANOVA, sediment mean grain size at the lower level significantly differed from

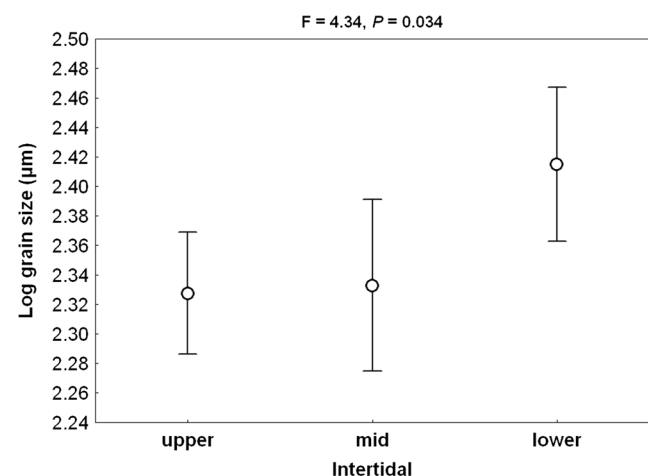


Fig. 2 Results of one-way ANOVA tests and mean values ($\pm 95\%$ confidence intervals) of sediment grain size across the intertidal zone (upper, mid, and lower) in the sandy beaches of TSB

the upper level, whereas mid and upper levels did not differ from one another (Fig. 2).

Meiofaunal Abundance and Diversity in the Sandy Beaches of TSB

The total estimated abundance (i.e., based on the 60 samples) for the meiofauna of TSB was of 76,572 organisms and included five higher taxa viz. Nematoda, Oligochaeta, Copepoda, Amphipoda, and Polychaeta (Table 1 in Online Resource 1). Nematodes were the most abundant group (86.8%), followed by oligochaetes (11.8%) and copepods (1.3%), together accounting for 99.9% of the identified organisms. In general, nematodes dominated the meiofaunal community in all sampled sites of TSB. The only exception was at the upper level of transect 4 (El Naranjo beach) where oligochaetes showed higher abundance (2514 vs. 1785 inds. 10 cm^{-2}). Although nematodes were not assigned to a lower taxonomic level, genera such as *Chaetonema*, *Daptonema*, *Metachromadora*, *Paradontophora*, *Rhynchonema*, and *Xyala* seem to be common in TSB. In particular, *Pselionema* was found in the lower and mid intertidal of all sandy beaches, but not in the upper intertidal (except in transect 7). Overall, diversity descriptors including S , J' , and H' were relatively homogenous across-shore (i.e., among intertidal levels) and along the sandy beaches of TSB. For example, mean values of H' were relatively low ranging from 0.10 to 1.03, whereas S and J' ranged from 2 to 4 and 0.08 to 0.82, respectively (Table 2 in Online Resource 1).

The total meiofaunal (ranging from 415 to 7702 inds. 10 cm^{-2}) and nematode abundances (ranging from 314 to 7601 inds. 10 cm^{-2}) varied similarly along the different sandy beaches of TSB, regardless of tidal level. Copepods, including nauplii, were also frequent in the sandy beaches of TSB, although with relatively lower abundances (i.e., when compared to nematodes and oligochaetes). The highest copepod abundances (> 200 inds. 10 cm^{-2}) were found in the upper level of transect 3 (Conalep beach) and in the mid level of transect 5 (El Ciprés North). Nematodes and oligochaetes occurred in all three levels of the intertidal along TSB, whereas copepods were mostly recovered in the upper and mid levels. Polychaetes and amphipods were less frequent, often found in low abundances (< 20 inds. 10 cm^{-2} , Table 1 in Online Resource 1).

With respect to the levels of beach disturbance, our analyses showed that meiofaunal and nematode abundances were significantly lower in beaches under medium to high anthropogenic impact (i.e., transects 1–3, 7–8), mostly due to the differences found in the upper level of the intertidal (Fig. 3a, b). For nematode abundance, medium to high disturbed beaches significantly differed from those under none to low disturbance, whereas for total meiofaunal

abundance, medium to high disturbed beaches differed from both none to low and low to medium disturbed beaches (Fig. 3a, b). Yet for diversity indexes, no significant differences were detected among beaches under different levels of disturbance.

Spatial Distribution of Meiofauna at TSB

Meiofaunal and nematode abundances showed a clear zonation pattern in the sandy beaches of TSB. Overall, the upper level showed the highest abundance, particularly in transects 4–6 and 9–10 (Fig. 4a, b). The pattern of higher abundances in the upper level was only disrupted in transect 7 (Corona beach), where the mid intertidal showed the highest abundance. The lowest abundance values were usually found in the lower level of the intertidal. Consequently, two-way ANOVA detected significant differences among transects,

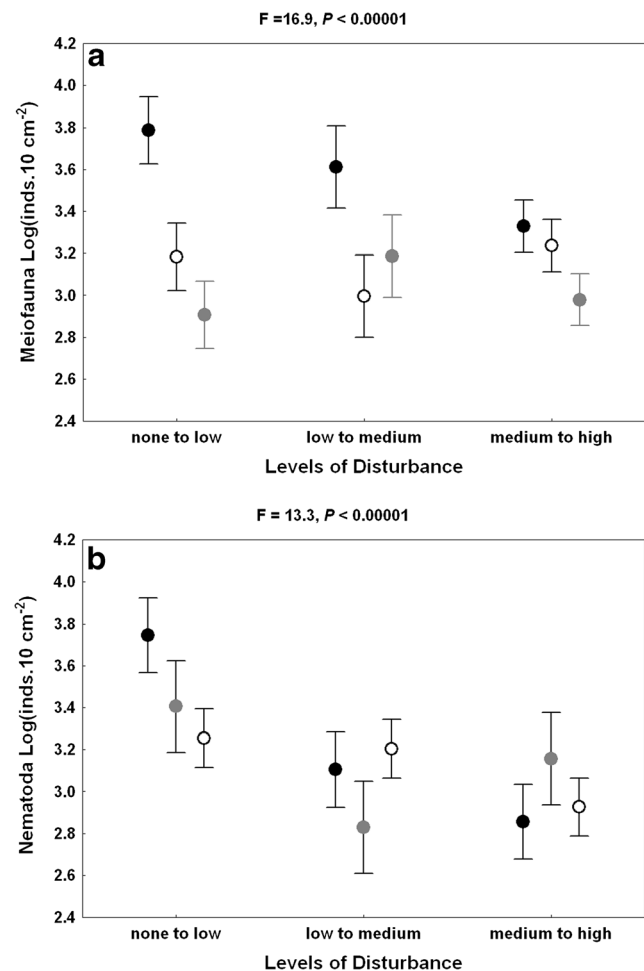


Fig. 3 Results of nested ANOVA tests and mean values ($\pm 95\%$ confidence intervals) of (a) total meiofauna and (b) nematode abundances among beaches under different levels of disturbance. Black, white, and gray circles represent the lower, mid, and upper intertidal levels, respectively

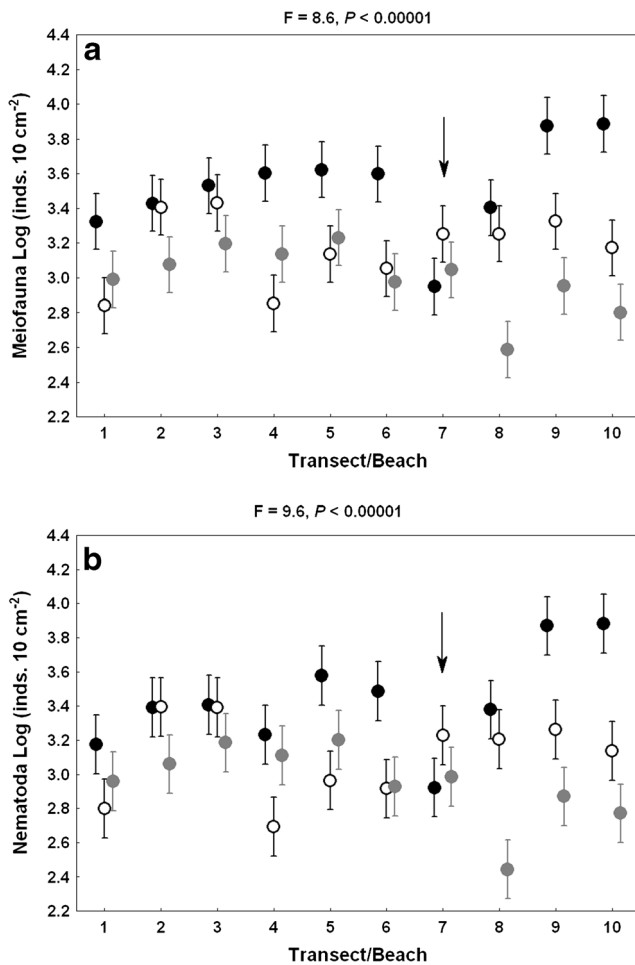


Fig. 4 Results of two-way ANOVA tests and mean values ($\pm 95\%$ confidence intervals) of (a) total meiofauna and (b) nematode abundances among sandy beaches of TSB. *Black*, *white*, and *gray circles* represent the lower, mid, and upper intertidal levels, respectively. Arrow indicates a change on the across-shore pattern

levels, as well as a significant interaction between both factors (Fig. 4a, b).

The nMDS analysis also detected this zonation pattern along the intertidal; samples representing the upper and lower levels were distributed towards the edges of the bi-dimensional plot, whereas mid-level samples appeared in the center, although relatively more widespread (Fig. 5a). ANOSIM analysis corroborated the significance of differences between the three intertidal levels (upper x mid: $R = 0.725$, upper x lower: $R = 0.825$, mid x lower: $R = 0.65$, $P = 0.001$ for all comparisons). According to the SIMPER analysis, copepod abundance (always $>35\%$ in all comparisons) was the main factor for such segregation among the intertidal levels (Table 2). However, when samples are grouped by levels of disturbance, no clear pattern is observed (Fig. 5b); ANOSIM analysis also confirmed the lack of significant differences among beaches (medium to high x low to medium: $R = -0.333$, $P = 1.0$; medium to high

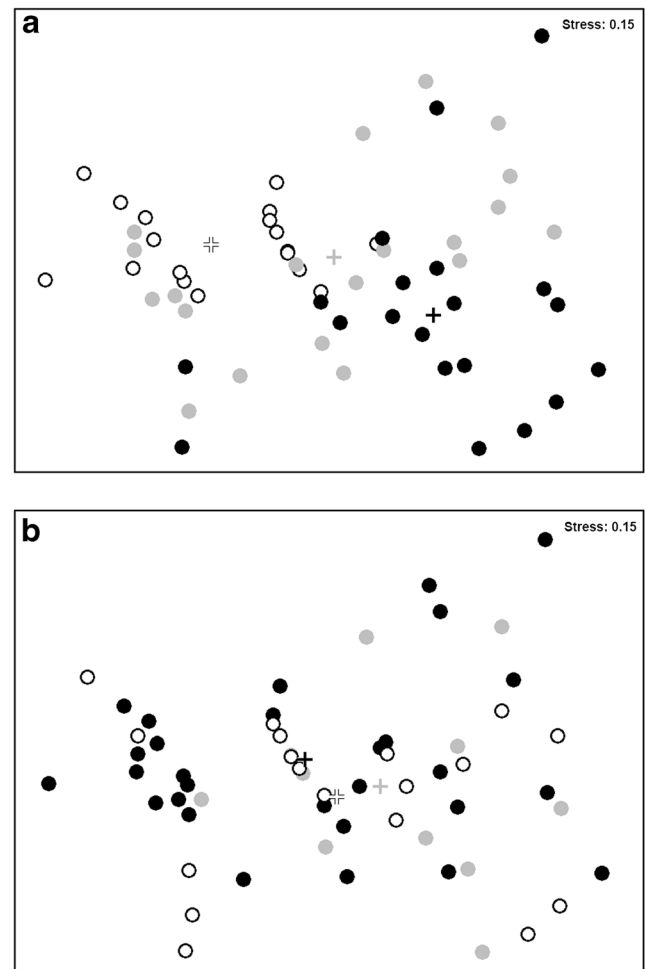


Fig. 5 Non-metric multi-dimensional scaling (nMDS) plot for transformed meiofauna abundance from (a) intertidal levels and (b) beaches under different levels of disturbance. Symbols are as follows: lower/none to low (*white*), mid/low to medium (*light-gray*), and upper/medium to high (*black*). Color-coded crosses indicate the center of dispersal for samples representing the intertidal and disturbance levels

x none to low: $R = 0.556$, $P = 0.2$; low to medium x none to low: $R = -0.296$, $P = 0.3$).

In addition to the zonation pattern exhibited by the meiofauna (i.e., abundance increasing from lower towards the upper intertidal), there is indication of a north-south disturbance gradient with respect to meiofaunal and nematode abundances (Fig. 6a, b). In general, lower abundances were found in the northern sites (e.g., transects 1–3) of TSB, near the Ensenada harbor, whereas higher abundances are found in the southern sites (e.g., transects 4–10, except transects 7 and 8, see discussion). Although this pattern varies across-shore, the disturbance gradient (most of the disturbed/impact sandy beaches are in the northern portion of TSB) seems to be more evident when meiofaunal and nematode abundances at the upper level are compared among the beaches (Fig. 6a, b).

Table 2 Results from the SIMPER analysis. Contributions (i.e., individual and cumulative) of each meiofauna taxon to differentiate the intertidal levels (U: upper, M: mid, L: lower). A dash (–) indicates no contribution

Meiofauna major taxa	Comparisons					
	Levels U x M		Levels U x L		Levels M x L	
	Contrib%	Cum.%	Contrib%	Cum.%	Contrib%	Cum.%
Copepoda	35.24	35.24	38.85	38.85	45.71	45.71
Oligochaeta	24.96	60.2	26.05	64.91	23.21	68.91
Nematoda	16.83	77.03	20.23	85.13	17.23	86.14
Polychaeta	16.46	93.49	14.87	100	–	–
Amphipoda	–	–	–	–	9.14	95.28

Discussion

Sandy Beach Meiofauna of TSB

This study evaluated the structure of meiofauna in 10 different sandy beaches of TSB, Baja California, Mexico. With respect

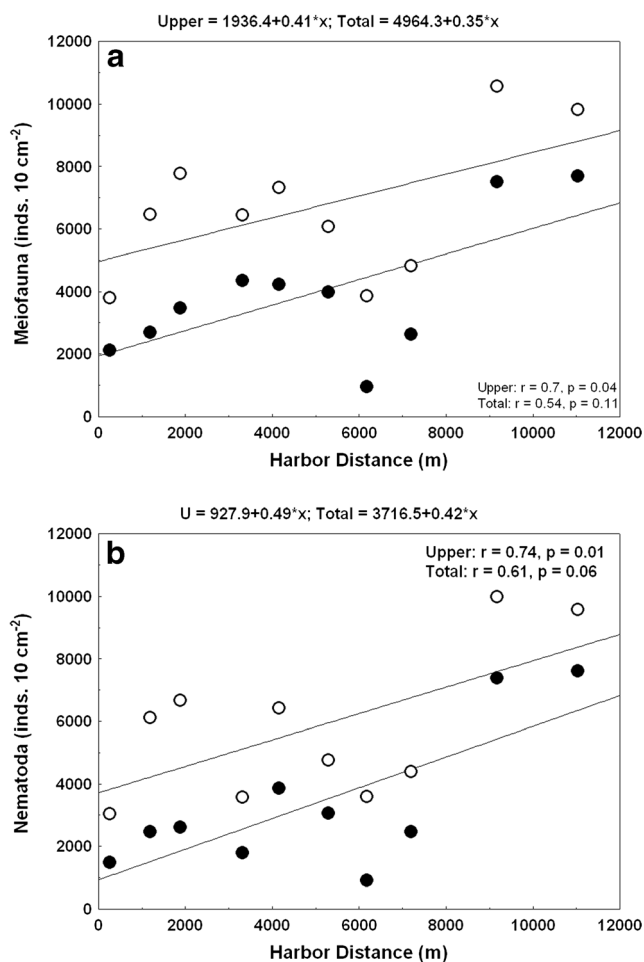


Fig. 6 North-south disturbance gradient for (a) meiofauna and (b) nematode abundances in relation to the distance from the Ensenada Harbor. Upper intertidal level and integrated abundances (i.e., across all three levels) are represented by black and white circles, respectively

to benthic communities, the majority of studies so far conducted in the area have focused on sublittoral sites of TSB [e.g., polychaetes (Rodríguez-Villanueva et al. 2003; Díaz-Castañeda and Harris 2004; Díaz-Castañeda et al. 2014), dinoflagellate cysts (Peña-Manjarrez et al. 2005), mollusks (Kuk-Dzul and Díaz-Castañeda 2016)]. Hitherto, no information was available about the intertidal meiofauna in the sandy beaches of TSB. Nevertheless, the values of abundance reported herein for meiofauna and the two most abundant groups (i.e., Nematoda and Oligochaeta) are comparable to those from sandy beaches in tropical, subtropical, and temperate areas (Rodríguez et al. 2001; Rodríguez 2004; Kotwicki et al. 2005; Gingold et al. 2010; Maria et al. 2013). Hooge (1999), studying the sandy beach (medium/coarse sand) of Big Lagoon, northern California, also reported nematodes and oligochaetes as the most abundant groups; yet for meiofaunal diversity, Hooge (1999) found eight major taxonomic groups, which is expected for coarser sandy beaches (Rodríguez et al. 2001; Rodríguez et al. 2003; Kotwicki et al. 2014).

Nematodes are generally the most abundant meiofaunal group in sandy beach habitats (Gheskiere et al. 2005b; Harriague et al. 2013; Kotwicki et al. 2014; Félix et al. 2016). In the sandy beaches of TSB it was no different. As nematodes represented 87% of total meiofaunal abundance, variations in their abundance greatly impacted total meiofauna abundance, notwithstanding the intertidal level or transect (Fig. 4a, b). Oligochaetes are also commonly found in sandy beaches, particularly in areas (e.g., wrack zone) where decomposition of organic material is high (Giere and Pfannkuche 1982). Félix et al. (2016) assessed the landscape visual quality of sandy beaches using natural/anthropogenic elements (e.g., presence or absence of buildings, armoring, vegetation) and related it with meiofaunal community. Accordingly, the authors noted that Oligochaeta abundance was higher in sandy beaches with lower visual landscape index (i.e., highly impacted/urbanized beaches). For TSB, oligochaetes were more abundant in the northern/more impacted sandy beaches (transects 1–4). Moreover, the high abundance of oligochaetes at the upper level of transect 4 (El Naranjo beach,

low to medium disturbance) might be related to a local input of organic matter (e.g., sand dune vegetation).

The low abundance of harpacticoid copepods at TSB is somewhat intriguing; copepods are often the second most abundant group especially in coarse well-oxygenated sediments, characteristic of reflective beaches (Coull 1999; Kotwicki et al. 2005; Moreno et al. 2006). However, sediment in the sandy beaches of TSB is mostly fine sand (i.e. less oxygen), which can reduce copepod abundances (McLachlan 1980; Rodríguez 2004; Levin et al. 2009). Human-induced hypoxia due to inputs of organic matter from sewage and agricultural and industrial activities are known to reduce diversity of sediments, particularly in well-populated areas [i.e., cultural eutrophication; Levin et al. (2009)]. Anthropogenic effects are likely to have a greater impact on copepods compared to other meiofaunal groups (Raffaelli and Mason 1981; Levin et al. 2009). However, no relationship between disturbance and copepod abundance was observed in this study. Although copepods are mostly distributed in the upper centimeters of the sediment (Joint et al. 1982; Kotwicki et al. 2005), our sample depth (about 10 cm) might also explain the overall low copepod abundance in TSB; copepods are known to vertically migrate to avoid turbulence and different species might display different vertical profiles. In fact, sampling of meiofauna at different depths has recovered different copepod abundances (Fricke et al. 1981; Joint et al. 1982; Hooge 1999).

Meiofaunal Zonation in TSB

Spatial distribution of meio- and macrofauna in sandy beaches is usually explained by zonation as a result of specific across-shore environment gradients [reviewed in Defeo and McLachlan (2005); Maria et al. (2016)]. Based on physical zones and distribution of macrofaunal organisms (e.g., crustaceans) the intertidal of sandy beaches might include: low, mid, and high intertidal zones (Dahl 1952); dry, retention, resurgence, and swash zones (Salvat 1964). While zonation patterns have been well established for macrofauna, with abundance and diversity often increasing towards the low intertidal, patterns of distribution for meiofauna are considerably more variable.

Gheskiere et al. (2004), evaluated the horizontal distribution of meiofauna in De Panne (a macrotidal, ultra-dissipative sandy beach), Belgium, and reported the highest abundance for meiofauna and nematodes near the water line, agreeing with the well-known macrofauna pattern. However, the highest nematode diversity was found in the mid tide level; the authors suggested that the mid-zone of the intertidal might be more suitable for harboring a higher diversity as it presents the optimal physical and chemical conditions across the beach slope (i.e., equilibrium hypothesis). Moreno et al. (2006) reported similar results for a micro-tidal sandy beach in the NW

of the Mediterranean Sea; in this case both the highest abundance and diversity were found in the low tide level [swash zone *sensu* Salvat (1964)].

Meiofauna and nematode abundances clearly showed a zonation pattern in TSB, with abundances increasing from the lower towards the upper level. Such pattern was constant throughout TSB, except in transect 7 due to heavy disturbance. Although conditions in the upper intertidal tend to be less favorable (e.g., higher temperatures, longer exposure periods) to organisms living in the sediment, differences on beach exposure, beach slope, sediment grain size, and geographic region, can influence the zonation pattern. Ansari et al. (1984) compared sheltered and exposed beaches and showed that the highest abundance for meiofauna were found in the upper and mid level, respectively, suggesting that wave action plays a key role in structuring the meiofauna of sandy beaches. Conversely, Hourston et al. (2005) showed that in sheltered sandy beaches with small tide range, zonation patterns could be fairly weak. In addition, Hourston et al. (2005) related the high nematode abundance and diversity with the stability of sheltered beaches, allowing colonization by nematodes and growth of primary food sources.

For temperate regions, Nicholas and Hodda (1999) also reported the highest nematode abundance in the mid and upper levels of Dolphin beach, Australia, suggesting that passive dispersal (i.e., nematodes are passively transported with the flow of sand and water) might explain the zonation patterns in high-energy sandy beaches with medium grain size. For reflective sandy beaches with steeper beach slope of southern Chile, Rodríguez et al. (2001) found the highest abundance of meiofauna in the mid and upper levels, whereas in dissipative sandy beaches meiofaunal abundance showed lower across-shore variation. Particularly, the authors found that nematode abundance was negatively correlated with grain size, thus being more abundant in the dissipative spectrum.

The aforementioned studies summarize the difficulty in determining patterns of distribution for meiofauna in sandy beaches. Although studies suggest that optimal conditions for meiofauna/nematodes occur in the mid-intertidal level (i.e., equilibrium hypothesis), a general zonation pattern cannot yet be established. The highest abundances for meiofauna in TSB were found in the upper level, which is still part of the retention (i.e., influenced by tidal oscillations) zone *sensu* Salvat (1964). Moreover, effects from temperature and desiccation are less pronounced in temperate zones. It is possible that the zonation pattern found in TSB might change as more across-shore sites are sampled. Recommendations for sampling sandy beaches similar to those of TSB include a higher number of sites and replicates (Schlacher et al. 2008). In addition, temporal variation must be accounted for when establishing patterns of distribution, as conditions might differ drastically among seasons (Hourston et al. 2005).

Meiofauna as an Indicator of Beach Disturbance

For TSB, Jiménez-Pérez et al. (1992) evaluated the effects of sewage on the macrofauna near the Ensenada harbor. Accordingly, the authors reported lower levels of macrofauna abundance and diversity for sites near the El Gallo stream (transect 1 in this study) related to sewage discharge. Similarly, this study showed that transect 1 displayed some of the lowest values of meiofaunal and nematode abundance, regardless of intertidal level.

Meiofaunal abundance also varied accordingly to beaches levels of disturbance as lower abundances were usually found in disturbed sites. Five of the 10 sandy beaches were characterized as highly disturbed beaches (transects 1 – 3, 7 and 8; Table 1). Transects 1 – 3, near the Ensenada harbor, are highly impacted by coastal development including the removal of sand dunes, sewage, human activity (e.g., presence of vehicles, domestic animals, debris), and the effects of the harbor *per se*. According to Muñoz-Barbosa et al. (2012), metal concentrations in the sediment close to the Ensenada harbor can potentially be toxic to biota. Also, these beaches are relatively close to Ensenada city, thus under stronger pressure due to human activities, especially during the summer. Moving away from the harbor area (north-south direction), sandy beaches (transects 4 – 10) displayed increasing meiofaunal abundance, except in transects 7 and 8. Coincidentally, Jiménez-Pérez et al. (1992) reported a healthier macrofauna community for sites south of the Ensenada harbor area, from Conalep beach towards El Ciprés beach (transects 3 – 5 of this study).

The coastline of Corona beach (transect 7) has been drastically modified due to coastal development (i.e., removal of sandy dunes, armoring, and urbanization; Table 1, Fig. 1 in [Online Resource](#)), reducing beach width. Thus, it is possible that the intertidal levels sampled in transect 7 do not correspond to the same levels in the other beaches. Human interventions are known to affect the benthic infauna of sandy beaches including the structure of meiofauna (Gheskiere et al. 2005b; Félix et al. 2016), macrofauna (Moffett et al. 1998; Lercari and Defeo 2003), and larger motile organisms [e.g., crabs, Schlacher and Lucrezi (2010)]. In the case of Faro beach (transect 8), which is highly visited by tourists during the summer (sampling period), the reduced abundance of meiofauna can be associated to the effects of trampling by humans and vehicles (Moffett et al. 1998; Davenport and Davenport 2006; Walker and Schlacher 2011).

The highest values of meiofaunal and nematode abundance were found in the extreme south of TSB (i.e., upper level of transects 9 and 10). In addition to the low levels of disturbance, these sandy beaches are located near to the Punta Banda estuary (PBE) mouth. It is possible that meiofaunal/nematode communities in this region of TSB benefit from a local input of nutrients. Tide amplitude in TSB ranges from 2 to 4 m (mesotidal) during spring tides, facilitating the transport

of sediment/organic matter from the PBE to the adjacent sandy beaches (Peynador and Méndez-Sánchez 2010). Also, current patterns of TSB, predominantly north-south and with eddies in the interior system (Mateos et al. 2009), might displace particles predominantly to the south of the PBE mouth.

Conclusions

This study is the first in characterizing the spatial distribution of meiofauna in the sandy beaches of TSB, thus creating a baseline that can be used in environmental monitoring programs. Specifically, this study showed that disturbance affected meiofaunal abundance, and to some extent altered the zonation pattern commonly observed in the sandy beaches of TSB. Future studies focused on the meiofauna of TSB might consider increasing the number of samples and taxonomic resolution of dominant taxa (i.e., nematodes), so that ecological patterns can better understood. These findings should be used as basis for management policies aiming to preserve/improve the quality and health of the sandy beaches in TSB, which are highly appreciated by both local residents and tourists (Peynador and Méndez-Sánchez 2010).

Acknowledgements The authors thank Mare Britannicum for funding this work through Lorax Consultores. We thank J. Sandoval-Castillo for help during collecting and processing of samples and G. Rendón-Márquez (Geology Department at CICESE) for assistance with sediment analyses. The authors also acknowledge the insightful comments and suggestions from three anonymous reviewers.

Compliance with ethical standards

Conflict of Interest The authors declare that they have no conflict of interest.

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