The relationship between sandy beach nematodes and environmental characteristics in two Brazilian sandy beaches (Guanabara Bay, Rio de Janeiro)

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ABSTRACT

We investigated if the differences in density and nematode communities of intertidal sediments from two Brazilian sheltered sandy beaches were related to environmental characteristics. The upper tide level (UTL) and the low tide level (LTL) of both beaches were surveyed in January (austral summer) and June 2001 (austral winter) during low-spring tides, by collecting samples of nematodes and sediments. Differences in density between beaches, tidal level and seasons, and nematode community structure were investigated. Sediments from both beaches were composed of medium to very coarse sand. The highest nematode densities were found at the UTL, and significant differences between beaches, tidal levels and months were found. A total of 54 genera were found and the genera composition on both sheltered beaches was similar to other exposed worldwide sandy beaches. The density and structure of the nematode community at both beaches clearly varied along the spatial and temporal scales. Gravel percentage was the most important variable explaining the spatial distribution of the nematodes, determining the four sub-communities; this suggests that the sediment characteristics influence the nematode community, rather than physical hydrodynamic forces. Temperature and salinity were suggested to be important variables affecting the temporal variation.

Key words: Brazil, free-living marine nematodes, hydrodynamic, granulometry, sandy beach.

INTRODUCTION

Sandy beaches are dynamic environments bordering many temperate and tropical coastlines, where they are extensively exploited commercially as recreational areas and used as buffer zones against the sea (McLachlan and Brown 2006). At first glance, these beaches may seem to be marine deserts; however, the sediment provides a three-dimensional habitat that provides a substratum for diverse endobenthic communities (Gray 2002). These communities include species of different sizes of organisms, such as micro-, meio- and macrobenthos. Among the meiobenthos, sandy-beach sediments are generally dominated by

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harpacticoid copepods and nematodes, with the dominance of one group over the other relating to grain size. The importance of the sediment for the distribution of animals on soft bottoms was first debated by Ford (1923) and an exhaustive discussion of this topic is found in Snelgrove and Butman (1994). The presence of nematodes as a group is independent of the sediment composition (Vanaverbeke et al. 2000), but, in general, nematodes are said to be highly dominant in sand finer than 300 μm, while harpacticoid copepods become more important in sediments coarser than 350 μm (McLachlan and Brown 2006). Several studies have demonstrated the importance of median grain size, silt content and sorting as key aspects structuring the composition and diversity of free-living nematodes (Wieser 1959, Heip and Decraemer 1974, Ward 1973, Vincx et al. 1990, Vanaverbeke et al. 2002). Wieser (1959) showed that the nematode species distribution in sandy-beach sediments is much better explained by granulometric changes than by tidal levels.

Several studies of sandy-beach nematodes show that the dominance of a nematode family is related to granulometric features (Sharma and Webster 1983, Gourbault and Warwick 1994, Nicholas and Hodda 1999, Gheskiere et al. 2004, Urban-Malinga et al. 2004, Calles et al. 2005, Hourston et al. 2005, Moreno et al. 2006, Mundo-Ocampo et al. 2007). Generally, sheltered areas with fine sand and mud are richer, while beaches exposed to oceanic waves are species-poor (Gray 2002). The aim of this study was to investigate if the differences in density and nematode communities of intertidal sediments of two Brazilian sheltered sandy beaches located in a protected bay are related to differences in sediment composition.

MATERIALS and METHODS

STUDY AREA

Guanabara Bay (22°24'-22°57'S and 42°33'-43°19') is a coastal inlet located in the second most densely populated state of Brazil, Rio de Janeiro, and has an area of 384 km^2. The bay is connected to the sea by an access 1.6 km wide (Kjerfve et al. 1997). Two well defined seasons occur in this area, a rainy (December to April) and a dry (June to October) season, which consequently leads to a regional seasonal pattern with lower salinities in summer and higher salinities in winter (Paranhos and Mayr 1993). Annual mean water temperatures range from 25°C at the surface to 23.7°C in the bottom layer (Paranhos and Mayr 1993). Salinity decreases from the outer bay (34.6) toward the inner areas (26.1) (Kjerfve et al. 1997). In general, the bay has calm waters with low swells and gentle winds, predominantly from the east (Amador 1997). This bay has undergone great anthropogenic impact since Brazil's colonization; human activities since then have led to major alterations of landscapes and changes in biological, physical and chemical features (Amador 1997). Its basin is densely urbanized, and pollution by untreated domestic sewage is considered to be the worst environmental problem in the bay, making it one of the most heavily impacted and degraded ecosystems in Brazil (Mayr et al. 1989). Areas of severe sewage contamination were identified by higher concentrations of coprostanol (Carreira et al. 2002). Bacterial activity reaches up to 7.35 μg C L^{-1} h^{-1} in the inner part of the bay where tidal circulation is restricted (Andrade et al. 2003). However, Guanabara Bay is considered one of the most productive marine ecosystems in the world, with carbon assimilation values ranging between 800 and 3,600 mg.C.day^{-1} and a mean net primary production of 0.17 mol.C.m^{-2}.day^{-1} (Rebello et al. 1988).

In this bay, two microtidal, sheltered sandy beaches, Bananal and Coqueiros, were surveyed in January (austral summer) and June 2001 (austral winter) during low-spring tides. Bananal Beach is located on the largest island in the bay (Ilha do Governador) in the middle of the bay. According to Mayr et al. (1989), this beach is located in a sector of intermediate water quality with medium- to coarse-sand sediments. Coqueiros Beach is located on a
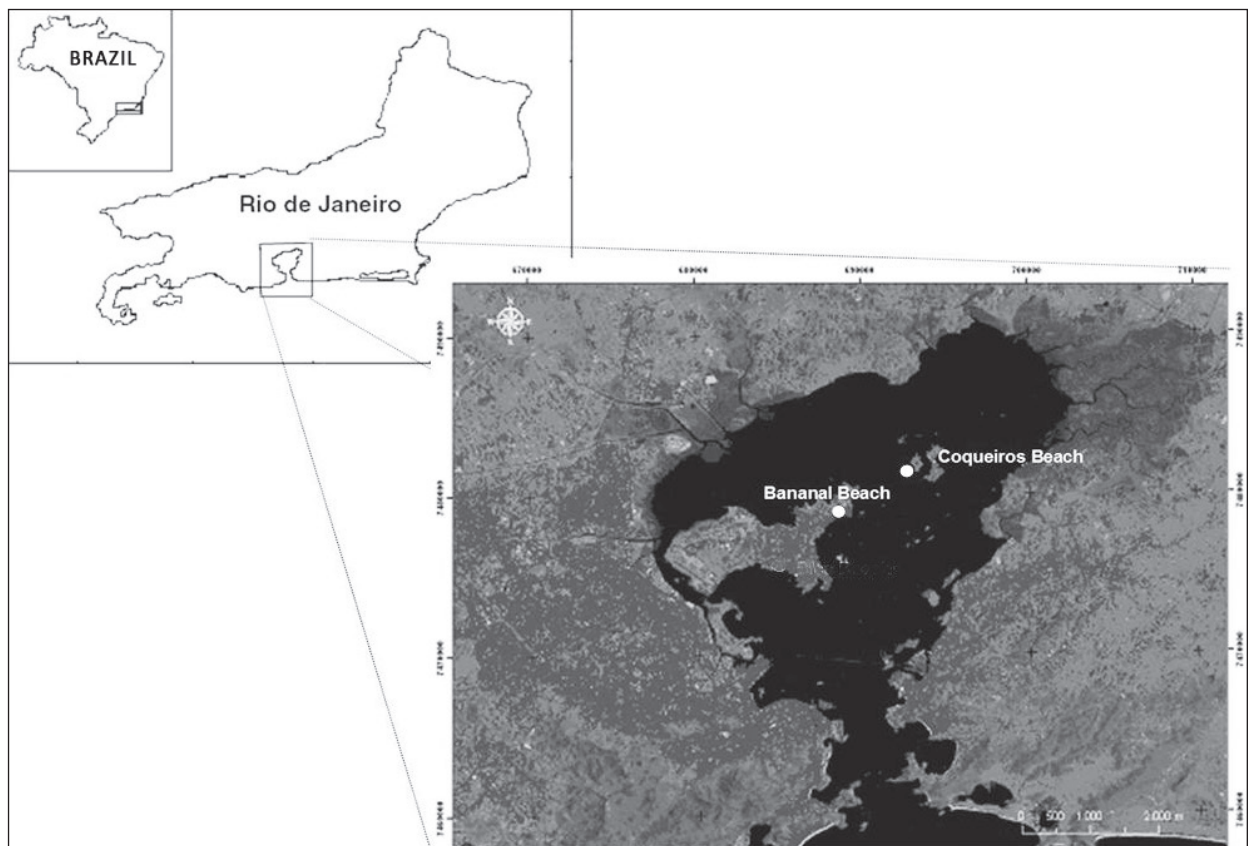
Fig. 1 - Guanabara Bay LANDSAT TM542 image, obtained by the Remote Sensing Laboratory of UFRJ. The locations of the beaches are indicated by white circles.

small island in the inner bay, where the best water quality is found because of the entrance of oceanic water during high tide (Mayr et al. 1989), and its sediment is composed of very coarse sand (Fig. 1).

Sampling Strategy and Laboratory Treatment

At both beaches, two stations were established: the low tide level (LTL) in the swash zone, and the upper tide level (UTL) 10 m above the LTL. At each station, triplicate meiofauna samples were taken using a 20-cm long PVC corer with an inner diameter of 3.6 cm, corresponding to a surface area of 10 cm^2, and immediately fixed with 4% formaldehyde. Another corer of the same diameter was used to collect sediment for sediment analysis. Sediment temperature was measured using a soil thermometer.

Nematodes were extracted from the sediment by sugar flotation (Esteves and Silva 1998) and sieved over 500-µm and 62-µm sieves. Nematodes retained on the 62-µm sieve were counted, and 200 individuals from each sample were picked randomly using a stereomicroscope and transferred to a solution of 5 parts glycerin, 5 parts ethanol and 90 parts distilled water. Finally, these nematodes were mounted on glass slides and identified to genus level using the pictorial keys of Warwick et al. (1998) and the Nemys database (Deprez et al. 2005).

Grain size analysis was performed through sediment sieving using an automatic shaker. The sediment fractions were defined according to the Wentworth scale (Bale and Kenny 2005).

STATISTICAL ANALYSIS

The differences in density between beaches, tidal level and seasons were tested by three-way analysis of variance (Beach, Tidal level, Season) using R (R Development Core Team 2011). Data were log transformed to assume a normal distribution and to fulfill the assumption of homogeneity of variances. Diversity was represented by K-dominance curves (Clarke and Warwick 2001). The nematode community structure was analyzed by non-metric Multi-Dimensional Scaling (MDS) using Bray-Curtis Similarity on non-transformed density data from each replicate sample. Differences between groups of data were investigated by a two-way crossed ANOSIM test. The genera that contributed most to the similarity within groups were identified by the SIMPER method. BIOENV was applied to investigate the granulometric parameter that best explained the spatial distribution of the nematode community composition. All these analysis were performed using the PRIMER v6.1 software package (Clarke and Gorley 2006).

The nematode composition was compared with 32 surveys of worldwide sandy-beach nematodes, in which beaches were grouped according to their degree of exposure. These surveys were based on peer-reviewed publications (Gray and Rieger 1971, Platt 1977, Sharma and Webster 1983, Gourbault and Warwick 1994, Gourbault et al. 1998, Nicholas and Hodda 1999, Gheskiere et al. 2002, 2004, 2005a, b, Urban-Malinga et al. 2004, 2006, 2008, Calles et al. 2005, Hourston et al. 2005, Moreno et al. 2006, Nicholas 2001, 2006, Nicholas and Trueman 2005, Calles 2006, de Jésus-Navarette 2007, Mundo-Ocampo et al. 2007, Gingold et al. 2010).

RESULTS

GRANULOMETRY

Sediments from both beaches were mainly composed of medium to very coarse sand (Table I). At Coqueiros Beach the median grain size corresponded to very coarse sediment, poorly sorted at

both tidal levels, with the highest contribution from gravel. At Bananal Beach the sand was mainly coarse, except at UTL in January when the median grain size corresponded to medium sand, and the sorting coefficient ranged from moderate at UTL to poorly sorted at LT. Considering the horizontal profile of both beaches, the highest median grain size, contribution of gravel, and contribution of silt and clay were found at LTL, except at Coqueiros Beach in January when the percentage of silt and clay was higher at UTL (Table I). The percentage of gravel increased in June, but there was no change in the median grain size or in the sorting coefficient.

TABLE I
Granulometric parameters of Coqueiros and Bananal beaches.

		Coqueiros beach		Bananal beach	
		UTL	LTL	UTL	LTL
January	mean grain size (mm)	1.472	1.621	0.433	0.885
	% of gravel	2.37	23.69	0.61	5.46
	% of silt and clay	0.40	0.24	0.17	0.47
	sorting coeficient	1.20	1.24	0.71	1.19
June	mean grain size (mm)	1.258	1.470	0.566	0.777
	% of gravel	5.26	26.18	2.18	10.79
	% of silt and clay	0.20	0.51	0.08	3.69
	sorting coeficient	1.26	1.37	0.92	1.96

TEMPERATURE

Temperatures showed similar patterns at both beaches: the same temperature was found at the UTL and the LTL in January (29°C) in both beaches, whereas in June the UTL show lower temperatures (22° at Coqueiros Beach and 24° at Bananal Beach) than the LTL (25°C at both beaches).

NEMATODE ASSEMBLAGES

The highest nematode densities were found at the UTL of both beaches, ranging from 880±217 to 3,148±430 ind.10 cm^{-2} (Fig. 2). The three-way ANOVA showed statistical differences between beaches, tidal levels and months separately, but no interaction was observed (Table II). Coqueiros Beach, UTL and June showed the highest density.
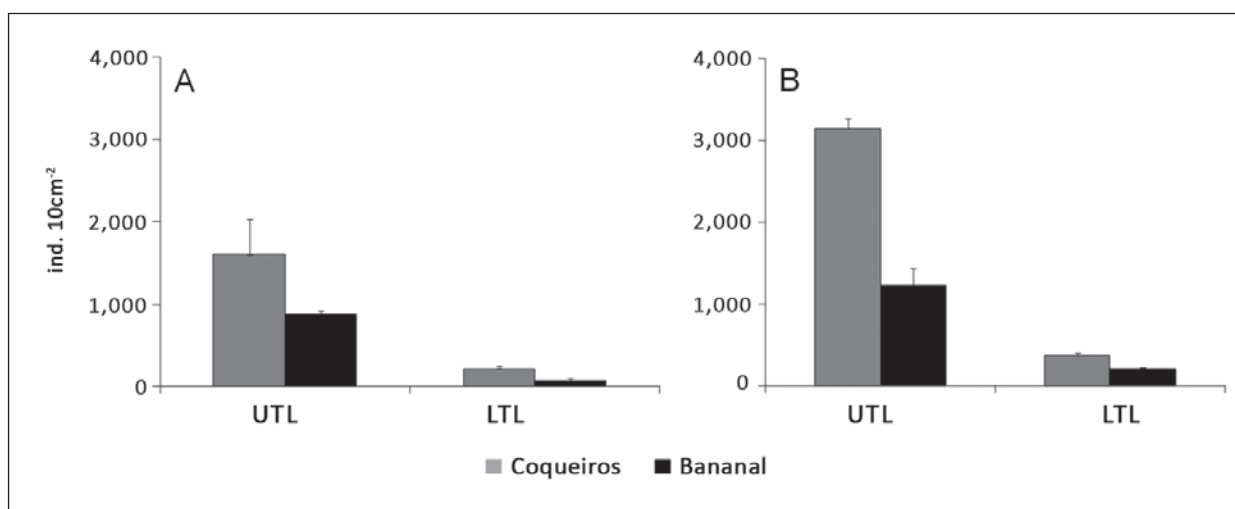
Fig. 2 - Mean density (ind.10cm^{-2} ± standard error) of nematodes at the two tide levels on the two beaches investigated. A: January, B: June. UTL: upper tide level, LTL: low tide level.

TABLE II
Result of three-way ANOVA for density.

	df	MS	F-value	p-value
Beach	1	0.83	556,900.0	**<0.01**
Level	1	51,631.00	3,459,571.0	**<0.01**
Month	1	0.55	366,269.0	**<0.01**
beach x level	1	0.00	0.3	0.58
beach x month	1	0.01	0.6	0.46
level x month	1	0.03	22,744.0	0.15
beach x level x month	1	0.06	39,633.0	0.06
Residuals	16	0.01		

Significant differences are indicated in bold.

A total of 54 genera were found at the two beaches, belonging to 25 families. Chromadoridae and Cyatholaimidae contributed the highest number of genera at Coqueiros Beach; at Bananal Beach, Chromadoridae, Desmodoridae and Oncholaimidae were equally dominant families (Fig. 3).

Dracograllus was the dominant genus in the UTL of Coqueiros Beach, with 42% and 34% of relative abundance in January and June, respectively. *Paracanthoncus* (24%) and *Nygmatonchus* (33%) were the dominant genera in the UTL of Bananal Beach in January and June, respectively. In the LTL, *Sabatieria* was the abundant genus at Coqueiros Beach, corresponding to 50% and 63% of the relative

abundance in January and June; and Theristus (75%, January) and *Chromaspirina* (23%, June) were most abundant at Bananal Beach (Appendix A). Comparison of the nematode composition with other beaches worldwide revealed that of the 54 genera found in this study, 46 have been reported from sandy beaches, including 35 for sheltered, 38 for intermediate and 39 for exposed sandy beaches.

The highest diversity was found in the UTL of both beaches in June, and the lowest diversity was found in the LTL of Bananal Beach. In June, the lowest diversity was found in the LTL of Coqueiros Beach (Fig. 4).

The multivariate analysis (MDS) clearly separated the nematode communities from the UTL to the LTL of both beaches. None of the communities of these tidal levels clustered together (Fig. 5A). There was a clear distinction between months within each beach and within each tidal level (Fig. 5B). The two-way crossed ANOSIM results confirmed that the nematode genera assemblages of these locations (R: 0.955, p = 0.001) and months (R: 0.593, p = 0.001) were significantly different.

The most abundant genus in each beach level was responsible for the similarity of the beach levels. In the case of the UTL, *Nygmatonchus* and
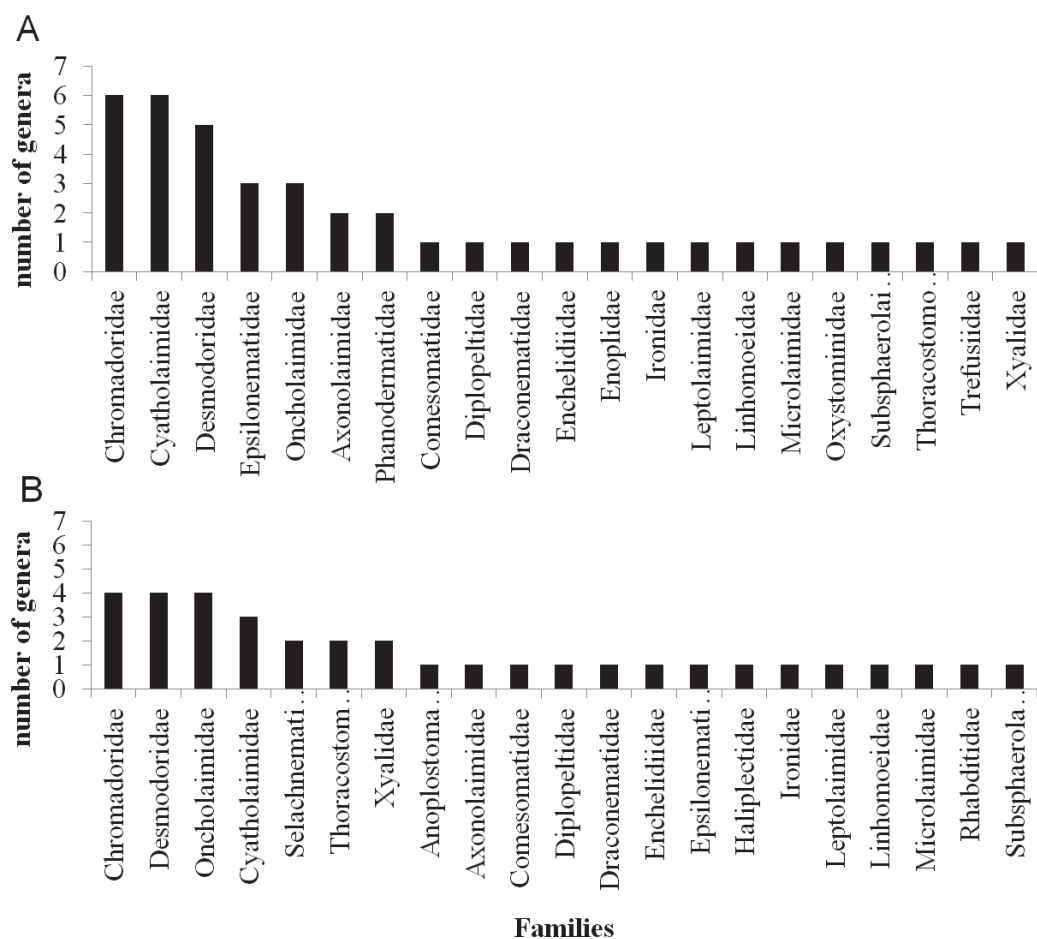
Fig. 3 - Number of genera per family found per beach. **A:** Coqueiros beach, **B:** Bananal beach.
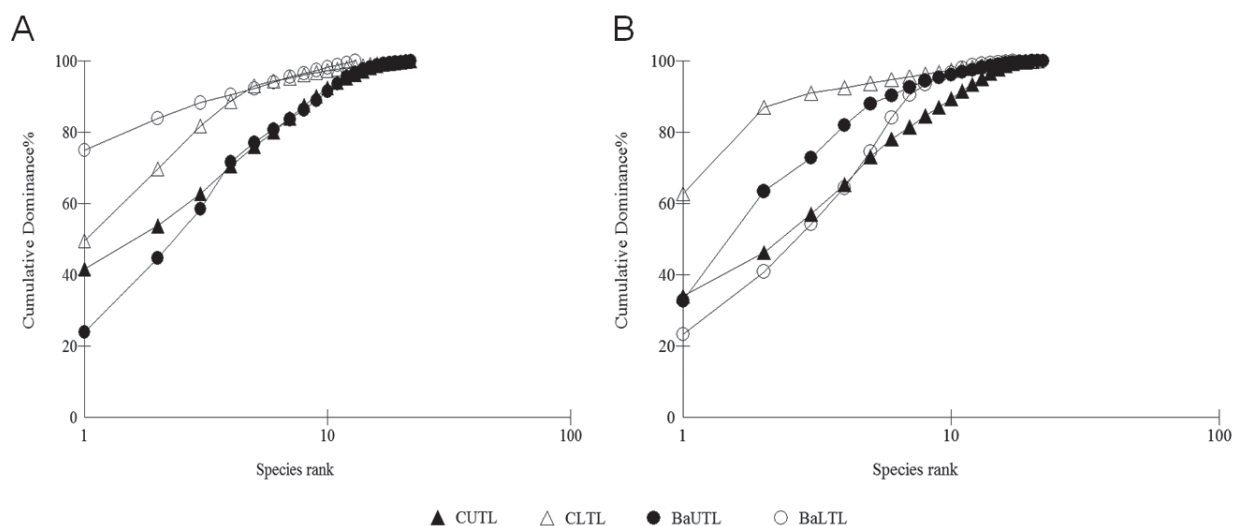

Fig. 4 - K-dominance curves for nematode genera data pooled over each tidal level. **A:** January, **B:** June. (CUTL: Coqueiros upper tide level, CLTL: Coqueiros low tide level, BaUTL: Bananal upper tide level, BaLTL: Bananal low tide level).
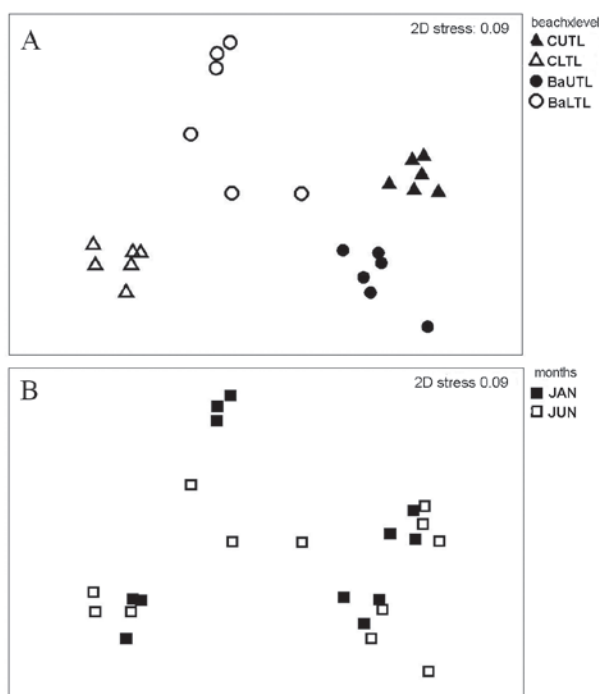
Fig. 5 - Nematode assemblages: output of non-metric Multi-Dimensional Scaling (MDS) based on non-transformed genus density. **A:** MDS of tidal levels and beaches; **B:** MDS for months. Abbreviations as showed in the previous figure.

TABLE III

SIMPER-list showing the contribution (%) of the most relevant genera to each beach and level, cut-off at 90%.

	UTL		LTL	
	Bananal (48%)	Coqueiros (63%)	Bananal (44%)	Coqueiros (77%)
Chromadorita	3	7		
Chromaspirina		18		
Desmodora				19
Desmodorella				9
Dracograllus		50		
Epsilonema		3		
Eurystomina				5
Metachromadora	17	4	11	
Nygmatonchus	36			
Oncholaimus		10		
Paracanthoncus	16			
Paracyatholaimus		10		
Sabatieria				60
Subsphaerolaimus	4			
Theristus			67	
Trileptium	3			
Trissonchulus	13	7		

Overall similarity for each beach level is given in brackets.

Dracograllus contributed most to the similarity within Bananal and Coqueiros beaches, respectively. In the LTL, *Theristus* and *Sabatieria* showed the highest similarity percentages within Bananal and Coqueiros beaches, respectively (Table III).

The BIOENV results showed that the contribution of gravel correlated best with the community structure ($\rho = 0.702$, $p = 0.001$).

DISCUSSION

SPATIAL DISTRIBUTION

The crossing of the cumulative curves of Bananal LTL and Coqueiros UTL did not enable us to distinguish the most diverse community in June, whereas in January higher diversity was observed in the UTL of Bananal, whereas higher density was found in the UTL of Coqueiros Beach in June. Considering that nematodes are highly abundant in sediments with a median grain size of 300 μm (McLachlan and Brown 2006), a high density would be expected to occur in the UTL of Bananal because the mean grain size is around this value. However, we observed the inverse; nematodes were much more abundant in very coarse sediments of 1.5 mm (UTL of Coqueiros). Although grain size directly affects the spatial and structural conditions of the interstitial matrix and indirectly determines the physical and chemical environment of the sediment, the most important characteristic of sands of different grain size is represented by their systems of interstitial spaces rather than solely the grain size (Wieser 1959). Sediment sorting is a principal factor determining meiofauna distribution (Hulings and Gray 1976, Urban-Malinga et al. 2004). In the UTL of Coqueiros Beach, the sediment was poorly sorted, meaning that there was a mixture of grades of sand that provides many more interstitial spaces for nematodes to inhabit. Coleman et al. (1997) also found that the number of individuals increased as the sediments became more poorly sorted.

TEMPORAL DISTRIBUTION

In tropical and subtropical areas, nematodes show seasonal shifts that are mainly related to food availability (Alongi 1990a). High densities of nematodes from northern and southern temperate sandy beaches occur during spring, summer and autumn because abundant food sources are provided due to the increase in primary production during spring and summer that persists into autumn (Boaden and Platt 1971, Sharma and Webster 1983, Nicholas 2001, Hourston et al. 2005). However, in tropical areas, food is not a limiting factor. The beaches studied are located in a bay with constant input of domestic sewage (Mayr et al. 1989). Therefore, the high density of nematodes during June, austral winter, may be related to the temperature, as previously demonstrated by Alongi (1990b). Esteves et al. (2004) and Maria et al. (2008) also observed that some nematode species have high peaks of abundance during the winter in a tidal flat, located in another bay near Guanabara Bay. Another factor that may explain the seasonal variation is the difference in salinity; January and June are in the rainy and dry seasons, respectively. As a consequence, lower salinities occur in summer and higher salinities in winter (Paranhos and Mayr 1993). Nematodes are able to withstand differences in salinities, but species from the upper shore are more capable of osmoregulating than those found in the lower shore (Foster 1998). This scenario agrees with our findings of high density in the upper tidal level during the dry season.

HYDRODYNAMIC X SEDIMENT CHARACTERISTICS

In general, sheltered beaches have a predominance of fine sediment particles, and exposed beaches have coarse sediments (McLachlan and Brown 2006). This expected pattern was not observed in either beach, although this departure from the normal pattern is easily explained by the origin of the grains, through pluvial sedimentation during the Pleistocene. These pluvial sediments have remained until now because of the low hydrodynamic characteristics of these beaches in the interior of Guanabara Bay, and the unavailability of fine sediments to settle (Amador 1997).

In both beaches, the type of sediment was clearly reflected in the dominant fauna. Chromadoridae, Cyatholaimidae and Desmodoridae were the dominant families in terms of genera. The higher number of similar genera in Coqueiros Beach, Bananal beach, and exposed worldwide sandy beaches indicates a similarity among the studied beaches and the latter morphodynamic beach types. Three of the most abundant genera are dominant or belong to dominant families in the sediment of exposed sandy beaches: *Dracograllus*, *Nygmathonchus* and *Theristus*. The two latter genera belong to the families Chromadoridae and Xyalidae, respectively. Chromadoridae is a dominant family in sediments of exposed sandy beaches (Urban-Malinga et al. 2004). Although Xyalidae is a dominant family in fine to medium sand (Gourbault and Warwick 1994, Nicholas and Hodda 1999, Gheskiere et al. 2004, Hourston et al. 2005, Moreno et al. 2006, Mundo-Ocampo et al. 2007), Theristus was also found to be a dominant genus in exposed and very coarse beaches (Gourbault et al. 1998, Urban-Malinga et al. 2004). Draconematids such as *Dracognomus*, *Dracograllus*, *Draconema* and *Paradraconema* occur in sediments ranging from medium to very coarse sand (Gheskiere et al. 2005a, A.M. Esteves (unpublished data) or coralline fragments (Gourbault et al. 1998, Netto et al. 1999, Raes and Vanreusel 2006), and their presence in these environments is attributed to their adaptation to substrate instability that is often associated with coarse substrates (Raes and Vanreusel 2006). Draconematids can attach themselves to large grains by using their ambulatory setae and caudal glands, avoiding being washed away by waves and current movements (Raes et al. 2006); in addition, a large

particle size is required for their atypical crawling locomotion, consisting of alternate movements with intervals of attachment and release of the anterior and posterior body regions (Stauffer 1924).

On the other hand, *Sabatieria*, the dominant genus in the LTL of Coqueiros Beach, occurs relatively infrequently in exposed sandy beaches (only 4 of 19 exposed beaches previously studied) and has no apparent relationship with this environment. For some *Sabatieria* species such as *S. punctata* and *S. celtica*, the contribution of fine sediments seems to be much more important (Vanreusel 1991), but surprisingly this genus was not found in the LTL of Bananal Beach where a high percentage of fine sediments was found. Smol et al. (1994) also reported this genus from sites with less than 5% silt. Perhaps its presence is related to the degree of pollution of the bay. *Sabatieria* is a genus that indicates poor ecological quality of the environment, because of its well-known tolerance to pollution (Moreno et al. 2011).

In general, the degree of exposure of a sandy beach is reflected in the sediment properties; very exposed sandy beaches often have intense hydrodynamism and medium to coarse sediments (McLachlan and Brown 2006). Therefore, the species occurring in highly hydrodynamic environments must have some adaptations to inhabit these beaches and to cope with rapidly changing conditions (Schlacher et al. 2008). As both beaches are sheltered, it is surprising to find a community adapted to high hydrodynamic forces. Sediment characteristics seem to better explain the community structure, since the gravel percentage is the sediment variable that better correlated with the nematode communities in both beaches. Therefore, the occurrence of nematode genera in an environment seems to be more related to the sediment characteristics, rather than to their ability to cope with intense physical disturbance. Morphological adaptations and species characteristics are important in favoring the survival of a genus or species in a dynamic environment, but

according to our results the sediment characteristics, rather than any hydrodynamic forces, drive the nematode community structure in sandy-beach sediments of the Guanabara Bay.

In conclusion, the density and structure of the nematode community at both beaches in Guanabara Bay clearly varied along the spatial and temporal scales. Gravel percentage was the most important variable controlling the spatial distribution of the nematodes, determining the four sub-communities (LTL and UTL of Bananal and Coqueiros beaches, separately); whereas temperature and salinity are suggested to be important for the temporal variation, differentiating the summer and winter communities of each tidal level within each beach.

ACKNOWLEDGMENTS

RESUMO

Foi investigado se a diferença entre a densidade e a comunidade de nematódeos dos sedimentos entre-marés de duas praias arenosas protegidas no Brasil estava relacionada com características ambientais. Durante as marés de sizígia de janeiro (verão austral) e junho (inverno austral) de 2001, amostras de sedimentos e nematódeos foram coletadas no médio litoral superior (UTL) e o médio litoral inferior (LTL). Diferenças na densidade e na estrutura da comunidade de nematódeos entre praias,

níveis de maré e estações do ano foram investigadas. O sedimento de ambas as praias foi composto por areia média ou areia muito grossa. A maior densidade de nematódeos foi encontrada no UTL e significativamente diferente entre praias, níveis de maré e meses do ano. Um total de 54 gêneros foi encontrado e a composição genérica de ambas as praias protegidas foi similar a de outras praias expostas ao redor do mundo. A densidade e a estrutura da comunidade de ambas as praias variou ao longo das escalas espacial e temporal. A porcentagem de cascalho foi a variável ambiental que melhor explicou a distribuição espacial dos nematódeos, determinando as quatro sub-comunidades; isso sugere que as características do sedimento controlam a comunidade de nematódeos em detrimento a forças físicas hidrodinâmicas. A temperatura e a salinidade foram sugeridas como variáveis ambientais importantes afetando a variação temporal.

Palavras-chave: Brasil, nematódeos marinhos de vida livre, hidrodinamismo, granulometia, praia arenosa.

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APPENDIX A

Relative abundance of nematodes genera at the two studied beaches, considering the tide levels
(UTL and LTL) and months (Jan=January and Jun=June). FT = feeding types.

Genera	FT	Coqueiros				Bananal			
		Upper		Lower		Upper		Lower	
		Jan	Jun	Jan	Jun	Jan	Jun	Jan	Jun
Acanthoncus	2A	0.00	0.00	0.17	1.07	0.00	0.00	0.00	0.41
Actinonema	2A	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.20
Anoplostoma	1B	0.00	0.00	0.00	0.00	2.56	2.34	0.00	0.00
Araeolaimus	1A	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00
Axonolaimus	1B	0.00	0.00	0.18	0.00	0.00	0.00	0.58	0.00
Choanolaimus	2A	0.00	0.00	0.00	0.00	3.65	0.94	0.00	0.00
Chromadora	2A	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00
Chromadorita	2A	7.85	7.73	0.69	0.56	5.46	0.61	1.59	1.83
Chromaspirina	2B	0.00	0.00	0.00	0.19	0.41	0.00	8.88	23.39
Desmodora	2A	0.00	0.00	12.06	24.25	0.00	0.07	0.00	10.12
Desmodorella	2A	0.00	0.00	20.11	1.48	0.00	0.00	0.00	0.00
Dracograllus	1A	41.65	34.01	0.00	0.29	0.00	0.51	0.00	0.00
Enoploides	2B	0.00	0.00	0.00	0.00	1.03	0.39	0.00	0.00
Enoplus	2B	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00
Epsilonema	1A	4.09	3.35	0.00	0.14	0.00	30.67	0.00	0.00
Eurystomina	2B	0.21	0.00	6.91	1.21	0.66	0.26	0.00	0.81
Haliplectus	1A	0.00	0.00	0.00	0.00	0.18	0.00	0.00	0.00
Kosswigonema	2B	0.00	0.00	0.00	0.00	0.00	0.00	0.86	0.00
Linhomoeus	1B	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00
Longicyatholaimus	2A	0.00	0.00	0.00	0.80	0.00	0.00	0.00	0.00
Cyatholaimidae type I	2A	2.62	0.34	0.00	0.00	0.00	0.00	0.00	0.00
Marylynnia	2A	0.00	0.00	0.23	0.00	0.00	0.00	0.00	0.00
Metachromadora	2B	3.84	10.84	0.34	0.59	13.05	9.11	4.39	17.53
Metaparoncholaimus	2B	0.00	0.00	0.29	0.00	0.00	0.00	0.00	0.00
Metepsilonema	1A	1.03	1.49	0.00	0.00	0.00	0.00	0.00	0.00
Metoncholaimus	2B	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.50
Microlaimus	2A	0.99	2.18	0.00	0.00	1.84	0.06	1.73	0.00
Molgolaimus	1A	0.17	0.00	0.00	0.00	0.16	0.00	0.00	0.00
Neochromadora	2A	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nygmatonchus	2A	2.21	2.39	0.00	0.00	13.78	32.79	0.00	13.33
Odontophoroides	2A	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00
Onchium	2A	0.00	0.00	0.41	0.43	0.00	0.00	0.81	0.20
Oncholaimidae type I	2B	0.00	0.00	0.00	0.00	0.00	0.00	0.66	0.00
Oncholaimus	2B	5.33	12.21	4.30	0.30	1.17	0.73	0.00	9.52
Oxystomina	1A	0.00	0.00	1.36	3.98	0.00	0.00	0.00	0.00
Paracanthoncus	2A	0.00	3.14	0.00	0.00	23.94	2.34	2.25	2.92
Paracyatholaimus	2A	12.10	8.32	0.18	0.64	0.16	0.64	0.00	0.00
Perepsilonema	1A	1.58	1.69	0.00	0.00	0.00	0.00	0.00	0.00

APPENDIX A (CONTINUATION)

Genera	FT	Coqueiros				Bananal			
		Upper		Lower		Upper		Lower	
		Jan	Jun	Jan	Jun	Jan	Jun	Jan	Jun
Phanoderma	2A	1.19	0.55	0.00	0.00	0.00	0.00	0.00	0.00
Phanodermatidae type I	1A	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Prochromadorella	2A	0.00	0.00	0.00	0.19	0.00	0.00	0.00	0.00
Rhabditis	1A	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.00
Rhips	2A	0.00	0.00	0.18	0.00	0.00	0.00	0.00	0.00
Sabatieria	1B	0.00	0.00	49.60	62.80	0.00	0.00	1.73	1.42
Southerniella	1A	0.00	1.10	0.00	0.00	2.09	0.00	0.58	0.00
Spilophorella	2A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20
Steineria	1B	0.00	0.00	0.00	0.00	2.73	0.77	0.00	0.00
Subsphaerolaimus	1B	0.33	1.77	0.00	0.16	2.95	1.80	0.00	0.00
Terschellingia	1A	0.00	0.00	0.00	0.19	0.00	0.00	0.00	0.00
Theristus	1B	0.99	4.99	0.84	0.47	0.46	0.35	75.00	10.18
Trefusia	1A	0.51	1.01	0.00	0.00	0.18	0.00	0.00	0.00
Trileptium	2B	0.14	0.00	0.40	0.00	2.56	6.06	0.00	0.00
Trissonchulus	2B	9.01	2.44	0.91	0.00	20.82	9.36	0.94	0.20
Viscosia	2B	3.69	0.00	0.00	0.13	0.00	0.00	0.00	1.22